WINGBEAT FREQUENCY OF BIRDS IN STEADY CRUISING FLIGHT: NEW DATA AND IMPROVED PREDICTIONS

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Summary

Wingbeat frequencies of 15 species of birds, observed in the field in level, cruising flight were compared with predicted frequencies, calculated according to the formula derived from an earlier sample of 32 species. All of the data were collected by the author, using the same methods throughout. The new observations were predicted well for species with low wingbeat frequencies, but were underestimated at the higher frequencies. The following revised proportionality gave the best fit of the wingbeat frequency (f) to the combined data set of 47 species:

$$f \propto (mg)^{1/2}b^{-17/24}S^{-1/3}I^{-1/8}\rho^{-3/8},$$

where m is the body mass, g is the acceleration due to gravity, b is the wingspan, S is the wing area, I is the wing moment of inertia, and ρ is the air density. As measurements of I were not available for most species, its exponent was combined with those of m and b, by assuming that $I \propto mb^2$. The following equation was fitted to the data on this basis:

$$f = m^{3/8}g^{1/2}b^{-23/24}S^{-1/3}\rho^{-3/8}.$$

These formulae are dimensionally correct, according to the rules derived in the earlier paper, and the equation is also numerically correct as it stands, without requiring a multiplication factor. For allometric comparisons between geometrically similar species, where body mass and wing measurements vary together (including wing moment of inertia), the expected relationship is $f \propto m^{-1/6}$. If the mass alone varies, owing to feeding or consumption of fuel, while the wing measurements and other variables remain unchanged, the expected relationship is $f \propto m^{1/2}$. These relationships apply to any dimensionally correct formula and are not affected by adjusting the coefficients within the dimensional constraints.

Key words: bird, flight, flapping, wingbeat frequency.

Introduction

Limits to frequency variation

The frequency with which a bird flaps its wings in flight cannot be too high, otherwise the force needed to accelerate the wing at each downstroke would be beyond that available from the pectoralis muscle and perhaps would incur the risk of breaking the muscle insertion, or even the humerus. The frequency cannot be too low either, as the strain rate in the muscles must be within a certain range as they shorten, if fuel energy is to be converted into work at an acceptable level of efficiency. A particular bird may vary its wingbeat frequency to some extent, depending on whether it is taking off, cruising horizontally, climbing or descending, but only a limited range of wingbeat frequencies is available for use by any particular individual bird or species. No heron could flap its wings at even the lowest frequency used by a starling. Skilled birdwatchers are well aware of this, consciously or otherwise, and often use small differences of wingbeat frequency to distinguish between similar and closely related species, at distances too great to see plumage details. Although a given bird's wingbeat frequency is under neural control to some extent, one may surmise that its mass and wing morphology, together with some environmental variables such as gravity and air density, define a 'natural' frequency, from which the bird cannot stray too far, in the same way that a pendulum has a natural frequency and can only be driven at frequencies close to this. If a natural wingbeat frequency exists, it does not follow that the bird is obliged to use it at all times. The general expectation would be that the bird would select a wingbeat frequency close to the natural frequency in sustained cruising flight, but might drive its wings above the natural frequency, perhaps to the limits of their structural strength, in high-power manoeuvres such as take-off.

Predicting wingbeat frequency

It is of great interest to be able to predict the frequency at which a particular bird will flap its wings, especially in sustained, level cruising flight, as this is one of the factors that determines the mechanical power output per unit mass of flight muscle (Pennycuick and Rezende, 1984). The simple statistical approach to this problem would be to measure the wingbeat

frequencies of a sample of birds, then use multiple regression analysis to determine how the frequency depends on such variables as body mass, wing span and wing area. However, there are two difficulties in applying this familiar approach to a problem which is partly physical in character. First, some of the independent variables of interest cannot be conveniently manipulated, especially the strength of gravity and the density of the air. Second, and perhaps more important, while the regression results in a predictive formula which may give a useful result, it is not guaranteed to represent the physics of the process correctly. Pennycuick (1990) devised a hybrid method, using a preliminary dimensional analysis to ensure physical correctness. Although this did not produce a unique solution, it identified constraints to which a physically valid solution must conform. Multiple regression was then used to select a solution which fitted the data without violating the physical constraints. The data used to calculate the regression were field observations of wingbeat frequency in level flight, derived from video recordings of 32 species of birds for which estimates of body mass, wing span and wing area had already been collected.

Physical constraints on wingbeat frequency

The dimensional analysis need not be repeated here in full, but an outline of the reasoning will help to show how new data have been used to modify the previous result. The first step was to make a list of variables, which were judged to be likely to affect the frequency, as follows.

Body mass	m
Wing span	b
Wing area	S
Wing moment of inertia	I
Acceleration due to gravity	$\boldsymbol{g}$
Air density	ρ

Air speed is not included in the list, because the birds were all observed in level, cruising flight. They were assumed, in effect, to be flying at a fixed multiple of their minimum power speed, which is compatible with earlier observations of the flight speeds of many species of birds on local flights (Pennycuick, 1982, 1987). If this is the case, then a change in any of the variables m, b, S, $\boldsymbol{g}$ or ρ will cause a corresponding change in the cruising air speed (Pennycuick, 1989), so that, under this restricting assumption, the air speed is not an independent variable. The six selected variables were reduced to five by combining the body mass and gravity as the weight $m\boldsymbol{g}$, so that the assumed proportionality relationship was:

$$f \propto (m\boldsymbol{g})^{\alpha}b^{\beta}S^{\gamma}I^{\delta}\rho^{\varepsilon}, \tag{1}$$

where α, β, γ, δ and ε are dimensionless numbers, whose values are initially unknown. As the wing moment of inertia (I) was unknown for most of the species represented in the field data, it was assumed for purposes of practical calculation that the moment of inertia depends on the body mass and wing span, thus:

$$I \propto mb^2. \tag{2}$$

Table 1. *Values of exponents chosen for proportionality 1*

Variable		Exponent	Pennycuick (1990)	Revised value
Body weight	$m\boldsymbol{g}$	α	1/2	1/2
Wing span	b	β	−2/3	−17/24
Wing area	S	γ	−1/4	−1/3
Moment of inertia	I	δ	−1/6	−1/8
Air density	ρ	ε	−1/3	−3/8

Under this assumption, proportionality 1 can be converted into a form in which I does not appear explicitly, but its influence is represented by modifying the exponents of m and b, thus:

$$f \propto m^{\alpha+\delta}\boldsymbol{g}^{\alpha}b^{\beta+2\delta}S^{\gamma}\rho^{\varepsilon}. \tag{3}$$

The frequency f has the dimensions of inverse time, and therefore the right-hand sides of proportionalities 1 and 3 must have the same dimensions. It was shown by Pennycuick (1990) that this places the following constraints on the values of the five exponents:

$$\alpha = 1/2, \tag{4}$$

$$\delta + \varepsilon = -1/2, \tag{5}$$

$$\beta + 2\gamma + 2\delta - 3\varepsilon = -1/2. \tag{6}$$

To select a particular set of values, conforming to the constraints expressed by equations 4–6, the predicted frequencies were compared with a multiple regression of the observed frequencies on body mass, wing span and wing area. This resulted in the first set of values shown in Table 1 (Pennycuick, 1990). Substituting them into proportionality 1 gives:

$$f \propto (m\boldsymbol{g})^{1/2}b^{-2/3}S^{-1/4}I^{-1/6}\rho^{-1/3}. \tag{7}$$

This was converted into a practical predictive equation, whose right-hand side has the same form as proportionality 3:

$$f = 1.08m^{1/3}\boldsymbol{g}^{1/2}b^{-1}S^{-1/4}\rho^{-1/3}. \tag{8}$$

The exponents are actually the same as in proportionality 7, but since the moment of inertia I is no longer included explicitly, its influence is incorporated into the exponents of body mass and wing span. The dimensionless multiplier 1.08 came from the multiple regression. It was noted that proportionality 7 and equation 8 could be amended by changing the values of the exponents, provided that any new combination of values still conforms to equations 4–6. In the present paper, new field data are added to the original data set, bringing the number of species to 47, on all of which wing measurements and wingbeat frequencies have been measured personally by the author, using the same methods throughout. A new 'best' set of values for the exponents is selected by an improved method, not involving multiple regression.

Materials and methods

Since the earlier paper of Pennycuick (1990), new observations of wingbeat frequency have been obtained on 15

Table 2. *Species observed and wing measurements*

Taxonomic name	English name	Mass (kg)	Span (m)	Area (m²)	Frequency ± S.D. (Hz)	V (m s⁻¹)	λ (m)	H
Diomedea exulans	Wandering albatross	8.55	3.01	0.583	2.49±0.11	15.0	6.02	2.00
Diomedea melanophris	Black-browed albatross	3.08	2.19	0.354	2.97±0.15	13.3	4.48	2.04
Macronectes giganteus/M. halli	Giant petrel	3.24	1.98	0.326	3.14±0.19	15.2	4.84	2.44
Procellaria aequinoctialis	White-chinned petrel	1.23	1.41	0.167	3.93±0.10	–	–	–
Daption capensis	Cape pigeon	0.418	0.875	0.0773	5.61±0.55	12.3	2.19	2.51
Pachyptila desolata	Dove prion	0.155	0.635	0.0469	5.42±0.36	11.1	2.05	3.23
Oceanites oceanicus	Wilson's storm-petrel	0.035	0.396	0.0215	7.65±0.60	10.4	1.36	3.43
Pelecanoides georgicus	South Georgia diving petrel	0.122	0.388	0.0197	12.3±0.64	–	–	–
Pelecanoides urinatrix	Common diving petrel	0.133	0.408	0.0221	12.3±0.64	–	–	–
Phalacrocorax atriceps	Blue-eyed shag	2.23	1.13	0.183	5.85±0.25	–	–	–
Catharacta skua	Southern skua	1.69	1.43	0.241	3.95±0.21	–	–	–
Larus dominicanus	Kelp gull	0.890	1.41	0.228	3.46±0.16	–	–	–
Chionis alba	Sheathbill	0.610	0.822	0.105	6.35±0.29	–	–	–
Anas georgica	South Georgia pintail	0.437	0.682	0.0646	7.62±0.23	–	–	–
Cygnus cygnus	Whooper swan	8.50	2.26	0.589	3.56±0.11	–	–	–

The last three columns are included for comparison with Pennycuick (1990).

V, observed mean air speed from Pennycuick (1982); λ, wavelength; H, advance ratio assuming a stroke angle of 1 rad.

Frequencies based on 63–1118 wingbeats per species (mean 310).

bird species, listed in Table 2. All of these except the whooper swan were South Atlantic seabirds, observed by video recording at sea from the British Antarctic Survey (BAS) ship *RRS James Clark Ross* between 31 December 1993 and 31 January 1994, from the Royal Navy frigate *HMS Norfolk* between 28 February and 2 March 1994, and on land during a stay at the BAS base on Bird Island, South Georgia, from 1 to 27 February 1994. The whooper swans were observed at the Wildfowl and Wetlands Trust's reserve at Caerlaverock, Scotland, between October 1994 and March 1995, also by video. The video recordings were taken with a Panasonic S-7 camcorder on S-VHS-C tape, under the European (PAL) video standard, and were then copied *via* an Amiga A3000 computer, using the genlock on an IV-24 board from GVP. Individual field numbers, generated by the Amiga, were superimposed on each field of the copy, which was made on a Panasonic FS-200 full-sized S-VHS video recorder. On playing back the tape through the FS-200, each field could be examined as a separate picture, identifiable by its field number, giving a time resolution of 1/50 s. In the case of birds that were flap-gliding (i.e. alternately flapping and gliding), the frequency recorded was that observed within a sequence of continuous flapping, not the average frequency over periods of flapping and gliding. Long sequences of continuous flapping were broken into segments of 20 wingbeat cycles, each of which was considered an 'observation'. The methods of counting wingbeat cycles, and of calculating wingbeat frequency and its standard deviation from counts of wingbeat cycles and fields, were the same as described by Pennycuick (1990).

Results and discussion

The ordinate in Fig. 1 is the mean frequency observed in cruising flight, and the abscissa is the predicted wingbeat frequency, calculated from equation 8 (the formula from Pennycuick, 1990). A constant value of 1.23 kg m⁻³ for air density was used for all the predicted frequencies, as all of the birds were observed near sea level, in actual air densities close to this standard sea-level value. A constant value of 9.81 m s⁻² was used for the acceleration due to gravity. If a point lies on the diagonal broken line, the observed and
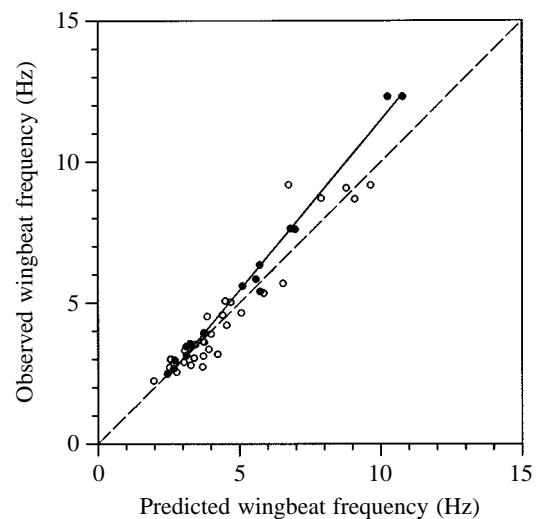

Fig. 1. Observed wingbeat frequency plotted against predicted wingbeat frequency from equation 8 (the formula from Pennycuick, 1990). Open circles, data from Pennycuick (1990). Filled circles, new data from Table 2. Standard major axis line fitted through new data points only, slope 1.21, r=0.994, N=15. The broken line represents a perfect fit of predicted and observed data.

predicted frequencies are the same. It can be seen that the majority of points for the new data lie above this line. The slope of the standard major axis line is also significantly greater than 1 (*P*<0.01), meaning that, although the observed and predicted frequencies agree well for birds with low wingbeat frequencies (large birds, or birds with large wings), the observed frequencies are higher than predicted at the higher frequencies. The two points at the top of the graph are for the two diving petrel species, which, like alcids, have higher wingbeat frequencies than other birds of similar mass, because their wings are adapted for underwater swimming. The predictive formula should be able to take account of any such adaptations, but has underestimated these high frequencies. Fig. 1 suggests that there may be some scope for adjusting the values of the exponents, in search of another valid combination of values, which will bring the predicted and observed frequencies closer together.

Selecting new values for the exponents

The new method of finding the 'best' set of values for the exponents was based on systematically varying these values, always selecting combinations that conformed to equations 4–6. First, it was noted that each of the exponents is confined to a narrow range. α is fixed ($\alpha=1/2$), and the other four exponents must all be negative, since an increase in any one of the corresponding variables (wing span, wing area, moment of inertia or air density) by itself would cause a decrease in wingbeat frequency. In that case, the values of both δ and ϵ are confined by equation 5 to the range 0 to $-1/2$. β and γ are similarly limited by equations 5–6 to a small range of negative values. Each combination was substituted into the expression on the right-hand side of proportionality 3, and this expression was used to calculate a predicted wingbeat frequency for each of the 47 species in the combined data set [from Pennycuick (1990) and Table 2 of this paper]. A standard major axis line was then calculated, relating the observed to the predicted frequencies. Systematically varying the exponents through the permissible ranges, and calculating the standard major axis line for each set of values, caused the slope of the line to vary both above and below 1, and also caused the correlation coefficient to vary up to a maximum of 0.973. The 'best' set of values was chosen according to the following criteria: (1) the slope should be as near 1 as possible, and (2) while satisfying the first condition, the correlation coefficient should be as high as possible. On this basis, the second set of fractional values in Table 1 was chosen, giving a slope of 1.004 and a correlation coefficient of 0.965. Fig. 2 shows the standard major axis line, calculated using these values. It is very close to the broken diagonal line, which represents a perfect fit. No constant of proportionality is needed, since the slope has already been adjusted to 1. The revised practical formula for predicting the wingbeat frequency is:

$$f = m^{3/8}g^{1/2}b^{-23/24}S^{-1/3}\rho^{-3/8}. \qquad (9)$$

This formula can be used for predicting the wingbeat frequency of a species whose mass, wing span and wing area are known,
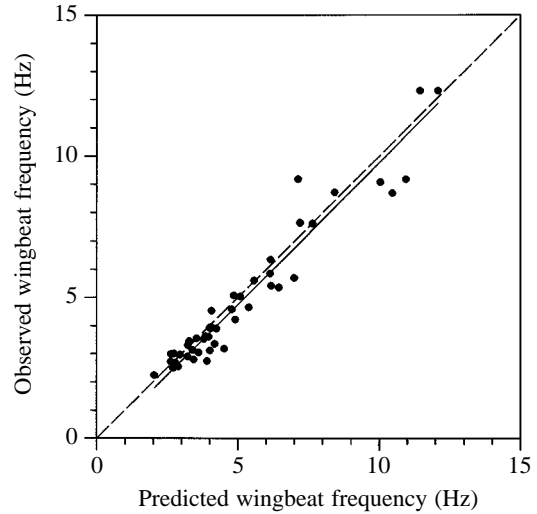

Fig. 2. Observed wingbeat frequency plotted against predicted frequency calculated from the revised formula (equation 9) using the combined data set from Pennycuick (1990) and Table 2. The slope of the standard major axis line is 1.004, *r*=0.965, *N*=47. The broken line represents a perfect fit of predicted and observed data.

but not for predicting the effect of changing the values of individual variables, because the exponents of *m* and *b* are based on the assumption that changes in the values of these variables will also change the wing moment of inertia according to proportionality 2. A change in the body mass of an individual bird in the course of a flight, or of the density of the air through which it flies, is not expected to affect the wing moment of inertia. To predict these effects on the wingbeat frequency, the form of proportionality 1 is required:

$$f \propto (mg)^{1/2}b^{-17/24}S^{-1/3}I^{-1/8}\rho^{-3/8}. \qquad (10)$$

Allometry of wingbeat frequency

When comparing a range of different species, the wingbeat frequency does not scale according to the exponent of *m* in either equation 9 or proportionality 10. This is because the wing span, wing area and wing moment of inertia are all functions of the mass and have to be included in the allometric argument. Specifically, in a series of geometrically similar birds (if any such existed), these variables would depend on the mass as follows:

$$b \propto m^{1/3}, \qquad (11)$$

$$S \propto m^{2/3}, \qquad (12)$$

$$I \propto m^{5/3}. \qquad (13)$$

Combining these with the the exponents of proportionality 10, the allometric relationship is:

$$f \propto (m)^{1/2}(m^{1/3})^{-17/24}(m^{2/3})^{-1/3}(m^{5/3})^{-1/8} = m^{-1/6}. \qquad (14)$$

Actually, the same result is obtained by using the original values of the exponents, from Pennycuick (1990), or any set of values conforming to equations 4–6. This result was also predicted on the basis of a somewhat different argument by

Pennycuick (1975), for cruising flight. For maximal exertion, as in take-off, the wingbeat frequency would be expected to vary with the −1/3 power of the mass, rather than the −1/6 power, following the classical argument of Hill (1950), which was based on the different assumption that the wingbeat frequency is limited by the mechanical strength of bones, tendons and muscles. The consequence of these different slopes is that, at some limiting value of the mass, the maximum wingbeat frequency (limited by structural strength) is only just sufficient to sustain cruising flight. If the mass increases further, cruising flight is no longer possible.

Effect of changing mass on wingbeat frequency

The effect of feeding, or using up fuel during a long flight, is to alter the mass while leaving the wing span, area and moment of inertia unchanged. This is not an allometric problem. The expected effect is expressed by the exponent α, and is that the wingbeat frequency should vary with the square root of the mass, other variables being held constant:

$$f \propto m^{1/2}. \qquad (15)$$

It remains to be seen whether birds actually do change their wingbeat frequencies according to proportionality 15, in response to changes of body mass. It is possible that they might not. If a bird's flight muscles were adapted to operate efficiently at a particular frequency suitable for typical combinations of the variables in equation 9, it might then not be able to deviate far from that frequency. It would be interesting to know whether individual birds do in fact adjust their wingbeat frequencies in response to changes of mass and air density, as this affects the power output available from the flight muscles.

Brent geese

Evidence that such an effect exists was reported by Guðmundsson *et al.* (1995), who observed the wingbeat frequency of brent geese (*Branta bernicla*) in Iceland in spring (mean 5.5 Hz), when the geese were about to set off across the Greenland ice cap to their breeding grounds in the Canadian arctic. The mean body mass at this stage of the migration cycle was estimated to be 2.01 kg. Brent geese from the same population had earlier been observed by Hedenström and Alerstam (1992) passing south-east Sweden in autumn, when their mean wingbeat frequency was 4.5 Hz, and mean mass 1.36 kg. Both populations were observed on the coast, at sea level, so that the air density may be assumed to have been near the standard sea level value of 1.23 kg m^{-3}. According to proportionality 15, the wingbeat frequency is expected to increase by a factor equal to the square root of the mass ratio, i.e. $\sqrt{(2.01/1.36)}=1.22$. The reported frequency increased by exactly this factor.

Whooper swans

The above observation suggested that it might be possible to exploit the effect of mass on wingbeat frequency, as an indirect method of estimating the mass of wintering whooper

Table 3. *Wingbeat frequencies (Hz) of whooper swans at Caerlaverock in early, middle and late winter*

Date		Level flight	Take-off	Climb-out
1 Nov 1994	Mean	3.53	4.03	3.97
	S.D.	0.097	0.194	0.132
	N	56	7	6
6 Feb 1995	Mean	3.58	3.96	3.98
	S.D.	0.086	0.201	0.199
	N	53	32	29
14 Mar 1995	Mean	3.57	3.89	3.98
	S.D.	0.118	0.185	0.185
	N	105	50	43
			Take-off + Climb-out	
All dates	Mean	3.56	3.95	
	S.D.	0.107	0.191	
	N	214	167	

swans (*Cygnus cygnus*), without catching them as is usually necessary. With this in mind, video recordings were made of whooper swans at the Wildfowl and Wetlands Trust's reserve at Caerlaverock, Scotland, on three occasions during the winter of 1994–1995, as listed in Table 3. The majority of the swans arrived at Caerlaverock from Iceland in the last week of October, a crossing which would require a swan of average size to consume around 2 kg of fat (Pennycuick *et al.* 1996). They were assumed to be light when their wingbeat frequency was first observed on 1 November, soon after their arrival in Scotland. On the second occasion (6 February), the swans had been feeding well, but were not about to migrate for another 4–6 weeks. On the third occasion (14 March), some swans had already left for Iceland, and the rest were expected to depart soon afterwards, so their mass was assumed to be augmented by fuel for the crossing. On each of these three occasions, the observations of wingbeat frequency were divided into three categories, level flight, take-off (meaning the first five wingbeats during the ground or water run, starting with the first full wingbeat) and climb-out (starting with the first full wingbeat after the feet were lifted off the ground or water). These samples were compared with each other using the *d*-test of Bailey (1959). No significant differences were found between take-off and climb-out on any date, and these two categories were therefore combined. The mean of the combined take-off/climb-out sample for all three dates (3.95 Hz) was significantly higher ($P \leqslant 0.01$) than the mean for level flight for all dates (3.56 Hz). However, no significant differences were found between means in any category, when comparing different dates.

Either the swans did not increase their mass during the course of the winter, which seems unlikely, or else there was no effect of mass on wingbeat frequency. If the latter was the case, then there must be some reason for the absence of any effect in whooper swans, when evidence that the expected effect does indeed occur was seen in brent geese. A possible

explanation is that these large birds are near the limits of performance, even when flying horizontally near their minimum power speed. Table 3 shows that they are capable of increasing their wingbeat frequency by about 11 % over the cruising value, for a few seconds at take-off, but their muscles may not be able to maintain the higher frequency in sustained cruising flight. The nature of these limitations, which result directly from large size, is further considered by Pennycuick *et al.* (1996).

Conclusion

There are limits to the consistency that can be claimed for the data presented here, even though all were collected personally by the author, using the same methods throughout. As is usual with field observations, the estimates of mass, wing span and wing area are means of samples for each species. These measurements were not known for individual birds. The birds were assumed to be flying level, at a fixed multiple of their minimum power speeds, but there was no way to check this, as the flight conditions were uncontrolled. Such data are adequate for establishing broad inter-species relationships, but when it comes to investigating the effect of changing body mass or air density on the wingbeat frequency of an individual bird, observations under controlled conditions will be needed on birds whose individual measurements are known. It may be possible to study the effect of mass changes in individual birds trained to fly for prolonged periods in a wind-tunnel, while Lishman's (1994) success at training birds to follow a microlight aircraft suggests that the effect of air density might be investigated by observing the same bird flying at different altitudes. The effect of gravity should not be forgotten just because it cannot be manipulated, although a direct test may have to wait until interstellar travel is more readily available to ornithologists.

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