

The strength of selection in the context of migration speed

Alasdair I. Houston

Centre for Behavioural Biology, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK (a.i.houston@bristol.ac.uk)

I use a model of avian migration based on maximization of overall migration speed to compare the strength of selection acting on foraging performance and flight speed. Let the optimal foraging behaviour be u^* and the optimal flight speed be v^* . It is shown that at this optimum, the ratio of the strength of selection on foraging to the strength of selection on flight speed is $\theta = -(u^{*2}P\gamma''/v^{*2}\gamma P'')$, where γ is the rate of energy expenditure during flight and P is the rate at which energy is gained during foraging. The dimensionless ratio P/γ is the ratio of time spent building up fuel to time spent flying which A. Hedenström and T. Alerstam showed was much greater than unity. Although θ depends on this ratio, it also depends on the curvatures of the functions, as represented by γ'' and P'' . I use this simple example to make some general points about the strength of selection.

Keywords: strength of selection; migration; flight speed; foraging

1. INTRODUCTION

Because the rate at which a bird or mammal uses energy is typically very much larger in flight than in other activities, it is tempting to believe that there must be strong selection pressure on flight behaviour. Hedenström & Alerstam (1997) present an analysis that is relevant to an evaluation of the strength of selection on flight speed. They show in the context of avian migration that a bird is likely to spend much more of the total journey time foraging than flying. They also show that the bird is likely to spend more energy on foraging than on flight. These results suggest that there may be stronger selection pressure on foraging than flight speed during migration, but this view cannot be substantiated without further analysis. In the absence of such an analysis, it is not clear if selection pressure should depend on time spent or energy spent. In this paper I use a migration model of Alerstam & Lindström (1990) in the form discussed by Hedenström & Alerstam (1995) to obtain results about the strength of selection acting on deviations from optimal foraging and optimal flight speed.

We can take the strength of selection acting on behaviour u to be $\partial F/\partial u$, where F is fitness (cf. the directional selection gradient, Lande & Arnold 1983). In the context of migration, Alerstam & Lindström (1990) introduced the idea of investigating various simple currencies that might be directly related to fitness. The case on which I will focus here is time minimization, i.e. the assumption that fitness is maximized by minimizing journey time or (equivalently) by maximizing the overall speed of migration, S . Then

$$\frac{\partial F}{\partial u} = \frac{dF}{dS} \frac{\partial S}{\partial u}.$$

It may not be easy to estimate dF/dS , which means that we cannot comment on the absolute magnitude of $\partial F/\partial u$ on the basis of $\partial S/\partial u$. We can, however, find the relative

magnitude of selection on behaviours u and v by means of the ratio

$$\frac{\partial S/\partial u}{\partial S/\partial v} = \frac{\partial F/\partial u}{\partial F/\partial v}.$$

If we are interested in the strength of selection for behaviour that maximizes migration speed, the analysis needs to be taken a bit further. When S is maximized then $\partial S/\partial u$ and $\partial S/\partial v$ are zero. In this case, the cost of deviation from the optimum will depend on higher order derivatives. Consider first a small deviation Δu from the optimal value u^* of u . It follows from a Taylor series expansion that the change in S is $\frac{1}{2}(\Delta u)^2(\partial^2 S/\partial u^2)$ plus higher order terms. In this paper I will work with the cost associated with a proportional change $\Delta u/u^*$. (This change is dimensionless.) The change in S as a result of this proportional change in u will be $\frac{1}{2}u^{*2}(\Delta u/u^*)^2(\partial^2 S/\partial u^2)$. Thus we can take $\frac{1}{2}u^{*2}(\partial^2 S/\partial u^2)$ to be a measure of the cost of a proportional deviation from u^* . By an analogous argument, the cost of a proportional deviation from the optimal value v^* of v is $\frac{1}{2}v^{*2}(\partial^2 S/\partial v^2)$. Both of these expressions are dimensionless. Once again we cannot measure the absolute effect of deviations from the optimum in terms of fitness, but we can estimate the relative magnitude by taking the ratio of these expressions.

2. THE MODEL

I consider the model of Alerstam & Lindström (1990) as extended by Hedenström & Alerstam (1995). The bird travels a distance D between refuelling sites. If it flies at speed v , it expends energy during flight at a rate $P(v)$. While on the ground the bird has a choice of foraging option. If it chooses option u , then its net rate of energetic gain is $\gamma(u)$. The time spent flying is D/v and the energy spent on flight is $(D/v)P(v)$. The time taken to replace this energy is $(D/v)(P(v)/\gamma(u))$ and so the total time T for the journey is given by the equation

$$T = \frac{D}{v} \left(1 + \frac{P(v)}{\gamma(u)} \right). \tag{1}$$

The overall speed of the migration is

$$S = \frac{D}{T},$$

$$= \frac{v\gamma(u)}{\gamma(u) + P(v)}. \tag{2}$$

As Hedenström & Ålerstam (1995) point out, S is maximized by maximizing the net rate of gain γ . The value of u that results in this maximum will be denoted by u^* . The optimal flight speed v^* can be found from the condition $\partial S/\partial v = 0$. From equation (2),

$$\frac{\partial S}{\partial v} = \frac{(\gamma + P)\gamma - v\gamma P'}{(\gamma + P)^2}. \tag{3}$$

It follows that v^* satisfies the equation

$$\gamma + P = vP', \tag{4}$$

(Ålerstam & Lindström 1990; Ålerstam 1991; Hedenström & Ålerstam 1995).

Two other speeds that are discussed in the context of optimal flight are the minimum power speed v_{mp} and the maximum range speed v_{mr} (see Hedenström & Ålerstam (1995) for a review). At v_{mp} , the rate of expenditure while flying is minimized, and hence the time that can be spent in the air per unit energy spent is maximized. At v_{mr} , the distance flown per unit of energy spent v/P is maximized. At v_{mp} , $P' = 0$, and at v_{mr} , $vP' = P$. Given that P' increases with v above v_{mp} , then these conditions together with equation (4) mean that $v_{mp} < v_{mr} < v^*$.

3. THE STRENGTH OF SELECTION

The strength of selection for optimal foraging behaviour is proportional to $u^2(\partial^2 S/\partial u^2)$ evaluated at u^* . It follows from equation (2) and the condition that $\gamma'(u^*) = 0$ that

$$\frac{\partial^2 S}{\partial u^2} \Big|_{u^*} = \frac{P(v)\gamma''(u^*)v}{(\gamma(u^*) + P(v))^2}. \tag{5}$$

The strength of selection for optimal flight speed is proportional to $v^2(\partial^2 S/\partial v^2)$ evaluated at v^* . From equations (3) and (4) it can be seen that

$$\frac{\partial^2 S}{\partial v^2} \Big|_{v^*} = -\frac{P''(v^*)\gamma(u)v^*}{(\gamma(u^*) + P(v^*))^2}. \tag{6}$$

Let

$$\theta = \frac{u^{*2}\partial^2 S/\partial u^2}{v^{*2}\partial^2 S/\partial v^2},$$

where both partial derivatives are evaluated at u^* and v^* . Then

$$\theta = -\frac{u^{*2}P(v^*)\gamma''(u^*)}{v^{*2}\gamma(u^*)P''(v^*)}. \tag{7}$$

(Exactly the same equation for θ results if we work with minimizing journey time rather than maximizing migration speed. Note that $\gamma''(u^*) < 0$ and so θ is positive.)

By definition, θ is the ratio of the selection pressure on foraging to the selection pressure on flight speed at the joint optimum. Equation (7) shows that the ratio $P(v^*)/\gamma(u^*)$ is one component of θ . P is the rate of energy expenditure during flight and γ is the net rate of energetic gain while foraging, so P/γ is dimensionless. It can also be seen that θ depends on the curvature of P and γ , as indicated by the second derivatives. P'' depends on the bird's power curve P , which in turn depends on the bird's morphology. γ'' depends on the foraging options that are available. As an example, let u be the bird's search speed, and assume that the rate at which it encounters food items is qu (cf. Ware 1975). Items have energetic content e and handling time h . The bird's rate of energy expenditure while foraging is $m + cu$. It follows that the gross rate of gain is $equ/(1 + hqu)$, and hence the net rate of gain $\gamma(u)$ is given by the following equation:

$$\gamma(u) = \frac{equ}{1 + hqu} - cu - m. \tag{8}$$

From the condition that $\gamma'(u^*) = 0$, it can be shown that

$$u^* = \frac{(eq/c)^{0.5} - 1}{hq}. \tag{9}$$

It can also be shown that

$$\gamma'' = \frac{-2eq^2h}{(1 + hqu)^3}. \tag{10}$$

It follows from equations (9) and (10) that

$$\gamma''(u^*) = -2q^{0.5}hc^{1.5}e^{-0.5}. \tag{11}$$

4. THE RATIO P/γ

We have seen that θ depends on the ratio P/γ evaluated at u^* and v^* . As Hedenström & Ålerstam (1997) point out, this ratio is equal to the time spent building up fuel at a refuelling site divided by the time spent flying between sites, i.e.

$$\frac{P}{\gamma} = \frac{\text{refuelling time}}{\text{flying time}}.$$

This ratio occurs in several other contexts. From equation (2) the overall speed of migration can be written as

$$S = \frac{v}{1 + P/\gamma}, \tag{12}$$

which makes it clear that the overall speed depends on just the flight speed and the dimensionless ratio P/γ .

The ratio P/γ also emerges if we consider the strength of selection on flight speed when speed is not optimal. At v_{mp} , $P' = 0$ and so it follows from equation (3) that

$$\frac{\partial S}{\partial v} \Big|_{v_{mp}} = \frac{1}{1 + (P(v_{mp})/\gamma)}. \tag{13}$$

At v_{mr} , $P = vP'$, and so from equation (3)

$$\frac{\partial S}{\partial v} \Big|_{v_{mr}} = \frac{1}{(1 + (P(v_{mr})/\gamma))^2}. \tag{14}$$

Because $v_{mr} > v_{mp}$ and P is an increasing function, the relative strength of selection satisfies the following inequality:

$$\frac{\left. \frac{\partial S}{\partial v} \right|_{v_{mp}}}{\left. \frac{\partial S}{\partial v} \right|_{v_{mr}}} > 1 + \frac{P(v_{mp})}{\gamma}. \quad (15)$$

5. DISCUSSION

In this paper I have used a model of flight speed and foraging during migration to investigate the strength of selection acting on deviations from optimal behaviour. The relative strength of selection on foraging as opposed to flight speed is $\theta = -(u^2 P \gamma'' / v \gamma P'')$, where all the functions are evaluated at the optimum. The dimensionless ratio P/γ is the relative allocation of time to building up fuel as opposed to flying. Hedenström & Ålerstam (1997) argue that this ratio is likely to be much larger than unity. This means that all else being equal, selection will be stronger on foraging than on flight. The equation for θ also shows that the ratio γ''/P'' is important, i.e. strength of selection depends on the curvature of the underlying functions.

The equation for θ is symmetrical, but there is an underlying asymmetry in the way that u and v interact. The optimal value of v depends on P and γ , whereas the optimal value of u depends on γ but is independent of P . Thus u^* can be found without knowing v^* , but v^* depends on u^* .

Charnov (1993) shows that dimensionless numbers can be used in the analysis of a range of problems in evolutionary biology. The dimensionless ratio P/γ occurs in several of the equations that I have obtained, including the selection ratios (equations (7) and (15)). Hedenström & Ålerstam (1997) show that the empirically derived allometric equations, based mainly on data from small or medium-sized passerines, imply that P/γ is roughly 7. If we take P/γ to be an approximate invariant for these birds (cf. Charnov 1993) then it follows from equation (12) that their overall speed of migration is about one-eighth of the flight speed, and the strength of selection on flight speed at v_{mp} is about eight times as great as it is at v_{mr} (equation (15)). If we do not assume invariance, then this relative strength of selection decreases as γ increases.

Hedenström & Ålerstam (1998) present an analysis of migration speed and obtain some general allometric equations. They calculated migration speed S at v_{mp} , v_{mr} and the optimal speed v^* for a range of species under the assumption that γ was equal to basal metabolic rate. They found that flying at v_{mr} instead of v^* reduced S by less than 1%, whereas flying at v_{mp} resulted in a reduction of between 65 and 76%. This led them to conclude that selection on flight speed is probably not very strong if speed is between v_{mr} and v^* . This analysis is based on a relatively large change in behaviour. In contrast, my analysis is based on small deviations either from v^* , v_{mr} or v_{mp} .

The model that I have used is simple. It ignores constraints on energy expenditure (see Houston (1993), Hedenström & Ålerstam (1995) and McNamara & Houston (1997) for discussion of the effects of such a constraint on optimal behaviour) and assumes that maximizing migration speed will maximize fitness (for a

broader discussion of optimal migration, see Ålerstam & Hedenström (1998) and Houston (1998)). These simplifications limit the conclusions that can be drawn about actual strengths of selection in the context of migration. Such a specific analysis is not, however, the main aim of the paper. I have used a model of migration to illustrate some general features of the relative strength of selection acting on two behaviours.

One general feature is that we cannot judge the relative importance of activities by comparing rates of energy expenditure. Flight is energetically expensive, but flight has to be paid for by foraging, and this puts pressure on foraging behaviour. This point also applies to comparisons of foraging behaviour and mating behaviour. Mating behaviour may be very expensive in terms of energy, and unlike foraging it makes a direct contribution to reproduction. It does not follow, however, that the strength of selection on mating behaviour will be greater than the strength of selection on foraging behaviour. As in the case of flight, the animal has to forage in order to gain enough energy to mate effectively, and as a result the strength of selection on foraging may be greater than the strength of selection on mating. Another feature of equation (7) that will hold in general is that the strength of selection will depend not just on the time allocated to activities but also on the consequences of changing behaviour. When we are considering deviations from an optimum, these consequences will be represented by the second derivatives of the functions that relate behaviour to performance. Any claim about the strength of selection that does not include the curvature of these functions is unlikely to be correct.

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