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PROVISIONING STRATEGIES OF PARENT BLACK TERNS

by

Clive V.J. Welham

B.Sc. (Zoology), University of Manitoba, 1983

M.Sc. (Zoology), University of Manitoba, 1986

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
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in the Department
of
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SIMON FRASER UNIVERSITY

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General Abstract

Optimal foraging theory assumes that individuals maximizing a given energetic currency maximize their fitness. A field experiment was designed to use flight speeds of black terns (*Chlidonias niger*) feeding their young to test predictions from optimal foraging models maximizing (1) the net energy gained per unit energy expended (Efficiency; EFF), (2) the net rate of energy intake (NREI), and (3) daily delivery rate (DR), respectively. Predicted speeds of the EFF model best matched the observed flight speeds. Maximizing efficiency resulted in the lowest delivery rate to the nest, but it was also the only currency that predicted adult daily energy expenditures within the theoretical limit (DEE_{max}) estimated for black terns (206 kJ/day; Kirkwood 1983).

I then used a simulation approach to predict the flight speeds of parent birds provisioning their young from the three optimal foraging currencies and a state variable model, and compared the fitness return for each model. EFF maximizing produced fitness estimates that were better than or equivalent to the two other foraging currencies over a wide range of parameter values. EFF was also the only currency (in addition to the state variable model) that predicted flight speeds which were consistently within the range of observed values for black terns. The state variable model resulted in higher fitness returns than the simple foraging currencies (particularly when feeding conditions were poor). Though the state variable approach illustrates the complexity of the allocation decisions parents might face, results suggest that EFF maximizing may provide a reasonable fitness return under a variety of conditions.

I investigated the provisioning response of parental black terns to experimentally-manipulated brood sizes above and below the modal size of 3. Broods were manipulated when chicks were about 5 (week 1) or 9 days (week 2) old. The number of prey items delivered per h increased significantly with brood size in week 1, but not in week 2. Using only the actual time spent foraging, the delivery rate of items per parent foraging-h also increased significantly with brood size in week 1. This suggests that parents with week-old chicks, in addition to lengthening foraging time, also increased provisioning effort in other ways. The delivery rate per parent foraging-h was lower in week 2, and did not appear to change significantly with brood size. A possible explanation lies in the fact that the proportion of daily energy supplied by different prey items varied significantly with chick age (when averaged over all brood sizes) but not brood size (with age constant). These results are in qualitative agreement with the predictions of a variance-sensitive model of behavior whereby parents attempt to minimize the probability that nestlings experience an energetic shortfall.

Dedication

Our family arrived in Canada in May, 1970. As with most immigrants, this land represented an opportunity for a better life. There must have been times when this seemed doubtful since, for my parents, the journey has been a difficult one. The wisdom of their decision, however, can be measured in the future they have provided for their children.

Unfortunately, our success also came at a price paid by loved ones left behind. Grandchildren are a link with the past and the hope for a better future. Separation from ones so young is a painful break in the chain.

And so it is with great pride that I dedicate this dissertation to my grandparents, Jack and Olive Welham, and my parents, Derek and Marion Welham. You showed me love and courage and for that I will always be grateful.

Acknowledgments

I owe much appreciation to the efforts of my senior supervisor, Ron Ydenberg. He has a talent for examining problems from a novel perspective and I hope to carry this lesson with me into the future. Ron also showed me how the beauty of an elegant theory (in this case, evolution by natural selection) lies in the paths that it leads to understanding. Thank you, Ron, for helping me become a scientist.

Many people provided assistance of one sort or another, in particular, Ralph Cartar, Mark Abrahams, Peter Nonacs, Karen Price, and John Reynolds. In this respect, Scott Forbes deserves mention. He encouraged me to join the Behavioral Ecology Research Group at SFU but, more importantly, spent considerable effort convincing me that "I had what it takes". I miss our boozed-up discussions.

I thank Larry Dill for illustrating the importance of an open mind - good and interesting ideas are everywhere if one chooses to look. Thanks too for just being a friend, Larry. Curling is truly the world's greatest sport.

Joan Sharp helped me develop the capability to convey ideas to new students in biology and served as a source of constant encouragement.

While performing field activities in Creston, Santo Wood displayed great powers of observation in locating breeding black terns. Thanks for always making me feel welcome. Speaking of feeling welcome, my family away from home was provided by Henry and Mary Czuchro. They fed and watered me and always ensured I was safe and sound. Friends for a lifetime.

Finally, I need to acknowledge the love and support of my spouse, Leslie Baldwin, and my son, Tristan. Leslie played an invaluable role in teaching me how to catch vast quantities of fish but, more importantly, she stuck with me through times that were difficult for us both. I know she's as proud of this dissertation as I am. Thank you, Tristan, for your patience on the many occasions when daddy couldn't play.

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CHAPTER I

GENERAL INTRODUCTION

Parental birds vary greatly in how they provision their offspring. For example, the White-tailed Tropicbird (*Phaethon lepturus*), a pelagic seabird, hatches only a single chick that is fed a large bolus of squid and fish every 15.7 - 16.7 h (Schaffner 1991). In contrast, a small passerine, the Blue Tit (*Parus caeruleus*), hatches as many as 15 chicks (Nur 1984) provisioned up to 1200 times a day by parents who usually return with only a single item each trip (Nur 1987). Though very different, each strategy is assumed to have evolved because it confers maximum fitness to the individuals of each species. An important problem in behavioral ecology is therefore to understand the selection pressures responsible for such a diversity of reproductive strategies.

One way to consider reproduction is within the context of each species' life-history. An essential feature of a life-history analysis is the idea of trade-offs between different life-history traits (Stearns 1989; see below). Trade-offs occur because two or more traits are limited by the same resource (for example, time or energy) so that investment in one trait is possible only at the expense of investment elsewhere (Lessells 1991). Though a number of potential trade-offs have been identified (see Stearns 1989), one of the most important is that between current reproductive effort and future reproductive potential (termed the cost of reproduction). Reproduction is costly because the benefits of further investment in present offspring are assumed to compromise the prospects for reproduction in the future (Charnov and Krebs 1974). Given the cost of reproduction, an optimal life-history strategy specifies that level of reproductive effort which will result in maximum lifetime reproductive success (LRS). In the case of Tropicbirds, annual adult survival is likely typical of most large seabird species (> 80%; Croxall and Rothery 1991) and the number of years that an adult lives to breed is the single most important component of LRS.

Consequently, parent Tropicbirds should invest relatively little into each reproductive event (hence, the single chick) in order to minimize any associate mortality risks. The opposite is true for the Blue Tit, however. Its probability of surviving to breed again varies from 10 - 50% (Nur 1984) so that parental LRS is heavily dependent upon reproductive success within a given year.

While a given life-history strategy might specify the optimal amount of total effort that should be invested in a particular breeding attempt, it is unclear how this translates into the details of parental behavior (see also Houston 1987). Why, for example, do parent tropicbirds provision their chick at regular (but long) intervals? Why don't Blue tits return with more items each trip, and so reduce the total number of trips per day? In these species, as in many other birds, nestling growth is dependent solely on the energy that the parent(s) bring back to the nest, and the energy costs of provisioning represent a significant proportion of total parental reproductive effort (Nur 1984, Bryant and Tatner 1988). An alternative approach is therefore to consider reproductive effort from the perspective of parental provisioning strategies. In central place foraging theory (CPF; Orians and Pearson 1979), a strategy is defined by a particular decision variable (for example, how many prey the parent should capture each trip, or the minimum acceptable prey size; see Stephens and Krebs 1986, for other examples), and its alternative values are then compared against some criterion (termed a currency). This currency is usually assumed to be the rate at which energy is delivered to the nest (Orians and Pearson 1979), though others also have been considered (see Chapter III for details). By maximizing a given currency the parent is assumed to maximize fitness (but see below).

Most tests of CPF currencies compare their predictions to behavioral observations collected over the short-term. What is generally not considered, however, are the long-term (i.e. life-historical) consequences of the predicted behavior. For example, Houston (1987) has demonstrated that if parental energy reserves are important for future survival, then the time necessary for parents to recoup energy expenditure can place important constraints on the rate at which food is delivered to the young. A new currency that took account of parental self-feeding time resulted in higher daily delivery when compared with three other commonly-used currencies. However, Houston (1987) used literature values to estimate the parameters necessary to test his hypothesis, and so his results have yet to be confirmed experimentally.

The energy cost of flight is an important component in any problem that addresses the provisioning strategies of birds. These flight costs are often estimated with equations developed from aeronautical theory (see Pennycuick 1989, for example). Several of these aerodynamic equations have gained acceptance in the foraging literature (for example, Blake 1985, McLaughlin and Montgomerie 1985, 1990, Welham and Ydenberg 1988, Gudmundsson et al. 1991) but their estimates of how the cost function varies in relation to flight speed can differ substantially (see Norberg 1990). Though these differences are likely to affect the predictions of a given currency, the use of a given equation in the foraging literature appears to be arbitrary (see examples given above). It should be possible, however, to compare predicted flight speeds from each equation to measured airspeeds under a specific set of ecological conditions (see below), and then determine which equation best fits the observations. For example, it is assumed that in order to successfully complete a long-distance migration at the minimum energy cost, most birds should fly at a speed maximizing the distance travelled per unit energy expended (Pennycuick 1989), often referred to as the maximum range speed (V_{mr}). Using three aerodynamic equations, I was able to determine which set of V_{mr} predictions best matched the flight speeds of migrating birds reported in the literature and, hence, which equation appeared to give the most realistic estimate of flight cost. The results of this analysis are presented in Chapter II.

In Chapter III, I use this equation as part of an experiment to compare predictions of flight speeds in parent Black Terns (*Chlidonias niger*) derived from two commonly-used central place foraging currencies, and Houston's (1987) daily delivery currency. This experiment considers explicitly the effect of parental self-feeding on the total daily food delivered to the nest. Recently, there has been considerable interest in whether parental energy budgets might not also be constrained by physiological mechanisms (the rate at which parents can process food through the gut, for example; see Wiener 1992). The development of these ideas can be traced to the work of Drent and Daan (1980) who suggested a limit to performance of 4 times the basal metabolic rate. Subsequent work has seen the introduction of a number of allometric relationships (reviewed in Wiener 1992). Hence, in addition to self-feeding time, I consider whether delivery rate might not also be constrained by physiological limits to parental energy expenditure using an allometric equation for maximum daily energy expenditure developed by Kirkwood (1983).

The relative ease with which its predictions can be tested under natural conditions has made a CPF theory a valuable tool to behavioral ecology. Nevertheless, the provisioning strategies of parental birds are undoubtedly much more complex than portrayed by these relatively simple currencies. One factor not considered, for example, is how the state of the parent (for example, its energy reserves) or the offspring might affect foraging behavior (Houston and McNamara 1985). Though the relative importance of state dynamics to behavioral decisions is widely appreciated (see Houston and McNamara 1988, Clark 1991), rigorous experimental tests of the predictions derived from these models are lacking. This may be due, in part, to the fact they require some measure of variation in the state variable which is often difficult to obtain (see Beauchamp et al. 1991, for an example in a provisioning context). Nevertheless, it is important to know whether the absence of state dynamics in CPF currencies seriously compomises their utility. In Chapter IV, I therefore use three CPF currencies to derive predictions of flight speed and expected fitness returns of Black Tern parents provisioning broods of normal size. These are compared to similar predictions made by a model incorporating the state dynamics of both parents and their offspring.

Though parental state is difficult to manipulate experimentally, it is possible to manipulate offspring condition and so determine its influence on parental provisioning decisions. One way is to alter brood demand through changes in brood size. When brood size is enlarged and chick demands increase, parents can respond in a number of different ways (these options and supporting references are detailed in chapter IV). One might be to simply increase the time spent provisioning at the cost of other activities, thereby increasing the total amount of food delivered across the day (as shown for example, by female Starlings *Sturnus vulgaris*; Tinbergen 1981). Another option is for parents to increase the delivery rate by changing their foraging tactics. This could be accomplished by (a) flying faster, (b) decreasing the amount of parental self-feeding (Lifjeld 1988, Kacelnik and Cuthill 1990), and/or (c) changing the prey selection criteria. In the latter case, a higher rate is often achieved by parents expanding the diet and delivering proportionately more smaller prey (so that the number of items/unit time increases). This usually means though that the quality of the diet (in energetic terms, for example; see Nur 1984) actually declines (Tinbergen 1981). Alternatively, parents could become more selective and instead return only with items of higher than average value. One drawback of this tactic is that there may also be a higher variance in the encounter rate associated with these items (since they are likely less abundant) which would depress delivery rate in the long-term. Parents might still gamble, however, on obtaining an above-average encounter rate over the short-term. A number of studies have provided evidence consistent with this idea of variance-sensitive foraging (see Caraco and Lima 1987, for examples) though the majority have been conducted on non-reproducing individuals. Consequently, its importance to the provisioning decisions of parental birds is largely unknown. Chapter V therefore considers whether the prey selection decisions of parent Black Terns might best be described in terms of variance-sensitive foraging. Offspring demand (and hence the parents' assessment of their requirement) was manipulated by creating brood sizes larger and smaller than the model size of 3. I was then able to compare the frequency distribution of prey sizes delivered to the nest with interpretations based on classical provisioning theory (which takes no account of the variation in prey availability; see above) and a model based on variance-sensitive foraging which assumes that parents attempt to minimize the risk their offspring experience an energetic shortfall.

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CHAPTER II

FLIGHT SPEEDS OF MIGRATING BIRDS: A TEST OF MAXIMUM RANGE SPEED PREDICTIONS FROM THREE AERODYNAMIC EQUATIONS

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ABSTRACT

Many temperate birds invest considerable time and energy to travel between their breeding grounds and wintering areas. It has generally been assumed that, to minimize the energy cost of migration (and thus maximize fuel economy), birds ought to fly at speeds that maximize the distance travelled per unit of energy expended (termed the maximum range speed, V_{mr}). I tested this idea by comparing literature reports of migration speeds for 48 avian species and comparing them to predictions of V_{mr} derived from three aerodynamic equations (Tucker, Pennycuick, and Greenewalt). No single equation made V_{mr} predictions that matched the full range of observed speeds. Species weighing 0.3 to 3 kg (Greenewalt equation) and 0.1 to 1 kg (Pennycuick equation) generally migrated at Vmr, but this represents only 42% (20/48) and 40% (19/48) of the total number surveyed, respectively. Deviations from V_{mr} outside these ranges varied systematically with mass. Lighter species almost always flew faster than V_{mr} while heavier species showed the opposite trend. The latter group is likely constrained to fly below V_{mr} due to limits on metabolic performance imposed by mass-specific scaling effects. The Tucker equation almost always predicted V_{mr} values that were less than observed speeds.

INTRODUCTION

Many avian species fly considerable distances in order to reach their breeding grounds, and the investment of time and energy necessary to complete this migration is substantial (Johnson and Herter, 1990). Hence, prior to departure, these birds feed intensively and store fat which is drawn upon as a fuel reserve during the trip. Fat reserves often need to be replenished *en route* and this is accomplished by feeding at one or more stopover locations. Though numerous investigations have been carried out on the fat deposition rates of migratory birds (see reviews by Odum, 1960, Berthold, 1975), only recently have ecologists considered the costs (extra weight that must be transported, for example) of accumulating fat reserves prior to departure.Using an optimization approach, for example, Alerstam and Lindström (1990) predicted optimal fat loads that depend on whether migratory strategies evolved to minimize time spent on migration, the associated mortality risk during migration, or to maximize fuel economy.

In addition to fat deposition, flight speed also can vary as a function of the migratory strategy (Alerstam and Lindström, 1990). Previous studies have suggested that to minimize the energy cost of migration (and thus maximize fuel economy) birds ought to fly at speeds that maximize the distance travelled per unit of energy expended (termed the maximum range speed, V_{mr}; Pennycuick, 1969, 1975, Tucker, 1974, Rayner, 1990). Alternatively, birds might fly at speeds that minimize the time spent on migration (while taking into account any extra time needed to recoup their energy expenditure). This time minimization hypothesis (Alerstam and Lindström, 1990) makes predictions of migration speeds which are higher than V_{mr} and depend upon the rate at which birds can replenish their energy stores (in contrast to V_{mr}, which is independent of feeding rate; see Alerstam and Lindström, 1990, Table 1). Though the departure fat loads of migrating Bluethroats (*Luscinia svecica svecica*) and Rufous Hummingbirds (*Selasphorus rufus*) were in qualitative agreement with the time minimization hypothesis (Lindström and Alerstam, 1992, see also Alerstam, 1991), its flight speed predictions have not yet been tested either directly or against the V_{mr} alternative.

Whether migration speeds are time or energy-selected (Alerstam and Lindström, 1990), is unknown. Furthermore, it may be some time before enough experimental evidence is accumulated to conclusively reject one idea in favor of another. To test predictions from the time minimization hypothesis, for example, both the feeding rate and subsequent flight speed of individual birds must be measured (Alerstam and Lindström, 1990). It is possible, though, to make predictions of V_{mr} for a given species using only a few parameters that are readily available in the literature. If migration speeds are consistently higher than predicted, this will at least allow rejection of V_{mr} as a general migration strategy. This is the approach used here.

METHODS

Flight speed selection criteria

I compiled literature reports of the flight speeds of migrating birds. Published speeds were acceptable only if: (1) they were instantaneous measurements. Speeds calculated from long distance trips were judged unreliable since the altitude of the migrating bird and the magnitude and duration of prevailing winds throughout the flight were unknown. (2) Wind speed and direction with respect to the bird was specified or, as in the case of some older records, wind conditions were stated as calm or nearly so. (3) There was an explicit assumption that the individuals were undergoing migration. Many older flight speed records were obtained from motorized vehicles by accelerating up to and then chasing birds for brief distances (e.g. Gignoux, 1921; Donald, 1928; Sooter, 1947; Cottam et al., 1942). Since these are probably estimates of maximum speed, all reports in this context were omitted with the exception of one estimate for the Barn Swallow (*Hirundo rustica* ; Harrison, 1931). In addition to fulfilling the above criteria, Harrison's subject is reported as flying parallel to the measuring vehicle, at a constant speed and in "normal" unhurried flight. Only airspeed records were used in the analysis. Some reports included only groundspeed records and these were converted to the corresponding airspeed (see below).

Predictions and Statistical Analysis

Using three aerodynamic models and their associated parameter values (see below), I made predictions of V_{mr} from details of 102 flights speeds in 48 avian species (see Appendix). To eliminate the lack of independence of multiple speed records on the same species, species-specific averages of both the predicted and observed speeds were calculated and then compared. I regressed the residuals (observed airspeed - predicted V_{mr}) against the log of mass (see below; logs were necessary to normalize the distribution) to look for any systematic deviation in the Vmr predictions. I also made predictions of the maximum sustained airspeed for each species and compared these values with V_{mr} predictions and the observed airspeeds.

All curve fitting procedures used Model I least squares regression (Sokal and Rohlf, 1981). Recently, Rayner (1985a) has criticized a similar analysis of flight speed data by Pennycuick (1982), in favor of a reduced major axis method (Sokal and Rohlf, 1981, p. 550). Pagel and Harvey (1988) have also questioned the use of Model I regression procedures to analyze data of this type. However, they also point out several drawbacks to the reduced major axis technique and instead favor calculating a slope from the major axis method (Sokal and Rohlf, 1981, p. 594). The reduced major axis and major axis methods are Model II procedures, applicable when both the dependent and independent variables are subject to error. Both methods would give an estimate for the slope slightly higher than Model I regression (Pagel and Harvey 1988). One difficulty with Model II regression (which is not true for the Model I procedure), however, is that the residuals are usually correlated with the independent variable, particularly if the correlation between the dependent and independent variables is low (Pagel and Harvey, 1988). Hence, a plot of the residuals against body mass would be biased since predicted V_{mr} and body mass are correlated (Pennycuick, 1975). I am confident therefore that Model I regression is better suited to this analysis (see also Pennycuick, 1987).

An important consideration in comparative analyses across taxa is whether the covariance between two traits results from common ancestry rather than parallel or convergent evolution (see Pagel and Harvey, 1988, for a discussion of this idea). In the former case (termed a taxonomic artifact; Ridley, 1983), species that are not of independent origin likely cannot be counted as statistically independent. Taxonomic artifact is likely unimportant in this analysis since most of the genera are represented only by a single species, and the maximum number of species in any given genus is only 3 (see Appendix).

Aerodynamic equations

I estimated flight costs using three equations derived from aerodynamic theory (Pennycuick, 1975, 1989, Tucker, 1974, 1975, and Greenewalt, 1975), two of which (Pennycuick and Tucker) have been used in a number of ecological models (for example, the Pennycuick equation by Blake, 1985, and Lindström and Alerstam, 1992; the Tucker equation by McLaughlin and Montgomery, 1985, 1990, and Welham and Ydenberg, 1988). Another method of estimating flight costs is based on vortex theory (Rayner, 1979). This approach takes into account the lift and thrust generated by the vortices created behind an animal's wings as it flies through the air. Unfortunately, the calculations involved are tedious, and the input parameters for many species are not well known (Norberg, 1990).

In the Pennycuick (1989) and Tucker (1975) equations, the total power required for flight (P_{total}) is assumed to be the sum of four components. 1. Parasite power (P_{par}) is the power necessary to overcome the drag generated by the bird's body (excluding the wings) as it moves through the air. 2. Induced power (P_{ind}) must be used to support the bird's weight in the air. 3. Profile power (P_{pro}) is required to flap the wings, and 4. Metabolic power (P_{met}) is used to maintain basic physiological functions. Equations describing parts 1, 2, and 4 are identical or very similar in each model (cf. Pennycuick, 1989, equations 3.3, 3.10, and p. 26, with Tucker, 1974, equations 5, 6, 48, and 51) and therefore are presented only in their basic form.

Parasite power is given as:

$$P_{par} = 0.5\ r\ V^3\ S_b\ C_{Db}, \qquad (1)$$

where r = air density, V = airspeed, S_b = frontal area of the body, and C_{Db} = the drag coefficient of the body.

Induced power is:

$$P_{ind} = k\ m^2\ g^2 / 2\ (S_d\ V\ r), \qquad (2)$$

where k = a dimensionless induced drag factor, m = body mass, g = the force of gravity, S_d = disc area (the area of a circle whose diameter equals the wing span), r and V are as defined above.

Metabolic power is:

$$P_{met} = 6.15\ m^{0.724} \text{ for passerines, and} \qquad (3a)$$

$$P_{met} = 3.73\ m^{0.723} \text{ for nonpasserines,} \qquad (3b)$$

where m is body mass in kg (Tucker, 1973).

Assumptions about profile power in the two models differ significantly. Tucker (1974, 1975) assumes that P_{pro} at a given velocity equals the sum of P_{par} and P_{ind} at that velocity, multiplied by a term incorporating the Reynold's number (see Vogel, 1981, for a discussion of Reynold's numbers) and a constant, to yield:

$$P_{pro} = 471 \ (\mu /(r \ m^{0.333} \ V))^{0.5} \ (P_{par}(V) + P_{ind}(V)), \qquad (4a)$$

where μ = air viscosity, and r, m and V are as defined above. Alternatively, Pennycuick (1989) argues that P_{pro} increases significantly only at airspeeds that exceed the maximum power output of most birds. P_{pro} is therefore entered as a constant but, like Tucker, is calculated in part from the sum of the P_{par} and P_{ind}. When plotted as a function of airspeed, this sum is curvilinear and its minimum is the absolute minimum power (P_{am}). P_{am} is then multiplied by a constant to yield P_{pro} (see Pennycuick, 1989, p. 25 for further details). Hence,

$$P_{pro} = 1.2 \cdot P_{am}, \qquad (4b)$$

where $P_{am} = \min(P_{par}(V) + P_{ind}(V))$.

In the Greenewalt (1975) equation, cost of flight is the sum of the parasite and induced powers only. Parasite power is given as:

$$P_{par} = (2.072 \ X \ 10^{-7}) \ S^{0.7} b^{0.3} V^{2.7}, \qquad (5)$$

and induced power,

$$P_{ind} = 7.879 m^{1.91} b^{-2} V^{-1}. \qquad (6)$$

S is the projected wing area (cm^2), b the wingspan (cm), and V and m are as defined above (in units of km/hr and g, respectively. The airspeed predictions were then converted to m/s for consistency with the other equations). Further details can be found in Greenewalt (1975).

To estimate total flight costs for a given airspeed (P_{total} (V)) requires only knowledge of bird mass and flight altitude. Species-specific mass estimates were calculated as the average of the mass of males and females. In many cases I was able to use weights derived from migrating species (Cramp and Simmons, 1977, 1980; Cramp, 1983, 1985). All other input variables can be estimated from allometric relationships, though actual measurements are always preferable and were used whenever possible (many of which were derived from Greenewalt, 1962; see Appendix).

Since the relationship between flight cost and forward airspeed is curvilinear, two characteristic speeds can be determined (see Alerstam 1991). The minimum power speed (V_{mp}) is found by setting:

$$d\,P_{total}(V) / dt = 0. \qquad (7)$$

However, the bird is flying at the maximum range speed (V_{mr}) when:

$$d\,P_{total}(V_a) / d\,V_g = 0, \qquad (8)$$

where V_g is the groundspeed resulting from flight at a given airspeed (V_a). In calm conditions, airspeed and groundspeed are equivalent. In a tailwind, however, groundspeed is increased for any given airspeed and the predicted V_{mr} decreases compared with the zero wind case (while the converse is true for a headwind; Norberg, 1990). The effect of wind speed (V_w) is determined by setting $V_g = V_a - V_w$, and requires knowledge of the two vectors (the following component and its associated perpendicular vector) that describe wind speed and direction with respect to the bird's speed and direction (see Norberg 1990, pp. 90-91). All V_{mr} predictions were corrected for wind speed whenever necessary.

Maximum power and velocity

From biomechanical considerations, the maximum specific power available (P_{as}) for flight at a given flapping frequency (f), can be approximated by the following equation (Pennycuick 1989, equation 7.14):

$P_{as} = 21.2\,f$ W/kg of flight muscle.

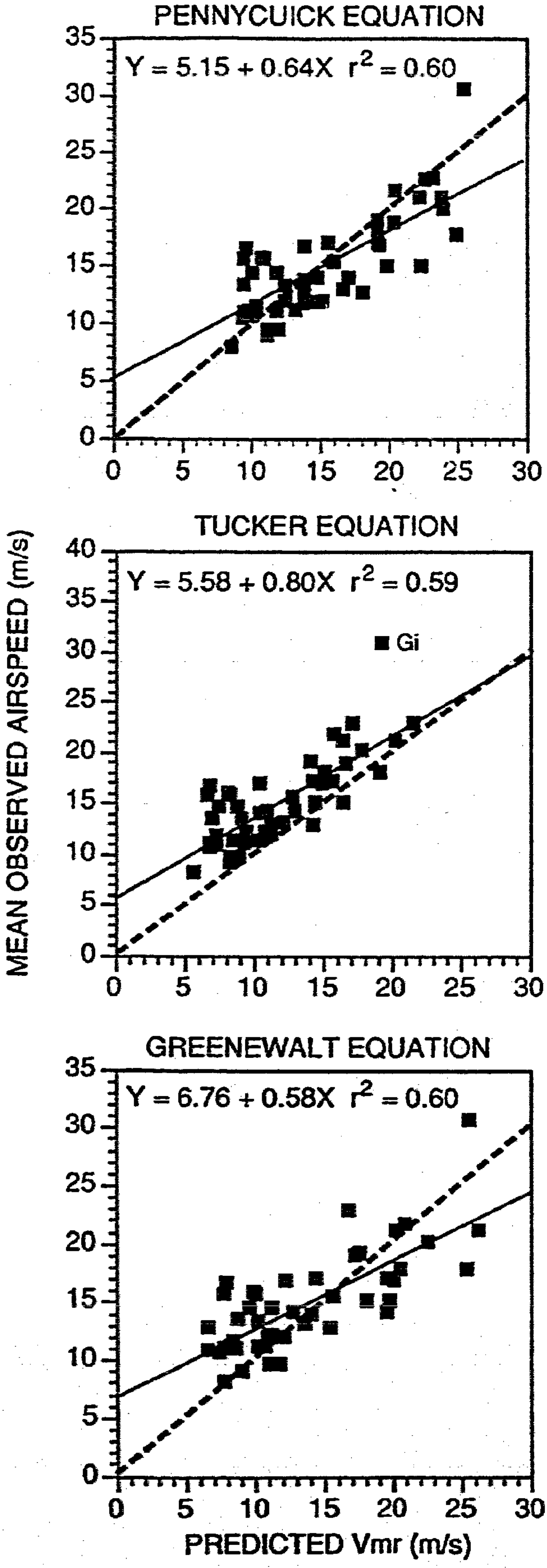
To estimate f, I solved the equation f $l^{1.15}$ = 3540 (Greenewalt 1962, Figure 10), where l is wing length (in mm, and which is assumed equal to one half the wing span; Greenewalt 1962). Recently, Pennycuick (1990) derived a relationship for flapping frequency that gives slightly different (though qualitatively similar) predictions to that used above. The sample of masses upon which it is based, however, is much more restricted, with only a single representative weighing less than 0.1 kg.

The airspeed at which $P_{total}(V)$ and the absolute power available to the muscles (P_{max}; W) are equal, is the maximum sustained airspeed (V_{max}). Pennycuick (1989) has suggested that P_{max} should scale with some power of the mass between 2/3 and 5/6. I estimated P_{max} by scaling P_{as} with mass^1. This was the lowest power at which the minimum P_{total} (V) estimates for at least two of the aerodynamic equations were always less than the corresponding P_{max} values for a given species, and (for one of the equations) gave V_{max} estimates for the two heaviest species that were less than their corresponding V_{mr} values (and close to V_{mp}; see Pennycuick, 1989 pp 90-91, for further discussion of this size-related scaling effect). I detemined V_{max} values for all species and each aerodynamic equation. Since estimates of P_{max} are based purely on theoretical considerations and have not yet received empirical confirmation, they may be subject to error. To compensate for this difficulty, I halved the P_{max} estimates and then derived a second set of V_{max} values for each equation.

RESULTS

Comparison of the V_{mr} predictions from the three equations shows that no single equation provided a strong quantitative fit to the observed airspeeds (Figure 2.1). In all three cases, the intercepts are significantly greater than 0

Figure 2.1. Mean observed airspeeds of 48 species of birds in relation to V_{mr} values predicted from the Pennycuick, Tucker and Greenewalt equations. In each case, the dashed line is the equality between observed and expected values and the equation describes the line of best fit. Symbol Gi under the Tucker equation is the outlier, *Gavia immer* (see text).


PENNYCUICK EQUATION
Y = 5.15 + 0.64X r² = 0.60
TUCKER EQUATION
Y = 5.58 + 0.80X r² = 0.59
Gi
GREENEWALT EQUATION
Y = 6.76 + 0.58X r² = 0.60
MEAN OBSERVED AIRSPEED (m/s)
PREDICTED Vmr (m/s)
0
5
10
15
20
25
30
35
40

($p < 0.001$), and the slope of the regression is significantly less than 1 for Pennycuick and Greenewalt ($p < 0.001$), but not Tucker ($p > 0.05$; 2-tailed tests). However, when a single outlier is eliminated from the Tucker regression (Outlier test, $p < 0.01$, Sokal and Rohlf 1981), its slope is also significantly less than 1 ($b = 0.734$, $p < 0.01$, $N = 47$). The Tucker equation consistently predicted migration speeds lower than observed, and this contrasts with the other equations which made some underestimates of V_{mr} at low observed airspeeds (particularly Greenewalt), and overestimates at high speeds (Figure 2.1).

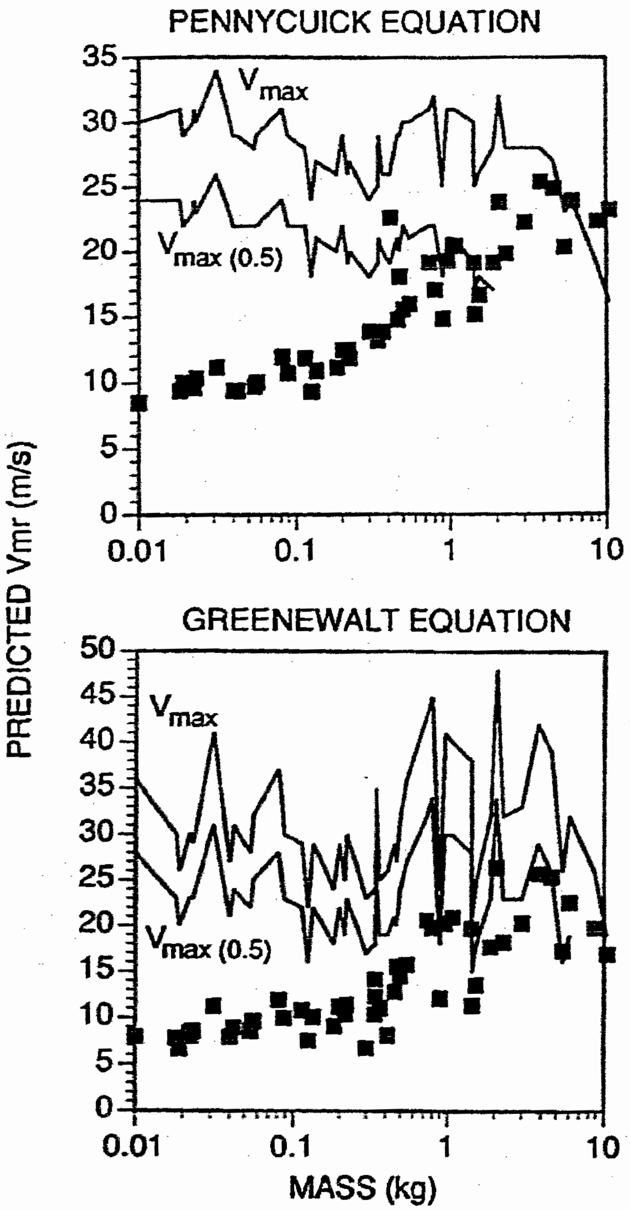
Results of the residual analysis showed a significant negative relationship with mass for the Pennycuick and Greenewalt equations, but the explained variation was low (Pennycuick $r^2 = 0.33$, Greenewalt $r^2 = 0.22$; Table 2.1). There was no significant relationship with body mass for the Tucker equation (Table 2.1). In general, the Greenewalt and Pennycuick equations made predictions of V_{mr} that were roughly equivalent to observed speeds for species weighing 0.3 to 3.0 kg (20/48 species) and 0.1 to 1 kg (19/48 species), respectively (these were the ranges at which the 95% confidence limits of the residual slope intercepted the 0 residual).

The relationship to mass between V_{max} and predicted V_{mr} values for the Pennycuick and Greenewalt equations are shown in Figure 2.2. I excluded the Tucker equation from this and the subsequent analysis since its predictions of the minimum flight cost for all species > 0.7 kg (a total of 16/48 species) exceeded the corresponding P_{max} values (this result is unrealistic since it suggests that these species are incapable of sustained flapping flight). Predictions of V_{max} show considerable variation between species of similar size as a result of large differences in wing span (and therefore flapping frequency). The difference between V_{mr} and V_{max} decreases with increasing

Table 2.1. Parameter values from the residual analysis

Equation	Slope	P	r^2
Greenewalt	- 2.18	< 0.01	0.22
Pennycuick	- 2.28	< 0.01	0.33
Tucker	- 0.90	0.08	0.06

Figure 2.2. The relationship between the mean predicted V_{mr} values (solid symbols) of the 48 species and their mass for the Pennycuick and Greenewalt equations. Each line is the velocity derived from estimates of maximum power output (V_{max}) and 0.5 times maximum output ($V_{max(0.5)}$), respectively. Truncation of the $V_{max(0.5)}$ line occurs because the predicted cost of flight at V_{mr} (derived from the aerodynamic equations) for heavier species exceeds the corresponding maximum output estimate.


PENNYCUICK EQUATION
V max
V max (0.5)
GREENEWALT EQUATION
V max
V max (0.5)
PREDICTED Vmr (m/s)
MASS (kg)
0
5
10
15
20
25
30
35
40
45
50
0.01
0.1
1
10

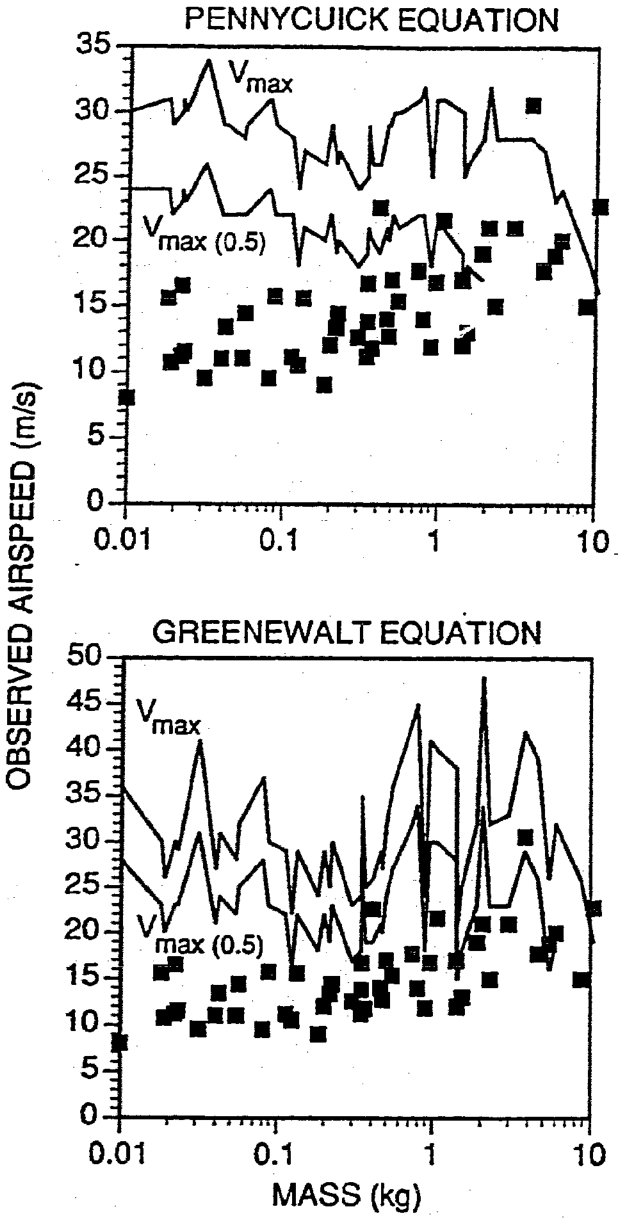
mass (Figure 2.2). With respect to the Pennyuick equation, its V_{mr} predictions for the majority of species weighing > 1 kg are very close to V_{max} and, in fact, exceed V_{max} for the two heaviest species. None of the predicted Vmr values from the Greenewalt equation exceed V_{max} and only for the very heaviest species (> 5 kg) are the two more or less equivalent.

V_{max} values from the Greenewalt equation almost always exceeded observed airspeeds though the two speeds converge as mass increases, and are within the V_{max} boundaries for the four heaviest species (Figure 2.3). This convergence is also apparent with the Pennycuick equation but the observed airspeeds are within the V_{max} boundaries at a much lower mass (about 1 kg; Figure 2.3).

DISCUSSION

Relatively few species appear to minimize the energy cost of migration by flying at V_{mr}. For example, smaller species have a surplus of power available for flight resulting from the large differential between V_{mr} and V_{max} and many use this extra power to migrate at faster airspeeds. This suggests that minimizing energy expended while migrating may be less important to these birds than other considerations, such as minimizing the time spent on migration, for example (see Alerstam and Lindström 1990, Lindström and Alerstam 1992, for further discussion of this point). Reducing migration time may be particularly important for birds which breed at high latitudes and make long-distance migrations to wintering grounds in southern latitudes. The short and unpredictable arctic summer might favor rapid flight to ensure arrival on the breeding grounds as early as weather permits, and a quick return in the autumn to staging areas further south. Many of the smaller species reported here do fit this description. For example, most of the shorebirds (see Appendix) and the

Figure 2.3. The relationship between the mean reported migration speeds (solid symbols) of the 48 species and their mass, for the Pennycuick and Greenewalt equations. See Figure 2.2 for details of V_{max} and $V_{max(0.5)}$.


PENNYCUICK EQUATION
V$_{max}$
V$_{max}$ (0.5)
35
30
25
20
15
10
5
0
0.01
0.1
1
10
OBSERVED AIRSPEED (m/s)
GREENEWALT EQUATION
V$_{max}$
V$_{max}$ (0.5)
50
45
40
35
30
25
20
15
10
5
0
0.01
0.1
1
10
MASS (kg)

passerines *Oenanthe oenanthe* and *Motacilla alba* are arctic breeders and migrate over at least 80° latitude (Johnson and Herter 1990). Furthermore, the few studies that have tested the time minimization hypothesis examined small migrants (including arctic breeding shorebirds), and results were consistent with its predictions (Lindström and Alerstam, 1992; Gudmundsson et al., 1991).

While the time minimization hypothesis might explain why observed airspeeds in species of low mass tend to exceed predicted V_{mr} values, it cannot explain the opposite trend in heavier species (predicted V_{mr} values which were almost always higher than observed airspeeds; Figures 2.2, 2.3). It appears instead that, for species weighing more than 1 kg, the V_{mr} predictions approach or exceed their maximum sustained power output (and hence the maximum sustainable airspeed, V_{max}; Figure 2.2). This scaling effect with size occurs because the minimum power necessary for flight increases with mass at a rate faster than power generated from mass-specific metabolic activity (Pennycuick, 1969, 1975). Hence, the total power available for flight declines as body mass increases. The lower airspeeds (relative to V_{mr} predictions) of large birds then appear to result from the fact they are flying at or very close to the upper limits of their metabolic performance. This point is particularly well illustrated by results of the Pennycuick equation (Figure 2.3).

Intermediate-sized species tend to migrate at about Vmr even though they are probably not constrained (by metabolic limits) to fly at this speed. Birds in this size range may be sufficiently large that they are less susceptible to short-term changes in weather conditions. Instead, selection has favored a more conservative migration strategy to ensure that stored reserves are never depleted to critical levels.

Though the primary aim of this study was not to evaluate the suitability of the costs-of-flight equations, several of the results call into question the validity of at least one of them. Most of the observed airspeeds for the largest species are higher than the predictions of V_{mr} from the Tucker equation (see Appendix), for example, which seems unlikely given the limits to metabolic performance discussed above. Furthermore, the actual flight costs predicted by the Tucker equation may be excessive since, for most of the heavier species, they exceeded the P_{max} limit. Alternatively, the Greenewalt equation may underestimate flight costs since it does not include either metabolic or profile power costs (see Models section). This will result in high predictions of V_{max}, which could explain why its V_{mr} predictions and the observed airspeeds are generally lower than V_{max} for almost all species (Figures 2.2, 2.3). It appears therefore that the Pennycuick equation may provide the most realistic estimate of flight costs in comparison with the other aerodynamic models.

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Appendix. Catalogue of species and their associated variables used in the flight speed analysis.

							Greenewalt		Pennycuick		Tucker	
Genus and species	Mass(kg)	Wing span (m)	Altitude (m)	Wind Angle (°)	Wind Speed (ms^{-1})	Mean reported airspeed (ms^{-1})	Mean Vmr (ms^{-1})	Vmax (ms^{-1})	Mean Vmr (ms^{-1})	Vmax (ms^{-1})	Mean Vmr (ms^{-1})	Reference
O. Passeriformes												
Parus caeruleus	0.010	0.24	5	0	0	8.0	7.9	36	8.5	30	5.9	Rayner, 1985b
Oenanthe oenanthe	0.018	0.26	5	0	0	15.8	7.8	30	9.4	31	6.8	Meinertzhagen, 1955
Hirundo rustica	0.019	0.33	5(4)	0(2) 180(2)	0,2,2,6.7	10.7	6.7	26	10.0	29	7.5	Harrisson, 1931 Meinertzhagen, 1955
Fringilla coelebs	0.022	0.31	5(2)	0,180	0,2	11.15	8.3	30	9.75	30	7.1	Gatter, 1979
Motacilla alba	0.022	0.28	5	0	0	16.5	8.0	30	9.8	31	7.0	Meinertzhagen, 1955
Fringilla montifringilla	0.023	0.31	5	180	2	11.5	8.5	29	10.3	30	7.6	Gatter, 1979
Passer domesticus	0.031	0.24	5	0	0	9.5	11.2	41	11.1	34	8.3	Rayner, 1985b
Sturnus vulgaris	0.081	0.39	5	0	0	9.5	11.9	37	11.9	31	9.0	Rayner, 1985b
Corvus brachyrhynchos	0.473	0.92	50	180	6.8	12.7	15.5	27	18.0	29	14.5	Tucker, Schmidt-Koenig, 1971
Corvus corone	0.46	0.85	5	0	0	14.0	12.8	29	14.7	29	11.0	Rayner, 1985b
O. Charadriiformes												
Calidris alpina	0.042	0.41	5	0	0	13.4	8.9	31	9.4	29	7.0	Rayner, 1985b
Calidris alba	0.056	0.43	5	0	0	14.4	9.6	32	10.0	29	7.5	Noer, 1979
Calidris canutus	0.088	0.5	5	0	0	15.7	10	30	10.7	29	8.1	Noer, 1979
Tringa totanus	0.134	0.63	5	0	0	15.6	10.1	29	10.9	27	8.3	Noer, 1979
Limosa lapponica	0.343	0.75	5	0	0	16.7	12.3	29	13.8	29	10.5	Noer, 1979
Numenius phaeopus	0.343	0.75	5	0	0	13.8	14.2	35	13.8	29	10.5	Meinertzhagen, 1955
Vanellus vanellus	0.218	0.85	5	180	2	13.3	10.4	25	12.4	26	9.3	Mildenberger, 1950

Pluvialis squatarola	0.224	0.77	5	0	0	14.4	11.4	30	11.8	27	8.9	Noer, 1979
Haematopus ostralegus	0.544	0.83	10(14)	c	d	15.34	15.7	36	15.9	30	12.51	Preuss, 1960
Sterna hirundo[e]	0.125	0.88	5	0	0	10.5	7.5	22	9.3	24	6.8	Raynor, 1985b
Larus atricilla[e]	0.3	1.13	50	112	6.6	12.6	6.7	23	13.6	24	11.5	Tucker, Schmidt-Koenig, 1971
Rissa tridactyla[e]	0.411	1.04	5(7)	f	g	22.59	8.1	26	22.6	26	21.7	Olden, Peterz, 1985
Larus argentatus[e]	0.895	1.47	5,50(3)	0(2),90 180	0,6.8(3)	11.88	12.125	24	14.78	25	11.38	Raynor, 1985b
O. Anseriformes												
Mareca americana	0.738	0.83	50	105	6.8	17.7	20.6	43	19.1	31	15.2	Tucker, Schmidt-Koenig, 1971
Clangula hyemalis	0.793	0.76	5	0	4.9	14.0	19.7	45	17	32	13.0	Spoirs, 1945
Anas acuta	0.97	0.88	50(3)	0,80,160	6.8(3)	16.8	20.23	41	19.23	31	15.0	Tucker, Schmidt-Koenig, 1971
Anas platyrhynchos	1.077	0.90	5,232.5	0,180	0,5.2	21.6	20.05	40	20.4	31	15.75	Bellrose, Crompton, 1981
Branta leucopsis	1.691	1.39	5	0	0	19.0	17.7	32	19.1	28	14.1	Raynor, 1985b
Somateria mollissima	2.05	0.94	5	0	0	21.0	26.4	28	23.8	32	18.1	Raynor, 1985b
Anser albifrons	2.273	1.48	5	0	0	15.0	18.2	32	19.8	28	14.5	Raynor, 1985b
Anser caerulescens	2.986	1.49	232.5(2)	0,180	3.5,3.7	21.0	20.35	33	22.2	28	16.45	Bellrose, Crompton, 1981
Branta canadensis	4.635	1.53	232.5(3)5 0	0(2),180 68	2.6,3.6, 3.4,6.8	17.7	25.42	39	24.86	27	19.1	Tucker, Schmidt-Koenig, 1971; Bellrose, Crompton, 1981; Wege, Raveling, 1984
Cygnus columbianus	6.05	1.86	5	0	0	20.0	22.6	32	23.9	24	17.9	Raynor, 1985b
O. Procellariiformes												
Oceanites oceanicus	0.04	0.4	5	0	0	11.0	7.9	27	9.4	29	6.9	Raynor, 1985b
Diomedea exulans	8.727	2.9	5	0	0	15.0	19.8	26	22.3	19	16.5	Raynor, 1985b

O. Apodiformes											
Apus apus	0.054	0.45	5	0	0	11.0	8.6	20	9.7	28	7.2	Rayner, 1985b
O. Falconiformes											
Falco sparverius	0.114	0.55	50	70	6.8	11.1	10.8	29	11.8	28	9.4	Tucker, Schmidt-Koenig, 1971
Falco tinnunculus	0.184	0.76	5	0	0	9.0	9.1	24	11.1	28	8.4	Rayner, 1985b
Accipiter nisus	0.2	0.63	5	0	0	12.0	11.2	29	12.4	29	9.5	Rayner, 1985b
Pandion haliaetus	1.528	1.58	5	0	0	13.0	13.6	25	16.6	26	12.1	Rayner, 1985b
O. Ciconiiformes											
Egretta caerulea	0.34	1.04	50(4)	0,90,112 180	6.8(4)	11.17	10.4	24	13.17	25	10.47	Tucker, Schmidt-Koenig, 1971
Egretta thula	0.360	0.97	50(3)	0,90,180	6.8(3)	11.8	11.07	25	13.0	26	10.03	Tucker, Schmidt-Koenig, 1971
Ardea cinerea	1.433	1.85	5	0	0	12.0	11.4	21	15.1	25	10.8	Rayner, 1985b
O. Columbiformes											
Columba palumbus	0.5	0.78	5	0	0	17.0	14.5	32	15.5	30	11.9	Rayner, 1985b
O. Gaviiformes											
Gavia stellata	1.423	1.11	5	0	0	17.0	19.7	38	19.1	30	14.3	Rayner, 1985b
Gavia immer	3.795	1.37	5,2057	110,0	6.9,11	30.6	25.7	42	25.4	28	19.3	Preston, 1951; Kerlinger, 1981
O. Gruiformes											
Grus grus	5.468	2.33	5,750	0(2)	0,10	18.8	17.25	26	20.3	23	14.8	Mildenberger, 1950; Alerstam, 1975

O. Pelecaniformes											
Pelecanus onocrotalus	10.5	3.15	382	0	0	22.7	16.9	19	23.2	16	17.1	Meinertzhagen, 1955

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[a] Unknown.

[b]. Not applicable.

[c] 0, 50, 60(6), 80, 100(3).

[d] 0, 0.6, 3.7, 4.5, 4.8, 5.6, 6.2, 7.9, 8.4, 9.0, 3.1, 8.6, 9.0, 9.1.

[e] F. Laridae (see text).

[f] 71, 93, 106, 109, 116, 132, 138.

[g] 13(4), 23, 14, 20.

CHAPTER III

EFFICIENCY-MAXIMIZING FLIGHT SPEEDS IN PARENT BLACK TERNS

From "Efficiency-maximizing flight speeds in parent black terns" by C.V.J. Welham and R.C. Ydenberg, *Ecology*, 1993, *74*, 1893-1901.

ABSTRACT

Optimal foraging theory assumes that individuals maximizing a given energetic currency maximize their fitness. Though models with different currencies (and assumptions) have been successful at describing forager behavior, discriminating between currencies has proven difficult because models optimizing different currencies often make similar predictions. A field experiment was designed to use flight speeds of Black Terns (*Chlidonias niger*) feeding their young to test predictions from optimal foraging models maximizing (1) the net energy gained per unit energy expended (Efficiency; EFF), (2) the net rate of energy intake (NREI), and (3) daily delivery rate (DR), respectively. Manipulating the distance an adult had to fly between a feeding enclosure and its nest enabled us to discriminate among the three currencies. Predicted speeds of the EFF model best matched the observed flight speeds. Maximizing efficiency resulted in the lowest delivery rate to the nest, but it was also the only currency that predicted adult daily energy expenditures within the theoretical limit (DEE_{max}) estimated for Black Terns (206 kJ/day; Kirkwood 1983).

The feeding enclosure represented an unusually profitable food source for the terns and this may have resulted in artificially high predictions for flight speed, particularly for the NREI and DR currencies. We therefore made another set of predictions from the three models using estimates of foraging success from parents who had never foraged from the feeding enclosure, and compared these predictions with measured flight speeds. The EFF model was again the best predictor of flight speeds even though none of the three models predicted energy expenditures in excess of DEE_{max}. Though the DR model resulted in the highest total daily energy delivered to the nest, this represented only a small gain relative to the NREI and EFF models. Black Tern parents may maximize

EFF because this currency is least likely to result in daily energy expenditures that exceed their metabolic limit.

INTRODUCTION

In optimal foraging theory (Pyke 1984), an animal is assumed to maximize its fitness by maximizing a given currency. A number of currencies have been proposed, and each makes different assumptions about the relationship between time, energy, and fitness. For example, maximizing efficiency (energy gained per unit energy expended, EFF), implies that energy expenditure is in some way limited, either as a result of a fixed total budget, or because it is costly to recoup. Alternatively, if foraging is limited by available feeding time, then a rate maximizing currency (for example, net energy gained per unit time, NREI) may be more appropriate (Stephens and Krebs 1986).

To date, most optimal foraging studies have treated the efficiency and rate maximizing currencies as alternative strategies (Kacelnik 1984, Schmid-Hempel 1987, McLaughlin and Montgomery 1990, for example; but see Ydenberg et al. 1993). It seems likely, however, that an animal will face limitations in both time and energy, and, for parents feeding offspring, Houston (1986, 1987) has shown that rate maximization neither minimizes the forager's energy expenditure rate, nor maximizes the energy it delivers to the nest over the day (see below). From a life-history context, Houston argues that parental foraging decisions should incorporate both the need for parents to meet their own energetic requirements, as well as those of their young. Houston (1986, 1987) therefore included a term for the time that a parent must spend self-feeding on each foraging trip to balance its own energy budget. His 'delivery rate' (DR) model resulted in a higher rate of energy delivery to the nest per day, than either the NREI or EFF maximizing currencies. Further, the optimal policy under the DR model depends upon the rate at which the parent can feed itself (in contrast to the other currencies; Houston 1987). If self-feeding rates are low, the DR predictions converge with those of alternative currencies (see Houston

1987, Tables 1, 3a). Conversely, when parents can feed themselves very quickly, they should provision their young at a very high rate.

Each of these currencies has been at least qualitatively successful at describing the foraging behavior of animals (Stephens and Krebs 1986, see Discussion). In some cases, however, more than one currency made predictions which adequately fit the data (Welham and Ydenberg 1988), or different currencies made similar predictions (Kacelnik 1984, Houston 1987). One further difficulty is that animals may face limits on performance that could constrain their behavioral options to levels below the predicted optimum. For example, Kirkwood (1983) derived an empirical relationship for maximum daily energy expenditure in animals that must maintain a balanced energy budget (see below for details); a limit that might be set by the ability of the gut to assimilate food (Peterson et al. 1990, Weiner 1992). In a theoretical model, Ydenberg et al. (1993) were able to demonstrate the importance of energy and time limitations to the foraging decisions of parental animals. When parental intake rate was constrained by the energy needed to power self-feeding, maximizing EFF ensured the highest total daily delivery to the central place. Similarly, when time needed for parents to recoup energetic expenditure limits total delivery, a low self-feeding rate relative to the rate of energy expenditure also favors efficient stategies. As the rate of self-feeding increases, however, foraging behavior deviates from efficiency in the direction of rate maximization. Experimental testing of models that maximize different currencies will thus be useful in determining how energy expenditure, time, and physiological limits on performance, affect the behavior of foragers.

Here we report the results of an experiment designed to achieve maximum discrimination between three foraging models maximizing (1) efficiency, (2) the net rate of energy intake, and (3) the food delivery rate to the nest. We use the three models to predict the flight speeds of Black Terns (*Chlidonias niger*) foraging to provision their young with fish from a stocked enclosure, and compare our predictions with measured airspeeds. For birds, flight speed can be a powerful tool to discriminate among these models (McLaughlin and Montgomerie 1985, 1990, Welham and Ydenberg 1988). We also calculate the total daily energy expenditures predicted by each model, and compare these values with a theoretical limit to daily energy expenditure (DEE_{max}) in the Black Tern. We use the equation for DEE_{max} of Kirkwood (1983), who derived the following allometric relationship for metabolizable energy intake based on estimates for 21 species of birds and mammals. For a species of mass, M (kg),

$$DEE_{max} = 1713\ M^{0.72} \quad \text{(kJ/d; SE of slope} \pm 0.008\text{)}. \qquad (1)$$

We then derive a new set of predicted airspeeds using the delivery rate maximizing currency but with daily expenditure constrained to DEE_{max}.

In our feeding experiment, fish were available to the terns only part of each day, and an individual's foraging decision might be based on its long-term expected rate of return. For Black Terns, this long-term rate is likely much lower than the rate attained during the experiment (see below). This would lead to lower predictions of airspeeds for the three currencies (particularly the DR maximizing model; see Houston 1987). We therefore also predict airspeeds from the three currencies using foraging parameters estimated from parents that had no access to the enclosure, compare these predictions with the observed airspeeds from birds using the enclosure, and again calculate the expected total daily metabolizable energy returned to the nest.

METHODS

The study was conducted during July 1987, 1988, and 1989 on the Creston Valley Wildlife Management Area, a 6800 ha managed marsh system near

Creston, British Columbia, Canada (49° 14' N, 116° 38' W). Black Terns return to breed in Creston in early to mid-May, and are present until mid-August. Nests consist of a floating mat of dead vegetation (Mosher 1986). The three eggs are usually laid in early June, and hatch after about 21 days of incubation. Chicks are capable of flight about 20 days after hatch but are fed by parents for at least several weeks after (pers. obs.). Adult insects (primarily damselflies of the family Coenagrionidae, and dragonflies of the family Calopterygidae) are the predominant prey for both parents and their young, though fish (usually year-class 1 yellow perch *Perca flavescens*) comprise about 10% by frequency of all prey items delivered (Mosher 1986). Parents bring only one prey item to the nest each trip.

Experimental protocol

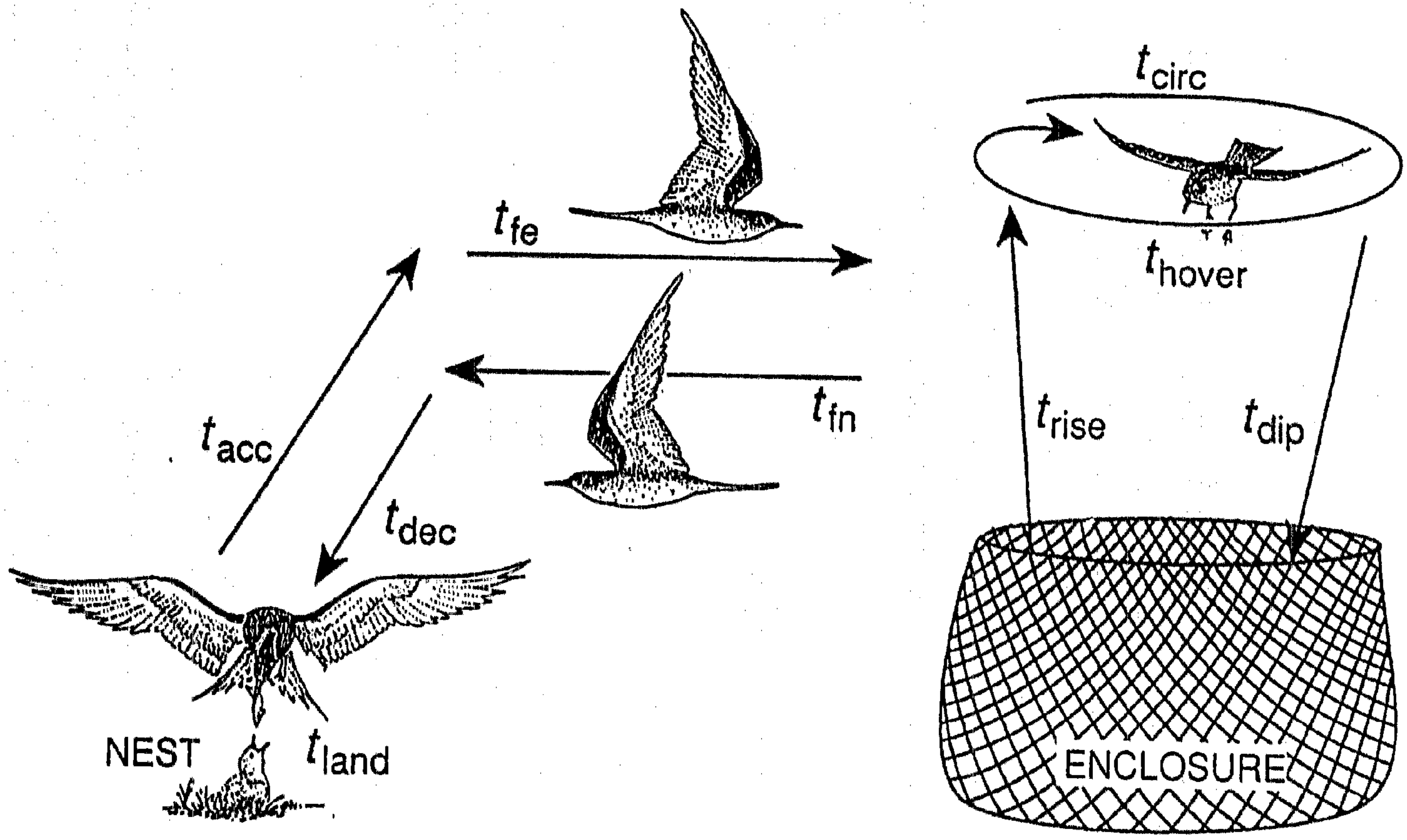
In June of each year we selected an area of marsh (about 75 X 75 m) with 50 - 80 pairs of breeding terns, and marked all nests containing eggs. Nests were checked daily to determine the date of clutch completion and to estimate hatching date. Several blinds were erected in the study area to observe parental foraging activities.

Prior to chick hatching, we constructed a mesh enclosure (size 4 X 4 X 0.2 m) in an area of the marsh frequented by foraging adults. We beach-seined the ditches that form part of the marsh drainage system in order to stock the enclosure daily with 800-1000 fish (yellow perch were used in 1987 and 1989, and largemouth bass *Micropterus salmoides* in 1988), about 3.2 ± 0.35 (SD; n = 80) cm in length (mean wet weight 0.31 ± 0.032 g). Previous observations (Welham unpublished) suggested that this was the average size of fish delivered to offspring prior to fledging. Hence, Black Terns returned to the nest with a single prey item of known size, and we therefore could make an accurate estimate of the energy gained on a given foraging trip. The artificially high density of fish also ensured consistent use of the enclosure and minimized any confounding effects associated with food depletion.

Every two days, the fish enclosure was moved to a different area of the marsh, with the exact location governed by its visibility to the observer. We altered the parents' travel cost by increasing the distance between the enclosure and a given nest, and this exaggerated the differences among the predictions of the three foraging currencies.

Observations were made on a total of 10 unmarked Black Terns (from 10 different nests) that provisioned their chicks with food from the enclosure. Offspring were between 10 and 12 days old to control for inter-brood variation in energetic demand, and all nests contained the maximum brood size of three. A typical foraging bout consisted of a series of trips between the nest and the enclosure. Each trip was described by a number of mutually exclusive behaviors (Figure 3.1) recorded using a portable tape recorder. If a nest was too far from the enclosure for a single observer to describe forager behavior accurately, or was obscured by emergent vegetation, a second observer relayed the behavioral observations through a radio headset. Adults travelled in a direct line to and from the enclosure. When at the enclosure, the bird usually circled several times before making a capture attempt. Capture attempts were assumed to occur when a bird dropped suddenly to the water surface, and then dipped its bill into the water. After an unsuccessful attempt, or if it consumed the fish, the bird resumed the circling behavior. These same behavioral sequences are normally used by terns pursuing fish, or insect prey close to the ground (personal observation). Adults usually made 3 or 4 attempts before successfully capturing a fish at the enclosure. Three adults (7, 9, and

Figure 3.1. Illustration of a typical foraging cycle. t_{acc} = time to accelerate to travel speed, V, t_{fe} and t_{fn} = the travel times from the nest to the enclosure, and vice versa, t_{circ} = time circling the enclosure, t_{dip} = time dipping to capture a fish, t_{hover} = time spent hovering, and t_{rise} = time to rise to circling speed or departure speed back to the nest. Not shown are rare occasions when individuals perched on the enclosure (see Table 3.1).


t_{fe}
t_{circ}
t_{hover}
t_{acc}
t_{fn}
t_{rise}
t_{dip}
t_{dec}
NEST
t_{land}
ENCLOSURE

10; see Table 3.1) also searched for fish while perching on the posts at the enclosure.

For a given individual, flight speeds from the enclosure to the nest (and vice versa), were measured to the nearest 0.1 m/s with a hand-held Doppler K15 radar gun (see Blake et al. 1990 for details; 5 nests) or by elapsed travel time (5 nests). Previous work has suggested that these techniques give comparable results (R.W. Blake, pers. comm.). Wind speed was measured with either a pendulum (Stong 1971) or rotating anemometer. A given foraging bout was terminated when the focal animal either ceased foraging, or captured a prey item while en route to the enclosure.

We also observed a total of 8 adults provisioning offspring at 5 separate nests, each with 3 chicks, none of whom was ever seen feeding at the enclosure. We estimated their average foraging success (number of items captured per unit of time spent foraging, excluding travel time) and round-trip delivery time (departure from the nest to subsequent arrival with a prey item).

Foraging model for each currency

Efficiency (EFF), a unitless currency, is given as

$$\mathrm{EFF} = \frac{\text{Net energy gained while foraging}}{\text{Energy spent while foraging}}$$

$$= \frac{E_{in} - t_e C_e + t_f(v) C_f(v)}{t_e C_e + t_f(v) C_f(v)}.$$

E_{in} is as defined above, t_e is the time spent foraging at the enclosure (see Table 3.1 for estimates of the individual components) with an energy expenditure rate C_e, $t_f(v)$ is flight time to and from the enclosure at a rate C_f.

TABLE 3.1. Means (SD) of the parameters estimated for terns feeding at the enclosure

	Average time spent in each activity (s)[a]								
Bird	t_{circ}	t_{hover}	t_{dip}	t_{land}	t_{rise}[b]	Fish per trip	One-way Distance (m)	Wind (m/s)	N
1	46.9 (34.9)[c]	23.7 (13.8)	2.1 (1.3)	4.7 (1.9)	2.7 (1.7)	1.14 (0.38)	68.6	1	7
2	32.5 (15.9)	0	2.9 (1.4)	0	2.8 (1.7)	1 (0)	92.9	0	8
3	15.3 (7.2)	1.0 (2.9)	1.5 (0.9)	0	1.7 (0.8)	1 (0)	141.5	0	11
4	11.3 (4.6)	8.2 (7.8)	2.3 (0.4)	0	2.4 (0.5)	1 (0)	149.2	0	8
5	45.2 (32.9)	14.5 (9.8)	3.5 (1.3)	4.3 (4.0)	4.7 (1.7)	1.2 (0.4)	151.7	0	7
6	118.0 (110.1)	6.3 (7.0)	4.0 (1.8)	3.3 (3.3)	5.0 (2.1)	1 (0)	172.3	1	8
7	43.2 (11.1)	61.3 (27.8)	6.4 (1.8)	72.6 (40.7)	6.2 (1.8)	1 (0)	185.5	3.4	13
8	58.8 (8.8)	13.4 (6.0)	10.3 (4.0)	1.0 (5.9)	7.1 (3.2)	1.5 (0.5)	484.0	2.2	8
9	97.0 (31.1)	9.9 (5.8)	9.7 (4.4)	16.7 (12.9)	3.5 (0.4)	1 (0)	484.0	0	11
10	47.5 (20.0)	5.5 (1.9)	13.8 (8.0)	22.3 (18.9)	5.9 (0.9)	1.53 (0.73)	484.0	1.1	15

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[a] See Figure 1 caption for a description of each behaviour category. The sum of these categories is the average time each indvidual spent at the enclosure, t_c (see text).

[b] Mean number of rises per trip was calculated by assuming each rise was of 1 s duration (see text).

[c] Standard deviation.

Similarly, net rate of energy intake (NREI; J/s) is

$$\mathrm{NREI} = \frac{\text{Net energy gained while foraging}}{\text{Time spent foraging}}$$

$$= \frac{E_{in} - t_e C_e + t_f(v) C_f(v)}{t_e + t_f(v)} \, .$$

Delivery rate to the nest (DR; J/s) is given by

$$\mathrm{DR} = \frac{\text{Prey energy}}{t_f(v) + t_e + t_e'(v)} \, .$$

Though $t_f(v)$ is as defined above, t_e is now the time spent at the enclosure to capture one fish. The t_e' term is the extra foraging time necessary for the adult to recoup the energy costs of provisioning young (see Houston 1986, 1987), and is the sum of two parts. Part 1 is the time spent self-feeding to recoup the energy expended while capturing and delivering a fish to the nest, and is equal to

$$te'(1) = \frac{[\text{travel cost}(v)] + [\text{average cost/fish}]}{[\text{average feeding rate}]} \, .$$

However, while foraging for time, te'(1), the bird is also expending energy at the average rate given above, which necessitates a further time foraging, te'(2).

$$te'(2) = \frac{[te'(1)] * [\text{average expenditure rate at the enclosure}]}{[\text{average feeding rate}]} \, .$$

For purposes of analysis, we have treated the self-feeding time as if the bird spent some extra fraction of each foraging trip in this activity. In practice, birds only occasionally engaged in self-feeding (probably because each fish was so highly profitable) but the two methods give equivalent results.

Energetic estimates

A.Cost of flight to/from the enclosure. The cost of flight was estimated using the equation provided by Pennycuick (1989). The cost, in J/s, is:

$$C_f = 1.1\ [(1.2(Mg)^2/2(S_d rv) + 0.5rv3S_bC_{db} + 1.2\ P_{am})/E + P_{ib}] \qquad (2)$$

where M is body mass in kg (= 0.053 ± 0.0046 SD for Black Terns, n = 6; Welham unpublished), g is acceleration due to gravity (9.8 ms^{-2}), S_d = wing disc area (m^2), r = air density at Creston (altitude 567 m; kg m^{-3}), v = airspeed (m/s), S_b = body frontal area (m^2), C_{db} = drag coefficient of the body, P_{am} is the absolute minimum power (J/s), E = metabolic efficiency (0.23; Pennycuick 1975), and P_{ib} = basal metabolic rate ($3.73m^{0.723}$; see Pennycuick 1975, 1989, for further details of these terms). To ensure consistency with our estimates of energetic gain, equation 2 is converted from its original form expressing the cost of flight in mechanical units, into its metabolic equivalent (cf. Pennycuick 1989, pp. 26-27).

The cost of accelerating to airspeed v was calculated as kinetic energy (in J; Oster, 1976):

$$\text{Acceleration cost} = 0.5mv^2/E. \qquad (3)$$

We also used this equation to estimate the cost of accelerating to the circling velocity (5.9 m/s , n = 9) after an attempted capture.

B. Cost of foraging at the enclosure. The energy expended by a tern while perched on the enclosure and when briefly transferring food to nestlings at the nest, was calculated using Kendeigh's (1970) equation of existence metabolism (EM) for non-passerines at 30 °C (log EM = -0.2673 + 0.7545 log M, where M is the mass in g), and converted to J/s. For lack of a better estimate, we assumed that this was also the cost of dipping into the enclosure to capture prey. The cost of hovering was estimated from the sum of induced and profile powers (see Pennycuick 1969, eq. 19 for details), except for one occasion when a tern was forced to contend with a prevailing wind of 3.4 ms^{-1}. In this case, the bird adopted a form of windhovering (sensu Videler et al. 1983), and we calculated the flight cost at a forward airspeed equal to the wind speed. The rate of energy expenditure when circling the enclosure was calculated using equation 2, at an airspeed of 5.9 m/s (see above).

C. Energy gain at the enclosure. We calculated the energy gained per fish as

Prey energy (J/fish) = Energy content/unit weight (J/g) X wet weight (g/fish) X digestive efficiency.

J/g estimates were 3807.4 for yellow perch, and 4351.4 for largemouth bass (Watt and Merrill 1975), and we used an average wet weight of 0.31 g/fish (see above). We used an estimate of 80% for digestive efficiency, the value used for other piscivorous birds (Kahl 1964, Kushlan 1977). Multiplying prey energy by the number of fish captured yields the gross energy intake per trip (E_{in}).

Predicted flight speeds

Using the time-energy budget data, we derived predictions of flight speeds from the three currencies in the following way.

Enclosure experiment. We first determined the cost to each adult of foraging at the enclosure, from the time spent in each behavior category (Table 3.1) and its associated energetic cost (as outlined above). Under the EFF and NREI currencies, the benefit was calculated as the average number of fish captured per trip, and the costs as the average time and energy spent foraging. For the DR currency, however, the benefit and costs were the respective energetic value, and time and energy expended in capturing a single fish. The remaining terms in each model were then calculated for each nest, and therefore travel distance, as a function of airspeed. We determined (by iteration) the travel speeds that maximized each foraging currency at a given distance. To compensate for wind effects which were strong in some cases (see Table 3.1), and the slightly greater weight of the parent on its trip back to the nest (due to the fish it was carrying), we calculated the predicted airspeed to and from the enclosure separately, and then averaged the two speeds. We then estimated the total daily energy expended at the predicted optimal flight speed for each currency, by varying foraging times up to a maximum of 16 h, the maximum set by available daylight. These estimates were compared to the DEE limit predicted for Black Terns by Kirkwood's (1983) equation.

To determine the effect on the DR currency of including DEE_{max}, we calculated for a 16 h day and using the foraging parameters of Table 3.1, the travel speed for each nest which maximized the total daily delivery, with the restriction that daily expenditures could not exceed DEE_{max}. We refer to this as the constrained delivery rate (DR_{con}).

Unmanipulated nests. To derive the parameter estimates necessary to predict the optimal flight speeds expected for naturally-foraging terns, we used prey capture and delivery rates from 8 individuals provisioning young with food obtained from locations other than the enclosure. Adults were capturing mostly damselflies and dragonflies (pers. obs.), and we estimated the capture rate (4.0 J/s) from the weighted mean prey value of 481 J/item (Cummins and Wuychek 1971, Orians 1980; including an assimilation efficiency of 80 %; Ricklefs 1973), and a mean inter-capture interval of 120 s/item (range 10 - 256 s; N = 521). The average interdelivery time to the nest (time from departure to subsequent arrival with a prey item) was 554 s. For a given adult, we also used the distance between its nest and feeding location to calculated the time available for foraging,

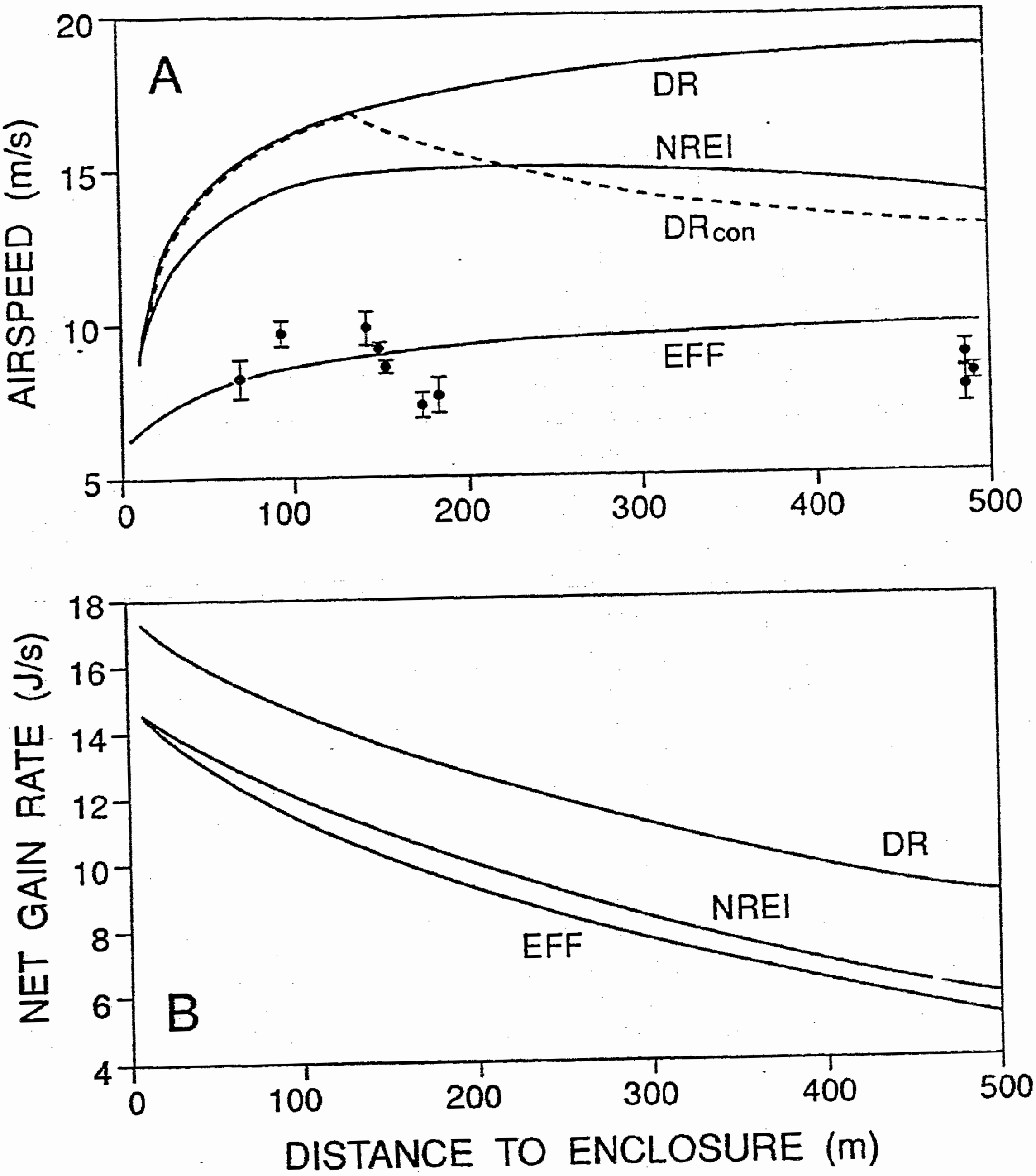
t_p = average time between deliveries (554 s) - (two-way travel distance/ travel speed).

Multiplying t_p by the average capture rate gave the total energy captured per trip. Adults foraged in a manner similar to that described in the enclosure experiment (see Figure 3.1), so we used the average rate of energy expenditure at the enclosure calculated over all 10 individuals (=1.94 J/s, excluding travel costs), as an estimate of the cost of capturing prey. Travel and acceleration costs at a given velocity were estimated from equations 2 and 3, respectively. For each nest, the predictions under the EFF and NREI models were simply those travel speeds that maximized each currency. The optimal policy under the DR currency, was that flight speed that maximized daily delivery rate. Predicted airspeeds were compared to mean observed airspeeds from the 10 individuals that foraged from the enclosure. We used the mean observed airspeeds in order to minimize the lack of independence resulting from multiple measurements on the same individual. We then determined the total daily energy delivered for each currency, and the total daily energy expended after 16 h of foraging.

RESULTS

The EFF currency provided the best prediction of the airspeeds observed during the enclosure experiment (Figure 3.2A). For each currency, Figure 3.2B displays the predicted net rate of gain associated with the optimal airspeed at each travel distance. Gain rates decline with distance at a decelerating rate, and the EFF currency predicts a rate considerably lower than the DR currency, but only slightly lower than NREI.

Figure 3.2. (A) Predicted airspeeds that maximize efficiency (EFF), net rate of energy intake (NREI), and delivery rate to the nest (DR) for the 10 nests, as a function of their one-way distance from the enclosure (see Table 3.1 for parameter estimates used to derive predictions, and corresponding sample sizes). DR_{con} refers to the predicted airspeeds for the delivery rate model when adult expenditure is constrained to the Kirkwood limit (see text). Also shown are the means and 95% confidence limits of the observed airspeeds for each nest. (B) The predicted net instantaneous gain rate (after subtracting parental foraging costs) for the three currencies in relation to the distance between the nest and the enclosure.


A
DR
NREI
DRcon
EFF
AIRSPEED (m/s)
5
10
15
20
0
100
200
300
400
500
B
DR
NREI
EFF
NET GAIN RATE (J/s)
4
6
8
10
12
14
16
18
0
100
200
300
400
500
DISTANCE TO ENCLOSURE (m)

The three models make more similar predictions when parameters from unmanipulated nests are used (Figure 3.3). However, the range of observed airspeeds consistently overlaps only the predictions of the EFF currency, particularly at travel distances less than 300 m (Figure 3.3). Many adults searched for prey in areas of the marsh close enough to permit at least some visual contact with the nest. Parents who travelled greater distances regularly flew back to and briefly circled their chicks before returning to forage (and likely incurring some cost in foraging time). From these observations, we estimated that adults captured more than 90% of prey items within 500 m of the nest (and often from much shorter distances), which accords well with our EFF predictions.

We calculated the total daily energy expended under each currency for varying lengths of available foraging time, and compared these values to the theoretical maximum daily expenditure limit of 206.6 ± 4.8 kJ/day, obtained from Kirkwood's equation (1983). For adults foraging at the enclosure, both the DR and NREI currencies predict expenditures in excess of the expected maximum for daily foraging times greater than 10 and 12 h, respectively (Figure 3.4). When the young are 10-12 days old, as in our study, adult terns forage 16 h per day (Welham unpublished). Hence, Black Terns that flew faster than the predicted airspeeds of the EFF currency would incur a negative energy budget. If they foraged from the enclosure for a full 16 h (according to the foraging parameters of Table 3.1) but constrained total daily expenditures to Kirkwood's predicted limit, the predicted airspeeds of the DR currency would be reduced by approximately 3 m/s. These predictions would still be consistently higher than the observed airspeeds.

Figure 3.3. The predicted airspeed that maximizes a given energetic currency (see Figure 3.2) in relation to the one-way travel distance, for black terns foraging a total of 16 h per day. Parameters were derived from observations of unmanipulated nests (see text). The solid horizontal line is the overall mean observed airspeed for the 10 manipulated nests ($n = 96$; see Table 3.1 for sample sizes of individual birds). Stippling shows the standard deviation of the mean. Values along the DR line represent the total daily kJ returned to the nest by a single parent under this currency, at a given foraging distance. Values in the stippled area are the percentage of daily DR (kJ/day) at the standard deviation of observed mean airspeed. Since energy expenditures for DR currency do not exceed DEE_{max} (see text), its predictions are also identical to those of the DR_{con} currency.

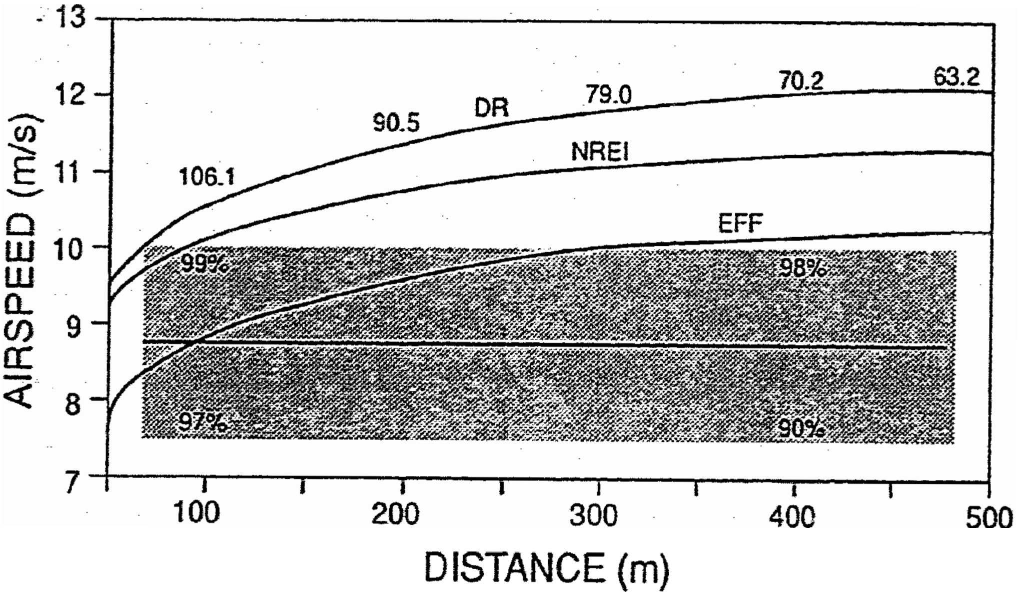
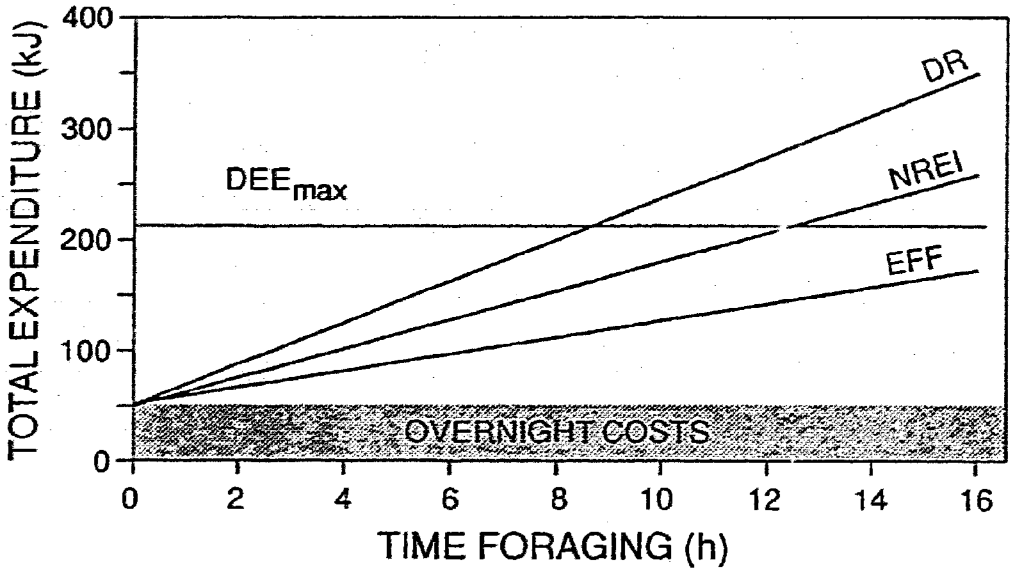

AIRSPEED (m/s)
13
12
11
10
9
8
7
DISTANCE (m)
100
200
300
400
500
DR
NREI
EFF
106.1
90.5
79.0
70.2
63.2
99%
98%
97%
90%

Figure 3.4. Total daily energy expenditure in relation to the total hours spent foraging per day. The lines were determined from the average (over the 10 nests) of the rates of expenditure at the predicted optimal airspeed for each currency. Also shown is the theoretical daily limit for black terns (horizontal line) derived from the equation of Kirkwood (1983; see text for details).


TOTAL EXPENDITURE (kJ)
400
300
200
100
0
DR
NREI
EFF
DEEmax
OVERNIGHT COSTS
0
2
4
6
8
10
12
14
16
TIME FORAGING (h)

Since the predicted flight speeds for the unmanipulated nests were lower than those from the enclosure experiment (cf. Figures 3.2A and 3.3), the expected flight costs for the birds was reduced considerably (compared to those using the enclosure), and this resulted in projections of daily energy expenditure for the three currencies that were always lower than the maximum limit. For example, our calculations indicate that foraging for 16 h at the flight speed maximizing DR would require only 60% (at 100 m) to 71% (at 1000 m) of DEE_{max}, and slightly less under the EFF and NREI currencies. Furthermore, Black Terns that fly at airspeeds maximizing either EFF or NREI would fly at slower speeds and deliver almost the same total daily energy, as birds using the speed maximizing the DR currency (Figure 3.3).

DISCUSSION

Though based on a relatively small sample (10 birds), our results clearly indicate that Black Terns provision offspring at flight speeds that are best predicted by the EFF maximizing currency. McLaughlin and Montgomery (1985, 1990) also found that flight speeds of adult Lapland longspurs (*Calcarius lapponicus*) feeding young were not significantly different from the EFF currency, and were less than the predictions of the delivery rate model of Norberg (1981; but see Houston 1986). Similarly, the observed crop load of honey bees (*Apis mellifera*) were more consistent with maximizing EFF than with NREI maximization (Schmid-Hempel et al. 1985, Schmid-Hempel 1987). In contrast, Welham and Ydenberg (1988) found that, for ring-billed gulls (*Larus delawarensis*), EFF maximizing best predicted patch residence times but observed flight speeds better matched the predictions of NREI maximizing. Unfortunately, our previous study (Welham and Ydenberg 1988) did not involve an experimental manipulation and, as a consequence, it was difficult to discriminate between both sets of predictions.

Two hypotheses have been proposed to explain why animals forage in accordance with efficiency maximization. Schmid-Hempel et al. (1985; see also Neukirch 1982) suggest that honey bee workers draw from a fixed life-time budget of metabolic performance so that expected lifespan declines in relation to the amount of flight performed (Schmid-Hempel and Wolf 1988, Wolf and Schmid-Hempel 1989; see also McLaughlin and Montgomery 1990). Hence, worker lifespan (and total energy delivered to the hive) is maximized by efficient energy expenditure while foraging. We have no data with which to evaluate this hypothesis for Black Tern parents but our results suggest several alternative explanations (see below). Alternatively, McLaughlin and Montgomery (1985, 1990) argue that, in most years, Lapland longspur parents can easily meet the food demands of their young, and so additional trips to the nest (above that predicted by the EFF currency) will not increase offspring fitness (since growth rates are already maximal). In contrast to both of these hypotheses, our hypothesis explicitly considers a limit on daily energy expenditure (Weiner 1992).

Our calculations from the unmanipulated nests suggest that adult terns normally use about 60-70% of DEE_{max}, and therefore could fly faster and deliver more food to their young. Black Tern nests often lose at least one chick to starvation (Mosher 1986, Welham unpublished), so the extra work by parents could translate into higher reproductive success (unless offspring cannot accommodate the extra food). Why their flight speeds were not more in accordance with the NREI or DR predictions is unclear, though the results of the enclosure experiment may provide an answer. Food could be obtained from the enclosure at a high rate, a situation analogous to when natural feeding conditions are particularly favorable. In our experiment, however, this resulted in airspeed predictions by the NREI and DR currencies in excess of the theoretical daily maximum (and this would presumably also occur under natural conditions). Exceeding this energetic limit is not sustainable because parents would be forced to draw upon stored energy reserves (Weiner, 1992). Furthermore, terns experience only a small reduction in daily energy delivered by flying slower than the DR predictions (Figure 3.3, see also McLaughlin and Montgomery 1990). It is also possible that increased work effort contributes to feather wear (McLaughlin and Montgomery 1990) or results in physiological exhaustion. These effects can be mitigated by foraging efficiently, thereby minimizing energy expenditure rates.

Terns could maximize total daily delivery while constraining daily energy expenditure to DEE_{max} (DR_{con}; see Figure 3.2A). The increase in total delivery over that of the EFF currency is small, however (see Figure 3.3). Furthermore, a possible disadvantage to this currency is that the parent is often at or near DEE_{max}, and if feeding conditions deteriorate, it may be unable to replace energy quickly enough to avoid an energetic shortfall. Further work is needed to evaluate these hypotheses.

Whether daily limits on physiological performance are important to the feeding decisions of parents is unknown, since few optimal foraging studies have assessed their predictions with respect to these limits. Kacelnik (1984) compared the work effort of parent starlings (*Sturnus vulgaris*) against a rule for maximum sustained working level of 4 times the basal metabolic rate (Drent and Daan 1980). He found that the optimal foraging currency which best explained his data, the FAMILY GAIN model (Gross rate of delivery to the nest - parental and brood metabolic rates; see Kacelnik 1984, equation 7), made predictions of performance that exceeded this rule. However, he found no indication that starlings reduced their average daily metabolic rate in response to the 4 BMR limit. This finding was corroborated in a subsequent study where parent starlings (Kacelnik and Cuthill 1990) allocated food in accordance with a model maximizing lifetime reproductive success rather than a model based on regulating parental energy reserves.

To assess the accuracy of predictions derived for naturally-foraging terns, we compared the expected daily energy delivered under the EFF currency, with published estimates of chick growth requirements. Unfortunately, no published data exist for Black Tern growth energetics and data available for other Larids are for species at least twice as heavy as terns (see Drent and Klaassen 1990). We used metabolizable energy estimates of growing dunlin (*Calidris alpina,* Scolopacidae) chicks since they have the same fledging age as Black Tern chicks (21 days), and similar growth patterns and asymptotic weights (0.044 vs 0.056 kg; see Drent and Klaassen 1990, Ricklefs 1974 for data on the dunlin, and Mosher 1986, for Black Terns). Though Black Tern chicks are fed by their parents while dunlin chicks feed themselves, young terns are active and mobile, and it is not unusual for the parents to lead a brood away from the nest (pers. obs.). At 10-12 days of age, we estimate that Black Tern chicks require 213-240 kJ/day for a brood of 3. Our estimates of energy delivered by two parents varies from 206 to 210 kJ/day at 100 m average one-way travel distance to 110.0 to 122.6 kJ/day at 500 m travel distance. The majority of foraging trips were less than 500 m, which puts our estimates of daily delivery close to the estimated requirements, and increases our confidence in the accuracy of the various energetic estimates used in our models.

As outlined earlier (see Introduction), the foraging models we considered are based on very different assumptions, and each has important implications for how selection may have shaped feeding behavior. The DR maximizing currency seems the most realistic biologically since it explicitly incorporates the energy budget of the parent as part of the foraging decision process. Our experimental design permitted the terns to recoup energy very quickly, and this currency predicted flight speeds considerably higher than measured airspeeds (and, in many cases, in excess of the estimated maximum sustainable working capacity). When we added a physiological limit to the DR currency its predictions were lower but still exceeded observed airspeeds. The success of predictions made by the EFF maximizing currency does suggest, however, that foraging, and hence reproductive success, in a number of species could be limited by the flight capabilities of parents. Our data suggest that terns may require a margin of safety with respect to daily energy expenditures to protect against an energy shortfall by parents. Efficiency maximizing might ensure expenditures are well within safe limits.

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CHAPTER IV

OPTIMIZATION OF PARENTAL BEHAVIOR IN A VARIABLE ENVIRONMENT: EVALUATION OF THREE SIMPLE FORAGING CURRENCIES

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ABSTRACT

We predicted the flight speeds of parent birds provisioning their young from three optimal foraging currencies (maximizing efficiency, EFF, maximizing the net rate of energy intake, NREI, and maximizing daily delivery rate, DR) and a state variable model, using parameter values derived from field data collected on Black Terns. We allowed prey intercapture intervals to vary randomly between days, and then compared the fitness return for each model (calculated as the expected reproductive success within a season, and expected lifetime reproductive success). EFF maximizing produced fitness estimates that were better than or equivalent to the two other foraging currencies over a wide range of mean/variance combinations of intercapture intervals. In addition, EFF was the only currency (in addition to the dynamic model) that predicted flight speeds which were consistently within the range of observed values for Black Terns. When foraging conditions were particularly favorable, flight speeds predicted by the NREI and daily DR models always resulted in parents exceeding a theoretical maximum daily energy expenditure limit. Consequently, parents tended to lose condition and this compomised fitness. The dynamic model resulted in higher fitness returns than the simple foraging currencies (particularly when feeding conditions were poor). Though the state variable approach illustrates the complexity of the allocation decisions parents might face, our results suggest that EFF maximizing may provide a reasonable fitness return under a variety of conditions. This could explain why, in a number of empirical tests, it has been a better predictor of forager behavior when compared with the rate currencies.

INTRODUCTION

The decisions of parent birds when provisioning their young should balance the cost of a given level of foraging effort against the benefits that accrue from the energy delivered. For example, delivering more food to the nest could produce some marginal fitness gain (like increased brood survival) but the rate at which the parent can work might be limited by its ability to dissipate heat (Clark, 1987), in increased mortality associated with foraging effort (Houston et al., 1988; see Schmid-Hempel and Wolf, 1988; Wolf and Schmid-Hempel, 1989, as examples), or because extra effort invested in current activities reduces the potential for future reproduction (Charnov and Krebs, 1974). This cost/benefit tradeoff has formed the basis for a number of models of parental foraging behavior.

One set of models assumes that reproductive success is constrained largely by limits on the time available to parents for provisioning offspring (limits set by daylength, for example). Under these conditions, strategies which maximize the energy gained per unit time spent foraging should be favored (Stephens and Krebs, 1986). A number of these rate maximizing models have been considered, including the gross (Orians and Pearson, 1979; Carlson and Moreno, 1982; Kacelnik, 1984) and net rate of energy intake (Welham and Ydenberg, 1988). Alternatively, if energy expenditure is in some way costly to the parent, then selection should favor provisioning stategies that are energetically conservative. In this case, parents might achieve maximum fitness by maximizing the energy gained per unit energy expended (efficiency maximizing; McLaughlin and Montgomerie 1985, 1990; but see Stephens and Krebs, 1986). In a different approach to this problem, Houston (1987) argued that if parental energy reserves are important for future survival, then the time necessary for parents to recoup energy expenditure can place important constraints on the rate at which food is delivered to the young. He therefore derived a new currency (daily delivery rate) that took account of parental self-feeding time. Using parameter values derived from the literature, Houston (1987) showed that this new currency resulted in higher daily energy delivered when compared with three other commonly-used currencies.

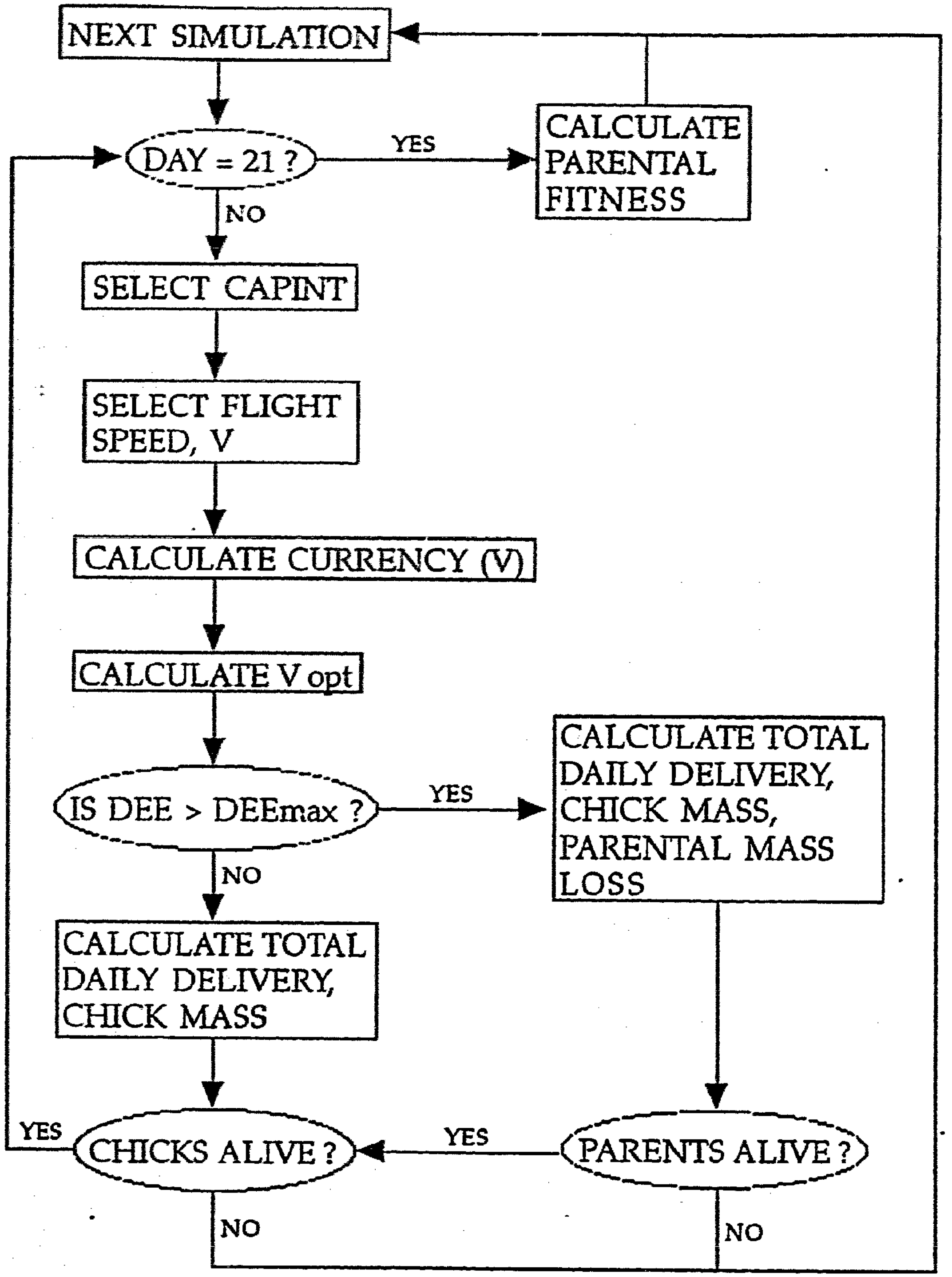
Though Houston's (1987) results for the daily delivery rate currency have yet to be confirmed experimentally, empirical evidence suggests that efficiency maximizing is often a better predictor of foraging behavior than other rate maximizing currencies. Recent examples include predictions of the amount of nectar collected by honeybee workers (*Apis mellifera*; Schmid-Hempel et al., 1985; Kacelnik et al., 1986; Schmid-Hempel, 1987), and the flight speeds of Lapland Longspur (*Calcarius lapponicus*; McLaughlin and Montgomerie, 1985, 1990) and Black Tern (*Chlidonias niger*; Chapter III) parents provisioning dependent young. Why does efficiency maximizing better explain the foraging behavior of parental birds?

Since the foraging studies reported above are conducted over a brief time period, one possibility is that the behavior predicted by rate maximization may not be sustainable in the long term (see Chapter III). In a recent paper, for example, Ydenberg et al. (1993) have demonstrated theoretically that in a provisioning context, when delivery rate is constrained by energy needed to power self-feeding, efficiency maximizing ensures the highest total daily delivery. Another possibility is that efficiency maximizing represents a Behaviorally Robust Strategy (*sensu* Clark and Mangel, 1986). In its natural world, an animal must cope with the complexities of an uncertain environment. One of the more important difficulties may be stochastic variation in energetic input and it is possible that foraging efficiently provides a reasonable rate of return under these circumstances.

One factor not considered by any of these currencies, is how the state of the parent (for example, its energy reserves) or the offspring might affect provisioning behavior (Houston and McNamara, 1985). Though the relative importance of state dynamics to behavioral decisions is widely appreciated (see Houston and McNamara, 1988; Clark, 1991), rigorous experimental tests of the predictions derived from these models are lacking. This may be due, in part, to the fact they require some measure of variation in the state variable and which for many animals is often difficult to obtain (Beauchamp et al. 1991; though Schmid-Hempel et al. 1993 review a number of examples in social insects). In this respect, it is useful to know whether the behavior and expected fitness returns predicted by the simpler optimal foraging currencies may closely approximate those made by a model incorporating state dynamics.

Here we use a simulation approach (Figure 4.1) to predict the flight speeds of parents provisioning dependent young with three optimal foraging currencies: maximizing the net rate of energy intake, maximizing efficiency, and maximizing daily delivery (see below for details). We make projections of the fitness consequences of provisioning at these speeds under conditions in which environmental quality varies unpredictably between successive days. These results are then compared with those obtained from a state variable model of parental provisioning behavior. Parameter estimates used in the models are derived from field studies of breeding Black Terns.

Figure 4.1. Schematic overview of the simulation procedure (see text).


NEXT SIMULATION
DAY = 21 ?
YES
CALCULATE PARENTAL FITNESS
NO
SELECT CAPINT
SELECT FLIGHT SPEED, V
CALCULATE CURRENCY (V)
CALCULATE V opt
IS DEE > DEEmax ?
YES
CALCULATE TOTAL DAILY DELIVERY, CHICK MASS, PARENTAL MASS LOSS
NO
CALCULATE TOTAL DAILY DELIVERY, CHICK MASS
YES
CHICKS ALIVE ?
YES
PARENTS ALIVE ?
NO
NO

Black Terns are marsh-nesting birds and usually lay a clutch of three eggs (Dunn, 1979). Offspring are semi-precocial and attain flight capability within 21 days of hatching. Newly hatched young are brooded full-time by one parent for the first 24 h, but the length of the daytime brooding period declines thereafter. Each adult returns to the nest with a single prey item at a time. A typical foraging trip consists of the flight to and from an area of the marsh where prey, usually insects or fish, are aggregated.

METHODS

Three simple foraging currencies

In this section, we present a simplified version of each of the foraging currencies (for a detailed description see Appendix 1). The two rate maximization currencies we consider are the net rate of energy intake (NREI), and maximization of daily delivery rate (DR). The net rate of energy intake is:

$$\mathrm{NREI} = \frac{\text{Net energy gained while foraging}}{\text{Time spent per trip}}$$

Delivery rate to the nest (DR) is given by:

$$\mathrm{DR} = \frac{\text{Energy gained from a single prey item}}{\text{Time spent per trip}} \cdot$$

The Efficiency maximizing currency (EFF) is given as:

$$\mathrm{EFF} = \frac{\text{Net energy gained while foraging}}{\text{Energy spent per trip}}$$

Predictions

Predictions of flight speed and reproductive success were made for each currency under conditions in which environmental quality, as measured by the mean prey intercapture interval, varies randomly between successive days. Variability in quality thus refers to between-day variance in the mean intercapure interval. For each of the respective foraging currencies and mean/variance combinations of intercapture intervals (Table 4.1), we ran a total of 75 simulations and then calculated our estimates of reproductive success. Preliminary analysis indicated that this was the minimum number of runs for which there was no appreciable change in the predicted outcome.

At the beginning of a given day in the brood-rearing period, one of five possible intercapture intervals was selected at random (CAPINT; see Figure 4.1). The standard deviation of each distribution of five intervals is referred to as sigma. Each intercapture interval was used throughout the entire day. We then determined the respective flight speeds which maximized each of the three currencies and calculated daily energy expenditures (DEE) for parents and offspring. If parental DEE was lower than theoretical predictions of maximum DEE (DEE_{max}; see Appendix 1), then the total daily food delivered to the nest (TDD) was calculated after subtracting energy consumed by the parent in self-feeding. TDD was then converted to mass gain by the offspring (see Appendix 1 for conversion efficiencies). At the beginning of the brood rearing period, we established a feeding hierarchy to which each chick was arbitrarily assigned a position. Each position was then maintained throughout a given simulation. On any given day, the chick in position 1 was always the first to receive food. If it reached satiation (see below), the chick in position 2 was fed and when (if) it

Table 4.1. Sample distributions of intercapture intervals (CAPINT; see text). Bold values show the mean for each distribution.

Sigma	CAPINT				
5	23.5	26.8	**30**[a]	33.3	36.5
10	17	23.5	**30**	36.5	43
15	21	30.5	**40**	49.5	59
20	15	27.5	**40**	52.5	65
25	18.5	34.3	**50**	65.8	81.5
30	12	31	**50**	69	88

[a] CAPINT distributions with higher and lower means (at a given level of sigma) were derived by adding or subtracting a constant to each combination.

became satiated, then chick 3 received food. This protocol mimicsthat observed under natural feeding conditions (Welham pers. obs.). When weighing less than 60 g, all chicks, if given the opportunity, ate the maximum amount of food they could metabolically process (see Appendix 1 for details of this limit). Whenever the mass of a given chick exceeded 60 g (usually after about 10 - 12 days; see Dunn 1979), it stopped gaining weight and only consumed enough food to fulfill its daily energy budget (DEB; see Appendix 1).

When parental DEE exceeded the maximum daily limit, TDD was calculated by assuming that parents only fed themselves enough on each trip to recoup expenditures up to this daily limit. Hence, in addition to calculating the mass gain of offspring (from TDD), we also determined the mass loss experienced by parents on that day. Note that, in contrast to the state variable model (see below), parents were able to only maintain or lose mass. Prior to the start of foraging on the next day, we calculated parent and offspring survival as a function of their respective masses according to the following rules.

Parents began the simulation at 65 g (which corresponds to the average maximum measured during the breeding season; Welham unpubl.) and were permitted to lose up to 30 g over the brood rearing period. Below 35 g, they were assumed to die of starvation. This limit was chosen since it is close to the minimum mass recorded for adult Black Terns in the wild (37 g; Cramp, 1985). We set no limits on the amount of mass loss per day, but in practice daily adult masses seldom dropped by more than about 3 g. All three chicks weighed 7 g at hatching (see Dunn, 1979). Since the survival of very young Black Tern chicks is closely correlated with the amount of food they receive (Welham, unpublished), we assumed that a chick weighing less than 35 g died if its energy consumption was insufficient to meet its minimum daily requirement (see Appendix 1 for details of this estimate). Chicks weighing more than 35 g could lose mass on a given day and still survive, as long as their final mass at the beginning of the next day (i.e., discounting overnight costs) did not drop below 35 g.

At the end of 21 days, we determined the masses of all surviving offspring. Chicks were assigned arbitrary probabilities of overwinter survival, based on their mass, as follows: 35 - 40 g, $p = 0.39$; 40.1 - 45 g, $p = 0.63$; 45.1 - 50, $p = 0.78$; 50.1 - 55, $p = 0.87$; 55.1 - 60, $p = 0.92$; 60.1 - 65, $p = 0.95$. Expected reproductive success (ERS) was then calculated as:

$$\text{ERS} = \Pr(\text{Chick 1 survives}) + \Pr(\text{Chick 2 survives}) + \Pr(\text{Chick 3 survives}). \quad (1)$$

Our second measure of fitness incorporated a survival cost to the parents associated with any mass loss experienced over the breeding period. Expected lifetime reproductive success (ELRS) is given as:

$$\text{ELRS} = \frac{\text{ERS}}{\Pr(\text{Adult dying overwinter})}, \quad (2)$$

where ERS is as above. The denominator is the probability that the parent dies as a function of its state and is given by:

$$1 - \Pr(\text{Adult survival}) = 1 - e^{-b(\text{adult mass})},$$

where $b = 0.015$. This value for b means that the highest survival probability of a Black Tern at its maximum mass (65 g) is 0.63. Though the actual mortality rate of adult Black Terns is unknown, our estimate is roughly equivalent to survival rates derived from other species of similar body mass (see Henny, 1972). Our equation for ELRS has been used in a previous analysis of present/future reproductive tradeoffs (Clark and Ydenberg,1990) and includes a number of underlying assumptions. One assumption is that expected reproductive success during one breeding episode correlates perfectly with that in future breeding attempts. For example, a parent bird that is expected to produce two young in the current breeding episode will also produce two young during the remaining breeding attempts, conditional upon survival. This is because overwinter survival prospects are assumed to be independent of age, and the variation in environmental conditions between years is equivalent to that experienced within years. Hence, the optimal parental strategy during a given season also is expected to be optimal in other years. If conditions were allowed to vary between years, future reproductive success would need to be treated as a variable (Beauchamp et al., 1991). Moreover, fitness in a fluctuating environment may have to be described with the geometric rather than the arithmetic mean of reproductive success (Mangel and Clark, 1988). Though our formulation of ELRS is a simplistic description of lifetime reproductive success, it does incorporate the basic trade-off between current and future reproduction.

A state variable model of parental provisioning

The simple currencies outlined above incorporate foraging rules that maximize energetic gain, but fail to to take account of the more general problem of maximizing parental fitness over the reproductive cycle. The state variable model addresses this problem.

During the breeding season, a number of parental actions can be taken and their value measured by the contribution each makes to parental fitness at the end of the nestling period. Hence, in the model developed in this section, Black Tern parents are expected to follow foraging rules that maximize the number and quality of young produced over the whole reproductive period. In contrast to the three simple currencies, parent Black Terns in the dynamic framework, not only select a particular flight speed, but also vary the amount of food allocated to the chicks versus self-feeding (see Kacelnik and Cuthill 1990).

The parental care model presented here is similar to that developed for starling (*Sturnus vulgaris*) parents by Beauchamp et al. (1991). In this respect, body mass represents the state variable, and the state of parents and their family determines the changes in expected payoffs that result from various parental actions. Further details of the analysis are given in Appendix 2. In order to compute changes in parental state during one day it is necessary to evaluate the efficiency with which adults accumulate mass from a given amount of energy. The limit on parental mass gain is dependent on both DEE_{max} (which is itself dependent on the rate at which food can be assimilated; see Peterson et al., 1990) and a factor, G_p, which expresses the efficiency by which energy consumed is converted to body mass. Tinbergen (1981) reported a value of 33 kJ/g for energetic efficiency in starlings but this estimate may vary widely between species (for example, Kersten and Piersma, 1987, report a value of 46 kJ/g for oystercatchers *Haematopus ostralegus*). Since the value for Black Terns is unknown, we have used the conversion factor reported for starlings, as both body size and diet are similar in the two species.

RESULTS

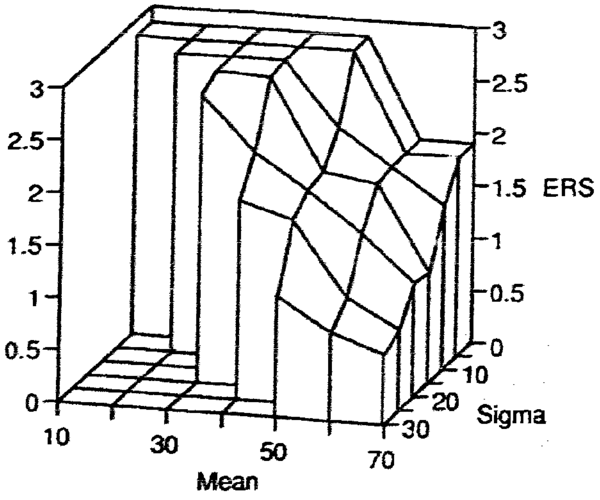
Expected reproductive success (ERS) varied with the three simple foraging currencies and with respect to a given mean/variance combination of intercapture intervals (Figure 4.2). For a given mean intercapture interval, ERS declined as the variance increased (with the exception of the EFF currency). Similarly, when the variance was held constant and the mean increased, ERSfirst increased then decreased for both rate currencies, but only decreased with the EFF currency (Figure 4.2).

The EFF currency seldom resulted in adults losing body mass (and thereby compromising survival), and this translated into higher ERS than the rate maximizing currencies, over a range of mean/variance combinations (Figure 4.2). When we restricted our comparison of the three currencies to cases in which fitness was limited only by chick survival, no single currency consistently predicted higher ERS (Figure 4.2).

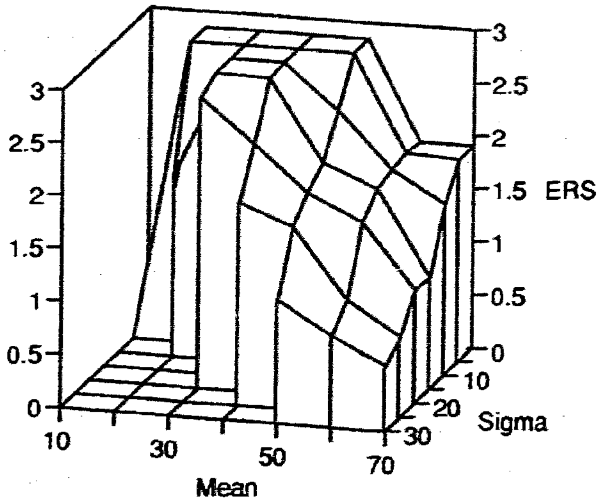
Any decline in adult mass usually had a marked effect on lifetime reproductive success (Figure 4.3). For example, there were 7 mean/variance combinations for the NREI currency, and 1 for daily DR, in which expected reproductive success was approximately equal to that for the EFF currency (< 1% difference). When we calculated lifetime reproductive success for these same combinations, however, the EFF currency consistently outperformed both rate currencies (by a range of 8.7 - 29.8 % for NREI, and 12.7 % for daily DR; Figure 4.3).

Figure 4.2. Expected reproductive success (ERS) from a given breeding attempt in relation to mean/variance combinations of intercapture intervals for each of three foraging currencies, maximizing efficiency, maximizing net rate of energy intake (NREI), and maximizing daily delivery rate (daily DR).

EFFICIENCY



NREI



DAILY DR

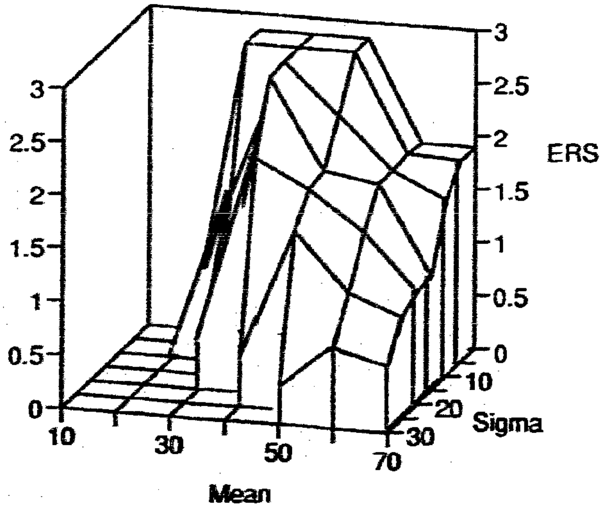
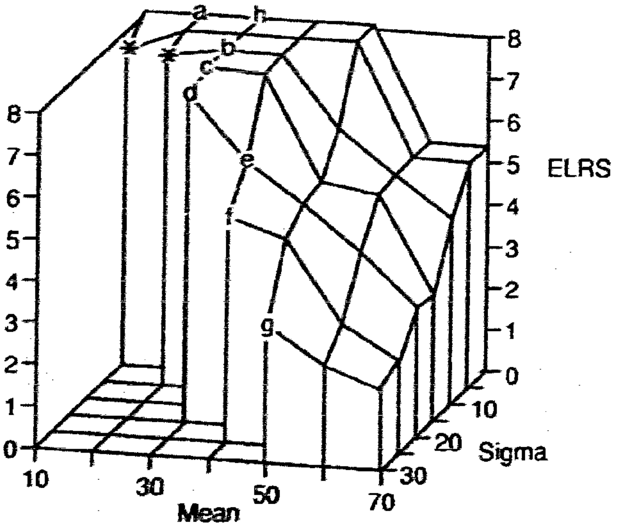
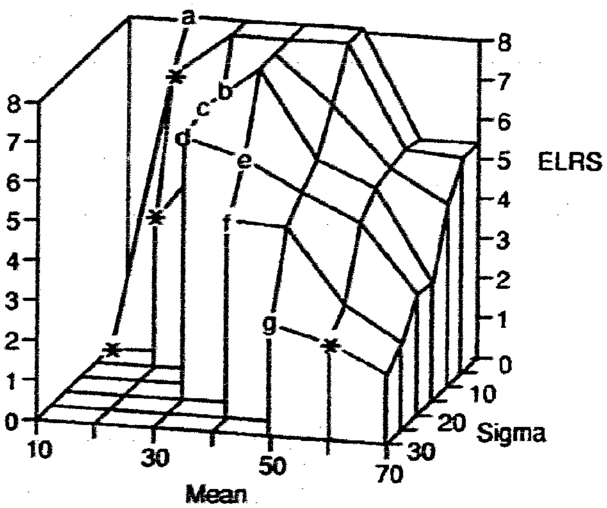


Figure 4.3. Expected lifetime reproductive success (ELRS) in relation to mean/variance combinations of intercapture intervals for each of three foraging currencies, maximizing efficiency, maximizing net rate of energy intake (NREI), and maximizing daily delivery rate (daily DR). Asterisks indicate the mean/variance combinations at which parents lost weight, and the letters are those combinations at which expected reproductive success for at least two currencies were equal (see Results) but ELRS was not.

EFFICIENCY



NREI



Daily DR

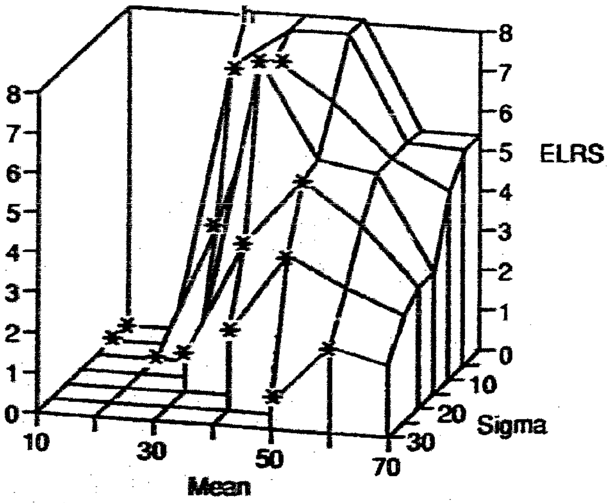


Figure 4.4 shows the expected fitness returns from the three foraging currencies and the state variable model. Since the results were qualitatively similar across all mean/variance combinations, we show values for only one series of means, at a sigma value of 25.0. Though the state variable model always outperformed the three foraging currencies (Figure 4.4) the differences did not vary uniformly. When the mean intercapture interval was low, there was a smaller difference between their predictions of expected reproductive success. However, EFF maximizing was the only currency whose predictions of lifetime reproductive success were consistently similar to those of the dynamic model. In addition, only the EFF currency and the dynamic model made predictions of flight speeds that were within the range measured for Black Tern parents provisioning young at natural nests (Figure 4.5). The rate maximizing currencies always predicted airspeeds that were higher than observed, regardless of the intercapture interval.

DISCUSSION

The model results suggest an important reason why the EFF currency might result in a higher fitness return than the rate maximizing alternatives. When feeding conditions were highly variable (relative to the mean), predicted flight speeds from the NREI and daily DR currencies often resulted in adults expending energy at a rate that exceeded their assimilation capabilities. These adults then exhibited a decline in mass which compromised both present and future reproductive success. In many species, the mass of adults provisioning normal-sized broods is often lower than that measured during incubation (Moreno 1989). However, the decline in weight usually occurs prior to or very

Figure 4.4. Expected reproductive success (ERS) and lifetime reproductive success (ELRS) estimates from three optimal foraging currencies and a dynamic programming (DP) model in relation to the mean intercapture interval and sigma value of 25.0.

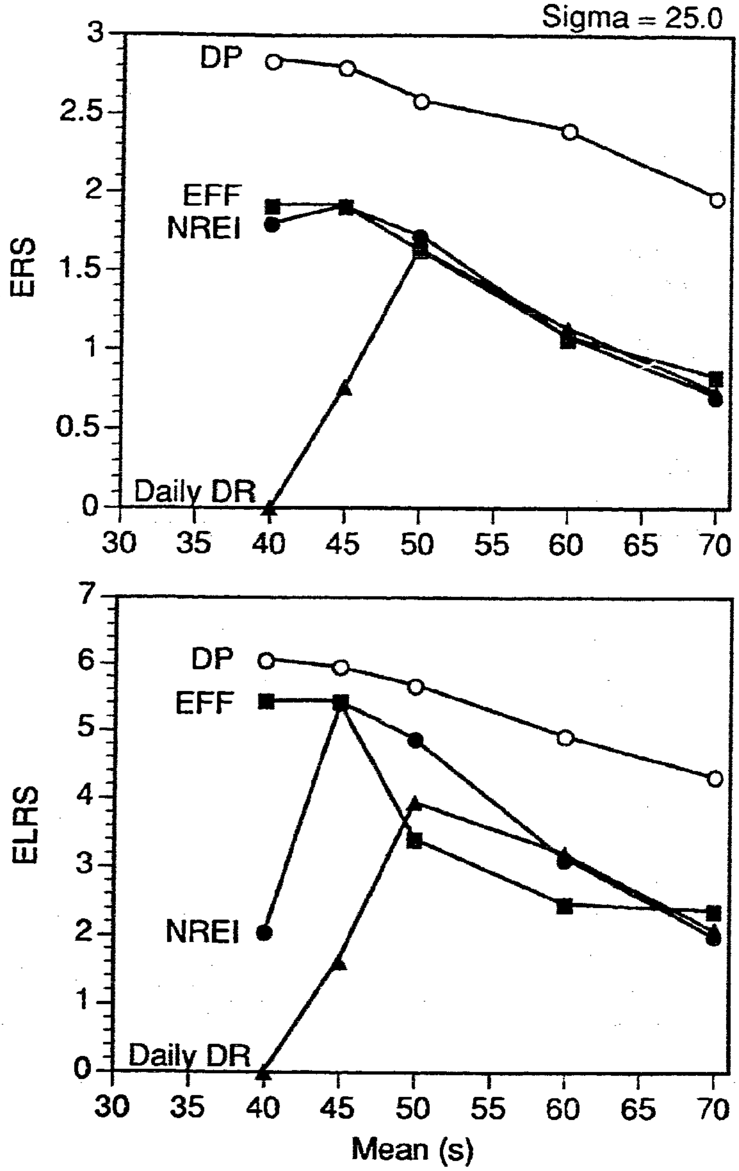
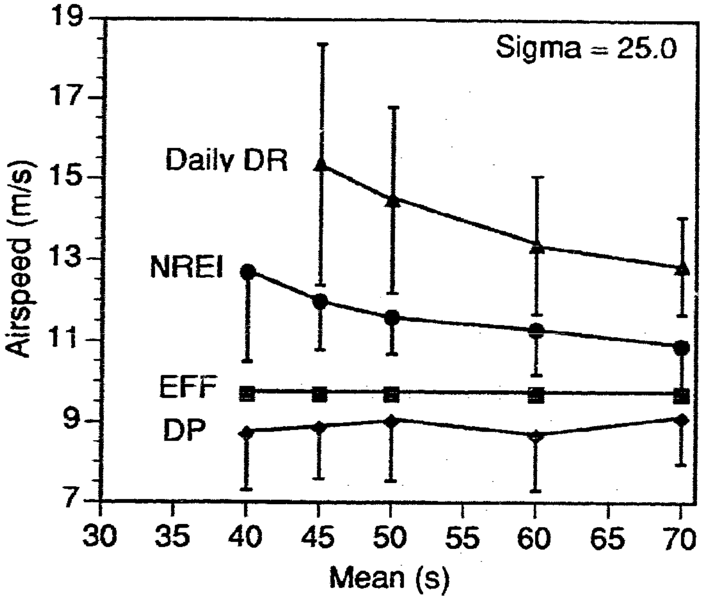

Sigma = 25.0
ERS
3
2.5
2
1.5
1
0.5
0
DP
EFF
NREI
Daily DR
30
35
40
45
50
55
60
65
70
ELRS
7
6
5
4
3
2
1
0
DP
EFF
NREI
Daily DR
30
35
40
45
50
55
60
65
70
Mean (s)

Figure 4.5. Predicted airspeeds from three optimal foraging currencies and a dynamic programming model, DP (based on maximizing ELRS; see Methods), in relation to the mean intercapture interval and a sigma value of 25.0. The mean and standard deviation of flight speeds measured in parent black terns is 8.8 ± 1.2 m/s (Chapter II; not shown).


Sigma = 25.0
Daily DR
NREI
EFF
DP
Airspeed (m/s)
19
17
15
13
11
9
7
30
35
40
45
50
55
60
65
70
Mean (s)

soon after hatching (Moreno, 1989), and so appears to be an anticipatory response to the demands of brood rearing (Freed, 1981, Norberg, 1981) rather than a result of physical exertion. The decline in parental mass exhibited by the rate currencies is therefore not consistent with these observations. On the contrary, the importance of parents maintaining body condition has been demonstrated in a number of species. For example, adult glaucous-winged gull (*Larus glaucescens*) parents who raised artificially enlarged broods lost condition and had lower overwinter survival than those raising smaller broods (Reid, 1987; see also Nur, 1988 for a similar example in blue tits *Parus caeruleus*).

The validity of the EFF and NREI currencies has been questioned by Houston (1987). He argued that when time spent self-feeding by the parent is incorporated into the foraging strategy (the daily DR model), neither currency maximized total daily food delivered to the nest. While Houston's (1987) reasoning may be correct, a shortcoming of his model is that it did not consider limits to the amount of food offspring can assimilate on a given day. Hence, while the daily delivery model might have resulted in the most food delivered, this did not necessarily translate into higher parental fitness since offspring have only a finite capacity for growth (set by these digestive constraints). Any currency which results in parents delivering enough food that offspring are growing at the maximum rate will therefore have equivalent fitness. This reasoning explains why, in cases where parents could successfully raise all 3 chicks without incurring any mass loss (see Figures 1 and 3), there were no discrepancies in expected fitness between the currencies (see also below).

When delivery rates limit the survival of at least some offspring (and parents do not experience a decline in mass), the extra food delivered under daily DR ought to result in higher growth rates and a reduced risk of starvation. Though not reported here, our results suggested that under the EFF and NREI currencies, chicks tended to gain mass a little more slowly than when parents foraged as daily DR maximizers. However, growth rates were not usually sufficiently depressed to seriously affect fitness (most chicks were were still able to attain their maximum mass at the time of fledging). A second factor mitigating the effect of a reduced delivery was brood size. Our broods were sufficiently small that any differential in daily delivery between currencies usually resulted in an equivalent amount of brood reduction (since, in contrast to a much larger brood, each chick's daily requirements constituted a high proportion of the total daily food delivered). A larger decrease in total daily delivery rate would be needed to affect brood size significantly. In addition, the decline in parental fitness resulting from chick starvation was often not offset by the marginal fitness returns from a higher delivery rate to the reduced brood (this argument also applies if parents can meet the maximum demands of reduced brood but not the minimum requirement of an extra chick).

Parental provisioning stategies that allow foragers to allocate resources dynamically had an advantage over any of the simple foraging currencies (particularly when the intercapture intervals were high), though the magnitude of this effect depended, in part, on how fitness was measured (Figure 4.4). When conditions improved, the discrepancy between the two approaches was reduced for at least one of the currencies (EFF maximizing; Figure 4.4). Under favorable circumstances, parents can forage in such a way that they easily meet their own requirements and those of their offspring, and allocation decisions have less of a consequence with respect to fitness. Whether the absence of state dynamics in optimal foraging studies is problematic appears to depend on (a) the particular currency under consideration, (b) how fitness is calculated, and (c) the prey capture rate. That EFF maximizing performed consistently better than the alternative currencies, and was the only currency (in addition to the dynamic model) which predicted flight speeds similar to measured speeds, suggests why it has received widespread empirical support (see Introduction).

Future foraging studies clearly need to evaluate the suitability of alternative currencies with regard to whether they are sustainable in the long-term (given limits to daily energy expenditure, for example). Moreover, the implications of foraging according to a particular currency should also be considered with regard to the role of environmental variability. Though the dynamic model illustrates the complexity of the allocation decisions parents might face, it is encouraging that a simple currency like efficiency maximizing appears to approximate optimal behavior under a range of foraging conditions. Whether it can successfully predict forager decisions in contexts other than reproduction remains to be seen.

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APPENDIX 1

We first give a detailed description of each currency and then outline the derivation of each of the terms. The net rate of energy intake at a given airspeed, V, is given as:

$$\text{NREI} = \frac{\text{Energy gained while foraging - energy cost per trip}}{\text{Time spent per trip}}$$

$$\text{NREI} = \frac{E_{in} - [C_a(V) + t_t(V)C_t(V) + (1+s_f(V))(\text{CAPINT})(C_p)]}{t_t(V) + (1+s_f(V))(\text{CAPINT})} .$$

E_{in} is the energy captured per prey item while foraging. The total energy cost per trip is the sum of three terms. The first is the acceleration cost from the nest ($C_a(V)$). The second term describes the total travel cost to and from the nest, $t_t(V)C_t(V)$, where $t_t(V)$ is flight time (to and from the patch), at a rate of expenditure $C_t(V)$. The final term is the cost to the parent of capturing a single prey item for the offspring plus any extra prey it consumes for self-feeding, $s_f(V)$ (for a derivation of this term, see below under Time costs: Capturing prey). Hence, the total time spent foraging in the patch is $[1+s_f(V)]$ times the intercapture interval (CAPINT). Multiplying this by the rate of energy expenditure, C_p, yields the total capture cost. The denominator gives the total time per trip (the sum of the time spent travelling and foraging in the patch). For purposes of analysis, we have treated the self-feeding time as if the bird spent some extra fraction of each foraging trip in this activity. In practice, birds might engage in self-feeding only occasionally but the two methods give equivalent results.

Daily delivery rate (DR) is the energy gained from capturing a single prey item (for delivery) divided by the time spent per trip:

$$DR = \frac{E_{in}}{t_f(V) + (1+s_f(V))(CAPINT)} \cdot$$

Note that the energy captured by the parent in self-feeding is expressed in the denominator as a time cost (see Houston, 1987 for further details).

Efficiency (EFF) is given as:

$$EFF = \frac{\text{Energy gained while foraging - energy cost per trip}}{\text{Energy cost per trip}}$$

$$EFF = \frac{E_{in} - [C_a(V) + t_t C_t(V) + (1+s_f(V))(CAPINT)(C_p)]}{[C_a(V) + t_t C_t(V) + (1+s_f(V))(CAPINT)(C_p)]}.$$

Parameter estimates

We made predictions of the optimal travel speed by estimating the components of the three foraging currencies in the following way.

Energy intake (E_{in})

Black Terns consume a number of species of small fish and aquatic insects (Chapter V). From detailed observations of foraging adults, we calculated an average value of 481 J/item (including an estimate of 80% digestive efficiency).

Energy costs

Flight

The cost of flight to and from a feeding area $C_t(V)$ was estimated using the aerodynamic equation provided by Pennycuick (1989) which incorporates the most recent modifications in the theory of bird flight.

The cost of accelerating to airspeed, V, was calculated as kinetic energy (in J; Oster, 1976):

$$C_a = 0.5mV^2/e\,, \qquad \text{(A2)}$$

where m is body mass (kg), and e is the conversion efficiency of mechanical to chemical energy (= 0.23; Pennycuick, 1975).

In Chapter III, a series of time budgets were constructed from 10 foraging Black Tern adults and after substituting energetic estimates for each behavioral component, the average rate of energy expenditure while capturing prey (excluding travel costs to the foraging area) was estimated to be 1.94 J/s. We used this as our estimate of the energetic cost to parents of capturing prey (C_p).

Overnight and brooding costs

Energy expended by the parent overnight (C_n) was estimated from equations for Existence Metabolism (EM) of non-passerines at 0 °C and 30 °C (Kendeigh et al., 1977; equations 5.28 and 5.35, respectively). We calculated an average EM from these two equations and then multiplied this value by the length of the overnight period (8 h), converted into seconds. To estimate the cost to the parent of brooding the chicks (see below), we used the equation for EM at 30 °C muliplied by the time spent in this activity.

Time costs

Travelling

To estimate the time costs of foraging, we first assumed that parents flew to a localized feeding area (termed a patch)100 m from their nest. This assumption is not unrealistic since many prey items captured by Black Terns were aggregated in schools (as in the case of fish) or concentrated in favorable breeding habitat (most insects; Mosher, 1986). Hence, after delivering a prey item to the nest, parents frequently returned to the same area and resumed foraging (Welham, pers. obs.). The travel time, $t_t(V)$, was therefore equal to 2 times the one-way distance/V, where V is the travel speed.

Capturing prey

For the NREI and EFF maximizing currencies, time spent foraging in the patch is the sum of two components (for clarity of presentation these are given in reverse order of their actual occurrence). The first is the time necessary to capture an item for delivery to the nest and which equals the intercapture interval (CAPINT; see Figure 4.1). The second component is the extra time that must be spent self-feeding in order to recoup the energy expended provisioning the young, and for overnight costs. This self-feeding time is a function of the number of prey items eaten by the parent per trip, $s_f(V)$, and the intercapture interval. Note that $s_f(V)$ depends on the rate at which energy is expended per trip and which varies, in part, with travel speed, V. We solved for $s_f(V)$ in the following way.

The total daily energy expended (DEE) by the parent is:

$$DEE = N\,C_{trip} + E_n + E_b, \qquad \text{(A3)}$$

where N is the number of trips/day, C_{trip} is the energy expended/trip, C_n is energy expended overnight, and C_b is energy invested in brooding the young.

However, the number of trips/day depends on the available foraging time and the time spent per trip:

$N = T_a/T_p,$ (A4)

where T_a is the total time available for foraging, and T_p is the total time spent per foraging trip. If the total number of prey the parent must consume (n) is:

$n = DEE/ E_{in},$ (A5)

where E_{in} is the energy value per prey item (see above), then the number of items consumed per parent per trip is:

$s_f(V) = n/N.$ (A6)

Substituting equation A5 into A6, followed by A3 and A4 yields:

$$s_f(V) = \frac{(T_a/T_p)C_{trip} + C_n + C_b}{E_{in}(T_a/T_p)}. \qquad \text{(A7)}$$

However, the total time per foraging trip (T_p) is the sum of the travel time, $t_t(V)$ and the time to self-feed, $s_f(V)$, plus capture one more item for delivery:

$T_p = t_t(V) + (1 + s_f(V))$ (CAPINT).

Total energy expended per trip (C_{trip}) is therefore:

$C_{trip} = C_a(V) + t_t(V)C_t(V) + (1 + s_f(V))(\text{CAPINT})(C_p).$

Substituting these equation for T_p and E_{trip} into equation A6, then rearranging terms gives:

$$s_f(V) = \left[C_a(V) + t_t(V)c_f(V) + (CAPINT)(C_p) + \frac{(C_n + C_b)(t_t(V) + CAPINT)}{T_a} \right] \left[\frac{1}{\frac{E_{in} - CAPINT\,(C_p + (C_n + C_b))}{T_a}} \right] \tag{A8}$$

Finally, the total number of daylight hours (16) sets a limit to the maximum time available for parents to forage. However, offspring are brooded continuously for the first 24 h after hatching and progressively less thereafter (so that by the time they are 9 days of age, both parents spend the entire day provisioning them; Chapter V). The time spent brooding (designated t_b) must therefore be subtracted from the maximum time available, to give the total time available for foraging, T_a. We used the following function to approximate t_b (in seconds) for the first 8 days of the brood-rearing period.

$t_b = (16 \times 3600)\ (1 - (\text{brood age}/8)^{.8})$.

After day 8, t_b was assumed to be 0.

Limits to DEE

The derivation of sf(V) given above assumes implicitly that the parent derives the full energetic value from the prey items it captures. There is evidence to suggest, however, that there are limits to the rate at which food can be assimilated across the gut (Peterson et al., 1990). Since activities such as flight are energetically costly, parents will be capable of maintaining a neutral energy budget only if their rate of energy expenditure is matched by the rate at which energy is assimilated. Hence, for each currency, we calculated daily energy expenditure (DEE; including a cost for self-feeding derived from equation A8) and compared this with an estimate of the maximum daily metabolic performance (DEE_{max}). We estimated DEE_{max} for a Black Tern parent of mass 0.063 kg, using the allometric equation of Kirkwood (1983). For a species of mass, M (kg),

$\mathrm{DEE}_{max} = 1713\ M^{0.72}$ (kJ/d; SE of slope ± 0.008).

If DEE exceeded DEE_{max}, we assumed that the parent consumed only enough items to match this metabolic limit (thereby incurring a negative energy budget). In this case, the number of prey consumed per trip in self-feeding is:

$$s_f(V)' = \frac{\mathrm{DEE}_{max}\,[C_a(V) + t_t(V)C_f(V) + \mathrm{CAPINT}C_p]}{E_{in}\,[\mathrm{DEEmax} - C_n - C_b - \dfrac{\mathrm{DEEmax(CAPINT)}C_p]}{E_{in}}} \qquad \text{(A9)}$$

Growth and mass loss

If parents or chicks (weighing > 35 g; see Methods) were unable to digest enough food to meet daily expenditures, they were forced to rely on stored reserves of fat. In this case, the decrease in mass was calculated by assuming that each g of fat yielded 25.3 kJ (Kendeigh et al., 1977).

We calculated chick growth (in g/day) by assuming that each chick weighing less than 60 g consumed enough food to maximize its growth rate. This maximum value was estimated from the equation for DEE_{max} given above. Unfortunately, the rate at which growing chicks convert energy intake into grams of body tissue is poorly known. Kendeigh et al. (1977) summarized daily energy budget (DEB) estimates for offspring of three species (one altricial and two precocial) and derived an allometric relationship for DEB in relation to chick mass (see Kendeigh et al., 1977, equation 5.78). We used this equation with published values for chick growth (Dunn, 1979) to estimate the DEB of Black Tern chicks. Empirical estimates from other tern species suggest that DEB increases linearly in the early phase of brood development (corresponding to the period of maximum mass gain) before reaching an asymptote (Drent and Klaassen, 1990). We therefore restricted our estimates of DEB to days 2 through 8 since this is the period of linear growth in Black Tern chicks (Dunn, 1979). By dividing these DEB values by the growth rate (g/day), we obtained estimates of the conversion efficiency for each day (kJ consumed/g increase in mass). We then averaged these and obtained a mean conversion efficiency (MCE) of 12.1 ± 2.2 (S.D.) kJ/g. Chick growth rate was then calculated as:

Growth (g/day) = (Total J consumed up to DEE_{max} - EM)/MCE,

where EM is existence metabolism (see above).

By about 10 days of age, the growth of Black Tern chicks reaches an asymptote at 60 - 65 g (Dunn, 1979). Empirical studies of DEB from chicks of other tern species with growth patterns similar to Black Terns, indicate that the rate of increase in DEB declines and then levels off as chicks reach their asymptotic weights (Drent and Klaassen, 1990). We used a simple step function to approximate this change in daily energy requirements by assuming that when the mass of a given chick exceeded 60 g, its DEB remained constant. We calculated DEB for these chicks from the equation for DEB given in Kendeigh et al. (1977).

APPENDIX 2

Here we give a detailed account of the dynamic model of flight speed in parent Black Terns. The model is developed over the brood-rearing period (21 days). Each day parents gather food for the young and themselves during a number of foraging trips. Time spent during a typical foraging trip can be broken down into the two following components: travel to and from the patch $t_t(V)$ at flight speed, V, and search for a single food item in the patch, CAPINT. Each prey item delivers E_{in} joules of assimilated energy. During one foraging trip, the proportion of time that is needed to search for a food item is a fraction of the total time per trip:

$$\mathrm{SEARCH} = \mathrm{CAPINT} / (\mathrm{CAPINT} + t_t(V))$$

where 1 - SEARCH = TRAVEL gives the proportion of time needed to bring the load back to the nest. Given that parents allocate a proportion (a) of the day to feeding young (to a maximum of 16 h; see below), we have

$$\mathrm{SC} = a\ (1\text{-}B)\ \mathrm{SEARCH}$$

$$\mathrm{TC} = a\ (1\text{-}B)\ \mathrm{TRAVEL}$$

which represent the proportion of the day devoted to the chicks that is needed to collect food (SC) and to travel to and from the patch (TC), respectively. The proportion of time during one day allocated to brooding by one parent, B, changes as a function of time, in a set fashion.

$B = 1 - (\text{chick age}/8)^{.8}$ (see Appendix 1 for further details).

The proportion of time an adult spends searching for food for itself is SP = (1- a) (1-B). Consequently, the total proportion of time spent searching for food by the parent is SP + SC. The foraging return (in grams) for a self-feeding parent when searching for food is

$$F_i = SP\ (E_{in}/CAPINT)\ DAY\ G_p$$

where DAY represents the number of seconds available to forage during one day and G_p converts energy intake into body mass increments (g body mass/J intake; see Methods: Predictions).

Given that the bird is foraging on day t, the energy state of a parent at the end of the day can be written as

$$X(t+1) = X(t) + \{ F_i - B\ C_b[X(t)] - (SP + SC)\ C_p - TC\ C_t[X(t), V] - C_n[X(t)] \} / msa$$

where C_b is the metabolic cost of brooding, C_p is the metabolic cost of searching for food, C_t the metabolic cost of travelling at a given speed, V, and C_n the metabolic cost of overnight rest. The variable msa was used to translate the body mass of the parent (a continuous variable) into an arbitrary scale (see Computational details). Notice that in this formulation, activity costs are expressed in grams per 16 h period. To derive these values, we used our estimates of energy expenditure (in J/s) associated with a particular activity and applied the following function: Costs (g/16 h) = Costs (J/s) DAY / 25300.

The energy state of a chick is given by the following equation:

$$Y(t+1) = Y(t) + \{ 2\ SC\ (E_{in} / CAPINT)\ DAY\ G_c - C_e[Y(t)] \} / msy$$

where C_e represents existence metabolism (see Appendix 1) converted to g/16 h (see above). G_c converts energy intake into body mass increments (g body mass/J intake), assuming a conversion efficiency of 12.1 kJ/g (see Appendix 1). msy translates body mass of the chick into an arbitrary state scale (see Computational details). Note that the energy received per chick on a given day is multiplied by 2 to account for delivery by both parents.

The terminal fitness function at time $t = T = 21$ is given by one of two functions. In the first formulation, the goal of parent Black Terns is to maximize the number and quality of young produced in the current reproductive episode (ERS; see Methods, equation 1), and in the second, parents trade-off current and future reproduction (ELRS; see Methods, equation 2). The dynamic programming algorithm for parent Black Terns can be expressed as:

$$F(x,y1,y2,y3,t,T) = \max_{a,V} \Sigma_i \, p_i \, F(x',y1',y2',y3',t+1,T)$$

with

$x' = \min(X(t+1), xmax)$

$y1',y2',y3' = \min(Y(t+1), ymax)$

p_i = probability that search time is CAPINT

The variables xmax and ymax represent the maximum state that a parent and a chick can attain respectively. We solved the dynamic algorithm numerically using a backward optimization procedure (Mangel and Clark, 1988) assuming a uniform distribution of CAPINT values.

The dynamic programming algorithm is based on the following fitness function:

$$F(x,y1,y2,y3,t,T) = \max E \{ \phi (X(T),Y1(T),Y2(T),Y3(T)) / X(t) = x, Y1(t) = y1, Y2(t) = y2, Y3(t) = y3 \}$$

Maximization of expected fitness is taken with respect to daily decisions about flight speed and allocation of food to the family given that the parents are in state x on day t and that the three chicks in the brood are in state y1, y2 and y3 respectively.

Implicit in the dynamic model algorithm is the assumption that only one foraging decision is taken each day. Hence, foraging decisions are not fine-tuned with respect to current environmental conditions, but correct with respect to the probability distribution of varying environmental states (cf. Beauchamp et al., 1991).

Computational details

Parental states were characterized by integer values between 0 and 10. State zero is the starvation level and state 10 is the maximum state allowed in the program. Offspring states could assume integer values between 0 and 6. We used the parameters msa and msy to translate body mass changes into the arbitrary scales for adults and offspring, respectively. We computed this for adults simply by dividing the range of body mass observed in the field (35-60 g; Welham unpubl.) by the number of parental states used in the model. Because chicks are growing during the nestling cycle, their range in mass changes with time. We used the following two functions, based on growth rates derived from the literature (Dunn 1979), to estimate this range.

$$\text{Minimum mass} = 35 / (1 + \exp(-0.42(t-10)))$$

$$\text{Maximum mass} = 65 / (1 + \exp(-0.42(t-10))).$$

Hence, for a given age (t; in days), we divided the range evenly between the offspring states.

Parents and young were subjected to food intake limitations that made it impossible for individuals to accumulate mass at too high a rate. We used the Kirkwood limit on energetic assimilation (Kirkwood, 1983) to compute the maximum amount of mass gain during one day. The maximum daily mass gain for parents is given by 207000 G_p, where 207000 represents the maximum amount of energy that can be assimilated by a bird weighing 55 g. For growing chicks, the Kirkwood limit was allowed to vary as a function of body mass, so that maximum daily mass gain also varied as a function of time.

The proportion of total food captured that was allocated to the chicks could assume integer values between 0 and 4, with each increment corresponding to a proportion of 0.25 (for example, an allocation value of 2 corresponds to half the foraging returns being allocated to the young). Within the brood, chicks were apportioned food according to the same allocation rule used for the simple foraging currencies (see Appendix 1).

Once optimal decisions were known for each combination of family states and nestling age, the program was run forward to find average trajectories across time of flight speed and allocation of food to the young. These trajectories can be compared directly with outcomes produced by the use of the simple foraging currencies. Simulations started on day 1 with parents and offsprings at the maximum state. We ran 100 simulations under each possible set of environmental conditions and fitness criteria. Average scores on a given day only included families that survived up to that day. We used a random number generator to select one of five possible daily values for search time CAPINT within the patch.

CHAPTER V

THE INFLUENCE OF BROOD DEMAND ON THE PROVISIONING TACTICS OF BLACK TERN PARENTS

Will be submitted as:

Welham, C.V.J. and R.C. Ydenberg.

ABSTRACT

We investigated the provisioning response of parental Black Terns to experimentally-manipulated brood sizes above and below the modal size of 3. Broods were manipulated when chicks were about 5 (week 1) or 9 days (week 2) old, and parents observed for two consecutive days thereafter. The number of prey items delivered per h increased significantly with brood size in week 1, but not in week 2. Consequently, week 1 offspring each received equivalent amounts of food regardless of brood size, but in week 2 chicks experienced a significant decrease in food delivery with brood size. This result could be accounted for, in part, by the fact that parents were able to increase the time they spent foraging in week 1 but not in week 2. The delivery rate of items per parent foraging-h increased significantly with brood size in week 1. This suggests that parents with week-old chicks, in addition to lengthening foraging time, also increased provisioning effort in other ways (by flying faster or decreasing the amount of self-feeding, for example). The delivery rate per parent foraging-h was lower in week 2, and did not change significantly with brood size. Thus, in week 2, parents did not deliver items as rapidly as they could have. A possible explanation lies in the fact that the proportion of daily energy supplied by different prey items varied significantly with chick age (when averaged over all brood sizes) but not brood size (with age constant). The difference in diet was the result of parents delivering more large prey and fewer, small items to older nestlings. These results are in qualitative agreement with the predictions of a variance-sensitive model of behavior whereby parents attempt to minimize the probability that nestlings experience an energetic shortfall.

INTRODUCTION

The rate at which parent birds expend energy to provison their brood has been suggested as an important determinant of clutch size (Masman et al. 1989). Energy expenditure may be costly to parents if, for example, it results in a decline in body condition which then decreases the prospects of future survival and reproduction (Charnov and Krebs 1974). Estimates of foraging effort in birds, however, indicate that parental energy expenditures are often well below the maximum possible (Weathers and Sullivan 1989, Masman et al. 1989). It seems then that parents lay a clutch size small enough to retain a margin of safety between expected and maximal demands, thus permitting a flexible response to changes in environmental conditions (Diamond and Hammond 1992). Results from brood manipulation studies that simulate increases in the energy requirement of nestlings, for example, suggest a number of options which parents can exercise in response to this variation.

One option is for parents to change the time allocated to particular activities. For example, Tinbergen (1981) found that female Starlings (*Sturnus vulgaris*) compensated for the extra demands of an enlarged and hungry brood, in part, by increasing the time spent foraging at the cost of time spent in other activities. A similar response has been documented in other brood manipulation studies (for example, Kestrels *Falco tinnunculus*, Dijkstra et al. 1990; Great Tits *Parus major*, Royama 1966).

There is evidence, however, that parents also change their foraging tactics in response to higher nestling demand. In addition to increasing foraging time, female Starlings also altered the composition of the nestling diet (Tinbergen 1981). When provisioning enlarged broods, they increased the proportion of leatherjackets (*Tipula paludosa*) relative to the other common prey, caterpillars (*Cerapteryx graminis*). This gave a higher return rate of biomass to the nest since leatherjackets were more abundant, but Tinbergen conjectured that the poor quality of these items may have eventually resulted in reduced nestling survival. Similar effects have been observed in other brood manipulation studies: parents increased the delivery rate (items/unit time) by returning with smaller prey items (see, for example, Lifjeld 1988, Smith et al. 1988 and references therein) though the quality of effort sometimes declined when measured in energetic terms (J/h; for example, Lifjeld 1988).

Another way that parental feeding tactics have been observed to change in response to brood demand concerns the allocation of energy captured between the adult and its offspring (see, for example, Tinbergen 1981, Martins and Wright 1993). Kacelnik and Cuthill (1990) compared the allocation of parental Starlings to predictions derived from two models. Their regulation model assumed that parents always consumed sufficient food to replace energy expenditures, while the alternative model was based on assumptions derived from maximization of lifetime reproductive success (LRS model). Overall, the LRS model better described allocation decisions, with parents giving more food to offspring (by lowering their rate of self-feeding) when both harvest rate and brood size were increased. The changes in the nestling diet discussed above might also be accounted for in this way. Under normal circumstances, prey below some minimum size might be consumed by the parent rather than delivered to the young (see Houston 1987). When brood demand is increased, however, the parent might reduce its self-feeding rate and instead deliver these items to the nest.

A third approach to foraging tactics considers the circumstances under which feeding decisions might be sensitive to the variation in food reward rather than simply to differences in the mean reward (as is implicit in many of the ideas presented above; see Houston and McNamara 1985). For example, if animals are at risk of not acquiring sufficient food to meet daily requirements, they should choose that reward which offers the greatest probability of meeting the requirement, even if it might also be the most variable (Stephens and Krebs 1986). Recent evidence consistent with this idea was provided by Cartar and Dill (1990; see Stephens and Krebs 1986, for further evidence). They examined the decisions of worker bumblebees (*Bombus occidentalis*) foraging to provision nests whose nectar reserves had been either experimentally depleted (which presumably reduced the potential for colony growth) or increased. Though each had the same expected rate of net energy intake, foragers from depleted hives preferred patches with the more variable reward than bumblebees whose honey pots had been enhanced. Whether the provisioning strategies of parent birds might better be interpreted within the context of variance sensitivity is unknown. One way to test this idea is to manipulate brood demand and then determine if any changes in parental provisioning behavior (prey selection, for example) are more consistent with predictions of variance sensitivity than the alternative explanations discussed above.

Here we describe the provisioning behavior of Black Tern (*Chlidonias niger*) parents in response to short-term variation in brood demand. Broods differing in size (from 1 to 5 chicks) and age (< 7 days old, and 8 - 14 days old) were created with the assumption that chicks in larger broods would pose a higher demand on parental provisioning effort. Parents were observed throughout the day to evaluate their response with respect to the above tactical options.

METHODS

The study was conducted during July 1989 and 1990 in the Creston Valley Wildlife Management Area, a 6800 ha managed marsh system near Creston, British Columbia, Canada (49° 14' N, 116° 38' W). Black terns return to breed in Creston in early to mid-May, and are present until mid-August. Nests consist of a floating mat of dead vegetation (Mosher 1986). The three eggs are usually laid in early June, and hatch after about 21 days of incubation. Chicks are capable of flight at about 20 days. Their diet consists entirely of food provided by their parents, who return to the nest with a single item each trip.

Experimental protocol

In June of each year an area of marsh (about 75 X 75 m) with 50 - 80 pairs of breeding terns was selected, and all nests that had eggs were marked. Nests were checked daily to determine the date of clutch completion and to estimate hatching date. Just prior to hatching, enclosures were constructed around 63 nests to limit brood mobility (it is common for parents to move the brood away from the nest after the chicks are about 14 days old; Welham pers. obs.). Each enclosure was built from chicken wire and measured approximately 2.5 X 2.5 m (depth 0.25 m). Several blinds also were erected around the study area from which to observe parental foraging activities.

Each of the 63 nests was assigned to one of two age-groups. The first group consisted of 43 nests, all with chicks less than 7 days old (mean age 4.1 ± 1.4 days; hereafter referred to as week 1 chicks). The remaining 20 nests (week 2) were observed when chicks were more than 7 but less than 14 days old (mean age 9.8 ± 1.5 days), the age at which growth rates are maximal (Dunn 1979, Mosher 1986). On the evening prior to observation, a series of chick manipulations were conducted on nests from both age-groups to create brood sizes from 1 through 5. To control for any confound associated with the addition of foreign chicks (assuming parents might be able to recognize their own offspring), we always attempted to also exchange the resident brood. Parents appeared to accept the foreign chicks readily though individual recognition may be important when chicks are older and more mobile.

All-day observations were conducted on parent Black Terns for 2 days following each manipulation. We were unable to observe all nests at any given time, so each day was blocked into 4 4-h periods, beginning at dawn (approximately 0530 h). On the first day, one set of nests was observed during the first and third periods, and the remainder during the second and fourth periods. This order was reversed on the second day. Following the 2-day observation period, all offspring were returned to their original nests.

Two observers recorded the time an adult was present at the nest, the estimated distance at which it foraged, the time an adult returned to the nest with a food item and, for a subset of nests, the type of prey delivered. Prey were categorized into 6 types: dragonflies (Odonata; small, medium, and large), damselflies (Ephemeroptera), small insects (mostly waterstriders; Heteroptera), and fish (yellow perch *Perca flavescens*). Insect larvae were also fed to offspring on occasion but these constituted such a small proportion of the total diet (<1 % by frequency) that they were excluded from analysis. Average energy values for each prey item are given in Table 5.1.

Statistical analysis

Foraging rates were analyzed by least squares regression or 2- way analysis of variance (ANOVA; with brood size and age as factors). An analysis of covariance (ANCOVA) was used to determine if the regression slopes differed significantly. In some cases, log transformations were necessary to normalize variance (Sokal and Rohlf 1981). Outliers were detected by t-tests

Table 5.1. Energy content of prey items fed to black tern chicks.

Prey	kJ/g	Mean Dry Weight (g)[a]	kJ/item
Dragonflies	21.4[b]		
Small		0.063 ± 0.006 (6)	1.35
Medium		0.075 ± 0.016 (6)	1.61
Large		0.280 ± 0.070 (9)	5.99
Damselflies	22.4[c]	0.016 ± 0.001 (8)	0.36
Waterstriders	20.9[d]	0.005 ± 0.001 (10)[e]	0.10
Fish	3.8[f]	0.310 ± 0.030 (80)[g]	1.18

[a] ± Standard Deviation. Sample sizes in brackets

[b] O. Odonata; Cummins and Wuychek 1971

[c] F. Zygoptera; Cummins and Wuychek 1971

[d] Estimated

[e] L. Rowe, pers. comm.

[f] Watt and Merrill 1975

[g] Chapter III

conducted on standardized residuals (Sokal and Rohlf 1981, p. 540) and were eliminated if statistically significant. Frequency data were arcsine transformed (Sokal and Rohlf 1981) and tested by week for brood size effects using a one-way non-parametric ANOVA. Differences contributed by each prey type to the proportion of total energy delivered to the nest were analyzed (after arcsine transformation) by multivariate analysis of variance (MANOVA).

RESULTS

The rate at which parents brought food items to nest increased significantly with brood size in week 1 but was marginally non-significant for week 2 (Figure 5.1A). The slopes of the two regressions differed significantly (ANCOVA $F_{1,56} = 4.29$, $p = 0.043$). The delivery rate of items per nestling was not significantly different from 0 in week 1 but showed a significant decline in week 2 (Figure 5.1B). The difference between these slopes was not quite significant, however (ANCOVA $F_{1,56} = 3.43$, $p = 0.069$).

Black tern parents in week 1 spent significantly less time present at the nest as brood size increased (one-way ANOVA: $H = 21.6$, $df = 4$, $p < 0.001$) but this was not true for week 2 ($H = 3.26$, $df = 4$, $p > 0.25$; Figure 5.2). In the latter case, parents of all brood sizes spent virtually all daylight h away from the nest.

The delivery rate of items per parent per foraging hour increased significantly in with brood size in week 1 but not week 2 (Figure 5.3); the ANCOVA test for interaction did not indicate a difference between the two slopes ($F_{1,56} = 1.49$, $p = 0.227$). An ANOVA, however, revealed highly significant effects of both week ($F_{1,57} = 13.06$, $p = 0.001$) and brood size ($F_{1,57} = 36.14$, $p < 0.001$) on delivery rate.

Overall, damselflies and dragonflies accounted for the majority of energy delivered to offspring in weeks 1 and 2 (Table 5.2). The proportions of prey

Figure 5.1. Mean (± S.D.) delivery rate per nest (A) and per chick (B) in relation to brood size and age. Regression equations in panel A are $y = 0.11 + 7.22\ x$, $r^2 = 0.61$, $P < 0.001$, $n = 41$ and $y = 0.01 + 4.74\ x$, $r^2 = 0.19$, $P = 0.06$, $n = 19$, for weeks 1 (squares) and 2 (circles), respectively. Regression equations in panel B are $y = 8.61 - 0.26\ x$, $r^2 = 0.01$, $P = 0.55$, $n = 43$ and $y = 12.75 - 2.18\ x$, $r^2 = 0.27$, $P = 0.04$, $n = 19$, for weeks 1 (squares) and 2 (circles), respectively. Lines of best fit have been added for signficant regressions only.

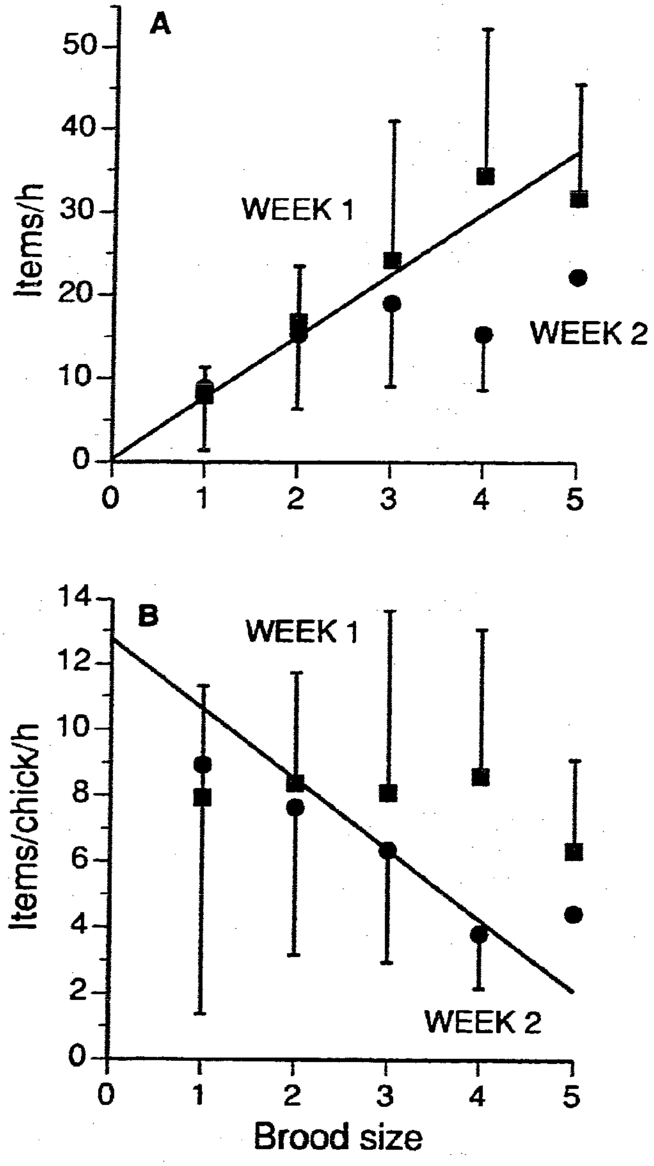

A
Items/h
50
40
30
20
10
0
0
1
2
3
4
5
WEEK 1
WEEK 2
B
Items/chick/h
14
12
10
8
6
4
2
0
WEEK 1
WEEK 2
0
1
2
3
4
5
Brood size

Figure 5.2. Percent of the day in which no parents (solid), 1 parent (diagonal lines), or 2 parents (stippled) were present at the nest in relation to brood size and age. Sample sizes (number of nests) are given in brackets.

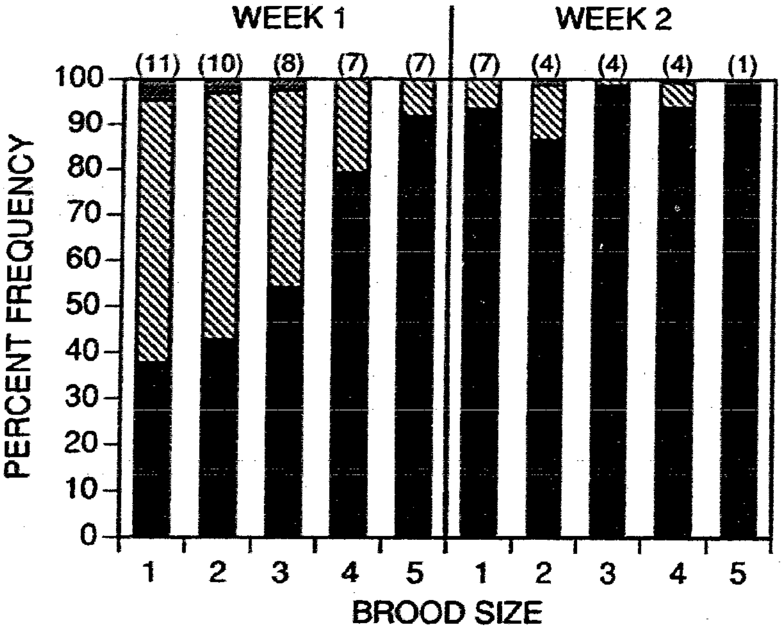

WEEK 1
WEEK 2
(11)
(10)
(8)
(7)
(7)
(7)
(4)
(4)
(4)
(1)
PERCENT FREQUENCY
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4
5
1
2
3
4
5
BROOD SIZE

Figure 5.3. Mean delivery rate per unit foraging time (± S.D.) in relation to brood size and age. Regression equations are $y = 0.08 + 5.76\ x$, $r^2 = 0.50$, $P < 0.001$, $n = 41$ and $y = 4.93 + 1.13\ x$, $r^2 = 0.12$, $P = 0.15$, $n = 19$, for weeks 1 (squares) and 2 (circles), respectively. A line of best fit has been added for the signficant regression only.

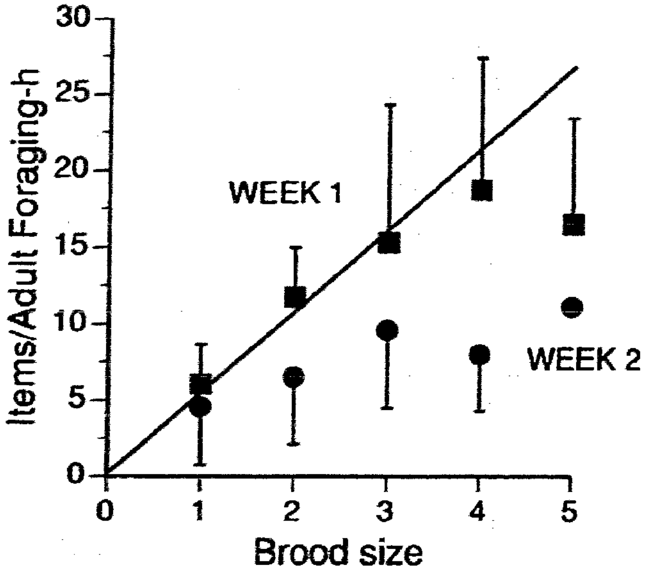

Items/Adult Foraging-h
30
25
20
15
10
5
0
WEEK 1
WEEK 2
0
1
2
3
4
5
Brood size

Table 5.2. Proportion of total joules returned to the nest by prey-type in relation to chick age and brood size. Sample sizes as in Figure 5.2. Note that the proportions for each column sum to 1.

	Week 1					Week 2				
	Brood size									
Prey	1	2	3	4	5	1	2	3	4	5
Dragonflies										
Large	0.05	0.08	0.06	0.17	0.22	0.38	0.29	0.19	0.12	0.56
Medium	0.08	0.12	0.02	0.07	0.10	0.06	0.13	0.02	0.07	0.10
Small	0.20	0.22	0.34	0.18	0.32	0.27	0.35	0.08	0.33	0.08
Fish	0.20	0.18	0.11	0.08	0.14	0.03	n[a]	0.09	0.08	0.07
Damselflies	0.43	0.38	0.45	0.49	0.22	0.25	0.23	0.59	0.38	0.18
Waterstriders	0.04	0.02	0.02	0.01	n	0.01	n	0.03	0.02	0.01

[a] negligible (< 0.01)

items did not vary significantly with brood size within weeks ($F_{24,168} = 0.65$, $p = 0.896$) but there was a significant difference across brood sizes between weeks($F_{6,48} = 2.40$, $p = 0.042$; the week X brood size interaction was not significant, $F_{24,168} = 0.84$, $p = 0.687$). Univariate F-tests showed that this age effect was largely a result of a significant increase in the proportion of large dragonflies ($F_{1,53} = 5.02$, $p = 0.015$, one-tailed test), and a decrease in the proportion of fish ($F_{1,53} = 2.89$, $p = 0.047$, one-tailed test) and waterstriders ($F_{1,53} = 2.74$, $p = 0.052$, one-tailed test), in the diet of week 2 chicks.

The daily energy delivered to the nest increased consistently with brood size in week 1 (Figure 5.4A). As a consequence, parents were able to adjust their provisioning effort to satisfy the demands of a larger brood (Figure 5.4B). Such was not the case in the second week. Parents doubled the daily energy delivered when brood size increased from 1 to 2 but the rate per nest declined to a relatively constant level for all larger brood sizes (Figures 5.4A). As a consequence, the delivery of energy per chick was constant initially (brood sizes 1 and 2) but then declined with further increases in brood size (Figure 5.4B).

Frequency distributions of the round-trip delivery time for each prey item are shown in Figure 5.5. Parents usually were able to deliver the two items of lowest caloric value in the shortest time (Figure 5.5A; see Table 5.1) while items of higher value were delivered over longer intervals (Figure 5.5 B, C). Consequently, the mean delivery time (and its associated varance) increased in relation to the average energy content of a given item (except for fish; Figure 5.5B).

DISCUSSION

In central place foraging theory (Orians and Pearson 1979), parents are assumed to achieve maximum fitness by maximizing the rate of food delivery to

Figure 5.4. Daily delivery rate to the nest (A) and per chick (B). For each panel, squares indicate week 1 chicks and circles are week 2 chicks.

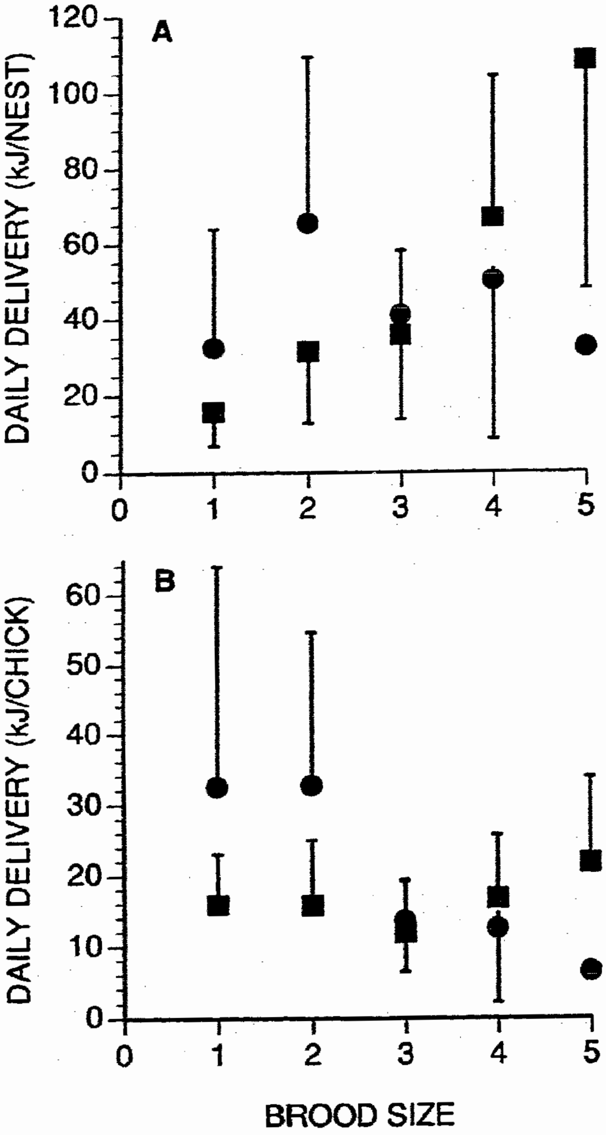
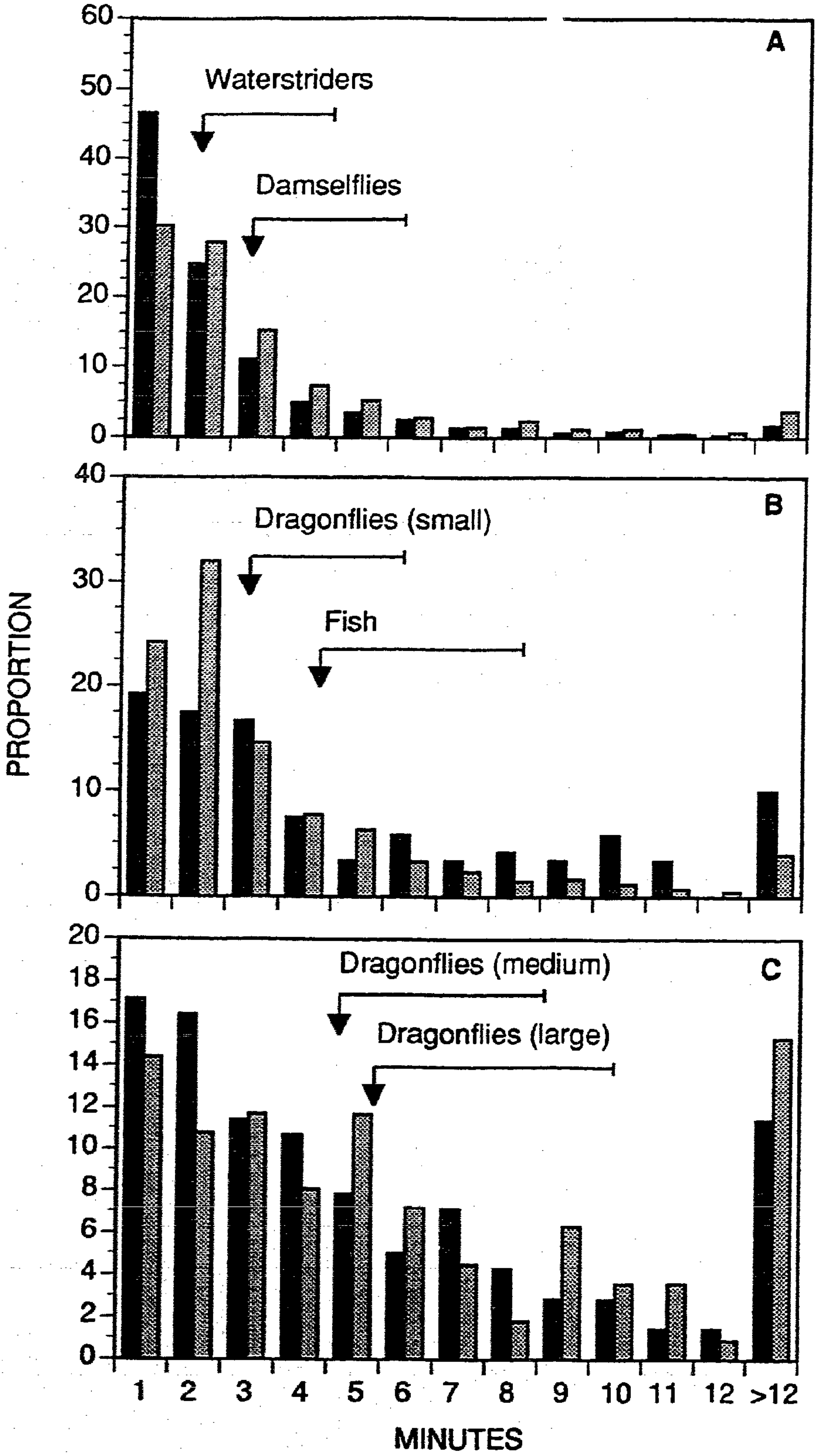

A
DAILY DELIVERY (kJ/NEST)
0
20
40
60
80
100
120
0
1
2
3
4
5
B
DAILY DELIVERY (kJ/CHICK)
0
10
20
30
40
50
60
0
1
2
3
4
5
BROOD SIZE

Figure 5.5. Frequency distributions (expressed in proportions) of the delivery times for each of 6 prey items, waterstriders and damselflies (N = 1130 and 988, respectively; panel A), fish and small dragonflies (N = 120 and 425, respectively; panel B), and medium and large dragonflies (N = 140 and 111, respectively; panel C). Solid bars are the distribution of the uppermost item listed in each panel. Also shown are the mean (vertical arrow) and standard deviation (horizontal bar) of the delivery times. Totals for each item were compiled from all 63 nests (see Methods).


A
Waterstriders
Damselflies
B
Dragonflies (small)
Fish
C
Dragonflies (medium)
Dragonflies (large)
PROPORTION
MINUTES
60
50
40
30
20
10
0
40
30
20
10
0
20
18
16
14
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
9
10
11
12
>12

the nest (Houston 1987). One interpretation of this theory suggests that parents should respond to variation in nestling demand simply by allocating more or less time to foraging, rather than changing aspects of the foraging cycle (prey selection, for example; Houston1987). In this study, Black Tern parents of week-old offspring increased the provisioning rate in relation to brood size (Figure 5.1), in part, because they decreased time spent at the nest (Figure 5.2; but see below). Other studies have demonstrated a similar change in the delivery rate with brood size. For example, parents increased both foraging time (Tinbergen 1981) and the delivery rate of items to the nest when Starling broods were experimentally enlarged (Tinbergen 1981, Westerterp et al. 1982). Feeding frequencies (items/unit time) in the great tit were significantly lower in reduced broods than either control or enlarged broods, but the latter two groups were not significantly different from one another (Smith et al. 1988). The increase in the item delivery rate in many of these studies was achieved by parents delivering prey that were either smaller and less profitable (though presumably more abundant; Smith et al. 1988), or of poorer quality (Tinbergen 1981, Westerterp et al. 1982). We found no evidence of such a change in the diet of week-old offspring (Figure 5.4). On the contrary, the largest brood size received proportionately more of the larger prey items (dragonflies, Table 5.1; see below).

Parents compensated effectively for the increase in brood size in week 1 (Figure 5.1B) but they delivered items to larger broods at a significanlty lower rate when offspring were 2 weeks old (Figure 5.1). In the latter case, all parents spent almost their entire day away from the nest, regardless of brood size, and so there was no opportunity to further increase foraging time (and thus overall delivery), as they had in week 1 (Figure 5.2). That the delivery rate per unit foraging time increased significantly with brood size in week 1 (Figure 5.3) indicates that parents must also have adjusted some other aspect of their behavior.

One possibility is that they increased effort by flying faster. A drawback to this tactic, however, is that it could increase the total energy budget to a point where parents exceed their capacity to recover expenditures through self-feeding (Wiener 1992). Estimates of daily energy expenditure indicate that, under normal circumstances, adult Black Terns can spend the entire day provisioning offspring without exceeding this limit (Chapter III). Though the extent to which parents could increase flight speed and not incur significant energy debt is unknown, they appear to have at least the potential of doing so. Alternatively, parents could expend energy at the same rate (i.e. fly at the same speed) but consume a smaller proportion of the prey captured (see for example, Kacelnik and Cuthill 1990). Unfortunately, Black Terns are almost exclusively aerial foragers (Welham pers. obs.), which made it difficult to obtain data on either flight speeds or self-feeding rates outside of our experimental situation that were sufficiently reliable to test these ideas.

There was a significant change in the overall diet of one versus two-week old chicks, with older broods receiving proportionately more large dragonflies (Table 5.2). However, estimates from a previous study suggest that, during the period Black Terns are breeding, dragonflies are not nearly as abundant as other, smaller prey (for example, damselflies; see Mosher 1986, Table 13). It seems that the decline in the delivery rate of items to older nestlings can be attributed simply to parents selecting prey that were less available (this could also explain the drop in delivery rate at the largest brood size in week 1; see Figure 5.3, Table 5.2). Why did parents change the diet of older chicks in favor of these larger items?

One reason for the change might be that prey availability differed between the two age-groups. This seems unlikely because the study site contained nests of both groups, there was considerable overlap in their breeding chronology, and parents tended to use the same foraging areas. Alternatively, if nest visitation increases the risk of predation (Lima 1987) then parents may have attempted to minimize the total number of deliveries to older offspring. In this case, the extra energy content of dragonflies would have to be sufficient to compensate for the reduction in delivery rate. This was generally not the case. Though daily energy delivered to the nest increased with brood size in week 1, in week 2 there was no relationship between brood size and daily delivery (Figure 5.4A). Other than nests containing 1 or 2 chicks, the amount of energy each chick received actually declined (Figure 5.4B). It seems that the lower delivery rate (both in terms of items and energy content) to older chicks is not due simply to parents minimizing time spent at the nest.

Another possibility is that parents may have altered their criteria for prey selection in order to minimize the risk of an energy shortfall. Stephens and Charnov (1982) provide formal analyses of this problem, the simplest of which is their z-score model. In one example of this model, a forager can choose between a variety of foraging options, each providing a reward that differs in mean and variance (this constitutes the forager's feasibility set). Stephens and Charnov (1982) then show how to select the option that minimizes the risk of an energy shortfall. In a provisioning context, various combinations of prey items delivered to nestlings might be considered as representing a feasibility set of parental foraging options since each combination has an expected return rate and an associated variance. We therefore examined whether this idea could be useful in explaining differences in diet between one and two week-old chicks.

Our results suggested that Black Tern parents easily meet the requirements of a young brood and can therefore respond to changes in demand simply by varying their provisioning effort (Figure 5.2, see above). Increased provisioning effort, however, may not be sufficient to meet the requirements of an older brood and this might force parents to change their provisioning tactics in an effort to minimize the risk of an energy shortfall. One option is to preferentially select prey of high energy content. If these items are less abundant, however, this will not necessarily increase the mean daily energy delivered but there may be a higher variance in total delivery. It has been argued that, given a choice between two options each with the same mean rate of return but differing in variance, a forager should favor the more variable option when the benefits of a higher return rate provide a disproportionate increase in fitness (see Reboreda and Kacelnik 1993). If Black Tern parents do indeed have difficulty in meeting the requirements of older offspring, any increase in the total amount of food delivered might improve their survival prospects considerably. In our case, the high energy content of dragonflies (Table 5.1) combined with the wide distribution of capture times associated with these items (Figure 5.5) suggests their prevalence in the diet could result in a high variance in total delivery. This might explain why, overall, these items were selected less in week 1 (when parents presumably have little difficulty in meeting offspring requirements) and their representation increased in the diet of older chicks (Table 5.2) even though it did not result in an increase in overall mean daily energy delivered (Figure 5.4). It should also be noted that for week-old chicks, the proportion of dragonflies in the largest brood was more than 20 % higher than for any other brood size in this age group (Table 5.2). It may be therefore that the addition of two extra chicks is sufficient to place these parents in an energy shortfall situation. Other studies that have manipulated brood size report an increase in the proportion of smaller prey items when demand was higher (see above). This change may not be inconsistent with the ideas proposed here, however, if these smaller prey actually represent the more variable option.

To date, most tests of variance-sensitive behavior restrict their protocol to one in which a forager can make a single choice between two options, presented simultaneously (for example, Caraco et al. 1980, 1990, Cartar and Dill, 1990, Reboreda and Kacelnik 1993). In this respect, the provisioning context considered here is much more complex. For example, the initial capture event is not mutually exclusive since the parent, while delivering that item, might encounter another of higher profitability (it then has the option of consuming the first prey, or discarding it, and delivering the second). Nevertheless, provisioning decisions that are sensitive to the variance in delivery may represent one more tactic available to parents.

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CHAPTER VI

GENERAL CONCLUSIONS

In their seminal paper, Drent and Daan (1980) presented evidence for the idea that energetic limits to performance play an important role in shaping patterns of reproductive effort in birds. They argued that, since parents can not exceed this metabolic limit without compromising their own prospects for survival, reproductive effort should reflect a balance between parental capacity and offspring needs. As a result, the reproductive strategies of parent birds should be relatively conservative with respect to energy costs in order to minimize the risks of excessive expenditure.

For many birds, offspring growth depends solely on the amount of food they receive from parents, and this activity can represent a large component of reproductive effort. Though provisioning effort is often considered from an optimal foraging perspective, few studies have attempted to assess the long-term consequences of the predicted behavior (Houston 1987). For example, it has been suggested that the optimal policy specified by at least some of the currencies may result in parents expending energy at a rate that is not consistent with a model of optimal reproductive effort based on life-historical considerations (Houston 1987). Parents are unlikely to forage at rates that compomise their own body reserves if adult mass at the end of the breeding season is positively correlated with future survival (Reid 1987 and references therein), and if fitness is strongly dependent on the number of breeding attempts.

By flying at speeds that provided the highest energetic benefit at the minimum cost (efficiency maximizing; see Chapter III), Black Tern parents were able to capture and deliver enough food to meet their own needs and those of their offspring at an energetic cost that likely did not exceed a maximum limit to daily energy expenditure. Such was not the case for the two alternative currencies (maximizing the net rate of energy intake and daily delivery rate), at least under conditions posed by the feeding experiment. Though both predicted a higher delivery rate than efficiency maximizing, it was at a level of work effort that was not sustainable.

Another important feature of biological design is the close quantitative match between the capacity of a particular physiological structure and the natural loads to which it is subjected (see Diamond and Hammond 1992). This follows from the fact that natural selection tends to eliminate unused capacities because they are costly to maintain. Nevertheless, actual capacity should exceed peak loads by some amount to permit a flexible response to changing environmental conditions (Diamond and Hammond 1992). In this respect, one benefit to parents of maximizing efficiency is that their daily energy expenditure is sufficiently low that they have some capability to increase provisioning effort up to the maximum limit, at least when offspring are young (though under natural conditions this may also be true of the rate currencies; see Chapter III). Hence, when brood size (and thus demand) was increased, parents with week-old offspring brought more food to the nest by foraging for longer periods in the day and also by increasing the delivery rate (Chapter V). Parents with older chicks spent the entire day away from the nest (regardless of brood size) but, in this case, the delivery rate did not increase with brood demand. One possibility is that these parents were provisioning at the maximum rate and so could not sustain any further increase in effort (see, for example, Masman et al. 1989).

While I was not able to establish whether provisioning effort in Black Tern parents was indeed constrained by limits to energetic performance, evidence from other species suggests that this may often be the case in species with small mass (Masman et al. 1989, Bryant and Tatner 1991). How the size of the reserve capacity affects parental provisioning options is unknown, however. In the case of Black Terns, their inability to sustain further increases in effort might have forced parents to change their provisioning tactics (by selecting larger but more variable prey items; see Chapter V) in order to meet the higher demands of an older brood. There is considerable evidence that forager decisions are sensitive to both the mean and variance associated with a reward (see, for example, Caraco et al. 1990, Cartar and Dill 1990). In birds though, the majority of these studies have been conducted on non-reproducing individuals. Hence, the role of variance-sensitive foraging in the decisions of parent birds warrants further consideration.

One of the shortcomings of 'classical' optimal foraging models is that the policy specified by a given currency does not depend on the forager's energy reserves (or those of its offspring) nor does it take account of any variation in feeding rate (see Chapter III). Houston and McNamara (1985) were able to demonstrate theoretically, using a state variable model, that when both of these factors are considered, the optimal policy can differ from that predicted by the classical optimal foraging approach. There are many circumstances when the inclusion of state dynamics is critically important to understanding the optimal behavior (Clark 1991, Houston and McNamara 1988) but conducting experiments to test these models is often difficult (see Chapter IV). The results from Chapter IV are encouraging, therefore, since they suggest that the predictions derived from optimal foraging models (particularly the efficiency maximizing currency) can, under some circumstances, closely approximate those made by a model incorporating state dynamics.

For the offspring of many species, their growth and survival depends upon the amount of food they receive. From the provisioner's perspective, however, foraging effort must reflect a balance between meeting its own needs and those of its offspring. In this respect, much of the work reported here has served to establish the conservative nature of parental provisioning effort.

Though other species have also been shown to forage in accordance with the predictions of efficiency maximizing, the reasons why this should be so are not well understood. My calculations for parent Black Terns, however, indicate that limits to daily performance may hold the key. By minimizing foraging costs, parents not only reduce the risk of excessive expenditure but also maintain a reserve capacity to permit a flexible response to changing conditions.

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