

S34-1 Current optimality models in avian migration

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Abstract Optimality models of bird migration are reviewed. The principal approach to simple optimality theory is presented, as well as main predictions and tests. We also discuss flight mechanical theory because migration theory builds extensively on such principles. This approach to the study of bird migration has proven very successful, and generated new directions of experimental work.

Key words Time, Fuel loading, Flight mechanics, Stopover decisions, Optimality modeling, Wind effects

1 Introduction

During the last decade, a migration theory has been developed as a theoretical foundation for understanding migration strategies and behaviors (Alerstam and Hedenström, 1998; Houston, 1998). This theory comprises a framework for predicting optimal policies regarding the process of migration, such as the length of stopover, at what fuel load to depart, and the influence of current winds on departure decision. It relies on the range equation, which is derived from the lift:drag ratio, and gives the potential flight range as a function of fuel load. Flight mechanical theory provides a model framework to analyse the forces and power components of birds in flight. Aerodynamic analysis leads to the so-called power curve, which is a relationship between the power required to fly and speed (Pennycuick, 1989). From this relationship it is possible to derive predictions about flight behavior.

A related analysis for gliding flight gives the glide-polar, relating sink rate to forward speed at force equilibrium to provide the input for predictions concerning soaring flight migration (Pennycuick, 1972). From analysis of the effect of winds, as the vector triangle between airspeed, ground speed and wind, predictions about optimal behavior of drift and compensation can be deduced (Alerstam, 1979; Alerstam and Hedenström, 1998). These are the main constituents of what we will loosely define as “optimal migration theory”: theory concerning the process and behavior of migration. Issues regarding the evolution of migration, and partial and differential migration patterns, may also be analysed from a theoretical viewpoint (Alerstam and Hedenström, 1998), but we do not consider such theoretical aspects in this paper. Figure 1 presents an overview of the components of migration theory and their relationships.

2 Fundamental equations

The flight range provided by a certain fuel load can

be derived from the effective lift:drag ratio, the energy density of fuel and the conversion efficiency of fuel (Pennycuick, 1975). The range shows a diminishing return function for added fuel because flight cost increases with body mass including added fuel, assuming that fuel energy density is constant; and flight cost will also increase due to increased pressure drag because fat stored subcutaneously increases the frontal area of the bird. Hence, flight range can be expressed as

$$Y = c \left(1 - \frac{1}{\sqrt{1+f}} \right),$$

where f is the relative fuel load ($f = (m/m_0) - 1$, where m is total body mass and m_0 is lean body mass), and c is a coefficient with distance dimension (Alerstam and Lindström, 1990; Alerstam and Hedenström, 1998). If the frontal area is unaffected by added fuel (an unrealistic assumption), the flight range is

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

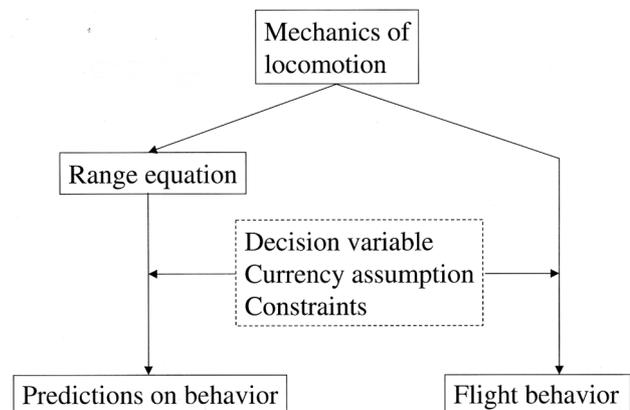


Fig. 1 Overview of bird migration theory and the interrelationship among its components

which is a curve of lesser penalty for carrying extra fuel than the first equation (Weber and Houston, 1997a; Alerstam and Hedenström, 1998). Both equations represent useful approximations of the relationship between range and relative fuel load. If the first range equation is rearranged to express fuel load as a function of potential flight distance f (Y), a useful relationship emerges for calculating the fuel load of a bird arriving overloaded at a new site, that is, a bird that had departed with more fuel than needed to fly the distance. Assuming a constant fuel deposition rate k and a constant energy density of fuel, and substituting kt for f in the range equation, the potential range can be expressed as a function of fuelling time $Y(t)$. Differentiating gives the instantaneous migration speed of the bird as

$$S = \frac{dY}{dt} = \frac{c}{2} k \cdot \frac{1}{(1+f)^{3/2}}$$

This equation gives the marginal rate of gain in flight range for a bird depositing fuel at a rate k , where S declines with increasing fuel reserves.

3 Predictions and tests about migration behavior

The optimal stay at a stopover site raises a fundamental question. Here we assume that the bird is accumulating fuel at a rate k , and that birds experience search/settling time and energy costs when arriving at a new stopover site (Rappole and Warner, 1976). A direct application of the range equation for two alternative fuelling rates is shown in Fig. 2. For the two rates shown ($k=0.04, 0.08$) and a search/settling time cost $t_0 = 3$ days and no energy cost ($f_0 = 0$), it appears that the optimal stopover period is $t^* = 13.2$ days for the low fuelling rate and $t^* = 9.6$ days and $f^* = 0.77$ for the high fuelling rate if both have a fuel load of $f^* = 0.53$ at

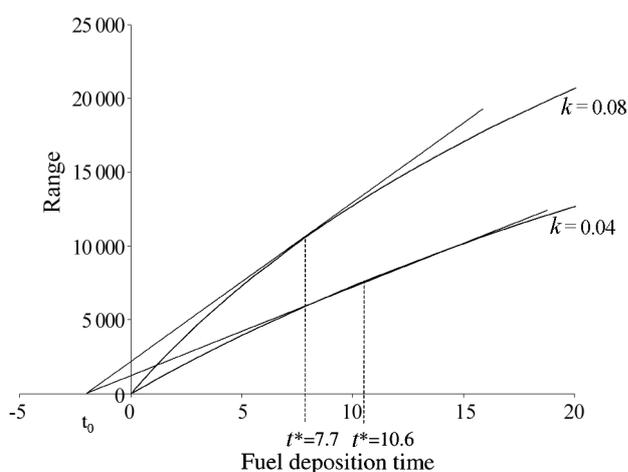


Fig. 2 Flight range as a function of fuelling time (t) at a stopover site

Two range curves representing $k = 0.04$ and $k = 0.08$ are shown, where the fuel load expressed as a proportion of lean body mass is $f = kt$. The optimal departure time for the two illustrated examples and $t_0 = 2$ days are: $t^* = 7.7$ days at $f^* = 0.62$ and $t^* = 10.6$ days at $f^* = 0.42$.

departure. Hence, with a high fuel deposition rate the bird should leave the stopover site with a higher fuel load than at low fuel deposition rates, but the fuelling time will be shorter at high deposition rates. The baseline model assumes an infinite total migration distance, whereas if migration is modelled as finite, the optimal departure load in relation to fuel deposition rate will increase in a stepwise manner, not as a continuous curve (Weber and Houston, 1997b). Hence, there will be windows where no change can be expected in departure fuel load across an interval of fuel deposition rates.

These general predictions have been tested several times by providing birds with food at artificial stopover sites, where mass gain and departure timing are monitored using color marked individuals and a remote-controlled balance. A few studies have reported data in qualitative, but not quantitative, agreement with the prediction (Lindström and Alerstam, 1992; Fransson, 1998), while similar experiments found no relationship between fuelling rate and fuel load at departure from the stopover (Dänhardt and Lindström, 2001). A number of possible explanations have been suggested for the mismatch between prediction and experimental data: (1) individual variation in expected migration speed (Lindström and Alerstam, 1992); (2) lack of response within intervals of fuel deposition rates, according to the step model of Weber and Houston (1997b); (3) birds may individually update expected migration speeds according to conditions experienced at the current site (Weber et al., 1999), (4) increased fuel loads that affect metabolic costs and reduce effective fuel deposition rate (Klaassen and Lindström, 1996); (5) applicable currencies other than time minimization, such as minimizing the total energy cost of migration (Hedenström and Alerstam, 1997); (6) variation in the expected speed of migration along the route (Lindström and Alerstam, 1992).

If birds use discrete stopover sites along their flyway, then one can predict scenarios for overloading and bypassing, depending on the relative quality of the stopover sites (Gudmundsson et al., 1991). If birds minimize the transport energy cost, they should stop at all useful sites along the route in order to carry the smallest possible fuel loads. On the other hand, skipping certain sites and overloads may become optimal for minimizing time. These predictions are derived from the third equation above. The predictions have not been tested experimentally, but observations of site use and nonzero fuel loads in birds arriving at stopovers are consistent with the predictions. Conditions and patterns of overloads and bypasses have been investigated theoretically by Weber et al. (1994), Weber and Houston (1997a) and Weber et al. (1998a, b).

More recently, Alerstam (2001) investigated optimal detours in birds using flapping flight. Since it is cheaper to fly with low fuel loads, it may be optimal to fly along a detour allowing frequent stops for refueling, rather than flying across an ecological barrier with a large fuel load at departure. Alerstam (2001) derived predictions for break-

even detours in birds, and provided numerous examples of birds taking a detour predicted by theory.

When accumulating fat before migratory flights, birds also seem to accumulate protein, mainly as increased flight muscle mass (Lindström et al., 2000). Weber and Hedenström (2000) derived predictions regarding the conditions when such physiological flexibility could be expected.

4 Flight behavior

The mechanical properties of flight have been modeled by various approaches, ranging from direct estimation of the forces acting on the flapping wing to characterization of the vortex wake (a bird's aerodynamic footprint) of the flying bird (Hedenström, 2002). In a popular approach, Pennycuick (1989) used an actuator disc, in which the bird is replaced by a circular disc of diameter equal to the wingspan. The oncoming airflow is considered as a circular tube, which is deflected downwards by the actuator disc and obtains an induced velocity. The induced power (P_{ind}) is inversely proportional to flight speed (U) and wing span (b). Another important power component arises from the pressure drag of the bird's body, usually called the parasite drag because it is not involved in generating any lift. Parasite power is proportional to U^3 and body frontal area and shape. There is as well a profile drag on the wings that has been shown to vary relatively little in the normal range of flight speeds, and is therefore usually considered as constant in that speed range. By adding together the three main power components of bird flight we get the power curve

$$P = \alpha + \beta \cdot U^{-1} + \gamma \cdot U^3,$$

where α , β , and γ are parameters that include bird morphology, body mass and certain physical constants. The power curve is illustrated in Fig. 3, where the characteristic U-shape is shown, and which immediately suggests several optimal flight speeds. First, from $dP/dU=0$ we get the minimum power speed which is associated with the cheapest flight cost per unit time. This is the best flight speed if flight duration is the main concern, irrespective of distance covered. Secondly, from $dP/dU=P/U$ we get the maximum range speed, which is associated with the minimum cost of transport. This is the best speed if energy expenditure per unit distance moved is important. Further optimal flight speeds can be derived from different currency assumptions (Hedenström and Alerstam, 1995).

5 Predictions and tests of flight behavior

It might be thought that the most straightforward approach here is to measure power output for a bird over a range of flight speeds by analyses of flight mechanics. Indeed, this has been tried several few times, but mainly by measuring the metabolic rate of flying birds (Butler and Bishop, 2000), which includes also the overall heat production by the bird. Thus changes in mechanical power output

may be masked. A few such studies do show a U-shaped relationship between metabolic rate and forward speed, while others show it as surprisingly flat. Direct measurement of mechanical power output has proven quite difficult to accomplish, but some recent technological advancements have made this possible (Dial et al., 1997; Pennycuick et al., 2000). Even though theory and experiments disagree in these studies, further experimentation is required for a critical evaluation of flight mechanics theory.

An alternative approach is to test the validity of predictions derived from the power curve. Depending on ecological context, we can expect birds to select one or other of the optimal flight speeds derived above. Skylarks (*Alauda arvensis*) seem to fly near their U_{mp} during song display while on migration their speed is $\geq U_{mr}$ (Hedenström and Alerstam, 1996). Such tests provide at best an indirect test of flight mechanics theory.

The power curve can also be used to derive predictions about flight speed adjustment in relation to head and tail winds. With a tail wind increment, a bird should reduce its flight speed from that in still air (Fig. 3), while in head winds it should increase it to remain at the optimal U_{mr} . That migrating birds actually do adjust their airspeed in relation to winds, as predicted, has been shown several times (Hedenström et al., 2002). Flight speed should also change with altitude because air density changes with altitude, a behavior also supported by recent radar tracking of migrating birds in the high Arctic (Hedenström et al., 2002). For a summary of different predictions about flight behavior on the basis of flight mechanics, see Hedenström (2003).

6 Prospects

The development of optimal bird migration theory over the last decade has been catalytic for bird migration research. Even if aspects of the theory are found to be wrong, it will have still served its purpose of pointing out

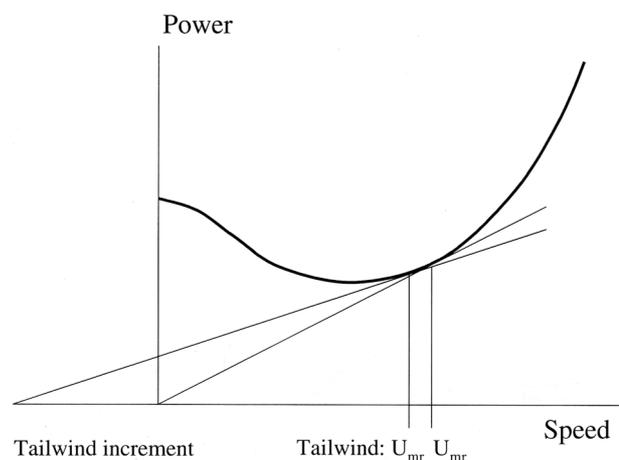


Fig. 3 Power in relation to forward air speed

This is a graphical representation of the last equation. How the optimal speed, U_{mr} , is affected by a tail wind increment is also shown.

what critical studies and experiments are needed. Studies on flight mechanics and the physiology of bird flight have also entered a new era with the deployment of modern low-turbulence wind tunnels (Pennycuik et al., 1997). New techniques for measuring the mechanical power output from birds, in particular, will be invaluable for evaluating flight mechanics theory.

Acknowledgements This research was supported by the Swedish Research Council.

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