This paper introduces some theoretical concepts based on optimality theory that may be applied to bat migration. Most predictions are based on flight mechanics and potential flight range. Optimal behavior will depend on the relevant immediate currency, such as safety, time, or energy. Predictions concern optimal flight speeds, stopover duration, fuel load at departure, and the adaptive use of winds. I also consider a criterion for fuel management when bats are migrating between summer and hibernation sites. The overall migration speed is predicted to be 46 km/day for a small (10-g) bat, and banding recoveries in Nathusius’s bat (Pipistrellus nathusii) showed a mean speed of 47 km/day. The timing of migration in bats that minimizes the time spent in migration is considered a result of the trade-off between seasonally increased length of the night (decreased in spring) and reduction of aerial insect abundance. Most predictions remains to be tested; the theoretical framework herein offers a point of departure when designing new field or laboratory studies of bat migration.

Key words: flight mechanics, flight speed, fuel load, hibernation, migration speed, migration theory

That bats perform seasonal migrations has been recognized from banding efforts that were initiated during the previous century (Fleming and Eby 2003; Griffin 1970; Hutterer et al. 2005). The ability to fly at relatively high speed is similar among bats and birds, and yet the incidence and extent of migration is lower among bats (Fleming and Eby 2003). This difference may be explained partly by the fact that the main survival strategy of bats during winter is hibernation, but it may be due to other more subtle differences as well. However, the actual process of migration in bats may be quite similar to that of birds, involving alternate periods of fuel accumulation and flight, the adaptive use of winds, and the use of external orientation cues. A theoretical approach based on optimality arguments, such as has been successfully applied to the migration of birds, therefore could be informative for understanding the adaptive and mechanistic significance of bat migration. For a review of bat migration patterns and which genera migrate, see Popa-Lisseanu and Voigt (2009).

Over about the last 40 years, a mechanical theory of flight has been developed and evaluated for birds (Pennycuick 1968, 2008), and basically the same theory also has been evaluated for a few bats (Carpenter 1986; Norberg 1990; Thomas 1975). By combining principles of flight mechanics and optimality reasoning, an ecological theory about migration strategies for birds has been developed over the last 2 decades (Alerstam and Hedenström 1998; Alerstam and Lindström 1990; Hedenström and Alerstam 1997). This theoretical framework allows the prediction of such variables as optimal strategies regarding timing of migration, flight step lengths, fuel loads at departure, and significance of winds. The theory has proved to be a useful tool in that it has suggested critical predictions, some of which have been tested by laboratory or field experiments (e.g., Hedenström 2008). A similar approach has not yet been applied to bat migration (Fleming and Eby 2003), which is a gap that I hope this paper will help fill. Even if some constructs of bird migration theory are directly applicable to bats, there may be differences in their basic biology that need to be considered in order to generate efficient and accurate predictions about bat migration. In this paper, I will outline some basic features of optimal migration theory as it can be applied to bats, and in a few cases illustrate or evaluate predictions on the basis of available data. I do not intend to give complete coverage of all aspects of migration theory, but rather deal with some issues that may be worth following up for migratory bats. I also will point out where data are lacking and what kind of information would be needed to evaluate assumptions and predictions presented here.

**The Mechanics and Energetics of Flight**

Predictions developed in this paper depend on 2 fundamental relationships derived from flight mechanics, which are briefly presented in this section: flight cost and flight range.

**Flight cost.**—In order to fly steadily, an animal has to overcome the pull of gravity by generating lift and overcome drag of body and wings by generating thrust. In steady-
powered flight, the flapping wings achieve both these functions so that 1 wing beat delivers a net force that balances total lift and drag. The mechanical cost of flight is usually divided into 3 components: the 1st is associated with generation of lift (or induced drag \( P_{\text{ind}} \)), the 2nd is due to drag of the wings (profile drag \( P_{\text{pro}} \)), and the 3rd is due to drag of the body (parasite drag \( P_{\text{par}} \)). There also is a power component due to inertia of the wings arising from acceleration of the wings at the turning points of the wing stroke, but this power component is considered to be small at cruising speeds (Hedrick et al. 2004; Norberg 1990) and therefore is often neglected. Detailed treatment of the basic principles of flight mechanics of bats and birds can be found elsewhere (e.g., Hedenström 2002; Norberg 1990; Pennycuick 2008). For the purpose of the present paper, I note that the 3 main power components are usually expressed as function of airspeed \( U \), and so total power required to fly can be written as:

\[
P(U) = a_0 U^{-1} + (a_1 + a_2)U^3,
\]

where \( P \) is mechanical power output and \( a_0, a_1, \) and \( a_2 \) include physical and morphological parameters. The 1st term on the right-hand side of equation 1 is the induced power, which declines with increasing airspeed, whereas the other 2 terms represent profile and parasite power, which increase with increasing airspeed. Pennycuick (1975, 2008) has argued that, in the range of typical cruising speeds, profile power changes relatively little with speed and is therefore often treated as a constant. The diverging trends of the power terms in equation 1 result in a U-shaped relationship between mechanical power required to fly and airspeed (Fig. 1), a relationship which I will refer to as the “power curve.” The model of equation 1 includes the mechanical power components of bat flight, whereas the animal actually expends a higher metabolic power than prescribed by this equation during flight. The ratio between mechanical power and total metabolic power is the energy conversion efficiency (e.g., Pennycuick 2008), which is typically about 20% for vertebrates. The conclusion in this paper is based on the assumption of constant conversion efficiency across all speeds, an assumption that remains to be critically evaluated for bats.

For flying vertebrates the power curve immediately suggests the existence of characteristic flight speeds associated with minimum power (\( dP/du = 0 \), \( U_{\text{mig}} \)), and maximum range (\( dP/du = P/U \), \( U_{\text{mr}} \)—e.g., Norberg 1990; Pennycuick 1975). Graphical solutions for these characteristic speeds are shown in Fig. 1.

It is difficult to measure directly the total mechanical power in a freely flying animal, and this has not yet been attempted for a bat. However, measures related to mechanical work (and hence power) have been obtained for a few species of birds flying in wind tunnels, with the general result of a U-shaped power curve such as shown in Fig. 1 (Askew and Ellerby 2007; Tobalske et al. 2003). In these studies, muscle work was estimated by measurements of muscle shortening and by applying the work loop method (Biewener 2003), where the net work is calculated as the area of the “loop” enclosed by the force-versus-length relationship during a contraction–lengthening cycle. Instead of measuring mechanical power output, researchers have often used flight metabolic rate as a proxy for power consumption, which is valid if the conversion efficiency between metabolic power input \( P_{\text{met}} \) and mechanical power output is constant across speeds. In the few studies of bats where flight metabolic rate has been measured using a respirometry mask in a wind tunnel, there is evidence in support of a U-shaped relationship between \( P_{\text{net}} \) and airspeed (Carpenter 1985, 1986; Thomas 1975).

**Flight range.**—The capacity to fly a certain distance without refueling is determined by the rate at which accumulated fuel is consumed. This rate depends on various factors such as overall body mass, wing and body morphology, and physiological efficiency of converting fuel into useful aerodynamic work. The aerodynamic cost is given by the fully parameterized equation 1, which would show that flight cost also depends on weight of the bat including the fuel load. The aerodynamic cost of carrying a fuel load arises due to the extra weight of the fuel and also to the increased frontal body area due to subcutaneous fuel deposits causing increased parasite drag. The 2-fold costs of carrying fuel result in a flight range \( Y \) of the form (Alerstam and Lindström 1990):

\[
Y = c[1 - (1 + f)^{-0.5}],
\]

where the coefficient \( c \) (of dimension distance) includes a number of factors, such as fuel composition, muscle work

![Fig. 1. Relationship between power required to fly (P) and airspeed for a bat in flapping flight—the “power curve.” The abscissa intersects the ordinate at value 0. The portion of the ordinate below the abscissa represents rate of fuel deposition (Pfuel). A tangent to the power curve (heavy line) from the point of relevant Pfuel gives optimal flight speed (Ump) associated with maximization of overall migration speed; where this tangent intersects the abscissa it gives migration speed (U_mig). U_cap is speed at minimum power and U_max is the speed at maximum range.](https://academic.oup.com/jmammal/article-abstract/90/6/1298/898078)
efficiency, bat morphology, and wind factor (Alerstam and Hedenström 1998). The fuel load ($f$) is expressed as a proportion of lean body mass ($m_0$) as $f = (m - m_0)/m_0$, where $m$ is body mass including the fuel. If the fuel is stored in a way that does not increase the frontal area significantly, the penalty of carrying extra fuel is less dramatic than suggested by equation (2a) and is written as:

$$Y = \frac{c}{2} \ln(1 + f). \quad (2b)$$

An alternative approach to obtain a range equation is to assume that the instantaneous rate of fuel consumption is a fixed proportion of the body mass, that is, $dm/dt = -xm$ (Delingat et al. 2008), where $x$ is the fraction of the body mass being consumed as fuel per hour. Integration from initial $((1 + f)m_0)$ to final mass $(m_0)$ yields flight duration, which multiplied by flight speed gives flight range as:

$$Y = \frac{U}{x} \ln(1 + f). \quad (2c)$$

In birds, values of $x$ typically vary from about 0.4% body mass/h in some extreme long-distance flying shorebirds, to 0.6% body mass/h in the blackpoll warbler (*Dendroica striata*—Nisbet 1963), and to 1–1.5% body mass/h in some other species (Alerstam 1981; Nisbet 1963). Because bats probably have somewhat higher drag than birds due to their protruding ears and less well streamlined bodies than birds, a provisional assumption could be $x = 1\%$ body mass/h for small bats. It should be noted that $x$ is likely to be scale- and shape-dependent and may thus vary among bats of different body size and airframe design.

A common feature of all versions of the flight-range equation is that flight range is a utility function of diminishing return of added fuel, which is why it becomes interesting to consider different optimality solutions for migration strategies. It should be noted that the assumptions underlying the derivation of flight range are purely aerodynamic properties except for equation 2c, which is based on empirical observation about the rate of mass loss during flight. There is as yet little empirical support for the assumption of mass-dependent flight cost differences in an individual bat that would occur during a long flight when significant fuel mass is lost. For an ideal bird (sensu Pennycuik 1975), it can be derived that power required to fly will vary due to within-individual mass change as $P \propto m^{7/4}$ (Dietz et al. 2007). Voigt (2000) measured the metabolic rate of horizontal flight of Palla’s long-tongued bat (*Glossophaga soricina*) in relation to mass changes during the pregnancy cycle, with mass variation between 9 and 13 g, and found that the flight metabolic rate varied as $P_{m_0} \propto m^{2.15}$. The scaling exponent was significantly different from 0 but not significantly different from the aerodynamic prediction ($P \propto m^{7/4}$), and so the only data available lend support for the assumption.

**Migration Strategies**

**Currencies of migration.**—Migration serves the purpose of transporting the animal in space to escape periods of competition or low resource levels (Alerstam et al. 2003), and because migration is a behavior not directly involved in reproduction, it should be carried out in a way that maximizes survival. The optimization approach is based on the assumption of some simple immediate currency and seeks a behavior that maximizes or minimizes this currency. The main optimization objectives assumed to apply to bird migration are safety, energy, and time (Alerstam and Lindström 1990). Safety is usually taken as avoiding predation, but also could include the selection of a migration route that avoids long flights across inhospitable terrain. During migration it may be difficult to locate and obtain food because unfavorable habitats must be crossed or because the bat arrives in unfamiliar habitats, and therefore it may be adaptive to save energy. Energy minimization could be achieved either by simply minimizing transport costs, or by minimizing the total energy used during the whole migration (Hedenström and Alerstam 1997). The latter currency, total energy cost, also involves an element of time because baseline maintenance energy costs will increase with duration of migration because they are directly proportional to time, and therefore some predictions derived on the basis of total energy cost of migration are similar to purely time minimization. In many situations there is a premium to those individuals that arrive 1st at the destination (Kokko 1999). In bats, this could be to claim the best sites for hibernation, the best sites for reproduction, or the best mates. In such situations selection may favor a fast migration. The immediate currency will be time, and the migration strategy is to minimize overall time of migration (Alerstam and Lindström 1990), which is synonymous with maximizing overall speed of migration (see below). In reality, it is perhaps unlikely that an animal is optimizing strictly 1 simple currency at any time, but more likely it is minimizing a combination of 2 or more immediate currencies.

Houston (1998) showed how optimal fuel load for departure in birds could be derived when simultaneously minimizing time of migration and predation risk. Ultimately, the overall currency of all animals is fitness, which is perhaps best measured as lifetime reproductive success, but it is not feasible to build models that use such a general objective to derive optimal behaviors during migration. However, the logic of using a simple immediate currency as proxy for fitness is that true fitness is a function of the simple currency.

**Fuel load.**—The optimal departure fuel load depends on balancing the cost of stopping over multiple times if flight steps are short and paying an establishment cost each time versus the increased flight costs of carrying heavy fuel loads needed if flight steps are long. We assume that upon arrival at a new stopover site a bat will pay an energy cost for searching and settling ($f_0$) and a time cost ($t_0$). The logic behind these costs is that it takes time before efficient foraging and fuel accumulation can start, either because of unfamiliarity with the new site or due to physiological adjustments needed before efficient fueling is commenced. During this searching and settling period stored energy is used (Hedenström and Alerstam 1997). Initial mass loss immediately after arrival at
a new stopover site is a common pattern among birds (Alerstam and Lindström 1990), but it remains to be shown if bats follow a similar pattern. When depositing fuel the bat is accumulating potential flight distance according to the flight-range equation (equation 2), which can be used to define speed of migration:

\[ S = \frac{Y(f) - Y(f_0)}{t + t_0}, \]  

where \( Y \) is the flight range according to equation 2, \( t_0 \) and \( f_0 \) are the searching and settling costs, and \( t \) is stopover time. By differentiating \( S \) with respect to \( t \) and setting the derivative equal to 0 we obtain:

\[ \frac{dY}{dt} = \frac{Y(f) - Y(f_0)}{t + t_0}. \]  

From this condition the optimal stopover duration \( t^* \) associated with maximum \( S \) is given. If the bat accumulates fuel at a daily rate \( k \), then the fuel load is \( f = kt \) after \( t \) days and the optimal fuel load \( f^* = kt^* \). Because \( df/dt = k \), we can substitute \( df \) with \( df/kt \) and \( t \) with \( f/kt \) in equation 4 to obtain the alternative criterion:

\[ \frac{dY}{df} = \frac{Y(f) - Y(f_0)}{f + kt_0}. \]  

The solution to this criterion can be illustrated graphically as shown in Fig. 2. The optimal fuel load at departure is given by constructing a tangent from a point in the 4th quadrant, representing the searching and settling costs, to the range equation. If the fueling rate \( (k) \) is increased (i.e., the starting point of the tangent is moved to the left) the optimal departure load is increased (Fig. 2), and if the searching and settling costs \( (t_0 \) and \( f_0) \) increase, optimal fuel load for departure also is increased. Notice that quantitative knowledge about the constant \( c \) of the range equation (equation 2) is not necessary to derive the optimal departure fuel load because \( c \) cancels out in the calculation.

An alternative currency to time minimization is the minimization of energy cost of transport, in which case the optimal fuel load is given by:

\[ \frac{dY}{df} = \frac{Y(f) - Y(f_0)}{f}, \]  

where variables are as defined before. The optimal fuel load \( f_{\text{min}} \) depends on \( f_0 \) and the range equation. This contrasts to time minimization, in that during minimization of energy cost of transport the bat should not be responsive to variation in \( k \) (Fig. 2).

If the criterion is minimization of total energy cost of migration, it can be shown that the optimal departure fuel load falls between the predictions dictated by equations 5 and 6 (Hedenström and Alerstam 1997).

Predation risk is usually assumed to be mass-related because increased mass reduces maneuverability (Hedenström 1992); therefore, predation risk may be elevated during migration when bats carry fuel loads. With mass-dependent predation risk an animal can opt for minimizing the ratio between predation risk and migration speed (Alerstam and Lindström 1990); this will modify the optimal fuel loads downward, compared with the case of purely minimizing time.

Migration to a hibernation site.—In temperate regions, many bats migrate to their winter hibernacula (Fleming and Eby 2003), which may be toward any geographic direction from the summer site. Bats accumulate fuel, mainly as fat, to be used as energy during their winter hibernation period. In cases when the hibernation site is to the north, it may be that the bats migrate to an area with fewer food resources than at the summer site. A relevant question for them then is whether to extend the stay at the summer site to accumulate fuel (fat) also for hibernation, or to 1st move to the hibernation site and accumulate the energy required after arrival there. Let us assume the bat is minimizing time to reach the required fuel level \( f_0 \) at the hibernation site, which involves migrating a distance \( D \) from the summer site. The fueling rate is \( k_0 \) at the hibernation site and \( k_1 \) at the summer site \( (k_1 > k_0) \). It will be beneficial to remain at the summer site and accumulate the fuel required for the migration and the following hibernation period if

\[ \frac{k_1}{k_0} > \frac{f_2 - f_1}{f_0}, \]  

where \( f_2 \) is the departure fuel load when \( f_0 > 0 \) (i.e., fuel for hibernation is brought along from the summer site) and \( f_1 \) is the fuel load if \( f_0 = 0 \) (i.e., fuel for hibernation is obtained at the site of hibernation). The criterion of inequality (equation 7) is illustrated graphically in Fig. 3. Whether fuel for hibernation also will be accumulated at the summer site or not will be determined by the ratio of fueling rates at the 2 sites and fuel requirement \( (f_0) \) for hibernation. The likelihood that bats will accumulate energy for hibernation before migration increases if distance \( D \) is short. There also could
be a situation where part of the hibernation fuel is accumulated at the summer site, and the remaining fuel is stored at or near the site of hibernation (cf. Alerstam 2006). The fueling strategy associated with migration–hibernation is analogous to that of overloading and capital breeding in migratory birds (Alerstam and Hedenström 1998; Hedenström 2006). A complication occurs if mating takes place at the hibernation site before entering hibernation, which may favor arrival as soon as possible with no surplus energy.

Flight speeds.—Flight mechanical theory suggests 2 characteristic flight speeds, speed at minimum power ($U_{mp}$) and speed for maximum range ($U_{mr}$; Fig. 1). Of these speeds, $U_{mr}$ is expected speed during migration associated with minimization of energy cost of transport, whereas $U_{mp}$ should be used when the objective is to maximize flight duration for a given amount of energy (e.g., Hedenström and Alerstam 1995). $U_{mp}$ is not expected during migratory flight, except perhaps in the event of disorientation when a bat is buying time until some reliable directional cue becomes available (Hedenström and Alerstam 1995). In time minimization there is an alternative optimal flight speed, $U_{mz}$, given by the criterion $dP/dU = (P + P_{fuel})/U$, which depends on the rate of fueling ($P_{fuel}$) expressed in the same unit as the power required to fly (Fig. 1; Hedenström and Alerstam 1995). In natural situations $P_{fuel}$ is probably rather low and $U_{mz}$ is close to $U_{mr}$, explaining why it may be difficult to distinguish between these 2 speeds on the basis of observation, given the usual variation in flight speed measurements.

Winds and wind drift.—Just as in birds, the characteristic flight speeds of bats are of the same order of magnitude as that of winds. The significance of winds is therefore potentially quite large, where a head wind of the same strength as the bat’s own airspeed will effectively prevent progress altogether. On the other hand, an equally strong tailwind will roughly double the potential flight range compared with migration in neutral winds. It can be shown that in order to maximize migration speed it pays the bat to be responsive to current winds (Weber et al. 1998). Wind responsiveness can act at different levels. The current wind situation may cause the bat to advance or postpone the time of departure from a stopover in relation to the optimum during neutral winds (Weber et al. 1998). Birds tend to depart on migratory flights on nights of tailwinds toward the expected migration direction (e.g., Åkesson and Hedenström 2000; Delingat et al. 2008). After the bat is in the air, flight may involve decisions about wind drift or compensation. Following Alerstam (1979b) and assuming a bat will spend a certain amount of energy on the next flight, the optimal heading (the direction of the velocity vector) for minimizing the remaining distance $D_{2}$ to the final goal depends on initial energy (i.e., potential flight distance) and initial distance $D_{0}$ to the goal. In a situation involving several flights and independently varying winds, a bat should allow wind drift to minimize the remaining distance $D$ to the goal (Fig. 4).

This amounts to allowing drift when far away from the goal, but successively increasing the amount of compensation as the goal is approached (Fig. 4; Alerstam 1979b). An analogous analysis can be made for the situation of altitudinal wind gradients (Alerstam 1979a), so that the best option is to exploit high-altitude strong winds and allowing partial drift, but to shift to low altitude and low wind speed during a 2nd leg of the flight with overcompensation toward the goal.

Liechti et al. (1994) showed that, for a bird (or bat) that aims at maintaining a constant track over ground and hence compensate for lateral wind drift, the optimal compensation is achieved by the condition:

$$P' = \frac{P}{U_{g}} U_{g}'$$  \hspace{1cm} (8)

where $U_{g}$ is speed over ground, $P' = dP/dU$ is the marginal gain in power cost with increasing airspeed $U$, and $U_{g}' = \ldots$
\( dU/dU \) is the marginal gain in ground speed with increasing airspeed. To achieve optimal compensation requires simultaneous adjustment of heading and airspeed, which may demand a lot of the bat. Partial drift and compensation require some reference to landmarks. However, orienting purely by a compass sense, such as stars or Earth’s magnetic field (e.g., Holland et al. 2006) will lead to full drift.

**Migration Speed**

Predicted migration speed.—Long-distance migration usually involves several cycles of fueling and movement toward the goal, and therefore the overall migration speed is the total migration distance divided by the total time of migration, that is, including time for refueling and movement (in the case of bat flight). Consequently, if only 1 flight is required to reach the destination, time of fueling before the single flight must be included when determining overall speed. Time for depositing an energy load \( T_{\text{fuel}} \) that covers a migration distance \( D \) is

\[
T_{\text{fuel}} = \frac{PDU}{(E_0 - C_0)^{-1}},
\]

where \( P \) is rate of energy consumption during flight, \( U \) is flight speed (with respect to air), \( E_0 \) is the rate of energy accumulation at stopovers, and \( C_0 \) is the rate of energy consumption when fueling (Hedenström and Alarstam 1995). By taking flight time as \( T_{\text{flight}} = D/U \), and writing the ratio between migration distance \( D \) and total migration time \( T_{\text{migr}} = T_{\text{fuel}} + T_{\text{flight}} \), the overall migration speed is obtained as:

\[
U_{\text{migr}} = \frac{U(E_0 - C_0)}{(E_0 - C_0) + P_{\text{flight}}}. \tag{9}
\]

It will be convenient to consider \((E_0 - C_0)\) as net rate of energy accumulation and denote it as \( P_{\text{fuel}} \). It can be noted that the ratio \( T_{\text{flight}}/T_{\text{fuel}} \) is equal to the ratio \( P_{\text{fuel}}/P_{\text{flight}} \), and overall migration speed is flight speed multiplied by a quantity that corresponds to the fraction of total time spent in flight \( T_{\text{flight}}/T_{\text{migr}} = P_{\text{fuel}}/(P_{\text{flight}} + P_{\text{fuel}}) \). A graphical illustration of the solution of \( U_{\text{migr}} \) is shown in Fig. 1, where power required to fly is plotted as a function of airspeed, and energy deposition rate is plotted along the downward-extended y-axis. Constructing a line from the point representing energy deposition rate to the point representing power required to fly and airspeed, we obtain the overall migration speed where this line intersects the x-axis (Fig. 1). Because the function between power required to fly and airspeed is typically U-shaped, we get the maximum possible migration speed by constructing a tangent from the relevant energy deposition rate to the power curve (Fig. 1). By substituting realistic values for the variables on the right-hand side of equation 9 we can calculate the resulting migration speed for a bat. Or alternatively, if migration speed is observed and all but 1 of the quantities on the right-hand side of equation 9 are known, the unknown quantity can be determined.

It is necessary to identify realistic values for the 3 variables in equation 9 in order to estimate overall migration speed of a small bat. I take Nathusius’s pipistrelle \((Pipistrellus nathusii; 7–10 \text{ g})—Schober and Grimmberger 1997\) as an example because data are available on migration speed, and not just flight speed, to compare with the prediction of equation 9 (Petersons 2004). Flight speed is expected to vary with body size in flying animals (Pennycuick 1975), and for small bats of about 10 g the flight speed should be about 7 m/s. The similar-sized Pallas’s long-tongued bat flies spontaneously at an average speed of 7.3 m/s in a 50-m-long flight corridor (Winter 1999). The 25-g lesser long-nosed bat \((Leptonycteris curasoae)\) commutes between feeding areas at a flight speed of 8.2 m/s (Sahley et al. 1993), whereas the 20-g pond bat \((Myotis dasycneme)\) commutes at 9.1 m/s (Britton et al. 1997), suggesting the assumption of 7 m/s is a realistic assumption for Nathusius’s bat.

Flight metabolic rate has been determined for a number of species and a recent compilation of data from the literature suggests the equation

\[
P_{\text{flight}} = 55.6M^{0.79},
\]

where \( P_{\text{flight}} \) is in watts and \( M \) is body mass in kilograms (Speakman and Thomas 2003). Body mass in Nathusius’s bat may vary between 7 and 10 g due to fat accumulation (Schober and Grimmberger 1997), and so we may take 8.5 g as a representative body mass for which the estimated flight metabolic rate is 1.3 W.

The most problematic quantity to estimate is rate of energy (fuel) deposition in bats because studies of fueling rate before or during migration seem almost nonexistent. No such data are published for the Nathusius’s bat, and so we must use data from other species. Bats also accumulate fat in preparation for hibernation and most data on mass or fat increase refer to this situation. A study of the fringed bat \((Myotis thysanodes)\) reports a mass increase of 7.58–10 g over a period of 11 days (Ewing et al. 1970). Assuming this mass change is fat (energy density \(37.6 \text{ kJ/g wet mass}—\) Jenni and Jenni-Eiermann 1998), this mass change corresponds to 0.1 W or 0.9 times basal metabolic rate, if we use a recently published allometric equation for basal metabolic rate in relation to body mass (Speakman and Thomas 2003). Another study of autumn mass change in the little brown bat \((M. lucifugus)\) reports an increase of 1.6 g (in males) over 13 days (Kunz et al. 1998), which corresponds to 0.054 W or 0.7 times basal metabolic rate. For birds, rate of fat accumulation is often reported as a percentage daily mass increase in relation to lean body mass (LBM), and, expressed this way, fat accumulation is 2.9% LBM/day and 1.8% LBM/day for the fringed and little brown bat, respectively. This is comparable to many bird species in natural situations (Lindström 2003), although in laboratory conditions birds may achieve much higher rates of fuel accumulation (Kvist and Lindström 2003). Certain species of bats track the phenology of their food when migrating (Fleming and Eby 2003; Moreno-Valdez et al. 2000). In such cases, the migration speed is determined by the rate of the "phenology wave," provided it is not faster than the maximum migration capacity of the bats.

Scaling of migration speed.—Equation 9 also can be used to derive the relationship between migration speed and body size, that is, how it scales across species. Let us assume isometric scaling of wing morphology \((b \propto m^{1/3})\), where \( b \) is wingspan...
and $m$ is body mass), characteristic speed and power required to fly scale according to an “ideal bird” (sensu Pennycuick 1975—$U_{\text{chat}} \propto m^{1/3} b^{1/2}$ and $P_{\text{flight}} \propto m^{5/3} b^{2/3}$), and that fuel deposition rate is proportional to basal metabolic rate ($P_{\text{fuel}} \propto m^{3/4}$—Hedenström and Alerstam 1998). After substituting these expressions into equation 9 and simplifying, it follows that:

$$U_{\text{migr}} \propto m^{-1/4}.$$  (10)

Hence, overall migration speed should decline with increasing body size. Wing morphology deviates somewhat from isometric scaling in some bat groups (Norberg and Rayner 1987), which will have the effect of increasing the exponent of proportionality (10) somewhat, but the exponent will still be negative (Hedenström and Alerstam 1998). Given a migratory bat species, there should be selection for decreasing body size if there is a selective premium for fast overall migration.

**Observed migration speed.**—On the basis of estimated quantities on the right-hand side of equation 1, we can now calculate expected migration speed. Using the highest estimate of $P_{\text{fuel}}$ (0.1 W) yields an overall migration speed of 46 km/day, whereas the lower estimate (0.054 W) results in 24 km/day. A migration speed of 46 km/day corresponds to a $T_{\text{flight}}/T_{\text{migr}}$ ratio of 1/14 and with 24 km/day the ratio is only 1/25. To the best of my knowledge the most comprehensive data available on migration speed in bats are from banding efforts in Latvia by Petersons (2004), who received records for 14 Nathusius’s bats banded and recovered in the same autumn. Considering accumulated distance for all recoveries, overall speed was 47 km/day with individual speeds ranging from 32 to 77 km/day. Evidently mean migration speed of Nathusius’s bats is close to that predicted for an energy accumulation rate of 0.1 W, and thus lends support for the assumptions used for calculating the prediction.

**Migration Routes**

Migrations of bats are relatively short and largely in temperate or subtropical regions where migration along great circles (orthodromes) makes little sense from a distance (energy)-saving point of view (see Alerstam and Pettersson 1991). However, at high latitudes and when the migration path has an east–west component, the great circle route may be considerably shorter than the rhumb line (loxodrome). Orientation along great circles involve continual change of direction, something that birds can achieve by a time-compensated sun compass but by not resetting the internal clock to local time as new time zones are entered (Alerstam et al. 2001). In principle, the same result can be achieved instead by using a star compass, but it is unclear if bats have that capability (Holland 2007). The migration routes of bats are perhaps most likely to be determined mainly by a magnetic compass (Holland et al. 2006) in combination with local topographic features and landmarks. After the 1st migration it is possible that adult bats acquire a navigational map as shown for some bird species (e.g., Perdeck 1958). However, bat migration may involve the passage of ecological barriers, such as seas and deserts. For example, the overall autumn migration direction of Nathusius’s bat suggests that some may cross the Baltic Sea (Petersons 2004). Depending on where the Baltic is crossed, the distance across open sea varies, whereas a likely flight between Latvia and northeastern Germany is up to 600 km. If we assume a range equation as equation 2c, a flight speed of 7 m/s, and an hourly fuel consumption of 1% of the body mass, then the potential flight range is $Y = 2,500 \times \ln(1 + f)$ km. A direct flight across the Baltic of 600 km would require a fuel load $f = 0.27$ with neutral winds. Alerstam (2001) derived the condition for the break-even detour that allows migration along a detour around a barrier but with the same energy cost as the direct flight, because the flight can be divided into multiple short steps each with a low fuel load and thus avoiding carrying heavy fuel loads. The limit to flight range with negligible fuel load is $Y_{\text{max}} = 2,500 f’/k$ km, which corresponds to 675 km; hence, the bat will be able to travel an additional 75 km at the same energy cost as a direct 600-km flight. The actual detour distance around the southern coast of the Baltic is approximately 780 km, and so the direct flight is the best option. That Nathusius’s bats actually do cross the Baltic in the autumn is supported by observations along the southern and southeastern coasts of Sweden (Ahlén 1997).

**Timing of Migration**

The optimal timing of migration depends on a multitude of needs and opportunities in the annual cycle of a bat. If minimization of migration time is the only variable considered, it may depend on the time available for feeding, which is during the night for bats. In birds, fueling rate depends on time available for feeding (Kvist and Lindström 2000), so that nocturnally migrating birds can maximize feeding time by using the entire daylight period for fuel accumulation and making migratory flights during the “free” nighttime. In this way, fueling rate and hence migration speed can be maximized. Bats are mainly nocturnal for both foraging and migratory flight, which means that they have to split their active period between these 2 tasks. In this respect, bats are comparable to diurnal bird migrants. In the Northern Hemisphere, day length gets shorter with progression of the season in autumn and longer in spring, which should select for late spring and early autumn migration in birds migrating in the Northern Hemisphere (Alerstam 2003). With constant food resources, the opposite pattern should apply to bats, because in autumn they would experience progressively longer nights, allowing for increased time for feeding and transport. However, for insectivorous bats a seasonal decline in food abundance is expected in autumn, which may balance the effect of day length. If such diverging selection pressures apply, it could lead to an optimal timing for migration as shown schematically in Fig. 5. With reversed gradients in spring, there is still an optimal time window for migration. In other bat species, such as the frugivorous Mexican long-nosed bat (Leptonycteris nivalis), timing of migration is driven by the phenology of plants providing nectar, as modeled by Moreno-Valdez et al. (2000).
The basic features of the migration model et al. 2007; Nyctalus noctula km and Alerstam 1992); SPECIAL FEATURE—BAT MIGRATION THEORY 1305

One problem with using banding recovery time for maximum speed of migration. Length of the night (as days get shorter) during autumn and broken migration for an insectivorous bat. Solid curve shows increase of food abundance during autumn, while the broken curve represents aerial insect abundance. The arrow indicates optimal time for maximum speed of migration.

**DISCUSSION**

In this paper I have introduced some theoretical ideas regarding optimality of bat migration. By suggesting specific predictions about expected migratory behavior in bats, observations or experiments can be devised to examine specific assumptions or predictions. The majority of predictions have not yet been evaluated, and purposely designed studies are needed to do so because existing data collected for other research objectives are unlikely to be useful. Some assumptions made here may not apply for bats, in which case more-appropriate assumptions have to be used to generate new predictions (see Parker and Maynard Smith 1990; Stephens and Krebs 1986). What are the elements of the optimality models that can be evaluated and how should it be done?

**Migration strategies.**—The basic features of the migration strategy models are that bats perform a multistep migration with alternate periods of stopover for fueling and flight toward the destination. There are some indications that bats spend time at sites that could be seen as stopovers (e.g., Eby 1991; Larkin 2006). An important issue is what is the rate of fuel deposition in bats? Several studies report on fat deposition in prehibernating bats (e.g., Ewing et al. 1970; Kunz et al. 1998; Pagels 1975), but few studies consider fueling for migration (but see O’Shea 1976; Townsend et al. 2008). A next step is to find out if bats are responsive to variation in fueling rate regarding the departure fuel load, because such variation would indicate an element of time minimization (Alerstam and Hedenström 1998). A positive relationship between fueling rate and departure fuel load is a common pattern among birds (Hedenström 2008). Diurnal foraging or flight during migration suggests a need to extend the time of activity, which also suggests time minimization. I have often observed such diurnal activities in noctules (Nyctalus noctula) on autumn migration. One may wonder why migratory bats have not developed diurnal flights to allow fueling during the whole night period as a mirror image to nocturnally migrating birds. Perhaps increased predation risk prevents diurnal flights in bats (Speakman 1991). In studies of birds, variation in the daily fueling rate ($\dot{k}$) has been created by clever supplemental food experiments (e.g., Lindström and Alerstam 1992); although this may be difficult to accomplish in bats there is certainly ample space for scientific creativity here.

Female bats in the Northern Hemisphere tend to migrate farther north than males in spring to form summer colonies (Cryan 2003; Fleming and Eby 2003). They also may migrate when pregnant, which adds to the nonfuel mass and affects the flight range. However, the basic migration strategy, that is, whether to migrate according to time or energy minimization rules, should not be affected with respect to these complicating factors. Many bird species also show sex-biased differential migration with females usually migrating farther to more-distant wintering areas (e.g., Ketterson and Nolan 1985). Spatial segregation between sexes thus occurs in different seasons in birds and bats.

**Flight behavior.**—A few attempts at comparing flight speed between different ecological situations have been made (e.g., Britton et al. 1997; Grodzinski et al. 2009), comparing foraging and commuting bats. The results suggest that bats fly more slowly when foraging and faster when commuting. A few measurements using radar (Bruderer and Popa-Lisseanu 2005) show rather high airspeeds (13 m/s) for commuting compared with foraging bats, but these trackings included portions of descent.

When it comes to the departure from stopover sites in relation to winds and whether bats show wind drift or compensation during flight, it is probably safe to assume that there are no such data available. By using small tracking devices (or radar) in combination with wind measurement, it should be possible to obtain relevant information. Mechanistic studies about the vision and orientation capacities of bats will be crucial when understanding if, how, and when bats are capable of compensating for winds. Wind tunnel studies also are providing new information about the aerodynamics and energetics of bat flight (e.g., Hedenström et al. 2007; Johansson et al. 2008), which will improve our knowledge about the flight-cost component of migration.

**Migration speed.**—One problem with using banding recovery or retrapping to calculate migration speed is, if there is a direct flight with short time between 1st and 2nd capture, it will overestimate the overall migration speed because fueling time is underrepresented. On the other hand, if too long a time has elapsed after banding, then speed will be underestimated because we may include time after the completion of migration. So far it has not been technically feasible to track individual birds or bats with satellite telemetry (Holland and Wikelski 2009). However, using small radiotransmitters it has been possible to follow individual passerine migrants on a number of nocturnal flights by means of car or aircraft (Cochrane 1987; Cochrane and Wikelski 2005), and during the initial flight after release in homing experiments with bats (Holland et al. 2006). Ultimately, we need to be able to track individuals throughout their migration in order to address...
questions about migration speed, migratory step lengths, and flight duration.

How does migration speed in Nathusius’s bat compare with that of birds? There are 2 compilations on migration speeds based on national banding schemes in Finland and Sweden (Ellegren 1993; Hildén and Saurø 1982). The mean migration speed of passerine species divided into 4 main categories for the Finnish and Swedish data are \( n = \) number of species): nocturnal long-distance migrants with wintering areas in the tropics (79 km/day, \( n = 13; 54 \) km/day, \( n = 14 \), nocturnal short- to medium-range migrants wintering in the temperate zone (48 km/day, \( n = 7; 45 \) km/day, \( n = 8 \), diurnal short- to medium-range migrants (52 km/day, \( n = 6; 35 \) km/day, \( n = 4 \), and partial or irrituous short-range migrants (28 km/day, \( n = 8; 20 \) km/day, \( n = 5 \). Although there is large variation in speed within categories, the mean migration speed of 47 km/day for Nathusius’s bats is close to that of birds with temperate wintering areas. Passerine birds with tropical winter quarters migrate faster, whereas the partial or irrituous bird migrants have lower migration speeds than the bats. Thus, migration speed in Nathusius’s bats is comparable to that of birds migrating a similar distance in winter within the temperate zone, as the bats do.

Even though migration speed of Nathusius’s bat appears similar to that of temperate migrant birds, the same speed may be realized by different combinations of the variables in equation 1. First, the flight speed was assumed to be 7 m/s for the bat, which is lower than that of similar-sized passerine bird species (Alerstam et al. 2007). Metabolic flight cost is very similar between birds and bats (Speakman and Thomas 2003), and so any differences in flight cost are likely to be small. The wake in Pallas’s long-tongued bat was found to be more complex than that of passerine birds (Hedenström et al. 2007), which may suggest that bats are less efficient in converting metabolic power into mechanical work. However, this remains a speculation until more-direct measurements of metabolic power and mechanical power output exist. Finally, comparing the energy deposition rate assumed for bats for lean body mass (2.9% LBM/day) with that of birds suggests that bats have a low rate of fuel deposition (Lindström 2003). In birds, fueling rates approach 10% LBM/day in small species, whereas during experiments involving supplemental food the fuel deposition rate may be as high as 20% LBM/day in long-distance migrants (Bayly 2007). However, in the European robin (Erithacus rubecula), which is a short-range migrant like Nathusius’s bat, the fueling rate was about 5% LBM/day in birds provided with supplemental food and less in birds feeding naturally (Dänhardt and Lindström 2001). One reason for relatively low fuel deposition rates in bats could be that their mode of foraging is aerial hawking, which is a very costly way of obtaining food. The barn swallow (Hirundo rustica), another aerial feeder, also has a relatively low fuel deposition rate of 2.1% LBM/day (Pilastro and Magnani 1997), although barn swallows migrate much faster than the bats (Hedenström and Alerstam 1998). The use of torpor by bats during the day in migration could be a way to conserve energy during daytime and hence to maximize fueling rate (Carpenter and Hixon 1988).

Bats are mainly nocturnal, which means they must divide their time between feeding and migratory flights, which is similar to diurnal migrants among birds. This leads to a compromise, although the actual number of nights bats that make migratory flights is rather low. Maximum migration speed has been assumed to be limited by the maximum capacity of processing and converting food into fuel (Hedenström and Alerstam 1998), which is often referred to as a metabolic ceiling (Hammond and Diamond 1997). However, experiments with birds show that the main factor limiting the fueling rate is the time available for feeding (Kvist and Lindström 2000). Whether bats are near or below such a metabolic ceiling when depositing fuel for migration remains unknown.

Future prospects.—As shown by studies of bird migration, optimality models have been important in advancing understanding about critical factors governing the process of migration. In this respect, the study of bat migration is still in its infancy. The rapid technological advancement of methods for tracking small, flying nocturnal animals such as bats will greatly help in addressing predictions put forth in this paper. Because of the lack of information about many aspects of bat migration, this paper aims to inspire studies examining the assumptions and predictions of optimality models. If refuted, the theory must be modified accordingly, which is likely to be the case in some instances because the basic theory was originally developed with bird migration in mind (Alerstam and Hedenström 1998). A next step could be to develop an annual-routine model (sensu McNamara and Houston 2008), with the aim of solving the overall life-history schedule for a bat all at once, including reproduction, migration, and hibernation. I have summarized the similarities and differences between passerine birds and bats for a number of feats related to migration in Table 1. A similar list is found in Fleming and Eby (2003), but Table 1 focuses more on parameters directly related to the migration process and performance. The content of Table 1 is naturally preliminary and it is my hope that investigations in the near future will extend and correct what is known about bat migration.

### Table 1: Summary of similarities and differences of some parameters related to migration between passerine birds and bats.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Passerine birds</th>
<th>Bats</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum migration distance (km)</td>
<td>≥2,000</td>
<td>2,000</td>
</tr>
<tr>
<td>Long sustained flights</td>
<td>Common</td>
<td>Uncommon</td>
</tr>
<tr>
<td>Fat loads</td>
<td>&gt;50% of LBM*</td>
<td>&lt;50% of LBM*</td>
</tr>
<tr>
<td>Fat deposition rate</td>
<td>≤20% of LBM*</td>
<td>≤3% of LBM*</td>
</tr>
<tr>
<td>Power curve U-shaped</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Mass-related flight cost</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Cruising speed (m/s)</td>
<td>&gt;10</td>
<td>&lt;10</td>
</tr>
<tr>
<td>Migration speed (km/day)</td>
<td>&gt;150</td>
<td>&lt;50</td>
</tr>
<tr>
<td>Wind responsive</td>
<td>Yes</td>
<td>Yes?</td>
</tr>
<tr>
<td>Magnetic sense</td>
<td>Yes</td>
<td>Yes</td>
</tr>
</tbody>
</table>

* LBM = lean body mass.
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LITERATURE CITED


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