THERMAL SOARING COMPARED IN THREE DISSIMILAR TROPICAL BIRD SPECIES, *FREGATA MAGNIFICENS, PELECANUS OCCIDENTALIS* AND *CORAGYPS ATRATUS*

By C. J. PENNYCUICK

Department of Zoology, University of Bristol, Woodland Road, Bristol BS8 1UG

SUMMARY

1. All three species were observed in straight flight, and circling in thermals, from Flamenco Island, Panama. Measurements were made by ornithodolite, an instrument which records a series of timed, three-dimensional position estimates, from which speeds, circle diameters and rates of climb can be calculated.

2. Mean lift coefficients in straight glides ranged from 0·72 to 0·84, except in slope soaring, where a mean of 1·6 was recorded for both the frigatebird and black vulture.

3. Mean circling radii were proportional to wing loading, and varied from 12·0 m for the frigatebird to 18·0 m for the pelican. Mean rates of climb ranged from 0·40 m s^{-1} for the black vulture to 0·57 m s^{-1} for the pelican. All species showed mean circling lift coefficients between 1·33 and 1·45, and angles of bank between 22·9° and 24·7°.

4. It is argued that the frigatebird is adapted to stay airborne continuously, day and night, for extended periods, by exploiting thermals over the sea under trade wind cumulus clouds. The low wing loading is seen as an adaptation to circling in narrow thermals, and the low disc loading as an adaptation giving low minimum power, when flapping cannot be avoided. Take-off appears to be possible only by dropping from an elevated perch, not from the ground or water surface.

5. The low aspect-ratio, tip-slotted wings of the black vulture are certainly less efficient for soaring, but appear to be better for upward take-off from the ground. The pelican also has tip-slotted wings. Although its aspect ratio is higher, it is still capable of taking off from a level water surface.

INTRODUCTION

This paper presents comparative observations, made in Panama, on three contrasting species of gliding birds. They were the magnificent frigatebird, *Fregata magnificens*, the brown pelican, *Pelecanus occidentalis*, and the American black vulture, *Coragyps atratus*. Although differing in habits and morphology, all three species could be seen soaring in thermals and slope lift, and in straight flight, from the same observation point. A few observations of flapping flight in Bigua cormorants, *Phalacrocorax olivaceus*, are also included.

Study area and general behaviour

Observations were made from the top of Flamenco Island, Panama, on 13 days between 21st May and 6th June 1980. Flamenco is the outermost of a series of three islands which are connected by a causeway, extending southwards from the mainland near Panama City, along the east side of the Pacific entrance of the Panama Canal. The nearby Naos Laboratory of the Smithsonian Tropical Research Institute provided a base for the project. Flamenco is a small, steep island. Its sides, although wooded, gave rise to a small area of slope lift in more or less any wind direction. The observation point was an exposed platform at the highest point on the north side of the island, about 90 m above sea level, giving a clear view to the north, and slightly obstructed views in other directions.

Taboga, Taboguilla and Urava Islands, about 14 km away to the south, supported large numbers of pelican nests, and were also used as roosts by frigatebirds. Birds from these roosts flew past Flamenco Island each morning on their way to forage in Panama Bay, with a reverse movement in the evening. While these movements were in progress, a constant stream of pelicans and frigatebirds passed close to, or over, Perico and Flamenco Islands, making use of slope lift and thermals in the vicinity of the islands. Bigua cormorants were also nesting on the outer islands, and participated in these movements.

Pelicans flew mostly in flocks, gliding or flap-gliding in vee or echelon formation. These flocks would maintain their coherence for short periods of slope soaring, all the birds in the flock turning together at the end of the slope. In thermals the flock structure gradually degenerated into a milling mass of pelicans circling in either direction. This behaviour differed from that recorded in African white pelicans (*P. onocrotalus*) (Pennycuick, 1972), and in European cranes (*Grus grus*) (Pennycuick, Alerstam & Larsson, 1980), which both maintained tight formations when circling. The only species seen behaving in this way at Flamenco Island was the Bigua cormorant. Flocks of cormorants were seen circling in thermals on a few occasions, although the usual behaviour of this species was to fly straight through thermals or slope lift, maintaining flapping flight.

Frigatebirds flew individually, with no apparent flock structure. They would circle in thermals and soar in slope lift, gliding whenever possible. They were also able to proceed in straight, continuous flapping flight when necessary.

Black vultures did not follow the same flight lines as the other species. They were abundant over Panama City, about 5 km away, where several hundred of them could often be seen soaring at the same time. They also foraged on the beaches along the causeway, and this brought them to Flamenco Island. They were most often seen gliding, and would soar in thermals or slope lift together with the other species. Like the frigatebirds, they did not show any apparent flock structure in flight.

Morphology

Body measurements of the three study species are listed in Table 1. 'Wing span' (b) is the distance from tip to tip of the fully outstretched wings. 'Wing area' (S) is the projected area of both wings, together with the portion of the body included between

■nem, according to the usual convention. Aspect ratio (A) and wing loading (Q) are derived from these as follows:

$$A = b^2/S \qquad (1)$$

$$Q = mg/S \qquad (2)$$

where m is the body mass, and g is the acceleration due to gravity.

The sources of the morphological data were heterogeneous, and no great precision can be claimed for them. The black vulture figures are the means from two adult females trapped on nearby Ancon Hill in the course of a project directed by Dr Neal Smith of the Smithsonian Tropical Research Institute, and measured by the author. The brown pelican data are from one adult female found floating in Panama bay, which appeared on dissection to be recently dead and in good condition.

Efforts to catch frigatebirds were unsuccessful, so the mass and wing area were taken to be the means for 10 individuals from Florida, recorded by Harrington, Schreiber & Woolfenden (1972). Although there is sexual dimorphism in this species, the sample sizes of flight observations were insufficient to investigate the effects of this on flight. The figures in Table 1 are the means for both sexes. Unfortunately Harrington *et al.* (1972) did not record wing spans. Aspect ratio was therefore measured directly, from six monochrome photographs of gliding frigatebirds, taken as nearly as possible from directly below. The wing span was then obtained by inverting Eqn. 1.

Table 1. *Body measurements*

Species	Mass kg	Span m	Wing area m^2	Wing loading Nm^{-2}	Aspect ratio
Frigatebird	1·52	2·29	0·408	36·5	12·8
Brown pelican	2·65	2·10	0·450	57·8	9·80
Black vulture	1·82	1·38	0·327	54·7	5·82

The differences of wing shape can be seen in the silhouettes of Fig. 1. These are derived from photographs of birds in flight, and are not exact projections of the wing planform. In particular the black vulture is slightly banked, which makes its aspect ratio appear even lower than it really is. Nevertheless the vulture does indeed have a wing of low aspect ratio and slight taper, in which the distal primaries are emarginated, so that a series of slots form at the tip when the wing is fully extended. This type of wing is typical of birds specialized for thermal soaring over land, including the New World vultures (Cathartidae), their Old World equivalents (Aegypiinae), storks (Ciconiidae) and cranes (Gruidae). The brown pelican has essentially the same type of wing, but the aspect ratio is much higher. The slotted wing tip is much less conspicuous in relation to the wing as a whole than in the vulture. In the frigatebird (another pelecaniform bird), the aspect ratio is higher still and the wing tapers to a ■oint, without slots.
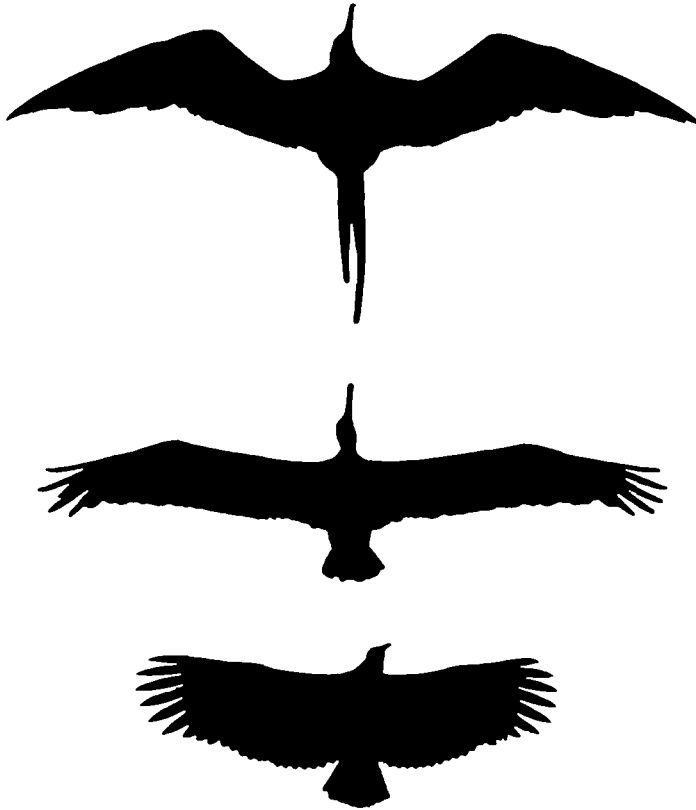
Fig. 1. Silhouettes made from photographs of birds in flight. From top to bottom: *Fregata magnificens, Pelecanus occidentalis, Coragyps atratus*.

METHODS

Flight measurements

Measurements of speed and rate of climb were obtained by ornithodolite. A full description of this instrument has been published elsewhere (Pennycuick, 1982*a*). The instrument (Fig. 2) consisted of a rangefinder on an alt-azimuth mount, fitted with photoelectric digital encoders for azimuth, elevation and range. In use, it was aimed manually to centre the image of the bird in the rangefinder window. The rangefinder (a coincident image type) was set by means of a large handle, geared to allow the range knob to be turned through its full travel with a quarter-turn of the wrist. On pressing a button adjacent to the aiming handle, the current readings of azimuth, elevation and range, and the time, together constituting an 'observation', were stored in the memory of a battery-operated Nascom 1 microcomputer. Several observations were accumulated before the bird passed out of range of the instrument, and these together constituted a 'run'. The run was concluded by typing in details of the species, the bird's behaviour, and the wind strength and direction from the computer's keyboard. The whole run, including these details, was then recorded on tape cassette, after which the computer's internal memory was reset, ready to accept the next run.
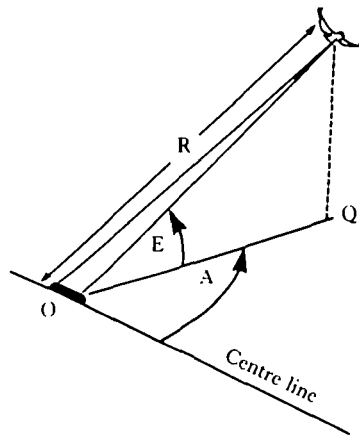
Fig. 2. The primary variables recorded by the ornithodolite were (1) the range, R; (2) the azimuth angle, A, between the instrument's centre line and the horizontal line OQ, which passes through the instrument and directly under the bird; (3) the elevation angle, E, measured upwards from OQ. The time of each observation was also automatically recorded.

The azimuth encoder allowed angles up to 64° either side of the centre line to be observed, in steps of 0·5°, while elevation could be observed up to 32° above and below horizontal, in steps of 0·25°. Time was incremented in steps of 0·1 s. It was estimated (Pennycuick, 1982a) that the instrument could be aimed at a bird in flight to within about ±1·5°, in both azimuth and elevation.

The rangefinder was initially fitted with an encoder disc covering 36·0–195·5 m, in increments of 0·5 m. Part way through the project, this was changed for another disc, covering ranges from 40–295 m in steps of 1 m, in order to increase the maximum range. A rangefinder calibration, carried out with the latter disc fitted, has been published previously (Pennycuick, 1982a). This shows a standard deviation of about 2·5 m at a range of 100 m, increasing to about 8 m towards the maximum range. The error would be expected to increase non-linearly, and may in fact be even greater than indicated by this test, at the longer ranges. At any rate, there is no doubt that the error must increase with distance, so that observations made at the longer ranges, permitted by the substituted encoder disc, would be subject to reduced precision. Naturally, birds flying close to the instrument were selected for observation whenever possible.

Wind measurement

Wind strength and direction were observed with a Mariner 1 anemometer set, of which the sensing unit consisted of a whirling-cup anemometer and a wind direction vane, mounted on a metal mast, 2 m above the level of the observation platform. The indicator unit, showing wind direction on a dial, and wind speed (in knots) on a 2-digit LED display, was mounted on the ornithodolite. The readings were taken immediately after each run, and entered via the keyboard. Calibration details for the anemometer have been published previously (Pennycuick, 1982a).

In the subsequent reduction of observations it was assumed, in effect, that the horizontal wind recorded by the anemometer was the same as that experienced by the bird 100–200 m away. In reality the wind must have been modified by the presence

of the islands and by thermals, besides which the anemometer reading itself would be
affected by the proximity of the ground. It was not possible to quantify these effects,
and they constitute a source of error in the conversion of groundspeeds to airspeeds.
This would increase the scatter in the airspeed estimates, although there is no reason
to suppose that any bias was introduced.

Reduction of observations

Observations of birds in straight flight were reduced as shown in Fig. 3. The
primary variables recorded for each observation were the azimuth, A, the elevation,
E, the range, R, and the time, t. The polar coordinates were transformed into rectan-
gular coordinates, x, y and z. The groundspeed was calculated by dividing the
horizontal distance (as opposed to the slant distance), travelled between successive
observations, by the elapsed time. The track direction was initially calculated relative
to the centre line of the instrument, and was then converted into the magnetic track,
by adding the magnetic bearing of the centre line, which was recorded for the whole
observing session. The groundspeed and track direction together constituted the
groundspeed vector. The wind was vectorially subtracted from this to give the air-
speed vector (airspeed and heading direction), as in Fig. 4. The vertical speed (rate
of climb) was obtained by dividing the increment in the z coordinate by the elapsed
time.

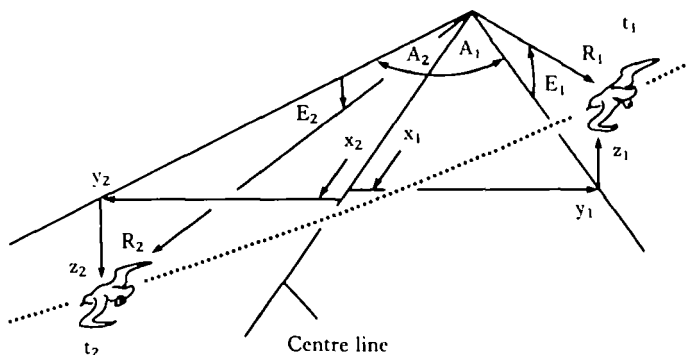Two methods were used to record circling flight. In the 'left–right' method

Fig. 3. In the analysis of straight flight the polar coordinates R, A and E were first transformed into
Cartesian coordinates x, y and z. Ground speed and track direction were calculated from the change
in position, projected on to the xy plane. Vertical speed (rate of climb) was found from the change
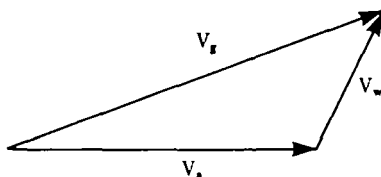in z. Time = t. From Pennycuick (1982b).

Fig. 4. The airspeed and heading direction (V_a) (also projected on the xy plane) were found by
subtracting the wind speed vector (V_w) from the groundspeed vector (V_g), found as in Fig 3.

[abbreviated LR), observations were taken as the bird appeared to reach the extreme left and right hand edges of the circle, as seen from the observer's position. In the 'near–far' method (NF), observations were taken as the bird passed the points nearest to, and furthest from the observer.

Fig. 5A illustrates an example in which the bird is flying steady circles relative to the air, but being drifted by the wind from right to left across the observer's line of sight. If this is observed by the RL method, as shown, the ground distance travelled is larger on the downwind halves of the circle than on the upwind halves. When the ground distance is transformed into the air distance, by applying the triangle of velocities as in Fig. 4, the effect of the wind is removed, revealing.a steady circle relative to the air, as in Fig. 5B. However, the positions of successive observations are still not exactly at opposite ends of a diameter, but move progressively round the circumference of the circle, as shown. This also happens with the NF method. It can be seen from Fig. 5B that the diameters of circles are, in general, slightly underestimated. The bias would be small compared with the scatter in the observations, and a correction was not attempted.

If the 'heading' is calculated, by the same method as for straight flight, it should change by approximately (but not necessarily exactly) 180° between successive pairs of observations. The expected result would be distorted by errors of position estimation,
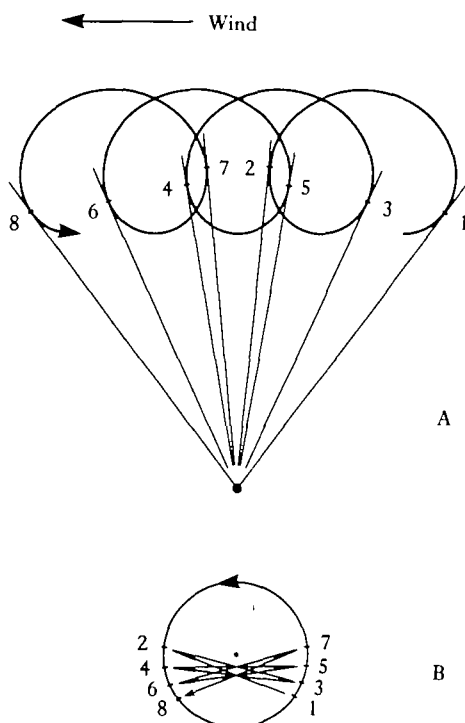

Fig. 5. A, Circling flight observed by the LR method. The bird is observed at eight points as it completes three and a half circles. Seven observations of circling radius and speed result. B, The bird's path relative to the air consists of steady circles. Successive position observations are approximately, but not exactly, at opposite ends of a diameter.

if these were appreciable in comparison with the diameter of the circle. In the subsequent analysis of the data, the changes of heading at successive observations were examined separately for RL and NF observations. The mean change of heading was 179·8° for RL observations, and 178·3° for NF observations. The circular statistic corresponding to standard deviation is the 'mean angular deviation' (explained by Batschelet, 1981), and this was 30·0° for the RL and 31·5° for the NF observations. It was concluded that neither method was appreciably more unreliable than the other, and the results from both were therefore pooled for the subsequent analysis.

The reduction of circling data differed from that of straight flight data, in that it was assumed that the bird travelled exactly half the circumference of a circle between each pair of observations. The air distance between observations, calculated as above, was taken as an estimate of 2r, where r is the radius of the circle, and the elapsed time as an estimate of $T/2$, where T is the circling period. The airspeed was then estimated as

$$V_a = 2\pi r/T \qquad (3)$$

Data processing

The output from the ornithodolite was obtained as a printed record of the encoder outputs and times. Small samples of the data were analysed in the field using a Hewlett Packard HP-67 card-programmable calculator. The data were later transcribed by hand to disc files on a 380Z computer at Bristol, on which all subsequent analysis was carried out. The procedures for transcribing and checking the data were as described elsewhere (Pennycuick, 1982b).

RESULTS

When recording data in the field, flight behaviour was first classified as either circling or straight flight, and these two types of records were treated differently in the subsequent analysis, as explained above. Straight flight was further subdivided into flapping, flap-gliding, slope soaring and gliding. The last category refers to gliding straight, but not along the slope, which usually occurred when a bird left a thermal to continue on its way, or arrived to join the slope lift after climbing in a thermal some distance away. The numbers of runs and speed observations (defined above) obtained on each species in each type of flight are listed in Table 2.

Straight flight

Mean airspeeds and standard deviations for straight flight are listed in Table 3. Mean airspeeds were first compared between flapping and flap-gliding flight. The 'd-test' given by Bailey (1959) was used for this and other comparisons of means. This is a modified t-test, for comparing the means of two samples of different size, whose standard deviations are not assumed to be equal. Only two species (frigatebird and pelican) were represented in the data for both flapping and flap-gliding flight, and neither showed a significant difference at the 5% level in mean airspeed. These two categories have therefore been pooled in Table 3. The few observations on flapping

Table 2. *Numbers of runs and speed observations*

Note that the number of speed observations in a run is one less than the number of position observations

| | Frigatebird | | Brown pelican | | Black vulture | | Bigua cormorant | |
	Runs	Obs	Runs	Obs	Runs	Obs	Runs	Obs
Flapping	16	40	6	11	0	0	15	28
Flap-glide	21	55	24	89	0	0	0	0
Glide	49	140	42	100	64	227	0	0
Slope soar	13	111	5	17	12	179	0	0
Circle RL	77	456	46	231	20	116	0	0
Circle NF	52	319	8	33	0	0	0	0
Other	13	104	3	11	0	0	0	0
Totals	241	1225	134	492	96	522	15	28

Total runs: 486
Total observations: 2267

Table 3. *Airspeeds in straight flight in m s^{-1}*

Numbers of observations are listed in Table 2.

| | Frigate bird | | | Brown pelican | | | Black vulture | | | Bigua cormoran | |
	Mean	s.d.	C_L	Mean	s.d.	C_L	Mean	s.d.	C_L	Mean	s.d.
Flap/flap-guide	9·30	1·96		9·53	2·73		No data			14·2	2·34
Glide	8·67	3·27	0·84	11·7	3·32	0·72	9·91	3·89	0·96	No data	
Slope soar	6·22	1·74	1·63	9·28	2·90	1·16	7·75	2·33	1·57	No data	

Bigua cormorants are included in this table, although no further data were obtained on this species.

The next comparison was between observations classified as 'gliding', and those classified as 'slope soaring'. In all species the mean speeds for slope soaring were at least 21 % slower than those for straight gliding. The differences were highly significant ($P < 0·001$) in the frigatebird and black vulture, though not in the pelican, for which only a small sample of slope soaring observations was obtained.

The lift coefficients corresponding to the mean speeds were calculated, using the wing loadings in Table 1, and are also listed in Table 3. The slope soaring lift coefficients were around 1·6 in the frigatebird and black vulture, which is about the same as the maximum values recorded in wind tunnel experiments on various species of live birds (Pennycuick, 1975). Slope-soaring frigatebirds and black vultures would tack back and forth along the slope, and the estimated lift coefficients may be regarded as representing minimum sink conditions. Pelicans would sometimes make a few beats back and forth along the slope, but more often simply routed longer glides so as to take advantage of a short segment along the slope. It is to be expected that they would not necessarily slow down to their minimum sink speed when doing this, so accounting for the lower lift coefficient of 1·16. This estimate is also subject to some doubt because of the small sample size (17 observations).

The 'gliding' observations may be considered representative of inter-thermal

glides, rather than flight at minimum sink. As expected, they show both higher mean
and higher standard deviations than the 'slope-soaring' observations. The lift co-
efficients corresponding to the mean speeds are quite high, ranging from 0·72
(pelican) to 0·84 (frigatebird), suggesting that inter-thermal speeds were mostly
rather low. Low inter-thermal speeds are appropriate for weak thermals, such as were
indeed recorded (below).

Circling flight

As explained above, the data yielded direct estimates of the circling radius (r) and
the time for one circle, or 'circling period' (T), from which an estimate of the airspeed
(V_a) could be derived. The basic equations for steady circling flight, relating these
variables with lift coefficient (C_L), angle of bank (ϕ) and air density (ϱ) are given by
Pennycuick (1971). For steadily maintained circling flight, the angle of bank is given
by

$$\tan\phi = V_a^2/gr \qquad (4)$$

where g is the acceleration due to gravity. The lift coefficient is then

$$C_L = 2mg/(r\varrho gS.\sin\phi) \qquad (5)$$

Table 4 contains a summary of the means and standard deviations for the different
species, for circling radius, circling period, airspeed in circling, and rate of climb.
Table 5 shows which interspecific differences in these variables were statistically
significant, using the d-test as above. Distributions for these four variables are shown
in Figs 6 to 9.

Table 4 also contains estimates for lift coefficient, Reynolds number and angle of

Table 4. *Measurements of circling flight*

Means with standard deviations where available.

	Frigatebird	Brown pelican	Black vulture
Circling radius (m)	12·0 ± 4·65	18·0 ± 6·51	17·1 ± 5·26
Circling period (s)	10·6 ± 2·02	13·3 ± 2·98	12·6 ± 3·02
Airspeed (m s^{-1})	7·19 ± 2·77	8·64 ± 2·95	8·78 ± 2·95
Rate of climb (m s^{-1})	0·48 ± 0·67	0·57 ± 0·56	0·40 ± 0·60
Reynolds number	4·1 × 10^4	5·9 × 10^4	6·6 × 10^4
Lift coefficient	1·33	1·45	1·35
Angle of bank (deg)	23·7	22·9	24·7
No. observations	775	264	116

Table 5. *Probabilities of differences between means in Table* 4

Abbreviations: Frig, frigatebird; Pel, pelican; BV, black vulture.

	Frig vs Pel	Frig vs BV	Pel vs BV
Circling radius	$P < 0.001$	$P < 0.001$	Not sig.
Circling period	$P < 0.001$	$P < 0.001$	$P < 0.05$
Airspeed	$P < 0.001$	$P < 0.001$	Not sig.
Rate of climb	$P < 0.05$	Not sig.	$P < 0.01$

nk. The lift coefficient has a strongly skewed distribution, because it is related to the inverse square of the airspeed, whose own distribution is more or less symmetrical (Fig. 8). For this reason, the lift coefficient given is that corresponding to the mean airspeed (not the mean lift coefficient) and the same method has been used to estimate the other two variables. All of these derived variables depend on morphological measurements, as well as on the flight measurements, and it was not considered feasible to calculate realistic indices of dispersion for them.

Circling radius

The mean circling radii listed in Table 4 are almost exactly proportional to the wing loadings listed in Table 1, as theory predicts (Pennycuick, 1975). The frigatebirds flew much smaller circles than did the other two species. The distributions (Fig. 6) show a few very small radii, suggesting an improbable degree of agility. These are presumably due to errors of position estimation or wind measurement. The same is no doubt true of some of the exceptionally large radii, but on the other hand some of these could be genuine. A circling bird would often make an unusually wide turn in the course of shifting the position of its circle, a manoeuvre known to glider pilots as 'centering in the lift'. The last circle was also often wider than usual, before the bird abandoned the thermal and set off in a straight glide.

Harrington *et al.* (1972) reported that the mean wing loading in magnificent frigatebirds was about 13 % higher in females than in males, and it was anticipated that a similar difference in mean circling radius might be observed between the sexes.
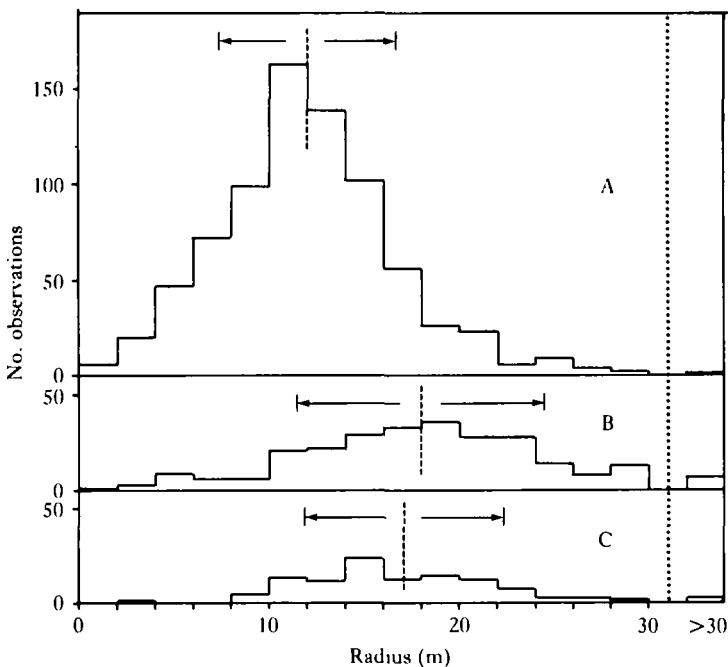

Fig. 6. Circling radius distributions. A, frigatebird; B, pelican; C, black vulture. Means and standard deviations are marked: their values, and the sample sizes, are listed in Table 4.

Table 6. *Circling radius in frigatebirds: means and standard deviations (in m) for males, females and immatures*

	Mean	S.D.	n
Adult male	11·7	5·23	174
Adult female	12·3	4·63	438
Immature	11·5	3·98	163

Adult males and females could be readily distinguished by plumage differences, and immature birds could be distinguished from adults, but not sexed. Means and standard deviations for males, females and immatures are listed in Table 6. The mean radius for females was only about 5 % greater than for males, and the difference was not significant at the 5 % level. The difference between immatures and females was just significant at this level, but the difference in wing loading in this case (or the sex ratio of the immatures) cannot be estimated.

Circling period

The circling period distributions (Fig. 7) do not show any anomalously low values, since the time at each observation was much easier to measure accurately than the position. Here again the mean values for the pelican and black vulture were close together, although just significantly different at the 5 % level. Both were considerably longer than the mean for the frigatebird.
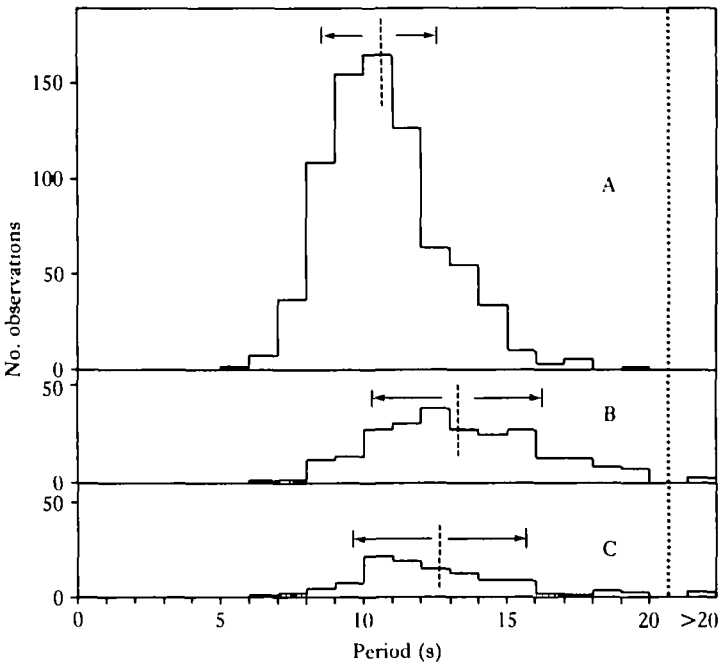

Fig. 7. Circling period distributions. Details as for Fig. 6.

Airspeed

The mean airspeeds for the pelican and black vulture were close together and not significantly different, but both were significantly higher than the mean for the frigatebird, more or less as expected from the differences in wing loading. Errors in observing position are reflected in the airspeed estimates, and the difficulty of estimating the wind at the bird's position also contributes to the errors. It is not unexpected that the distributions (Fig. 8) show examples of both improbably low and improbably high speeds.

Rate of climb

The distributions of rate of climb (Fig. 9) all show means at modest positive values, but also include a substantial number of negative observations. A negative observation means that a circling bird lost height in the course of half a circle. Some of these observations (and also the high positive ones) could be due to errors of position estimation. On the other hand it is quite usual in gliders, when soaring in such weak thermals, to continue circling even if height is lost in the course of a particular half-circle. This can occur because the circle is not correctly centred in the thermal, and the pilot's (or bird's) response may be to shift the circle, rather than to leave the thermal.

It was anticipated that the low wing loading of the frigatebird would give it a low minimum sinking speed, and that this, combined with the small radius of turn would result in the best rate of climb in thermals. The frigatebird did indeed show a slightly better mean rate of climb than the black vulture, though the difference was not
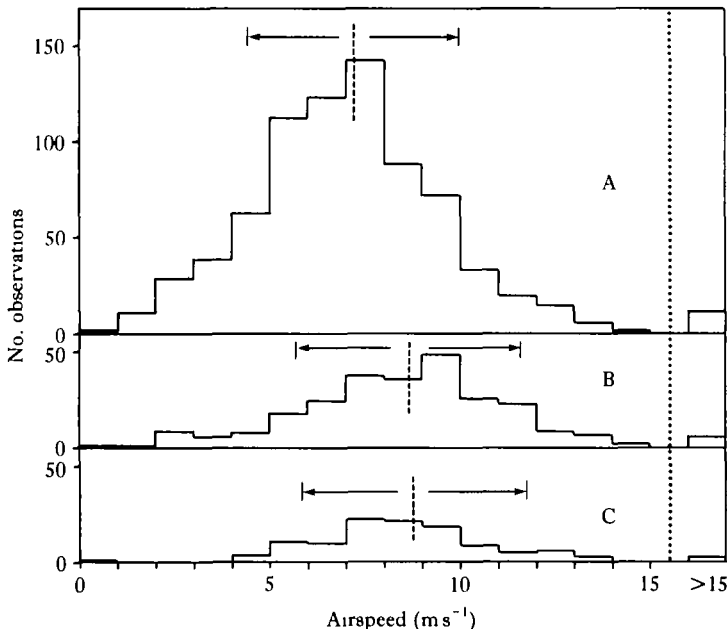
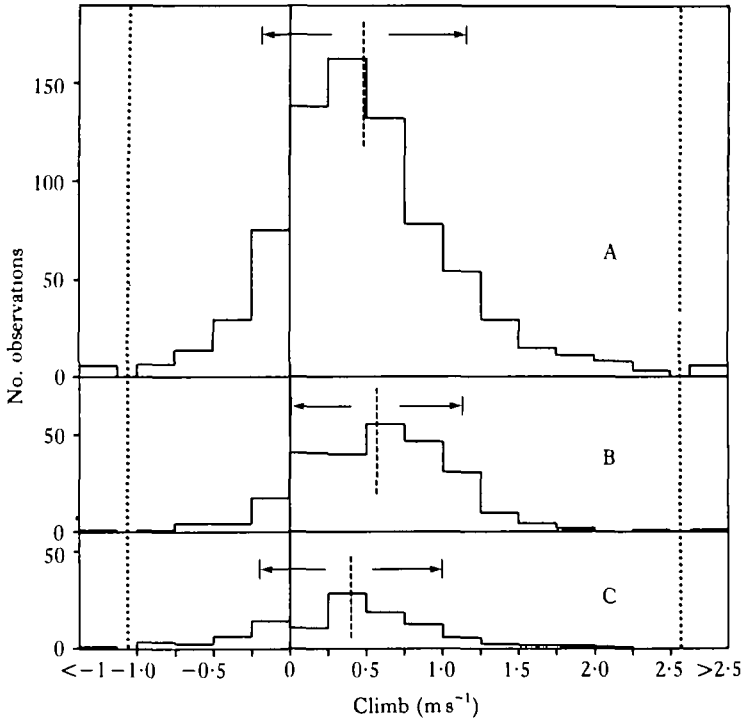Fig. 8. Airspeed distributions in circling. Details as for Fig. 6.

Fig. 9. Rate of climb distributions in circling. Details as for Fig. 6.

significant. Contrary to expectation, the pelican showed the highest mean rate of climb, significantly greater than that of either of the other two species.

Lift coefficient and angle of bank

Angles of bank and lift coefficients were calculated from the mean values of the other variables, according to Eqns 4 and 5. These estimates (Table 4) show a striking uniformity between the three species. The lift coefficients varied from 1·33 to 1·45, and the angles of bank from 22·9° to 24·7°.

DISCUSSION

It is clear that all the three species under discussion made extensive use of thermals, and might reasonably be regarded as being adapted to thermal soaring as their main method of locomotion. In that case, the major morphological differences between them (illustrated in Fig. 1) have to be accounted for in terms in differences in the flight requirements imposed by their different ways of life.

The broad, tip-slotted wing

Both the pelican and the black vulture have the tip-slotted wing generally considered to be typical of birds which soar in thermals over land. Both have similar wing loadings and were observed circling at similar radii. The pelican's significantly better rate of climb in weak thermals comes as no surprise in view of its much higher aspe**

ratio (Table 1). That being so, it is far from clear why the black vulture's aspect ratio should be so low. It is clear from general theory, and from experience with gliders, that a low aspect-ratio wing cannot possibly be advantageous for gliding performance as such. It is also clear, from the existence of albatrosses (Diomedeidae), that viable gliding birds with aspect ratios up to 14 can evolve (Pennycuick, 1982b). Earlier calculations (Pennycuick, 1971) indicated that if African vultures were to adopt an albatross-like wing shape, there would be a small penalty in their ability to exploit very narrow thermals, but a considerable improvement in all other aspects of both climbing and cross-country performance. Similarly, as a result of practical experience, modern gliders designed for thermal soaring generally have aspect ratios of at least 18.

It seems likely that all soaring birds would evolve high aspect-ratio wings if soaring performance were the only requirement to be satisfied, but that some are obliged to accept a reduction in soaring performance in order to satisfy some other requirement. Whatever this requirement is, it must be shared by such groups as American vultures (Cathartidae), their Old World equivalents (Aegypiinae), storks (Ciconiidae) and cranes (Gruidae), but not by marine soaring birds. Qualitative comparison of the three study species suggests that the requirement is connected with take-off performance. Fig. 10 illustrates the most difficult take-off requirement for each species. The frigatebird (A) takes off only from elevated perches such as trees, never from level ground or from the water. It can accelerate past its minimum power speed by dropping from the perch, and is not required to exert high power at a low speed. Pelicans (B) also use elevated perches, but in addition they alight on the water, and have to take off from it. This imposes the more difficult requirement of having to accelerate to the minimum power speed along a horizontal surface. Black vultures (C) feed on the ground, and have the even more difficult requirement of taking off directly on to a climbing path, to clear obstructions.

The comparison suggests that a low aspect-ratio wing is best for exerting high power
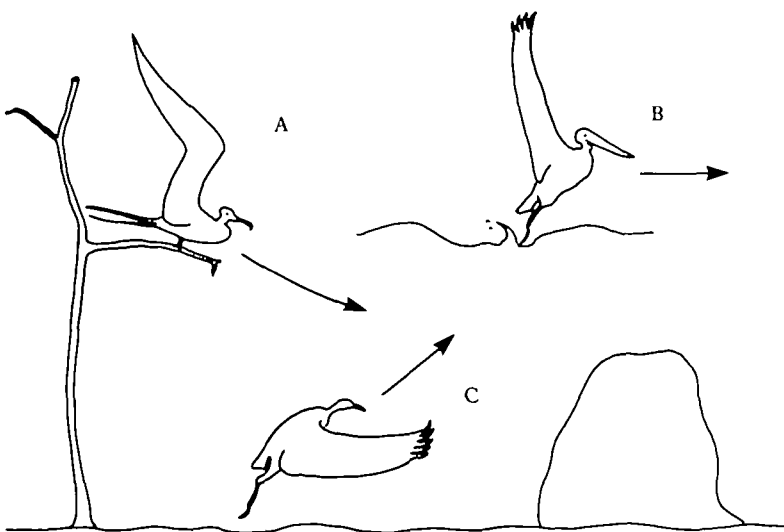

Fig. 10. Most difficult take-off condition. A, frigatebird; B, pelican; C, black vulture. (See text.)

at a low forward speed, although it is not entirely clear why this should be so. The tip‖ slots may be seen as an adaptation minimizing the deleterious effects of the low aspect ratio on gliding performance. Their appearance and arrangement is strongly reminiscent of the 'wing-tip sails' tried experimentally by Spillman (1978) on a low aspect-ratio aircraft wing. He observed a substantial reduction of induced drag, especially at high lift coefficients such as those observed in the present paper for circling and slope soaring.

Distribution and movements of frigatebirds

Frigatebirds (Fregatidae) are very different from other seabirds, both morphologically and in a number of other respects. The general biology of the group has been reviewed by Nelson (1975), who considers that their unusual characteristics follow from their specialized food requirements. Apart from their well-known habit of kleptoparasitism, frigatebirds feed mainly by swooping down and snatching food items, usually flying fish or small squid, from the sea surface, without alighting. This relatively time-consuming and unreliable method of feeding leads, according to Nelson, to their unusually long breeding cycles, and their distribution over the 'blue-water tropics', where their favoured food is to be found. It first became clear from the ringing studies of Sibley & Clapp (1967) that *Fregata ariel* ranges widely over the open ocean, and is not confined to the vicinity of land. Nelson (1975) concluded from sighting records and other evidence that this is true of all five species of *Fregata*. He also noted that frigatebirds have never been recorded alighting on the water, and are not suitably adapted to do so. These two observations together imply that frigatebirds must be able, like swifts (Apodidae), to remain airborne continuously, day and night, for extended periods. It would appear that thermals over the sea are the main source of energy enabling them to do this.

It has long been known that convection occurs over the sea, and is used by soaring birds. Woodcock (1940) made detailed observations of herring gulls (*Larus argentatus*) soaring off the east coast of the U.S.A. between 16°–45° N. The gulls soared only if the sea surface temperature was at least 2 °C warmer than the air overlying it. In light winds they circled in thermals which were evidently of the columnar or 'dust-devil' type, whilst in stronger winds they were sometimes able to glide directly into wind, indicating that convection took the form of horizontal vortices.

The trade wind zones

It seems from Woodcock's descriptions of conditions and cloud formations that the good soaring conditions were in the southern part of his study area, in the zone of north-easterly trade winds. It seems likely that the distribution of frigatebirds is in fact limited to the trade wind zones, rather than to the tropics as such, because the meteorological characteristics of those zones provide them with the conditions they require for extended periods of continuous flight with minimum expenditure of energy.

A general description of the weather in the trade wind zones was given by Malkus (1956), who pointed out that these zones cover some 40 % of the earth's surface, compared to about 30–35 % for the zones of mid-latitude westerlies. A review of more recent studies is given by Augstein (1980). The trade wind zones are characterized by▮

'north-easterly winds in the northern tropics, and south-easterlies in the southern tropics. The trade winds thus converge on the equatorial zone which lies between them. Within the trade wind zones, the air is transported equatorward over progressively warmer water, so heating the atmosphere from below, and giving rise to convection. The typical cloud formation is 'trade wind cumulus' consisting of small cumulus clouds whose base remains relatively constant at about 600 m ASL. These look very similar to the cumulus clouds which indicate the presence of thermals over land. Trade wind cumulus differs from cumulus over land, however, in that it shows little diurnal variation. Cumulus over land builds up during the day as the land surface warms, and disperses at night as it cools. The temperature differential between the sea surface and the air over it shows much less diurnal variation, leading presumably to continuing convection at all hours of the day and night. At any rate, trade wind cumulus formations seen at night by moonlight look identical with those seen during the day, and it seems likely that the thermals also continue during the night.

Little seems to be known about upward air velocities in trade wind thermals, but they are most probably modest. Malkus (1953) found that 1–$2\,\mathrm{m\,s}^{-1}$ was typical within the cumulus clouds, with a maximum of $4\cdot3\,\mathrm{m\,s}^{-1}$. Vertical velocities below the clouds would most probably be less. The mean rate of climb of around $0\cdot5\,\mathrm{m\,s}^{-1}$, recorded at Panama, may well be representative of rates of climb likely to be achieved at sea.

Reasons for frigatebird wing shape

As compared to other birds of similar mass, frigatebirds have unusually large wing areas, and unusually large wing spans. These two characteristics do not necessarily occur together, and may be seen as separate adaptations. The large wing area results in a low wing loading, which in turn allows the bird to fly in circles of small radius. If frigatebirds are indeed adapted to use thermals under trade wind cumulus clouds, as suggested above, the implication is that these thermals are particularly narrow. This is a point which could be investigated.

The unusually large wing span is, of course, beneficial for efficient gliding flight, but this may not be its primary function. It results in a low disc loading, which in turn leads to a low minimum power in flapping flight. Although trade wind weather is unusually predictable, there must be occasions when thermals fail, and then the frigatebird's problem is to remain airborne for the lowest possible expenditure of power. Swifts (Apodidae) have the same problem, and they too have evolved unusually long wings in relation to their mass.

Sexual dimorphism

All frigatebird species show marked sexual dimorphism, the males being smaller, and having lower wing loadings than the females. The effect of varying wing loading on soaring performance has been discussed at length elsewhere (Pennycuick, 1971, 1975). A low wing loading allows the bird to fly in small circles, and hence to exploit narrow thermals, but also obliges it to glide slowly in between thermals. A compromise is needed when cross-country performance is important, especially if there is a need to make progress against the wind. Harrington *et al.* (1972) attempted to account for the dimorphism of *F. magnificens* in terms of the wind strengths observed

at different roosts. A more general interpretation is suggested by the work of Diamond (1972, 1973) on the same species. He suggests that the dimorphism extends to the breeding cycle, and that males breed every year, whereas females breed only every other year. He found that the males departed from the breeding colony soon after the chicks were big enough to be left unattended, leaving the females to feed the chicks from then on. This would mean that the females would need adequate cross-country performance for out-and-return foraging trips while raising the young, whilst the males would not. This might well dictate a higher wing loading for females.

CONCLUSION

The comparative picture which emerges is that the brown pelican soars in thermals in the course of movements between roosting and feeding areas, and perhaps on seasonal migrations as well. The black vulture does this too, and also soars as a means of patrolling in search of food. The magnificent frigatebird uses thermals to remain aloft continuously, day and night, over the open sea, and has an unusually low wing loading, presumably for circling in very narrow thermals. Each species has the most efficient (i.e. highest aspect-ratio) gliding wing which can be reconciled with its most difficult take-off requirement. The frigatebird has the easiest take-off requirements (downward take-offs only), and the highest aspect-ratio wings. The pelican requires horizontal take-offs, and has lower aspect-ratio wings with inconspicuous tip slots. The vulture requires climbing take-offs, and has very low aspect-ratio wings with prominent tip slots.

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