On the Aerodynamics of Animal Flight in Ground Effect

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SUMMARY

Flight in ground effect above a flat, smooth surface may give an animal considerable performance advantages, including a reduction in cost of transport of up to 15%, and a reduction in mechanical flight power of as much as 35%, compared with values for flight out of ground effect. Previous theories modelling the phenomenon have either been incomplete or marred by typographical errors. A complete lifting line theory of flight in ground effect with a fixed wing is developed, and instructions are given so that it may be applied to animals such as skimmers, pelicans and myotid bats which fly and forage close above water. Several predictions are made about likely flight behaviour in ground effect, and about the appropriate flight morphology for taking advantage of the potential performance improvements. The most important conclusion, differing from previous analyses, is that slow flight performance in ground effect is very poor, owing to the horizontal air velocity induced around the wing in the presence of the ground.

1. INTRODUCTION

When an animal or an aircraft flies close above a plane surface the aerodynamic properties of its wings are altered as a result of the interaction of the vortices on the wing and the wake with the surface. This phenomenon is known as 'ground effect', and has a significant effect on flight performance during take-off and landing. The dominant effect is a reduction in the induced (i.e. vortex) drag, and hence a saving in the thrust required for level flight. Various specialized aircraft have been designed to take advantage of ground effect, and it has often been argued that it is used by certain birds and bats which fly over water. The species involved include petrels (Withers 1979), pelicans (Hainsworth 1988), skimmers (Rhynchopidae) (Withers & Timko 1977; Blake 1983, 1985), ospreys, fish eagles and fishing owls (*Ketupa*), fishing bats of the genera *Noctilio* (Noctilioninae, Phyllostomidae) and *Pizonyx* (? = *Myotis*, Vespertilionidae) (Norberg & Rayner 1987), and trawling myotid bats of the subgenus *Myotis* (*Leuconoë*) (Aldridge 1988; Jones & Rayner 1988, 1991); for general discussions see also Kistyakovskii (1967) and Norberg (1990). All of these animals habitually fly low and level close to water surfaces while foraging or commuting. Ground effect is also used over land by certain raptors, and is likely also to be important in take-off for heavily loaded water birds such as swans, rails and divers, and for large land birds such as vultures and bustards which on level ground require a take-off run into the wind.

Although there are several theoretical aerodynamic approaches to the ground effect problem (see below), only two models (those of Reid (1932) and McCormick (1979)) are quoted in the biological literature. Although the underlying reasoning of these models is correct, and equivalent to that developed in this paper, both are incomplete, and the model of McCormick is in error, at least in the form in which it is printed and usually quoted. Here I develop a complete theory for a fixed wing in ground effect, based on a steady-state lifting-line wing model, and use this to show how ground effect is likely to affect the flight performance of an animal close above a surface.

2. EXISTING THEORIES

The principle of ground effect is that the airflows around the animal's wing and induced by the wake vortices interact with the ground, and this interaction has the effect of altering the flow regime around the wing. The problem is usually modelled by developing a vortex image system which ensures that the airflow perpendicular to the ground plane is zero. For the case of a straight wing in level flight over a smooth surface the appropriate image system is simply the mirror of the wing and wake vortices (figure 1). The parent vortex system comprises a line vortex lying on (or bound on) the wing, and a trailing vortex sheet (or the equivalent rolled-up vortex pair) behind the wing. If the animal is flying at height h above the ground, the image system is the same line vortex and vortex sheet, at height $-h$ below the ground, and with equal but opposite vortex circulation (Betz 1912).

It is a relatively straightforward, if somewhat tedious, computation to find the induced velocity on the wing caused by the parent vortices (which as a first approximation are the same as those in flight away from the ground plane) and by the image vortices, and from this to derive the total induced drag. The velocity induced by the image of the trailing vortex sheet has a positive vertical component, and therefore the tendency of the ground effect is usually to reduce total induced drag.

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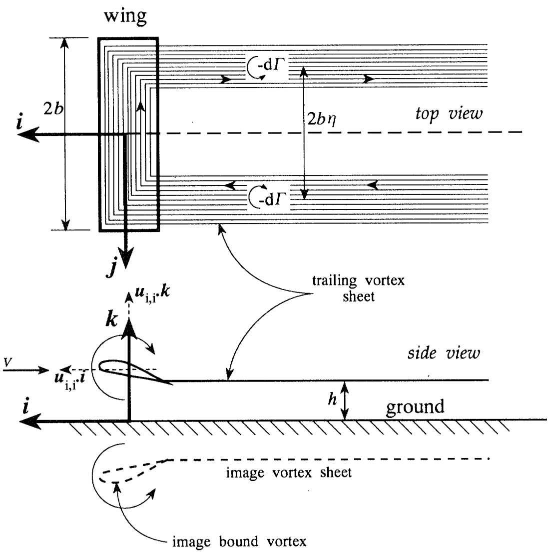

Figure 1. The wing as a lifting line, with its wake system as a vortex sheet, and the image vortex system (broken line), showing definitions of notation and of unit reference vectors $\boldsymbol{i}, \boldsymbol{j}, \boldsymbol{k}$. The wake vortex and its image are taken as coplanar to derive the lifting line induced downwash and induced drag. In practice the vortex sheet will roll up into a trailing vortex pair which convects downwards; the roll-up process, and the rate of convection, will both be altered in ground effect. The sense of the induced velocity on the wing due to the image system is indicated as dashed vectors. (After McCormick (1979).)

This calculation has been done by several authors (see, for example, Prandtl 1919; Wieselsberger 1921), and in the form quoted by Reid (1932; table VIII, p. 173) forms the basis of most studies of animal flight in ground effect (see figure 2 below). Hummel (1973) has reviewed the extensive older aeronautical literature. If b is the wing semispan, the Prandtl–Wieselsberger–Reid results for a straight, elliptically loaded wing can be approximated by the formula

$$1-\sigma = (8.72+0.1b/h)/(7.4+2.1b/h), \tag{1}$$

(Suh & Ostowari 1988) for $0.25 \leqslant h/b \leqslant 1$, in which σ is the induced drag factor denoting the relative reduction in induced drag. Induced drag $D_{\mathrm{i,ge}}$ in ground effect is determined from induced drag D_{i} out of ground effect by

$$D_{\mathrm{i,ge}} = D_{\mathrm{i}}(1-\sigma). \tag{2}$$

Note that Reid used b to represent the full wingspan, which is twice the value used in this paper, where b represents the semispan (denoted s by Suh & Ostowari (1988) and Laitone (1989)).

An alternative formula was given by McCormick (1979), based on modelling the image wake as a pair of line vortices equivalent to the vortex sheet in strength and spacing (i.e. momentum). This is printed as

$$1-\sigma = (8h/b)^2/[1+(8h/b)^2]; \tag{3}$$

in this form it contains a typographic error, omitting a factor of π, and should read

$$1-\sigma = (8h/\pi b)^2/[1+(8h/\pi b)^2] \tag{4}$$

(Laitone 1989); again, b is the wing semispan. The amended version of this equation given by Spedding (1987) and Hainsworth (1988) is incorrect, but the values in McCormick's (1979) figure 7.4 are correct to equation (4). (The incorrect formula used by Spedding and Hainsworth is numerically approximately correct, and use instead of equation (4) would not alter their conclusions that ground effect reduces induced drag.) Laitone (1989) has given an improved version of equation (4) as

$$1-\sigma = [1-2/\pi+(8h/\pi b)^2]/[1+(8h/\pi b)^2], \tag{5}$$

which is a significantly better approximation to Prandtl's original results in the range $h/b > \frac{1}{2}$, but is inaccurate at lower heights, and does not preserve the expected limit $\sigma \rightarrow 1$ as $h/b \rightarrow 0$. In the analysis below, σ is calculated exactly by numerical integration, and a second parameter τ is introduced for which there is no convenient algebraic approximation.

The major limitation of this theory is that it models only the vertical component of the induced velocity which modifies the downwash caused by the wake, but it neglects the induced velocity caused by the bound vortex on the image of the wing. This transverse image vortex induces a forwards velocity in the wing (figure 1), which subtracts from the translational velocity of the wing (the flight speed) and has the effect of increasing the effective angle of attack (Reid 1932); thus flight with the same total lift is possible only with an enhanced angle of incidence or circulation. In aeronautical practice the horizontal induced flow is generally ignored (but see Hummel (1973)), for two reasons. First, its effect is usually understood to be small, unless the wing is close to the ground or the flight speed is low (the lift coefficient or circulation is high). Second, ground effect is most significant to conventional aircraft during take off and landing, when flight speed and height above the ground are unlikely to be constant, and the main design concern is to fly safely. A more logical paradigm for birds and bats is to maintain level flight at a constant height above the ground, in the most economic way (minimum power or minimum cost of transport, for instance). This alters the problem significantly, and in this case it is no longer possible to neglect the forwards induced velocity and the associated reduction in lift. To develop a theoretical model of this situation it is useful first to consider lifting line theory for free flight and to review some of its predictions.

3. LIFTING LINE THEORY

Lifting line theory assumes that the bound vorticity on the wings can be modelled as a straight line vortex, of circulation Γ varying across the wingspan; for full derivation see, for example, Glauert (1947), Milne-Thompson (1958), McCormick (1979), Jones (1990). This theory forms the foundation of theoretical low-speed aerodynamics, and is implicitly the basis of most theoretical models of animal flight treating the wings as fixed lifting surfaces (see, for example, Pennycuick 1968, 1989; Tucker 1973; Greenewalt 1975). In the form given by these authors, and summarized here, the theory does not take account of thrust generation by the flapping wings, but it is an appropriate starting point for modelling ground effect for a flying animal; see Rayner (1986, 1992) for an unsteady three-dimensional form of lifting line theory which accounts for wing flapping and quantifies the influence of thrust generation on induced drag. Observations of the vortex wakes of gliding birds and bats (Spedding 1987; Rayner 1992; J. M. V. Rayner & A. L. R. Thomas, unpublished data) confirm that the lifting line model is remarkably accurate for vertebrate wings.

(*a*) *Derivation of lift*

As the wing moves forwards at speed V, lift is generated by the interaction of the bound vortex on the wing and the relative airflow, and is perpendicular to both; the lift per unit span of the wing is given by the Kutta–Joukowski theorem as

$$\boldsymbol{\delta L} = \rho V \Gamma(\eta)\, \boldsymbol{k}, \tag{6}$$

where ρ is the air density, and $\boldsymbol{k}$ is a vertical and upwards unit vector. Circulation varies across the wingspan, and in this paper is taken to follow elliptic loading, that is

$$\Gamma(\eta) = \Gamma_0(1-\eta^2)^{\frac{1}{2}}, \tag{7}$$

in which η parametrizes the span station across the wing, from -1 to 1, and Γ_0 is the circulation of the bound vortex at the midpoint of the wing (i.e. at the body). Elliptic loading is the circulation distribution which minimizes induced drag for a wing generating given lift. Although it is usually assumed to be the optimum for animal flight design, this assumption is untested, and appears to be incorrect: it is certainly too simple. Other loading distributions which maximize thrust for given weight, or minimize wing structural weight for given lift, may be preferable (Rayner 1986; Jones 1990). (Interestingly, elliptic loading is not the optimum (minimum induced drag) distribution for a fixed wing in ground effect (de Haller 1936).) However, a number of features make the elliptic loading solution the most straightforward for this analysis, and it is assumed throughout this paper; the results derived here are not formally correct for other lift distributions, but variation of the spanwise loading curve within reasonable limits has only a small effect on performance in ground effect, and the error probably falls within the range that would be resolved experimentally or observationally in animals.

From equation (6) the total lift across the full wingspan is calculated as

$$\boldsymbol{L} = 2\int_0^1 \rho V \Gamma(\eta)\, b\boldsymbol{k}\, \mathrm{d}\eta = \tfrac{1}{2}\pi\rho b V \Gamma_0 \boldsymbol{k}. \tag{8}$$

This result can be derived analogously by equating the lift force on the wing to the downwards rate of convection of air momentum by the vortex wake generated by the wings; the two quantities are identical. (At this point the reader should be reminded that the wake vortices are essential to flight, as without them there can be no lift; authors who write of the elimination of the wake vortices as a desirable means of saving energy in flight are mistaken. What is essential is generation of wake vortices that convect the appropriate momentum most 'efficiently', that is presumably with minimum energy or maximum safety factor.)

In steady level flight the lift force must balance weight $-Mg\boldsymbol{k}$, so that wing root circulation is determined as

$$\Gamma_0 = 2Mg/\pi\rho b V. \tag{9}$$

Lift acts vertically, perpendicular to the flight path, and no work is done against it in level flight. Work must be done against the drag force, which represents form, friction and pressure drags on the wings (profile drag) and body (parasite drag), and the energy cost of generating the wake vortices (induced drag).

(*b*) *Derivation of drag*

Induced drag is usually computed as the Joukowski force arising from the interaction between the bound wing vortex and the air velocity $\boldsymbol{u}_{\mathrm{i}}$ induced in the region of the wing by the wake vortices; this force is analogous to the lift, modelled in equation (6), generated by the interaction of the horizontal airstream $-V\boldsymbol{i}$ with the bound vortex. To calculate $\boldsymbol{u}_{\mathrm{i}}$ the vortex sheet and the bound vortex on the wing are decomposed into horseshoe vortices, each centred at the midpoint of the wing, and with span $2b\eta$ and circulation $-\mathrm{d}\Gamma = -(\mathrm{d}\Gamma/\mathrm{d}\eta)\,\mathrm{d}\eta$. (See figure 1 for notation and definition of reference axes.) Write $\boldsymbol{w}(\boldsymbol{p}, \boldsymbol{q}, b', \gamma)$ for the velocity induced at $\boldsymbol{p}$ by a horseshoe vortex centred at $\boldsymbol{q}$, of width b', and strength γ, and stretching to $-\infty$ along the $\boldsymbol{i}$ axis (the appropriate formulae for $\boldsymbol{w}$ are given in textbooks; see, for example, Milne-Thompson 1958, ex.IX.13). It is usual to model the wake vortices as a vortex sheet coplanar with the wing; in practice the sheet rolls up into a vortex pair, which convects downwards slowly under its self-induced velocity. For a straight, flat wing the induced downwash on the wing (and hence the induced drag) is computed equivalently from the rolled-up and convected vortex pair, or from the undeformed planar vortex sheet; the latter approach is normally used in lifting line theory, and is adopted here.

The total velocity induced at point $\boldsymbol{p} = (0, b\eta, h)$ on the wing is given by

$$\boldsymbol{u}_{\mathrm{i}}(\eta) = -\int_0^1 \boldsymbol{w}\left(\boldsymbol{p}, \boldsymbol{q}', b\eta', \frac{\mathrm{d}\Gamma}{\mathrm{d}\eta'}\mathrm{d}\eta'\right), \tag{10}$$

where $\boldsymbol{q}' = (0, 0, h)$. The integration is straightforward, provided care is taken with the singularity when $\eta' = \eta$, and leads to the familiar, and felicitous, result that with elliptic loading the induced velocity on the wing is vertically downwards and independent of position on the wingspan, and is given by

$$\boldsymbol{u}_{\mathrm{i}}(\eta) = -\Gamma_0 \boldsymbol{k}/4b. \tag{11}$$

At this point the formal derivation of lifting line theory usually proceeds with the assumption that circulation is unknown, and the Kutta condition is applied at the trailing edge of the wing to determine the circulation in terms of wing planform, flight speed V and the local pitch (or geometric angle of incidence) of the wing. This is not necessary here for I assume that the loading distribution is elliptic, and that an animal's elastic and deformable wing can in some way adjust to maintain this distribution. The details of this process need not concern us here, although departures from elliptic loading in ground effect may have a small additional effect on performance.

Induced drag can be expressed by analogy with equation (6) as

$$\delta \boldsymbol{D}_{\mathrm{i}} = \rho \boldsymbol{u}_{\mathrm{i}}(\eta)\cdot \boldsymbol{k}\Gamma(\eta)\,\boldsymbol{i}, \tag{12}$$

so that total induced drag is

$$\boldsymbol{D}_{\mathrm{i}} = 2\rho b \int_0^1 \boldsymbol{u}_{\mathrm{i}}(\eta)\cdot \boldsymbol{k}\Gamma(\eta)\,\boldsymbol{i}\,\mathrm{d}\eta = -\tfrac{1}{8}\pi\rho\Gamma_0^2\boldsymbol{i}. \tag{13}$$

Computation of the other components of drag is relatively straightforward; for fixed wings the sum of profile and parasite drags can be expressed in the form

$$\boldsymbol{D}_{\mathrm{p}} = -\tfrac{1}{2}\rho S C_{\mathrm{D}} V^2 \boldsymbol{i}, \tag{14}$$

where S is wing area, and C_{D} is a drag coefficient related to the shape of the body, the cross sectional profile of the wings and the shape of the wingtip. Any possible variation in C_{D} with speed (or Reynolds' number) is ignored here, as is any potential increase in the profile drag component of C_{D} with lift coefficient as a result of boundary layer thickening. In flapping flight the profile drag component of C_{D} must be modified to account for the movement of the wings relative to the body: see Pennycuick (1968) and Rayner (1979, 1986) for alternative treatments of this problem.

(*c*) *Derivation of performance curve*

The total drag acting on the animal can be computed as the sum of induced, parasite and profile drags from equations (13) and (14) as

$$D(V) = \tfrac{1}{8}\pi\rho\Gamma_0^2 + \tfrac{1}{2}\rho S C_{\mathrm{D}} V^2; \tag{15}$$

by substituting for Γ_0 from equation (9), drag can be expressed as a function of flight speed as

$$D(V) = [(M^2g^2)/(2\pi\rho b^2 V^2)] + \tfrac{1}{2}\rho S C_{\mathrm{D}} V^2. \tag{16}$$

The rate of working against drag DV is the mechanical power output $P(V)$ by the animal, and therefore

$$P(V) = DV = [(M^2g^2)/(2\pi\rho b^2 V)] + \tfrac{1}{2}\rho S C_{\mathrm{D}} V^3. \tag{17}$$

This equation is the basis of the familiar U-shaped mechanical power curve for a flying bird or bat, in which induced power varies with flight speed as V^{-1}, and profile and parasite powers rise as V^3. Equation (17) can be compared with equivalent formulae given for birds by, for instance, Pennycuick (1968) and Blake (1983, 1985), but as – like those models – it ignores the effect of wing flapping, it is equally applicable to fixed-wing low-speed aircraft. Deviations from elliptic loading are usually accommodated by introducing an additional parameter into the induced drag term, known as the Munk or Ostwald span efficiency; as this analysis is confined to elliptic loading, the span efficiency is identically unity, and so is omitted here.

From the power-speed curve it is usual to define the characteristic minimum power speed V_{mp} at which power is minimum ($\partial P/\partial V = 0$), and minimum cost speed $V_{\mathrm{m,c}}$ at which drag D or cost of transport P/MgV are minimum ($\partial D/\partial V = 0$). Strictly, V_{mc} should be the speed at which total metabolic power in flight is minimum, including heat generated by the flight muscles and the cost of basal metabolism. However, the difference in speed is slight, and for this analysis V_{mc} is to be understood as the speed at which mechanical drag is minimal, or, equivalently, at which the weight to drag ratio is maximal.

These characteristic speeds, the associated powers P_{mp} and P_{mc}, and the minimum cost of transport $C_{\mathrm{mc}} = P(V_{\mathrm{mc}})/MgV_{\mathrm{mc}}$ can be used to characterize the animal's flight performance. The minimum cost speed can be obtained by differentiation of equation (16) as

$$V_{\mathrm{mc}} = \sqrt{\{(Mg)/[\pi\rho b\sqrt{(SC_{\mathrm{D}}/\pi)}]\}}, \tag{18}$$

and the circulation and drag at this flight speed are obtained by substitution as

$$\Gamma_{\mathrm{mc}} = 2\sqrt{\{[Mg\sqrt{(SC_{\mathrm{D}}/\pi)}]/(\pi\rho b)\}}, \tag{19}$$

and

$$D_{\mathrm{mc}} = Mg\sqrt{(SC_{\mathrm{D}}/\pi)}/b. \tag{20}$$

It is convenient to use these values to normalize the drag–speed curve. Write $v = V/V_{\mathrm{mc}}$, $\gamma = \Gamma/\Gamma_{\mathrm{mc}}$ and $d = D/D_{\mathrm{mc}}$. Then the horizontal force balance in equation (15) becomes

$$d(v) = \tfrac{1}{2}\gamma(v)^2 + \tfrac{1}{2}v^2, \tag{21}$$

and the vertical force balance in equation (9) relating speed and circulation becomes

$$\gamma(v)\,v = 1; \tag{22}$$

non-dimensional mechanical power is given by

$$p(v) = \tfrac{1}{2}v^{-1} + \tfrac{1}{2}v^3. \tag{23}$$

It is useful to define a non-dimensional parameter c by

$$c = 2\sqrt{(C_{\mathrm{D}}/\pi A)}, \tag{24}$$

where $A = 4b^2/S$ is the aspect ratio, which measures the shape of the wings. From substitution in equation (20) the minimum drag becomes

$$D_{\mathrm{mc}} = Mgc, \tag{25}$$

so it can be seen that c is equivalent to the inverse of the maximum weight to drag ratio, or to the mechanical cost of transport for flight at V_{mc}. This parameter characterizes the entire effect of wing and body morphology on the non-dimensional solution for flight in ground effect.

4. THE LIFTING LINE IN GROUND EFFECT

As explained above, the change in flight performance when in ground effect is determined from the induced velocity resulting from the image vortex system. By analogy with equation (10) this is given by

$$\boldsymbol{u}_{\mathrm{i,i}}(\eta) = \int_0^1 \boldsymbol{w}\left(\boldsymbol{p}, \boldsymbol{q}'_{\mathrm{image}}, b\eta', \frac{\mathrm{d}\Gamma}{\mathrm{d}\eta'}\right)\mathrm{d}\eta', \tag{26}$$

where $\boldsymbol{q}'_{\mathrm{image}} = (0, 0, -h)$, and again $\boldsymbol{p} = (0, b\eta, h)$. I know of no analytical solutions to this integral. The

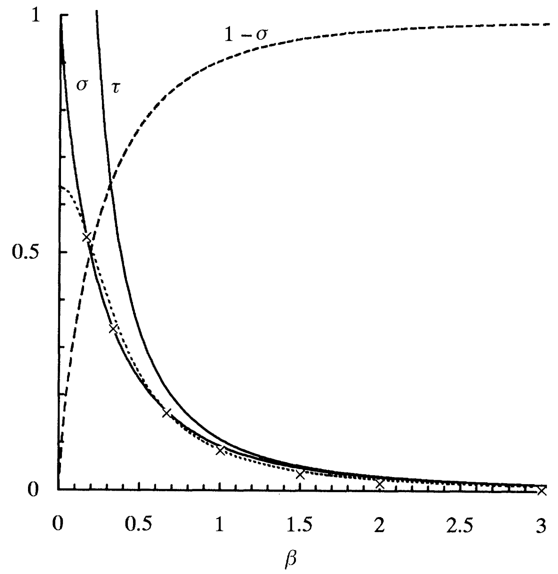

Figure 2. Computed ground effect interference coefficients σ and τ as a function of height/wing semispan $\beta = h/b$, from equations (30) and (31). Crosses mark the tabulated values of Reid (1932), after Prandtl (1919) and Wieselsberger (1921), and the light dashed line connecting them is Laitone's approximation (equation (5)), which is inaccurate for $\beta < 0.5$. The induced drag factor $D_{\mathrm{i,ge}}/D_{\mathrm{i}} = 1-\sigma$ is the ratio of induced drag in ground effect $D_{\mathrm{i,ge}}$ to induced drag in free flight D_{i}, and is shown as the heavy dashed line. Computations were performed on a Tandon 486sl microcomputer with programs in Microsoft Basic PDS 7.1 written by JMVR.

induced velocity is proportional to Γ_0/b, and otherwise depends only on $\beta = h/b$; it can be written as $\boldsymbol{u}_{\mathrm{i,j}}(\eta)\cdot\boldsymbol{i} = (\Gamma_0/b)\,g(\beta,\eta)$ and $\boldsymbol{u}_{\mathrm{i,j}}(\eta)\cdot\boldsymbol{k} = (\Gamma_0/b)f(\beta,\eta)$, where g and f are functions determined by numerical integration. It can be deduced from the sense of the induced velocities in figure 1 that both are positive for $|\eta| \leqslant 1$. The spanwise velocity component $\boldsymbol{u}_{\mathrm{i,i}}\cdot\boldsymbol{j}$ can be considerable on some parts of the wing at small values of β; although this may have some implications for the stability of the bound vortex, it can be ignored as it does not give rise to an induced drag force, being parallel to the bound wing vortex, and symmetric on the two halves of the wing.

The induced drag resulting from the imaging can be computed as

$$\boldsymbol{D}_{\mathrm{i,i}} = 2\rho b\int_0^1 [\boldsymbol{u}_{\mathrm{i,i}}(\eta)\cdot\boldsymbol{k}\;\boldsymbol{i} - \boldsymbol{u}_{\mathrm{i,i}}(\eta)\cdot\boldsymbol{i}\;\boldsymbol{k}]\,\Gamma(\eta)\,\mathrm{d}\eta, \tag{27}$$

or

$$\boldsymbol{D}_{\mathrm{i,i}}(\beta) = 2\rho\Gamma_0\int_0^1 [f(\beta,\eta)\,\boldsymbol{i} - g(\beta,\eta)\,\boldsymbol{k}]\,\Gamma(\eta)\,\mathrm{d}\eta; \tag{28}$$

this force acts forwards, reducing induced drag, and downwards, reducing lift. It can be normalized by the induced drag $D_{\mathrm{i}} = -\boldsymbol{D}_{\mathrm{i}}\cdot\boldsymbol{i}$ out of ground effect (equation (13)), and be written as

$$\boldsymbol{D}_{\mathrm{i,i}}(\beta)/D_{\mathrm{i}} = \sigma\boldsymbol{i} - \tau\boldsymbol{k}, \tag{29}$$

where σ and τ are functions of β alone, given by

$$\sigma = \frac{16}{\pi}\int_0^1 f(\beta,\eta)\,\frac{\Gamma(\eta)}{\Gamma_0}\,\mathrm{d}\eta, \tag{30}$$

and

$$\tau = \frac{16}{\pi}\int_0^1 g(\beta,\eta)\,\frac{\Gamma(\eta)}{\Gamma_0}\,\mathrm{d}\eta. \tag{31}$$

σ is the same as the quantity discussed above (equations (1)–(5)), the induced drag factor; τ is the equivalent quantity for the vertical force balance, and as will be demonstrated below can be viewed as a circulation factor. The variation of σ and τ with non-dimensional height β is shown in figure 2.

5. GROUND EFFECT AND FLIGHT PERFORMANCE

The effect of the ground on performance can readily be computed from σ and τ. The vertical force balance (equation (9)) becomes

$$Mg = \tfrac{1}{2}\pi\rho bV\Gamma_0 - \tfrac{1}{8}\pi\rho\tau\Gamma_0^2; \tag{32}$$

this implies that the animal must increase circulation Γ_0 (presumably by supinating the wing, to increase the local angle of incidence) to compensate for the reduced relative air stream past the wing caused by the image of the bound vortex. The horizontal force balance (equation (15)) becomes

$$D(V) = \tfrac{1}{8}\pi\rho\Gamma_0^2(1-\sigma) + \tfrac{1}{2}\rho SC_{\mathrm{D}}V^2. \tag{33}$$

In normalized form these may be written

$$1 = \gamma(v)\,v - \tfrac{1}{2}\tau c\gamma^2, \tag{34}$$

and

$$d(v) = \tfrac{1}{2}\gamma^2(1-\sigma) + \tfrac{1}{2}v^2. \tag{35}$$

The normalized solution depends only on non-dimensional height β and the cost of transport parameter c. The equations can be solved to give circulation as

$$\gamma(v) = [v - \surd(v^2 - 2\tau c)]/\tau c \tag{36}$$

(the negative branch of the square root is taken as γ must vary as v^{-1} when $\tau = 0$), and drag as

$$d_{\mathrm{ge}}(v) = [(v^2-\tau c) - v\surd(v^2-2\tau c)]\,(1-\sigma)/\tau^2c^2 + \tfrac{1}{2}v^2. \tag{37}$$

Mechanical power output for steady level flight in ground effect is obtained as $p_{\mathrm{ge}}(v) = d_{\mathrm{ge}}(v)\,v$.

To show how performance changes when in ground effect it is necessary to determine appropriate values of c (equation (24)). Aspect ratio in birds ranges from approximately 5 to 20, with an average around 8; most birds fall in the range 6.5–12, and few birds approach the upper end of the range (Rayner 1988). Aspect ratios in bats are slightly lower, falling in the range 5–12 (few species have $A > 10$), and averaging approximately 7 (Norberg & Rayner 1987). Estimation of total drag coefficient C_{D} is more problematical: reliable experimental data are scarce, and are completely lacking for bats and for smaller birds. Values of the order of 0.05 (based on wing planform area S) were estimated in flapping flight at cruising

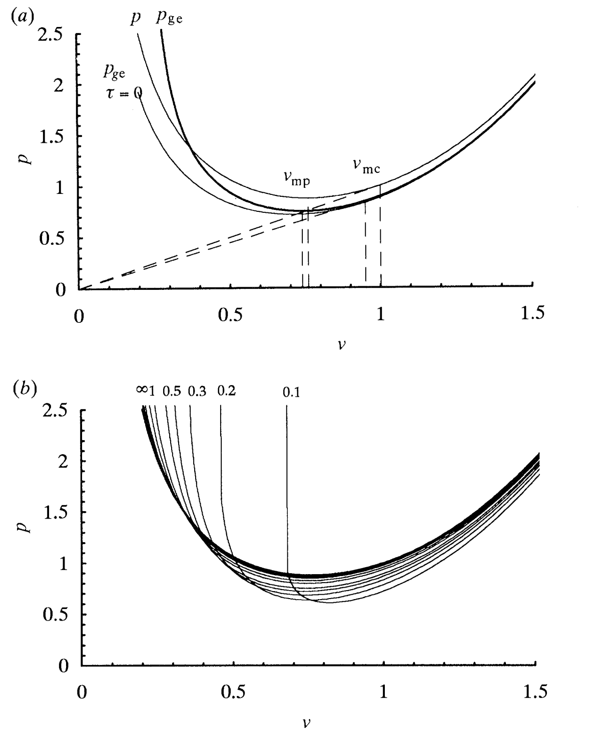

Figure 3. Non-dimensional mechanical power–speed curves for flight in ground effect. Flight speed, $v = V/V_{mc}$; mechanical flight power, $p = P/P_{mc}$ (*a*) performance for $\beta = 0.5$, $A = 8$, $C_D = 0.05$, i.e. $c = 0.089$. The curves shown are power out of ground effect p, in ground effect p_{ge}, and the erroneous values for flight in ground effect with τ ignored. Neglect of τ has little effect above v_{mp}, but at lower speeds greatly underestimates p. Characteristic flight speeds (indicated by the broken lines) decrease slightly in ground effect, and the corresponding power is reduced by some 15%. (*b*) the family of power curves for a range of values of $\beta = h/b$ (0.1, 0.2, 0.3, 0.4, 0.5, 0.75, 1.0, 1.5, 2, 3, ∞; ∞ corresponds to flight out of ground effect). As height decreases, power drops at higher speeds, but increases dramatically at lower speeds, with an accompanying dramatic rise in power below the minimum power speed v_{mp}. By controlling its height the animal could access the envelope of these power curves, thus obtaining a 25% reduction in total power at speeds between v_{mp} and v_{mc} if it can fly as low as $\beta = 0.2$. At greater distances from the surface ($\beta > 1$) a change in height has very little effect on performance, particularly at low speeds.

speeds by Rayner (1979); values for larger birds may be somewhat smaller, because of boundary layer transition, whereas values for the smallest birds and bats might be appreciably greater. However, C_D is unlikely to fall outside the range 0.03–0.08. This implies a median value of $c = 0.089$ ($A = 8$, $C_D = 0.05$), with an approximate extreme range of c from 0.06 to 0.14. The lowest (most economic) values correspond to higher aspect ratio and lower drag coefficients (i.e. greater streamlining). These values are consistent with estimates of mechanical cost of transport by Rayner (1979, 1990) and Norberg & Rayner (1987).

Figure 3 shows how ground effect modifies the non-dimensional mechanical power, $p_{ge} = d_{ge}\,v$, with the median value of c. Figure 3*a* illustrates performance curves out of ground effect, and in ground effect at height $\beta = 0.5$; the figure also shows the in-ground-effect curve with $\tau = 0$, to illustrate the influence of the horizontal component of the image induced flow (and the consequence of neglecting this quantity). Induced drag retains its approximately v^{-2} behaviour, at least unless τ is large, although this is not obvious from equation (37). At $\beta = 0.5$ there is a reduction in power p from 1 to 0.894 (10.6%) at the minimum cost speed $v = 1$, and a slightly greater saving of 14.3% from 0.877 $(= (\frac{2}{3})^{\frac{3}{4}})$ to 0.753 at the minimum power speed $v = (\frac{1}{3})^{\frac{1}{4}} = 0.760$. There are modest reductions (2.5 and 5.0% respectively) in the minimum power and minimum cost speeds, and by reducing speed by a factor of 0.95 the animal can maximize the reduction in cost of transport to 0.891 (10.9%). At speeds below v_{mp}, power p_{ge} rises sharply, and soon exceeds the power for flight out of ground effect.

As expected, performance savings in ground effect depend on height, and at heights below $\beta = 0.5$ the savings in power can be considerable: power at v_{mc} reduces by 24.3% at $\beta = 0.3$, and by 29.9% at $\beta = 0.2$, whereas the minimum costs of transport at these heights are reduced by 17.5% and 23.0% (figure 3*b*). These considerable savings underline the potential importance of ground effect as a source of energy savings in flight for animals which are able to take advantage of it. Note that, if the horizontal flow due to the image of the bound vortex were ignored ($\tau = 0$), it would be concluded erroneously that ground effect reduces power at all speeds. The effect of this error is confined mainly to speeds around or below v_{mp}; at speeds close to v_{mc} omission of the horizontal induced velocity modelled by τ has only a marginal effect.

The square root in equation (36) imposed the limit $v^2 - 2\tau c > 0$. This corresponds to the condition that the horizontal component of the image induced velocity $\boldsymbol{u}_{i,i}\cdot\boldsymbol{i}$ cannot exceed the forwards flight speed V; in fact the animal cannot approach close to this limit, because the wing would be likely to stall as the circulation γ increases sharply. This situation is potentially important at low flight speeds or very low flight heights. Approach to this limit is the explanation of the sharp increases in induced drag below v_{mp}, and these increases occur at progressively high speeds as the animal flies closer to the surface (figure 3*b*). Thus, animals are likely to avoid this situation, and it probably has little real biological significance. However, by varying its flight height an animal can access the (lower) envelope of a family of performance curves, and, if this effect is useful, it should fly closer to the surface at higher flight speeds.

This analysis also predicts that speed selection according to mechanical performance criteria may become more critical for an animal flying in ground effect, because as height falls the minimum of the mechanical power–speed curve becomes more pronounced, and there is only a limited range of speeds at which the lowest powers can be achieved. This may be particularly critical for bats feeding over water surfaces, for which low flight speed may increase the likelihood of detecting small, catchable prey items, but high speed can increase the area searched for prey in given time (Jones & Rayner 1991): at around or below the minimum power speed these animals may experience a

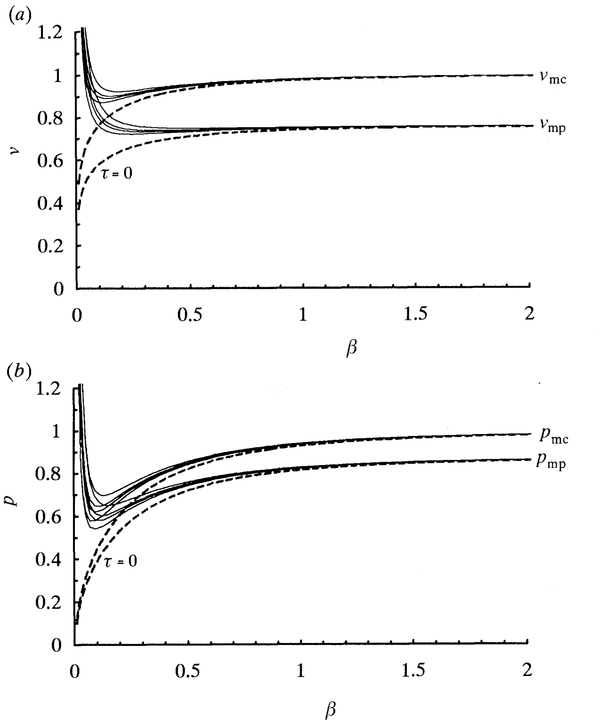

Figure 4. Characteristic non-dimensional flight (*a*) speeds v_{mp} and v_{mc} and (*b*) powers p_{mp} and p_{mc} for flight at varying height, with aspect ratio $A = 5$, 8, 10, 15 and $C_{\mathrm{D}} = 0.05$. In each group of curves the lower curves correspond to higher aspect ratios. There is a pronounced minimum in power for β in the range 0.08–0.12, which is lower than the heights accessed by animals; the minima for speeds are more shallow; that for minimum power speed v_{mp} falls in the same range as the power optima, but that for minimum cost speed v_{mc} is somewhat higher, decreasing from 0.52 at $A = 5$ to 0.29 at $A = 15$, and this matches the measured range for some birds and bats. The solutions out of ground effect are given by $v_{\mathrm{mc}} = p_{\mathrm{mc}} = 1$, $v_{\mathrm{mp}} = 0.760$, $p_{\mathrm{mp}} = 0.877$. The solutions with $\tau = 0$ are also shown: this (incorrect) model would predict that characteristic speed and power fall continually with decreasing height. $\beta = h/b$; $v = V/V_{\mathrm{mc}}$; $p = P/P_{\mathrm{mc}}$.

trade-off between being low, and therefore close to their prey, or being somewhat higher, and therefore flying more economically.

If an animal intends to fly economically in ground effect, it will presumably select flight speed by the same criteria as in free air (e.g. minimum activity time or energy, maximum net energy gain, or minimum cost of transport). The last of these is the most straightforward to define and calculate, and corresponds to the minimum $\partial d_{\mathrm{ge}}/\partial v = 0$. Out of ground effect the minimum occurs by definition at $v = 1$, $d = 1$. In ground effect the minimum cost speed v_{mc} is less than 1, so if this criterion is realistic, and if they are able to make the appropriate adjustments, birds and bats commuting in ground effect should reduce air speed compared with flight out of ground effect. (The prediction is not necessarily robust for foraging animals, for which other criteria may dictate speed (Jones & Rayner 1991).) I know of no reliable observations that might test this prediction. *Myotis daubentoni* foraging over water did fly more slowly than in free air (Jones & Rayner 1988), but the similar and closely related *Myotis adversus* did not (Jones & Rayner 1991); however, low speeds may occur also because of a change in their manner of prey location and capture (as described above). As height reduces both characteristic speeds, and the mechanical powers at those speeds, also reduce, down to a critical height (which depends on wing morphology); at lower heights the speeds and the associated powers both rise (figure 4). This implies that there is – at least theoretically – an optimum height at which the animal can fly most slowly and with least power. The optimum heights for minimizing flight power, cost of transport or commuting speed v_{mc} are generally very low, and in the range $\beta = 0.1$–0.2 (depending slightly on c), but the lowest minimum power speeds are obtained at $\beta = 0.3$–0.4; for median c the optimum β is 0.36 (falling to 0.24 if aspect ratio rises to 15), although the minimum is shallow (figure 4*a*). Typical flight heights for pelicans and skimmers in flapping flight are in the range $\beta = 0.4$–0.5 (Withers & Timko 1977; Hainsworth 1978), whereas myotid bats may fly lower, in the range 0.3–0.4 (Jones & Rayner 1991). The height for bats is fortuitously close to the optimum (although it would be unwise to believe the explanation is given this simply), but the values for birds are higher than predicted. There are several reasons why this is not surprising. A minimum height may be set by the need to avoid contact between the tips of the flapping wings and the water surface, and at very low heights circulation would be high, and the wing would risk stall (this last constraint may be more significant for birds than for bats, which with elastic and flexible wings are better adapted for slow flight or high lift conditions (Rayner 1986)). Moreover, the sharp rises in characteristic power and speed below the optimum height imply that at this height the animal would experience control problems in maintaining a steady height. Finally, the animal may simply benefit from flying at a modest height, to avoid the possibility of being trapped by predators, or to allow it to scan a wider area of the water surface for food.

6. ESTIMATION OF GROUND EFFECT PERFORMANCE

The following procedure summarizes the method of estimating the effect of the ground on flight performance.

1. Determine the appropriate height h over the surface, and the animal's wingspan $2b$, and from these determine the relative height $\beta = h/b$. Also compute the minimum drag to weight ratio c from equation (24). If in doubt the value 0.05 is probably the best currently available estimate of C_{D}; it is inadvisable to use drag values determined for isolated wings or wing–body combinations in wind tunnels, as these rarely mimic free flight conditions.

2. Use the value of β to determine the interference coefficients σ and τ, either by reading values from figure 2, or by evaluating equations (30) and (31) numerically.

3. Estimate the animal's flight performance in steady level flight in free air. This may comprise a prediction of minimum cost (maximum range) speed

V_{mc} and mechanical flight power $P_{\mathrm{mc}} = D_{\mathrm{mc}} V_{\mathrm{mc}}$ (for instance, from the multivariate allometric equations given by Norberg & Rayner (1987) and Rayner (1990), or from equations (18) and (20)), or a prediction of the mechanical power against speed curve for the appropriate range of speeds, derived from a theoretical model such as those of Pennycuick (1968, 1969, 1989), Tucker (1973), Greenewalt (1975) or Rayner (1979, 1986, 1992). Power should be measured as mechanical power, that is the rate of increase of the kinetic energy of the air, rather than total metabolic power. It would be inadvisable to use a metabolic power against speed curve determined for flight in a wind tunnel, as wind tunnels also give rise to wall interference problems akin to those in ground effect, and do not mimic conditions in steady, level, free flight. Either:

(4) If only minimum cost mechanical power and speed have been determined, the power against speed curve for free flight may be estimated from equation (23). The power curve for steady level flight in ground effect is obtained from equation (37) with the appropriate values of σ, τ and c. If speed is so low that $v^2 - 2\tau c < 0$, there is no solution, and flight is impossible.

Or:

(5) If a known mechanical power curve $P(V)$ is available, this may be corrected for the effect of the ground as

$$P'_{\mathrm{ge}}(V) = P'(V)\, d_{\mathrm{ge}}(v)/d(v), \tag{38}$$

where $d(v)$ is given by equation (23), and $d_{\mathrm{ge}}(v)$ by equation (37); $v = V/V'_{\mathrm{mc}}$, where V'_{mc} is the minimum cost speed for the known power curve $P'(V)$. Again care should be taken at low speeds, and if $v^2 - 2\tau c < 0$ there is no solution and flight is impossible.

(6) If an estimate of circulation is required, this may be obtained from equations (19) and (36). Mean lift coefficient can be estimated as $C_{\mathrm{L}} = \frac{1}{2}\pi c A \gamma_{\mathrm{ge}}(v)/v$.

7. DISCUSSION

This analysis has given rise to a number of predictions concerning ground effect, the most significant of which is that flight in ground effect provides performance improvements, provided that flight speed is not too low. This is at variance with previous models, which implicitly ignored the effect of the induced velocity due to the image wing. A number of other more detailed predictions may prove testable, provided experiments or observations of sufficient resolution, and with suitable controls for other influences on behaviour, can be determined: (i) an animal cannot fly very slowly in ground effect; (ii) for power or range economy an animal should reduce speed when commuting in ground effect; (iii) an animal should show less tendency to vary flight speed at any given height when in ground effect, particularly when it is flying slowly, at or around the minimum power speed; and (iv) when varying flight speed over a surface an animal should reduce height at higher flight speeds. This last prediction is perhaps the most easily tested, and is indeed supported by casual observations. Birds such as pelicans frequently commute by flying low over water, and there is no doubt that this behaviour is to exploit ground effect (Hainsworth 1988). Even if the birds aim to fly at minimum cost speed, for range economy, they should alter speed in response to wind. Thus, in a head wind they should increase air speed, and accordingly should reduce height to maximize the benefit of ground effect. By doing this they may also be flying into the wind's boundary layer, and would benefit from lower wind speeds.

In this paper I have treated primarily the aerodynamic consequences of ground effect, and predicted its influence on simple, readily defined characteristic performance measures. Other factors may dictate an animal's choice of flight height or flight behaviour, and may overlay – or indeed completely outweigh – aerodynamic factors. When close to a surface an animal may have less space in which to escape a potential aerial predator. It may be searching for food, and may be able to scan a broader area (albeit with perhaps less resolution) when flying higher. And in flapping flight the animal should avoid excessive contact between the wingtips and the water surface, particularly if such contact were liable to alert potential prey.

The analysis in this paper has been based on lifting line theory for a straight, fixed wing. The conclusions have been presented in the form of non-dimensional correction factors to circulation, speed, drag and power, and it seems reasonable to propose that these factors might be applied with acceptable accuracy to estimates of performance from more realistic models derived with other assumptions, and perhaps including the aerodynamic effects of wing flapping. In the absence of a theory of ground effect wake interactions for a three-dimensional flapping wing there seems to be no alternative to this suggestion. The main predictions outlined above are likely to remain qualitatively correct, even if the precise numerical values are not appropriate. Other limitations may be more significant. It is recognized that the lifting line ground effect model may become inaccurate at very low heights, as the wing cannot retain a sensible circulation distribution in the presence of the image induced flows (see, for example, Küchemann 1978), and because the boundary layer flow induced on the upper surface of the ground plane may be unstable and may separate unsteadily in some ranges of Reynolds' number (see, for example, Harvey & Perry 1971; Doligalski & Walker 1984; Ersoy & Walker 1985; Walker *et al.* 1987). Lifting surface theory (see, for example, Hummel 1973) can resolve some of these problems, but its predictions do not differ materially from those of lifting line theory in the likely biological range of heights. At very low heights, or for very low aspect ratios (< 5), neither of these models is appropriate, and it is usually necessary to use an asymptotic or conformal mapping solution (Widnall & Burrows 1970; Kida & Miyai 1973; Newman 1982; Tuck 1983).

Potentially the most serious limitation to this model of ground effect is its neglect of wing flapping. This produces two separate problems that are not formally treated correctly. Profile drag should include the additional work done against the relative air flows in flapping, as well as in forwards translation; this effect was nominally included by enhancing the value of C_D to allow for the additional drag force (following Rayner 1979), but as wingbeat kinematics change with flight speed, it is unlikely that profile drag will remain proportional to v^2. Perhaps more important is the neglect of the enhanced induced drag reflecting thrust generation in addition to weight support; to generate thrust the vortex wake elements cannot lie at a constant distance from the surface at all times of the wingbeat. This problem has implicitly been treated here by taking mean values of σ and τ corresponding to the mean height of the body, but as induced velocities do not vary linearly with height this procedure may appreciably underestimate the interference coefficients when the animal is flying very close to the surface. This problem can be resolved only with a complete theory modelling the three-dimensional wake of the animal and the temporal and spatial variation of the induced air flows. The reason for its significance is that if, at the bottom of the downstroke, the wingtip is close to the surface, it is also close to its image vortex, and therefore the induced flows are large; the wingtip may stall if the horizontal induced velocity approaches flight speed, or it may be necessary to alter circulation dramatically; even if lift can be sustained on the distal part of the wing, induced drag from that segment of the wing may be large for short periods. There is some evidence that animals flying in ground effect attempt to avoid these problems. Pelicans gliding over water fly at a much lower altitude ($\beta = 0.31$) than when they are flapping ($\beta = 0.50$) (Hainsworth 1988). Skimmers (Withers & Timko 1977) and myotid bats (Aldridge 1987) adopt an asymmetric wingbeat in which the downwards excursion of the wing below the body has a much lower amplitude than the upper half of the wingbeat. However, skimmers do occasionally allow their wingtips to touch the water (Withers & Timko 1977), so the effect may not always be significantly detrimental.

It is helpful to ask if there is any sensible morphological design for making best use of ground effect. The calculations reported here show a weak variation of the solution with aspect ratio, over the range typical for birds and bats, although some of this variation may be masked by our ignorance of the appropriate values for the total drag coefficient. By every measure higher aspect ratio wings and streamlined bodies are favoured, allowing not only lower absolute power and cost of transport (Norberg & Rayner 1987; Rayner 1979, 1988, 1990), but also greater potential relative savings from flight at the same height. Further, when aspect ratio is low, the minima of the power–speed curves become very acute at low height, making slow flight in ground effect virtually impossible. Most animals that fly in ground effect have relatively high aspect ratios: for instance, some of the highest aspect ratios in microchiropteran bats are found in Noctilionae (Norberg & Rayner 1987), and the *Leuconoë* myotids generally have higher aspect ratios than other non-trawling myotids (Norberg & Rayner 1987). Skimmers (Rhynchopidae), like their close relatives the gulls, have large, high aspect ratio wings. (Flying fish (Exocoetidae) also have high aspect ratio 'wings' or pectoral fins.) However, caution is needed before associating these observations with the theoretical predictions. High aspect ratio (i.e. long) wings may increase the likelihood of the ground interference problems discussed above, but are generally favoured for most flying vertebrate lifestyles, and it is features of the habitat which have dictated the evolution of shorter, and aerodynamically inefficient, wings (Rayner 1988). These constraints are likely to be less acute in the marine birds for which habitual use of ground effect is most common.

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