FLIGHT OF AUKS (ALCIDAE) AND OTHER NORTHERN SEABIRDS COMPARED WITH SOUTHERN PROCELLARIIFORMES: ORNITHODOLITE OBSERVATIONS

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SUMMARY

Airspeeds in flapping and flap-gliding flight were measured at Foula, Shetland for three species of auks (Alcidae), three gulls (Laridae), two skuas (Stercorariidae), the fulmar (Procellariidae), the gannet (Sulidae) and the shag (Phalacrocoracidae). The airspeed distributions were consistent with calculated speeds for minimum power and maximum range, except that observed speeds in the shag were unexpectedly low in relation to the calculated speeds. This is attributed to scale effects that cause the shag to have insufficient muscle power to fly much faster than its minimum power speed. The wing adaptations seen in different species are considered as deviations from a 'procellariiform standard', which produce separate effects on flapping and gliding speeds. Procellariiformes and the gannet flap-glide in cruising flight, but birds that swim with their wings do not, because their gliding speeds are too high in relation to their flapping speeds. Other species in the sample also do not flap-glide, but the reason is that their gliding speeds are too low in relation to their flapping speeds.

INTRODUCTION

This paper records ornithodolite observations of flight speeds in 11 seabird species, comprising several different adaptive types. They are compared with earlier observations (Pennycuick, 1982*b*) on a set of procellariiform species, which covered a wider range of body mass, but were more homogeneous in other ways. The species in the present set can be seen as deviating from a 'procellariiform standard', in various ways, which affect their flight performance and style of flight.

Study area

Flight speed measurements were made between 28 June and 9 July 1986 on the island of Foula, in Shetland. Foula is an isolated island of about 12 km² projected area, centred at 60°08′ N, 2°04′ W, about 24 km west of the main island of Shetland, and noted for its concentrations of breeding seabirds. A detailed account of its birds, and the status of their populations in recent years, has been compiled by Furness

(1983). Most flight observations were made from the southern tip of the island, where continuous streams of birds could usually be seen flying around the South Ness, between the main breeding areas on the western cliffs and feeding areas to the east.

MATERIALS AND METHODS

Body measurements

The body masses of Shetland birds listed in Table 2 are means for breeding adults, weighed during July over a period of years, and kindly supplied by Dr R. W. Furness (personal communication). The number in each sample is listed as n_m. The gannet mass is from means of breeding adults weighed at the Bass Rock and Ailsa Craig by Nelson (1978). The masses for South Georgia birds are means for breeding adults, published by Croxall & Prince (1980). Wing measurements were taken by the author, the number in each sample being listed as n_w. The measurements of Shetland birds were collected during a visit to Fair Isle, Shetland, in 1975, except for five great skuas measured on Foula during the present study. Those of South Georgia birds were collected on Bird Island, South Georgia in 1979–1980.

Flight speed measurements

Flight speeds were measured by ornithodolite. The instrument and method of operation were essentially the same as described by Pennycuick (1982a,b, 1983). The same 'Mariner 1' anemometer set was used as on previous occasions, mounted on a pole 2·8 m above ground. A 'run' consisted of a series of timed, three-dimensional positions of the bird in space, and a speed 'observation' was obtained by comparing each two successive positions. The Nascom 1 computer, originally used to control the instrument, was replaced by an Epson PX8 battery-powered computer, connected via a home-made parallel interface. After each run, the bird's groundspeed, track direction, airspeed, heading, height and vertical speed were calculated and displayed immediately on the PX8's liquid crystal display. Two BASIC programs, incorporating machine-code routines to control the ornithodolite, were used, one for aligning and testing the instrument, and the other for acquiring and recording data. The raw ornithodolite data (not computed speeds etc.) were recorded as a tape file on the PX8's built-in microcassette recorder. On return to the laboratory, the tape files were transferred from the PX8 to disc files on a Nascom 2 computer. All subsequent analysis was done by BASIC programs on the Nascom 2.

RESULTS

The species on which new flight observations are reported are listed in Table 1, with two-letter identifiers which are used in subsequent tables and graphs. This is to distinguish them from South Georgia seabird species reported on by Pennycuick (1982b), which are also listed in Table 1, with the three-letter identifiers used in the earlier publication. Some additional South Georgia species, not covered in the earlier

paper, are included in Table 1. Table 2 shows morphological data for the same set of species, classified into three functional groups. Measurements of observed and calculated speeds, and other quantities derived from these, are listed for the Shetland species in Table 3.

Reynolds number and parasite drag

The 'mean flapping speed' (V_{mf} in Table 3) for each species is the mean airspeed for observations in which the bird was either flapping or flap-gliding. Reynolds numbers, based on this speed, are listed in Table 3 for the body and the wing. The body Reynolds number is based on the diameter of a circle whose area is the same as the maximum cross-sectional area of the body, which is itself estimated from the mass as indicated by Pennycuick (1975). The wing Reynolds number is based on the mean chord. Body Reynolds numbers ranged from 61 000 (kittiwake) to 127 000 (gannet), and wing Reynolds numbers from 77 100 (razorbill) to 161 000 (great skua, great black-backed gull, shag).

To estimate the speeds for minimum power and maximum range (V_{mp} and V_{mr}) an estimate is needed for the drag coefficient of the body, in order to calculate its effective flat-plate area. Prior (1984) reported from wind tunnel measurements that the drag coefficients of the bodies of ducks, geese and swans declined as Reynolds number increased through the range observed here, levelling off at about 0·2 (or a

Table 1. *Species codes used in subsequent tables and figures*

Foula birds (present study)

Fa	Puffin	*Fratercula arctica*
Ua	Guillemot	*Uria aalge*
At	Razorbill	*Alca torda*
Cs	Great skua	*Catharacta skua*
Sp	Arctic skua	*Stercorarius parasiticus*
Rt	Kittiwake	*Rissa tridactyla*
Lm	Great black-backed gull	*Larus marinus*
La	Herring gull	*Larus argentatus*
Fg	Fulmar	*Fulmarus glacialis*
Mb	Gannet	*Morus bassanus*
Pa	Shag	*Phalacrocorax aristotelis*

South Georgia birds (from Pennycuick, 1982*b*)

WAN	Wandering albatross	*Diomedea exulans*
BBA	Black-browed albatross	*Diomedea melanophris*
GHA	Grey-headed albatross	*Diomedea chrysostoma*
STY	Sooty albatross	*Phoebetria palpebrata*
MAC	Giant petrel	*Macronectes giganteus/M. halli*
WCP	White-chinned petrel	*Procellaria aequinoctialis*
CAP	Cape pigeon	*Daption capensis*
PRN	Dove prion	*Pachyptila desolata*
WIL	Wilson's storm petrel	*Oceanites oceanicus*
SDP	S. Georgia diving petrel	*Pelecanoides georgicus*
CDP	Common diving petrel	*Pelecanoides urinatrix*
BES	Blue-eyed shag	*Phalacrocorax atriceps*

little less) at Reynolds numbers above 200 000. It would appear that the value of 0·43 assumed by Pennycuick (1975) for the parasite drag coefficient of any bird, on the basis of measurements on the domestic pigeon (*Columba livia*) and Rueppell's griffon vulture (*Gyps rueppellii*), is too high for birds with well-streamlined bodies, flying at Reynolds numbers of 60 000 and above. The speeds for minimum power (V_{mp}) and maximum range (V_{mr}) were estimated by the method of Pennycuick (1975), using a value of 0·25 for the parasite drag coefficient for all species. Probably the drag coefficient should be a declining function of Reynolds number, which would have the effect of slightly decreasing the speed estimates for the birds that fly at lower Reynolds numbers, and *vice versa*. However, the effect would be small, and Prior's results, as presented, would not allow such a function to be estimated with a sufficient degree of precision to justify this added complication.

Table 2. *Morphological data*

Species	n_m	n_w	Mass (kg)	Wing span (m)	Wing area (m²)	Wing loading (N m⁻²)	Aspect ratio	C_{L1}
Albatrosses, petrels and storm-petrels								
WAN		3	8·73	3·03	0·611	140	15·0	1·16
BBA		3	3·79	2·16	0·356	104	13·1	1·08
GHA		1	3·79	2·18	0·352	106	13·5	1·10
STY		1	2·84	2·18	0·338	82·4	14·1	1·04
MAC		4	5·19	1·99	0·331	154	12·0	1·19
WCP		2	1·37	1·40	0·169	79·5	11·6	1·05
CAP		2	0·433	0·875	0·0773	55·0	9·90	0·98
PRN		5	0·168	0·626	0·0460	35·8	8·52	0·86
WIL		3	0·038	0·393	0·0219	17·0	7·05	0·69
Fg	350	3	0·815	1·13	0·124	64·5	10·3	0·97
Auks and diving petrels								
Fa	150	20	0·398	0·549	0·0369	106	8·17	1·25
Ua	100	3	0·950	0·707	0·0544	171	9·19	1·46
At	50	3	0·620	0·661	0·0462	132	9·46	1·39
SDP		3	0·114	0·381	0·0200	55·9	7·26	1·05
CDP		2	0·137	0·393	0·0221	60·8	6·99	1·05
Other seabirds								
Cs	40	6	1·35	1·37	0·214	61·9	8·77	0·81
Sp	12	5	0·390	1·05	0·117	32·7	9·42	0·75
Rt	37	3	0·387	0·965	0·101	37·6	9·22	0·79
Lm	5	1	1·56	1·69	0·317	48·3	9·01	0·71
La	80	1	0·940	1·31	0·181	50·9	9·48	0·81
Mb	89	1	3·01	1·85	0·262	113	13·1	1·16
Pa	43	4	1·81	1·04	0·158	112	6·85	0·91
BES		1	2·23	1·13	0·183	120	6·98	0·92

The species groupings correspond to the lines in Figs 2 and 4.

n_m, number in each sample for mass measurements; n_w, number in each sample for wing measurements; C_{L1}, lift coefficient when the gliding speed equals the minimum power speed.

Table 3. *Flight data for the Foula birds*

Sp.	n_f	V_{mf} (m s^{-1})	$Re \times 10^{-3}$ Body	Wing	V_{mp} (m s^{-1})	V_{mr} (m s^{-1})	V_{mf}/V_{mp}	C_L at V_{mf}	C_L (mean)	V_{zw} (m s^{-1})	Wind effect	Sig.
Fa	200	17·6	82·2	81·4	11·8	19·4	1·49	0·56	0·63	17·2	−1·09	<0·05
Ua	178	19·1	120	102	13·9	22·7	1·37	0·76	0·82	17·9	−0·72	NS
At	50	16·0	88·4	77·2	12·5	20·5	1·28	0·84	0·91	16·2	−0·77	<0·05
Cs	72	14·9	105	161	11·3	18·6	1·32	0·45	0·54	15·6	−1·09	NS
Sp	20	13·3	64·3	102	8·5	14·4	1·56	0·30	0·33	11·2	−0·59	NS
Rt	18	13·1	61·0	94·8	8·9	14·9	1·47	0·36	0·40	9·17	−0·82	<0·05
Lm	25	12·4	90·0	161	10·6	17·6	1·17	0·51	0·64	11·6	−0·69	<0·01
La	16	11·3	70·8	107	10·2	16·9	1·11	0·65	0·67	10·2	−0·25	NS
Fg	104	13·0	77·8	98·3	10·5	17·4	1·24	0·62	0·75	13·0	−0·72	<0·01
Mb	32	14·9	127	146	12·6	20·7	1·18	0·83	0·94	14·2	−0·76	<0·05
Pa	103	15·4	117	161	14·2	23·2	1·08	0·77	0·83	14·5	−0·68	<0·01

Sp., species (see Table 1); n_f, number of observations; V_{mf}, mean observed airspeed; Re, Reynolds number; V_{mp}, minimum power speed; V_{mr}, maximum range speed; C_L, lift coefficient; V_{zw}, zero-wind speed; Sig., significance; NS, not significant.

Wind regression

For each observation, the difference between the groundspeed and the airspeed was used as a measure of 'tailwind component'. If the groundspeed is greater than the airspeed, then there is a tailwind, and *vice versa*. The effect of a tailwind on airspeed was represented by calculating linear regressions for each species, in which the ordinate is airspeed, and the abscissa is (groundspeed − airspeed). Similar regressions for petrels and albatrosses (Pennycuick, 1982*b*) were quoted by Rayner (1985) as an illustration of the respective merits of different methods of calculating the slope of the line. Rayner concluded that the reduced major axis method, which makes no distinction between the dependent and independent variables, is more appropriate in this case than the regression method, which recognizes one variable as dependent and the other as independent. As Rayner noted, neither variable is under the control of the observer, and errors in the measured airspeed appear in both variables. However, it can be argued that the tailwind component is imposed on the bird, and is therefore the independent variable, whereas the airspeed at which the bird elects to fly represents its response, making this the dependent variable. As the point seems to be arguable, the regression calculation is retained here, primarily to render the results directly comparable with the earlier observations.

As in the petrels and albatrosses observed by Pennycuick (1982*b*), the slopes of the regression lines were negative for all species, that is, the birds responded to a tailwind by reducing their airspeed, and increased speed in response to a headwind. This is the expected response, as explained by Pennycuick (1978). Seven of the 11 correlation coefficients were significant at the 5 % level or beyond. The regression coefficients are listed in Table 3 as 'wind effect', together with an estimate of significance. The y-intercept of each regression line is listed as the 'zero-wind speed' (V_{zw}), that is, an estimate of the airspeed at which the bird would fly in zero wind.

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Airspeed histograms

Fig. 1 shows histograms of observed airspeeds for all species, in flapping and flap-gliding flight. The minimum power speed (V_{mp}), and maximum range speed (V_{mr}), calculated from the mass and wing span by the method of Pennycuick (1975), are listed in Table 3, and also marked on each histogram, together with the percentages of observations falling below V_{mp}, and above V_{mr}. In all species, both the mean observed airspeed (V_{mf}) and the zero-wind speed (V_{zw}) fall between the calculated values for V_{mp} and V_{mr}.
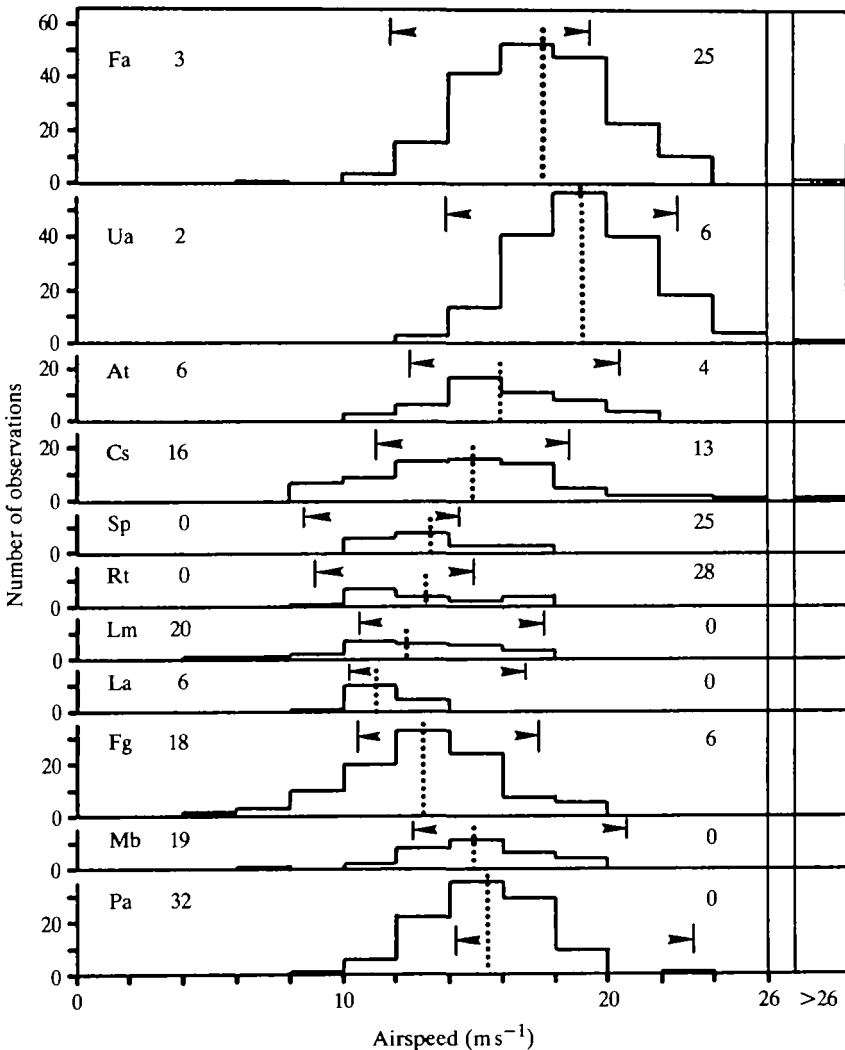
Fig. 1. Airspeed histograms for flapping and flap-gliding flight. The species codes on the left are identified in Table 1. The mean airspeeds are shown as vertical dotted lines. The speeds for minimum power (V_{mp}) and maximum range (V_{mr}) are shown as thin vertical lines with left- and right-pointing arrowheads, respectively. The numbers on the left and right are percentages of observations falling below V_{mp} and above V_{mr}.

Of the three species that showed large percentages of observed speeds above the calculated maximum range speed, the puffin also showed a significant negative correlation between airspeed and vertical speed. The reason appears to be that many of the puffins passed the observation site in a shallow dive, on their way from nearby cliff nesting areas to the sea, and increased their speed accordingly. The other two species (arctic skua and kittiwake) were represented by small samples, dominated by birds flying at increased speed against headwinds. Their zero-wind speeds were much less than their mean speeds (Table 3). Several species showed large percentages of observations below the calculated minimum power speed. Of these, the great skua, great black-backed gull and fulmar were reducing speed in some observations as they made use of slope-lift along the cliff. Gannets were flying well out from the cliff, but were often seen reducing speed and looking down, presumably at fish. The shag is the only species whose speed distribution is not easily explained in terms of behaviour. It showed the highest percentage of observations below V_{mp} (32 %), and none above V_{mr}. The shags were flying steadily along over the sea, and were not slope-soaring, preparing to land or looking out for prey. Their speed distribution calls for another explanation (see below).

Lift coefficients

Lift coefficients for the gliding phase of flap-gliding flight were calculated for each observation from the formula

$$C_L = 2\,mg/\rho V^2 S. \tag{1}$$

The ratio mg/S is listed in Table 2 as the wing loading, m being the mass, g the acceleration due to gravity, S the wing area, and V the airspeed. The air density (ρ) was calculated separately for each run from the temperature and pressure, which were recorded on the data tapes. In the case of a bird in flapping flight, equation 1 gives the lift coefficient that would apply if the bird were gliding at the observed speed. The speed distributions of Fig. 1 are fairly symmetrical, consequently the lift coefficient distributions are skewed, on account of the inverse square relationship of equation 1. Because of this, the mean lift coefficient for each set of observations is generally different from (higher than) the lift coefficient corresponding to the mean speed (V_{mf}). Both lift coefficients are listed in Table 3.

DISCUSSION

Flight style

Flap-gliding is the characteristic style of powered, cruising flight in 'normal' Procellariiformes – that is, albatrosses, petrels and storm-petrels, but excluding diving petrels (Diomedeidae, Procellariidae and Hydrobatidae but not Pelecanoididae). Among the species in the present sample, the gannet also regularly flap-glides in cruising flight, but the others typically flap most or all of the time. A bird that flap-glides when cruising must be able to flap reasonably efficiently, at a speed not too far from that for the best glide ratio in gliding flight. The required flapping
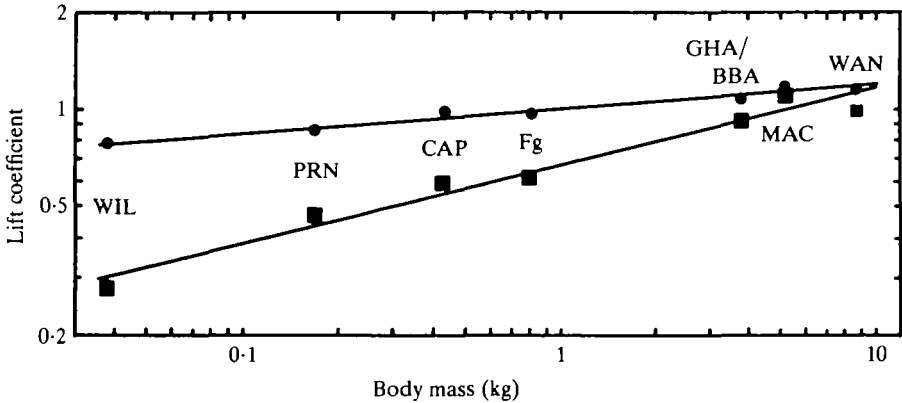
Fig. 2. Lower line: lift coefficients corresponding to mean airspeed in flapping and flap-gliding flight for Procellariiformes other than diving petrels. Upper line: lift coefficient for gliding at a speed equal to the calculated minimum power speed in the same species. The species codes are given in Table 1.

speed cannot be too much above or below the best gliding speed, otherwise the gliding phase of the flap-glide will be unacceptably inefficient.

One might suppose that the normal Procellariiformes, whose body masses range from about 30 g to 9 kg, would choose a constant value of the lift coefficient for the gliding phase of flap-gliding flight, but this is not so. These lift coefficients were determined by Pennycuick (1982b) for seven procellariiform species, and ranged from 0·28 for Wilson's storm petrel to 1·08 for the giant petrel. These results are plotted (together with the new value for the fulmar) as the lower line in Fig. 2. It shows that the lift coefficient varies with the 0·24 power of the body mass. The slopes of all the lines of Figs 2 and 4 were calculated by the reduced major axis method, as recommended by Rayner (1985).

Relationship of flapping to gliding speeds

Another way to represent the problem is to ask: at what value of the lift coefficient would the gliding speed be equal to the minimum power speed? This question can be answered from body measurements alone. The resulting value of the lift coefficient is listed as 'C_{L1}', along with the morphological data in Table 2. It is determined as follows. The minimum power speed, on the assumptions of Pennycuick (1975), is given by

$$V_{mp} = 0.760k^{1/4}m^{1/2}g^{1/2}\rho^{-1/2}A^{-1/4}S_d^{-1/4}, \tag{2}$$

where k is the induced power factor, m is the body mass, g is the acceleration due to gravity, ρ is the air density, A is the equivalent flat-plate area of the body (equal to the actual cross-sectional area times the body drag coefficient), and S_d is the disc area. S_d can be expressed in terms of the wing span, and A can be replaced by a function of the body mass, after Pennycuick (1975). If this is done, and numerical

values of 1·2 for k and 0·25 for the body drag coefficient are assumed, equation 2 can be expressed as:

$$V_{mp} = 4.19m^{1/3}g^{1/2}\rho^{-1/2}b^{-1/2}, \tag{3}$$

where b is the wing span. The gliding speed (V_g) is simply

$$V_g = \sqrt{(2\,mg/\rho C_L S)}. \tag{4}$$

If we now set the gliding speed equal to V_{mp}, and solve for the lift coefficient, the result can be expressed as

$$C_{L1} = 0.114m^{1/3}\Lambda/b, \tag{5}$$

where Λ is the aspect ratio, defined as

$$\Lambda = b^2/S. \tag{6}$$

C_{L1} being dimensionless, the numerical constant in equation 5 has the dimensions of (mass$^{-1/3}$ × length). These curious dimensions result from the substitution of a function of the mass, in place of the cross-sectional area of the body. If the latter were used explicitly, equation 5 would take a more overtly dimensionless form. The upper line in Fig. 2 represents C_{L1} plotted against body mass for normal Procellariiformes. Like the observed lift coefficient, C_{L1} also increases with mass, but only as the 0·077 power of the mass. The line converges with the one for observed flap-gliding lift coefficients at a body mass of 10·9 kg, and a lift coefficient of 1·21. This means that if an 11-kg albatross were to fly at V_{mp} during the flapping phase (which is too slow for efficient flapping flight), it would have to glide at a lift coefficient of 1·2 (which is too high for efficient gliding). It may be noted that the largest species, the wandering albatross, deviates below the line, that is it flies somewhat faster than the relationship predicts, and thus at a lower lift coefficient. It would appear that the largest species do not have sufficient muscle power to fly much faster than V_{mp}, and thus have no choice but to fly at a speed too low to be efficient. Not surprisingly, they avoid powered flight whenever possible, and rely heavily on soaring. At the other extreme, C_{L1} for the Wilson's storm petrel is lower than that for the large albatrosses, but far above the lift coefficient at which it actually flies. It was noted by Pennycuick (1982*b*) that only this smallest species actually flies at a speed near its calculated maximum range speed.

Species adapted to wing-propelled swimming

The three auks (Alcidae) are the only species in the present sample that use their wings in a flapping motion for propulsion under water. An incipient form of this adaptation can be seen in underwater films of plunge diving boobies (Sulidae), which steer with the partially opened wings. However, these birds do not show the penguin-like motion seen in the auks, and their forward motion seems to be derived from the momentum of the dive, or from buoyancy when returning to the surface, rather than from flapping the wings. In the Southern Hemisphere, the diving petrels (Pelecanoididae) swim in a similar way to the auks, and are generally considered to be convergent on them. Since water is some 800 times denser than air at sea level, it is

remarkable that auks and diving petrels can use the same wing, and even a similar motion, for propulsion in both media. The flapping frequency is, of course, much lower in water, and the wings are held with the wrist and elbow joints sharply flexed.

Pennycuick (1986) has represented this and other adaptations by considering them as deviations from a theoretical 'standard seabird'. The latter is defined by a mass, wing area and wing span that fall in the centre of the allometric series of the normal Procellariiformes. The 'standard seabird' is like a medium-sized petrel, close to the fulmar. Variations in size from the standard generate the procellariiform series of flap-gliding seabirds. The wings of boobies are indistinguishable from the standard on this basis, but adaptation for wing swimming leads to a deviation from the procellariiform lines, in the manner shown in Fig. 3. As compared to normal Procellariiformes (or boobies) of the same mass, auks and diving petrels show reduced wing span and wing area, with little change in the aspect ratio. This process is carried to extremes in penguins and other flightless wing swimmers, in which the wing is presumably optimized for swimming. Birds that swim in this manner, but also retain the power of flight, have to settle for an intermediate degree of reduction.

It is obvious that reduction of both wing span and area in the manner of Fig. 3 will lead to an increase of both gliding and flapping speeds. Less self-evidently, it was noted by Pennycuick (1986) that the gliding speed is more strongly affected than the flapping speed. If the 'standard' bird (upper outline in Fig. 3) normally proceeds by flap-gliding, then the bird with the reduced wing will not be able to do so. Its flapping speed will be faster than that of the normal bird, but its gliding speed will be faster still, so that it is no longer possible both to flap and glide at the same speed. Therefore auks and diving petrels do not flap-glide, but proceed by continuous
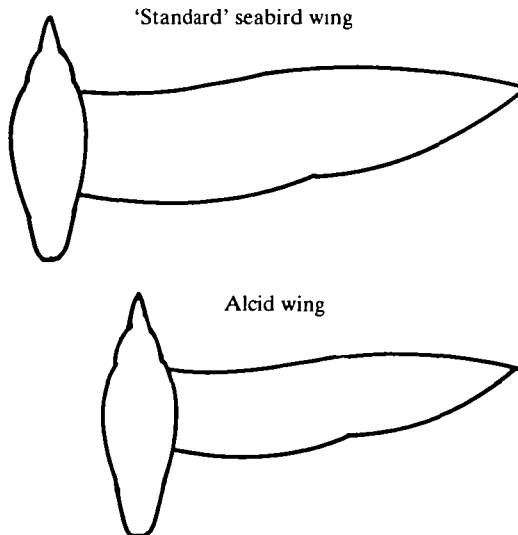

Fig. 3. The alcid wing may be considered as derived from a petrel-like 'standard seabird' by reducing the span and area, with little change to the aspect ratio, or to the size and mass of the body.
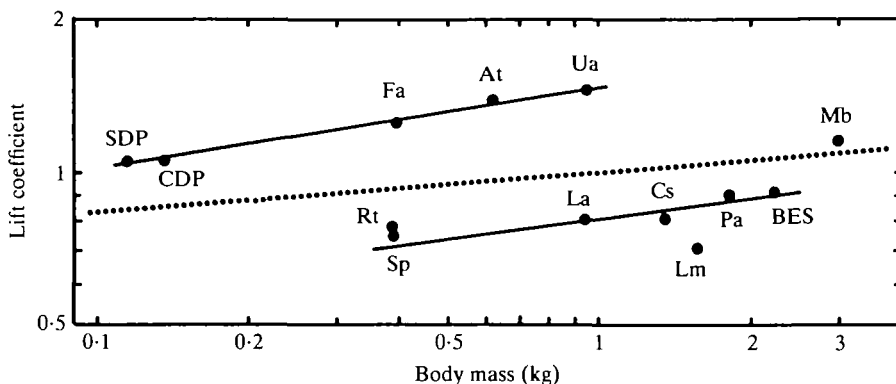
Fig. 4. Lift coefficient for gliding at a speed equal to the calculated minimum power speed. Upper line: alcids and pelecanoidids. Lower line: larids, stercorariids, phalacrocoracids. Middle (dotted) line: Procellariiformes other than diving petrels, transferred from the upper line of Fig. 2. Data are from Table 2; the species codes are given in Table 1.

flapping. This does not mean that these birds are unable to glide. The three species of auks in the present sample do glide when slope-soaring along cliffs in strong winds. Presumably they do so at airspeeds above their normal flapping speeds. Regrettably, this conjecture could not be tested directly, as no suitable observing site was found on the cliffs, from which ornithodolite observations of gliding auks could be obtained. The difficulty was to find a site at which meaningful readings could be obtained from the anemometer. Suitable sites most probably do exist on other islands with less precipitous cliffs.

The effect can be seen indirectly by considering C_{L1}, the lift coefficient for gliding at the minimum power speed. This is much higher in auks than in normal Procellariiformes of similar mass (Table 2; Fig. 4). The top line in Fig. 4 represents C_{L1} for the three auks and two diving petrels in Table 2, for comparison with the dotted line, which is the procellariiform line transferred from Fig. 2. With a value of 1·46 for C_{L1}, the guillemot would be almost stalled if it attempted to glide at its minimum power speed. The mean flapping speed for guillemots was 1·37 times the estimated V_{mp} (Table 3), but this is evidently still too slow for flap-gliding to be practicable. Values of C_{L1} for the diving petrels, with body masses below 150 g, are near those for albatrosses. The latter flap-glide, whereas the diving petrels do not. Probably there are two reasons for this. First, the albatrosses are obliged by lack of muscle power to fly not much faster than their minimum power speeds, whereas the diving petrels, like the auks in the present survey, probably fly considerably faster than this. Second, the albatrosses can probably glide efficiently at higher lift coefficients than diving petrels, because of the higher Reynolds numbers at which they fly.

Other adaptations

The seven remaining species in the Shetland sample comprise three gulls (Laridae), two skuas (Stercorariidae), the shag (Phalacrocoracidae) and the gannet

(Sulidae). Their values for C_{L1} are plotted on Fig. 4, together with that for the blue-eyed shag. The lower line is fitted through this group of points, excluding that for the gannet. The points for this more heterogeneous group of species show considerably more scatter about their line than do the normal Procellariiformes or the wing-swimming species. The point for the gannet falls very near the normal procellariiform line. As noted by Pennycuick (1986), gannets and boobies are indistinguishable from normal procellariiform birds on the basis of their wing span or area, and, like Procellariiformes, they flap-glide in cruising flight. Gulls, skuas and cormorants mostly flap continuously in cruising flight, but not for the same reason as the wing-swimming birds. Their C_{L1} values fall below the normal procellariiform line (lower line in Fig. 4), which means that their gliding speeds are lower than their flapping speeds, rather than higher as in the wing-swimmers. When gulls, skuas and cormorants glide, they do so at speeds slower than their cruising speeds in flapping flight, rather than faster.

Landing manoeuvres

Birds with a low C_{L1} change from flapping to gliding as they slow down, whereas those with a high C_{L1}, if they happen to be gliding, have to change to flapping before they can reduce speed. A gull or cormorant preparing to alight on the water, first stops flapping and glides, as it decelerates prior to touching down, whereas an auk continues flapping as it flies on to the surface. An auk preparing for a cliff landing will often approach the cliff in a shallow, fast, gliding dive. It pulls up to approach the landing ledge in a steep, decelerating climb, and as it slows down, it changes from gliding to flapping, invariably flapping vigorously just before touching down.

Anomalous speeds in the shag

As noted above, the mean flapping speed observed for the shag was only 1·08 times the calculated minimum power speed, and 32 % of the observations were below V_{mp}. The observations were not distributed upwards towards the calculated maximum range speed, as in other species, and there were no observations over V_{mr}. The high estimates for V_{mp} and V_{mr} (14·2 and 23·2 m s^{-1}, respectively) reflect the fact that the shag's wing span (1·04 m) is very short in relation to its mass (1·81 kg). To reduce the estimate for V_{mp} to, say, 12 m s^{-1} (which would remove the anomaly) one could argue that the induced power is much lower than assumed. On present assumptions, the wing would have to behave as though its span were about 1·35 m, which seems improbable. Alternatively, the parasite drag, or perhaps the wing profile drag, would have to be very much greater than assumed. This does not seem likely either, as such an assumption, applied to the auks, would produce an anomaly in the other direction.

The best interpretation seems to be that shags, unlike the other species, really do undertake foraging flights at speeds only a little above their minimum power speed. The observation may reflect a simple scale effect, which has been discussed elsewhere (Pennycuick, 1975). As flying animals increase in size, the power required to fly increases more steeply than the power available from the muscles. There is some value of body mass at which a bird of a particular morphological type has only just

enough power to maintain its maximum range speed in level flight. As the bird is scaled up further, its muscle power becomes insufficient to reach V_{mr}, and the speeds available to it become restricted to a progressively narrower range about V_{mp}. The dimensional argument predicts the trend, but does not supply a numerical estimate for any particular combination of mass and wing span at which flight at the maximum range speed should no longer be possible. The present observations suggest that the shag is beyond this point. If this interpretation is correct it can be used as a calibration, to insert numerical values into the dimensional theory.

REFERENCES

CROXALL, J. P. & PRINCE, P. A. (1980). Food, feeding ecology and ecological segregation of seabirds at South Georgia. *J. Linn. Soc. (Biol.)* **14**, 103–131.

FURNESS, R. W. (1983). *The Birds of Foula*. Ambleside: Brathay Trust.

NELSON, J. B. (1978). *The Gannet*. Berkhampstead: Poyser.

PENNYCUICK, C. J. (1975). Mechanics of flight. In *Avian Biology*, vol. 5 (ed. D. S. Farner & J. R. King), pp. 1–75. New York: Academic Press.

PENNYCUICK, C. J. (1978). Fifteen testable predictions about bird flight. *Oikos* **30**, 165–176.

PENNYCUICK, C. J. (1982a). The ornithodolite: an instrument for collecting large samples of bird speed measurements. *Phil. Trans. R. Soc. Ser.* B **300**, 61–73.

PENNYCUICK, C. J. (1982b). The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. *Phil. Trans. R. Soc. Ser.* B **300**, 75–106.

PENNYCUICK, C. J. (1983). Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificens, Pelecanus occidentalis* and *Coragyps atratus. J. exp. Biol.* **102**, 307–325.

PENNYCUICK, C. J. (1986). Flight of seabirds. In *Seabirds: Feeding Ecology and Role in Marine Ecosystems* (ed. J. P. Croxall). Cambridge: Cambridge University Press.

PRIOR, N. C. (1984). Flight energetics and migration performance of swans. Ph.D. thesis, University of Bristol.

RAYNER, J. M. V. (1985). Linear relations in biomechanics: the statistics of scaling functions. *J. Zool., Lond.* A **206**, 415–439.