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AERODYNAMICS AND HYDRODYNAMICS OF THE 'HOVERING' FLIGHT OF WILSON'S STORM PETREL

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SUMMARY

Wilson's storm petrel (*Oceanites oceanicus*) characteristically feeds by 'hovering' over the water surface, but its technique for this is unlike that of other flying vertebrates. The kinematics and aerodynamics of this 'hovering' flight were investigated to determine the possible sources of lift; various non-aerodynamic sources of lift were discounted. It is suggested that the storm petrel soars into an ambient, horizontal wind, and thus is not hovering in the usual sense. Such soaring into a horizontal wind is only possible if some thrust component counteracts the bird's aerodynamic drag, and it is shown that the hydrodynamic drag of the feet through the water is adequate to balance aerodynamic drag. The bird is thus analagous to a kite, where the tension in the string counterbalances the aerodynamic drag of the kite.

The movements of the storm petrel's wings during 'hovering' suggest that the bird may use the wing-flip mechanism for generation of high lift coefficients (Weis-Fogh, 1973, 1976). Such high lift coefficients are required for the bird to 'hover' under calm conditions, when ambient wind velocity is less than 5 m s^{-1}. Use of the wing-flip mechanism would enable the bird to 'hover' at lower ambient wind velocities. Ground effect also contributes to the bird's ability to 'hover'.

This analysis of the flight behaviour of Wilson's storm petrel indicates that its 'hovering' is an energetically inexpensive foraging stragegy which is probably available only to small, surface-feeding birds with low wing-loading.

INTRODUCTION

Wilson's storm petrel, or Mother Carey's chicken (*Oceanites oceanicus* Kuhl 1820), is a widespread, common, oceanic bird which, like other storm petrels (Hydrobatidae; Procellariiformes), feed on surface plankton, oil, small fish, squid and debris. The birds characteristically 'flutter' or 'hover' over the water surface while feeding (Roberts, 1940; Watson, 1966). Indeed, the common name, petrel, is presumably derived from the biblical account of St Peter's attempt to walk on water,

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because of the illusion of the storm petrel's 'walking on water' while feeding (Serventy, Serventy & Warham, 1971).

The 'hovering' flight of Wilson's storm petrel is unique among flying vertebrates because the flight actions are unlike the normal hovering, or slow forward flight, of other birds. The birds patter their feet on the water surface, with wings fully extended, or held almost motionless over the back to form a dihedral (Roberts, 1940; Serventy *et al.* 1971). It is well known that many birds soar by utilizing updraft from waves, slopes or thermals. Soaring or gliding has a lower metabolic cost than flapping flight (Baudinette & Schmidt-Nielsen, 1974). However, the flight pattern of Wilson's storm petrel, while feeding, appears to be unlike the typical soaring patterns of other birds.

In view of this unique form of flying or 'hovering' by Wilson's storm petrel, I have undertaken an aerodynamic and hydrodynamic study to evaluate the various source(s) of lift. The possible mechanisms for lift generation considered here include conventional and novel aerodynamics, and hydrodynamic lift derived from surface tension, impact loading of the water by 'pattering' the feet on the surface, and use of the feet as parachutes when they are submerged.

METHODS

Body mass and wing span of Wilson's storm petrel were obtained from Roberts (1940), and additional data for wing span and wing area were measured for a specimen in the Transvaal Museum.

A 16 frame s^{-1} cine film of Wilson's storm petrel 'hovering' under calm conditions was made available to me from the D. R. Dickey Film Collection (Biology Department, U.C.L.A.). Wing and leg movements during hovering flight were studied using a frame-by-frame film analyser.

The various power requirements for flapping flight (induced, parasite, and profile powers) were estimated for Wilson's storm petrel using the equations of Tucker (1973) and Pennycuick (1969, 1975). It was necessary to take ground effect into account because of the proximity of the storm petrel to the water surface during feeding (see Withers & Timko, 1977).

The sink angle (θ) for a gliding storm petrel was calculated as $\theta = 90 - \arctan (L/D)$, and sink velocity ($V_s$) was calculated as $V_s = V \tan \theta$, where L is lift (= body weight), D is drag and V is the ambient wind velocity (Pennycuick, 1972).

The lift generated by a wing was calculated as $L = \frac{1}{2}\rho V^2 SC_L$, where L is lift (Newtons), ρ is air density (1·18 kg m^{-3}), S is the projected wing area (m^2) and C_L is the lift coefficient. The value of C_L is probably maximum at about 1·5, assuming conventional aerodynamics, but C_L of 3 or more are possible if novel mechanisms for lift mechanism are used (Weis-Fogh, 1973, 1976).

The drag force acting on a body submersed in water is calculated as, $D = \frac{1}{2}\rho V^2 AC_D$ where D is the drag (Newtons), ρ is the water density (about 1025 kg m^{-3} for sea water), V is the velocity (m s^{-1}), A is the projected area (m^2) and C_D is the drag coefficient. For a disc, C_D is approximately 1·2 (Granet, 1971).

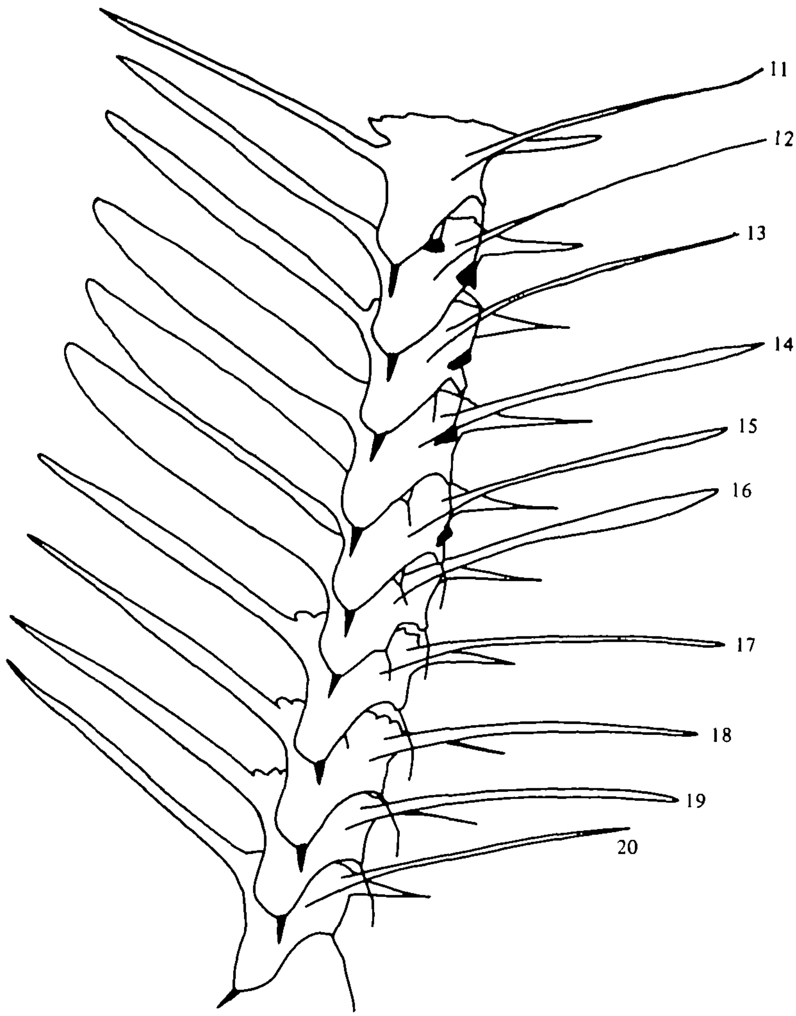

Fig. 1. Kinematics of hovering flight of Wilson's storm petrel during 'hovering'. Numbers indicate successive frame numbers (1 frame = $\frac{1}{16}$ s).

RESULTS

The average body mass of Wilson's storm petrel is 0·034 kg, wing length is 0·15 m, wing span is 0·40 m (Roberts, 1940; Stokes, 1963; Murphy, 1936; Watson, 1966). Wing span of the specimen examined at the Transvaal Museum was 0·395 m; wing area was 0·0174 m^2; wing disc area ($\frac{1}{4}\pi$ span^2) was 0·123 m^2. Hence, wing loading (weight/wing area) was 19·3 N m^{-2} and aspect ratio (AR = span^2/wing area) was 9·0. These morphometric data are compared in Table 1 with other values for *O. oceanicus* (Warham, 1977), with predicted values for *O. oceanicus* using the models of Greenewalt (1975), and with data for other storm petrels (Ainley, Morrel & Lewis, 1974). Wilson's storm petrel has a higher aspect ratio, and lower wing loading and wing disc loading, than predicted, but is similar to other storm petrels.

The wing movements of a Wilson's storm petrel during hovering are shown in

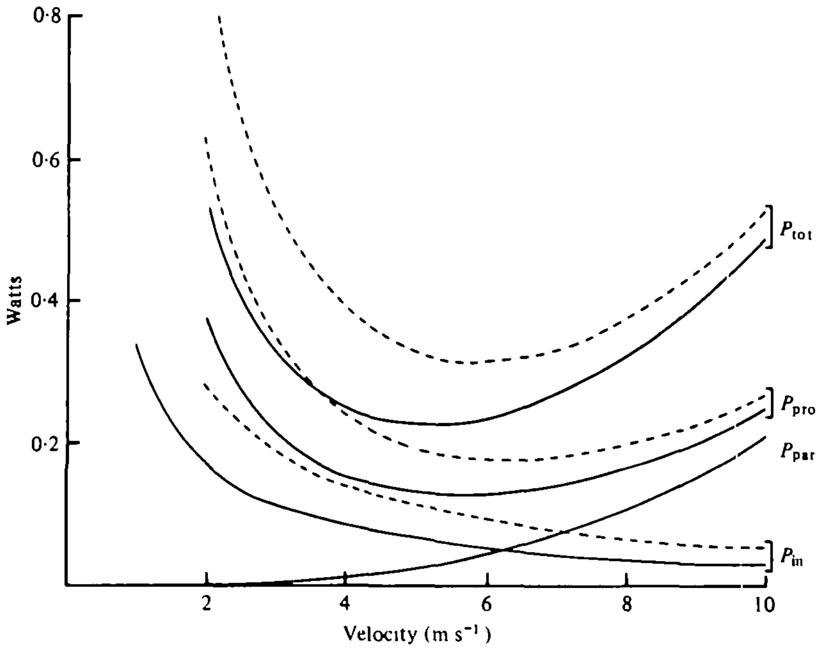

Fig. 2. Total aerodynamic power requirement (P_{tot}), profile power (P_{pro}), parasite power (P_{par}) and induced power (P_{in}) of a Wilson's storm petrel at different relative air velocities. Broken line is for absence of ground effect, solid line is with ground effect (σ = 0·4). All values were calculated after Tucker (1973).

Fig. 1. The storm petrel showed virtually no movement of the wings in either a vertical or horizontal plane, in marked contrast to other hovering birds which sweep out almost the entire wing disc area. The storm petrel showed rapid pronation and supination of the wings, with pronation occurring over 2·5 frames, and supination over 3·5 frames.

The storm petrel held its legs almost vertically while hovering, with the feet held either above or below the water surface. Some slight flexion and extension movements of the legs were noted. The petrel moves down slightly relative to the water surface during the film sequence, as can be seen from the disappearance of the feet (Fig. 1).

The aerodynamic analyses after Tucker (1973) and Pennycuick (1969, 1975) yield qualitatively similar results, but differ quantitatively primarily because of differences in estimating profile power. The results using Tucker's analyses are presented in Fig. 2, for the absence of ground effect (interference coefficient σ = 0) and with a gap/span ratio of 0·2 (σ = 0·4).

Ambient wind has a significant effect upon the generation of lift. An upward-directed wind can support a soaring bird and allow it to remain motionless with respect to the ground. A horizontal wind, such as would be encountered by a storm petrel over calm water or in troughs between waves, cannot maintain the bird motionless, as the bird must either decrease in altitude to overcome its aerodynamic drag, or else somehow accelerate in the direction of the wind. The former situation is apparent from the glide polar of Wilson's storm petrel (Fig. 3) where the sink velocity is always negative, with the lowest rate of sink being 0·9 m s^{-1} at an ambient wind velocity of about 5 m s^{-1}.

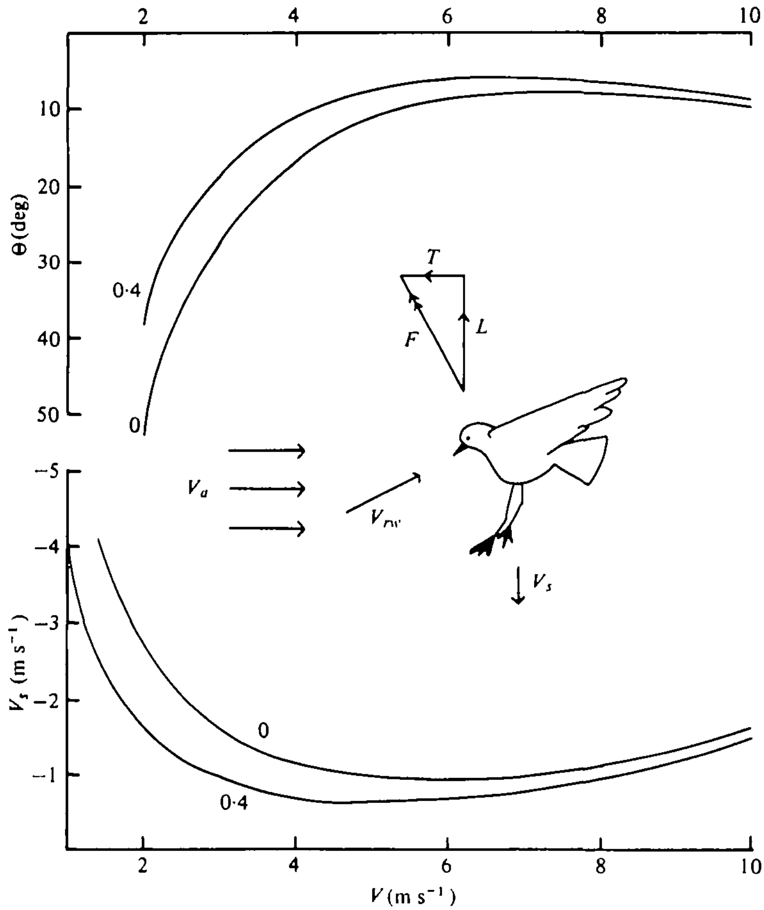

Fig. 3. Sink angle (θ) and sink velocity (V_s) of a Wilson's storm petrel at different relative wind velocities. Insert shows forces acting on bird during gliding; L is lift, T is thrust, F is aerodynamic force, V_a is ambient wind velocity, V_{rw} is relative wind velocity. Curves are for ground effect interference coefficients of 0 and 0·4.

However, storm petrels may soar into a horizontal wind if the feet provide sufficient hydrodynamic drag to counteract the bird's aerodynamic drag. If each foot of the petrel was 0·0004 m^2 in area, then the required velocities for the feet to move through the water to neutralize aerodynamic drag ($V = (2D/\rho AC_D)^{\frac{1}{2}}$) are much lower than the relative wind speed (Fig. 4). Calculations of the rate of change in velocity of a bird simply holding its feet in the water, and starting at zero initial velocity with respect to the water, indicate that the bird rapidly (within 1 s) attains its terminal velocity.

DISCUSSION

The flight behaviour of Wilson's storm petrel in normal forward flight is to 'dip and rise with the undulations of the sea' (Roberts, 1940), and they are probably slope soaring off the wave surfaces. The feet are lowered only during feeding and appear to 'patter' on the water surface, with both feet lowered three or four times in

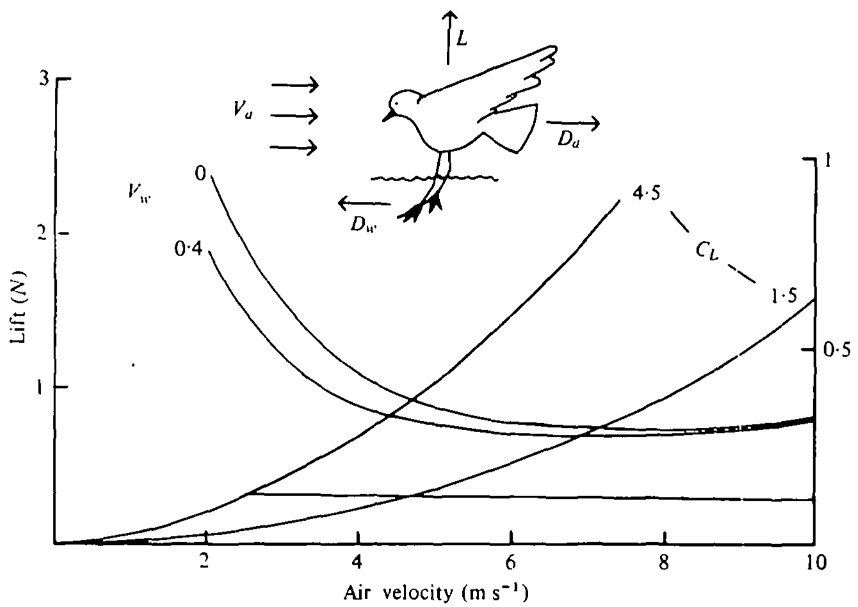

Fig. 4. Lift generated by Wilson's storm petrel at differing relative wind velocities with lift coefficients (C_L) of 1·5 and 4·0, and the velocity at which the feet must move through the water (V_w) for their hydrodynamic drag to equal the aerodynamic drag. Inset shows forces acting on bird while 'hovering' with feet submerged; L is lift, D_a is aerodynamic drag, D_w is drag of the feet in water, V_a is the relative wind velocity. Horizontal line shows lift = body weight.

quick succession (Roberts, 1940). During feeding the wings are held almost motionless, either to the sides or over the back to form a dihedral (Serventy *et al.* 1971). The birds feed almost exclusively in this manner; they rarely settle on the water or dive to obtain food (Roberts, 1940). When feeding, the storm petrels appear to orientate themselves in the same general direction (see plate 4 of Roberts, 1940), probably to face into the ambient wind.

Strong wind conditions make it difficult for the birds to fly, presumably because of their very low wing-loading, and the birds seek shelter in the wave troughs where there is relatively calm air (Roberts, 1940). Holding the wings in a dihedral probably assists stability under such conditions. In the strongest winds the petrels appear to feed by slope-soaring a few inches above the windward wave slopes (Roberts, 1940).

Direct observations of Wilson's storm petrel, and kinematic analysis (Fig. 1), suggest that the bird can 'hover' over calm water when feeding. However, the wing movements while feeding are unlike those of other hovering vertebrates, and consequently the mechanism(s) for 'hovering' may be unique. Alternative methods of lift generation to flapping flight and conventional aerodynamics include:

(1) water surface tension acting on the feet;
(2) impact loading of the water surface by the feet;
(3) retardation of the bird's sink rate by 'parachuting' on its feet;
(4) use of ambient wind to soar like a kite;
(5) novel mechanisms for generation of aerodynamic lift (Weis-Fogh, 1973).

Surface tension. The surface tension of water at 20 °C is 0·074 N m^{-1} (Walshaw & Dobson, 1972). The surface tension acting on the storm petrel's feet, even assuming that each foot has a circumference of 0·1 m, is only 0·02 N (4% of the bird's weight). Furthermore, the feet are often totally submerged, and the surface tension of the legs would be negligible.

Impact loading. Considerable forces can be generated through impact loading of water. Watanabe (1933) demonstrated that the magnitude of the impact force of discs was dependent upon the mass and the impact velocity, and that the impact force could considerably exceed the weight. A storm petrel impacting with the water surface at 0·1 m s^{-1} would experience a force of perhaps 0·01 N (3% body weight) (calculated from equations of Watanabe, 1933). Large impact forces at high impact velocity could not, however, assist the petrel in hovering. The petrels probably never impact with the water surface at velocities as great as 0·1 m s^{-1}, when the impact force is only 3% of body weight. The petrels do not appear, while hovering, to vigorously patter their feet on the water surface, and the feet are often totally submerged. The legs of storm petrels are ill-suited to sustaining even moderate forces and the birds have considerable difficulty in walking on land; the wings are used to assist their clumsy attempts at walking (Roberts, 1940). Furthermore, impact forces are of short duration, and a quickly falling object such as a storm petrel would fall rapidly through the water surface (unpublished observations).

Soaring. The glide polar of Wilson's storm petrel demonstrates that the minimum sink velocity (about 0·9 m s^{-1}; Fig. 4) is too great for the bird to remain at the water surface for a significant period of time while sinking in a conventional glide, into a horizontal wind.

The petrels could slope soar under strong wind conditions, but cannot slope soar under calm conditions when there are essentially no wave slopes. It is possible for a bird to remain stationary in a horizontal wind if there is some thrust component which can counteract its aerodynamic drag. Otherwise, the bird loses relative wind velocity, its capacity to generate lift diminishes, and it must eventually sink to prevent stall. Wilson's storm petrel could move its feet through the water at much lower velocities (0·3–0·5 m s^{-1}) than the wind velocity required for lift = weight and generate sufficient hydrodynamic drag to counteract its aerodynamic drag. The storm petrel is analogous to a child's kite; whereas the child and the string provide the tension to balance aerodynamic drag, the storm petrel uses its feet as 'anchors'.

The storm petrel could paddle its feet at the required velocity and remain stationary with respect to the water surface; it could allow itself to be moved across the water surface at velocities of 0·3–0·5 m s^{-1}; or it could use any intermediate between these two choices. Looking for food items while being blown passively across the water surface could be a suitable foraging strategy for the storm petrel, since the metabolic cost of gliding is considerably lower than the cost of flapping flight (Baudinette & Schmidt-Nielsen, 1974). When the petrel must be stationary in order to pick up a food item, it could either paddle its feet to be stationary, or alter its wing posture and go into a conventional glide, thereby becoming stationary and also automatically dropping onto the food item.

The storm petrel would have to soar into an ambient wind of about 5 m s^{-1} to obtain sufficient lift, according to conventional aerodynamic theory (Fig. 5). However, it is unlikely that storm petrels are restricted from hovering under ambient wind velocities less than 5 m s^{-1} since they can do so under quite calm conditions. There

Table 1. *Morphometrics of Wilson's storm petrel*

(Values from text, Warham, 1977 (*a*), values predicted from Greenewalt, 1975 (*b*), and values for other storm petrels from Ainley *et al.* 1974 (*c*).)

	Body mass (kg)	Wing span (m)	Wing area (m^2)	Wing disc area (m^2)	Wing loading ($N\ m^{-2}$)	Wing disc loading ($N\ m^{-2}$)	Aspect ratio
Wilson's storm petrel (text)	0·034	0·40	0·017	0·12	19·3	2·7	9·0
Wilson's storm petrel (*a*)	0·039	—	0·015	—	26	—	—
Shore-bird model (*b*)	0·034	0·30	0·012	0·08	28	4·2	4·9
Passerine model (*b*)	0·034	0·32	0·015	0·08	22	4·2	6·8
Ashy petrel (*c*)	0·040	—	0·019	—	20	—	—
Leaches petrel (*c*)	0·042	—	0·024	—	17	—	—

are no pertinent data at present to test this hypothesis, but the birds are not necessarily limited to the use of conventional aerodynamics.

Novel lift mechanisms. There are two novel mechanisms – the wing clap and the wing flip, which result in greater lift coefficients than are possible from conventional aerodynamics (Weis-Fogh, 1973, 1976). There is no indication that storm petrels use any mechanism analogous to the wing clap. However, the kinematic study provides some evidence for the wing flip. Wing flip occurs when a wing twists (i.e. pronates) from the base of the wing towards the tip. This motion induces circulation around the wing and results in unusually high lift coefficients. Wing flip may also confer great manoeuvrability through slight variation in the path of the wing tips (Weis-Fogh, 1973). Weis-Fogh (1973, 1976) demonstrated the probable use of wing flip by syrphid and aeschnid insects, and suggested that other insects and vertebrates (such as kestrels and petrels) with low wing loading might also benefit from wing flip. Wilson's storm petrel is very lightly loaded compared to predictions for either passerines or shore-birds of the same body mass (Table 1). The kinematic analysis (Fig. 1) demonstrates that the wing movements of Wilson's storm petrel during 'hovering' are dissimilar to those of other flying vertebrates, and that there is a rapid pronation/supination of the wings.

The cine film, however, did not have sufficient time resolution to demonstrate a basic requirement for wing flip – delayed elasticity. During pronation the leading edge of the wing must twist, and the trailing edge remains stationary as the twisting progresses from the wing base to the tip (Weis-Fogh, 1973). High-speed photography (200–400 frames s^{-1}) should be able to resolve whether there is delayed elasticity in large wings, such as those of storm petrels.

Although the wing flip establishes a useful, anterior vortex which is bound to the wing, there must be some translational movement of the wing for shedding the posterior vortex. Wilson's storm petrel, if it does use wing flip, must obtain the translational velocity from the ambient wind, as there are no significant movements of the wings themselves. This is in contrast to the insects which have pronounced translational wing movements, with wing flip superimposed on this motion (Weis-Fogh, 1973, 1976).

Ground effect diminishes the bird's aerodynamic drag, particularly at low wind velocities (Fig. 3), and consequently decreases the velocity at which the feet must move through the water to balance aerodynamic drag (Fig. 5). Ground effect does not alter the lift generated by the wings (Reid, 1932).

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