AERODYNAMIC THEORIES OF FLIGHT
VERSUS PHYSIOLOGICAL THEORIES

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In 1963 I reviewed published studies of the rate of weight-loss in small birds while migrating, and suggested a "reasonable average" for their power consumption during flight (Nisbet 1963). Raveling and Lefebvre (1967) have reviewed the data again, incorporating two studies of pigeons published in the interim, and they suggested that my figure for small birds was much too low. While their conclusion may be correct, it is not in fact supported by their statistical analysis.

There are three serious objections to their treatment of the published data, as summarized in their Figure 1.

(1) They used two theoretical calculations (points C and G) to support their own theory, which is contrary to all principles of scientific method. In fact, the modification of Odum's theory which they quoted (point G) is almost identical to their own theory, so its use to support theirs is entirely circular.

(2) They included an experimental study of a hovering hummingbird (point A), although hovering flight is mechanically different from forward flight, and is known to obey different scaling laws (Greenewalt 1962).

(3) They took an unweighted average of their data, although there are marked differences in reliability between different measurements. In fact, standard errors have been attached to most of the estimates (Nisbet 1963: Table 9), and at least two of them deviate significantly from Raveling and Lefebvre's regression line, which is therefore unacceptable as a statistical fit to the data.

Table 1 summarizes the estimates of power consumption in forward flight which were used by Raveling and Lefebvre, and includes an estimate of the statistical weight to be attached to each estimate on the basis of random errors in measurement. Assuming that power consumption in flight is proportional to the n 'th power of total body-weight, the *weighted* estimate of n obtained from the data in Table 1 is $0.94 \pm .029$. This figure is midway between the two extreme theoretical predictions, 0.744 from physiological theory (Raveling and Lefebvre 1967) and 1.167 from aerodynamic theory (Wilkie 1959); it is significantly different from both. It is markedly different from Raveling and Lefebvre's estimate of 0.799, because they included some high figures for small birds which were either non-comparable (A, C and G) or of low statistical reliability (B and J).

My figure of 0.94 is the best statistical estimate of n available from the measurements of free-flying birds in Table 1. It is not necessarily a good estimate, however, because there were systematic

TABLE 1. PUBLISHED ESTIMATES OF POWER CONSUMPTION IN FREE-FLYING BIRDS

Estimate*	Species	Total weight (g.)	Power consumption (kcal./hr.)		Statistical weight
			Mean	% standard error	
B	*Vermivora peregrina*	10.9	1.83	50	0.3
D	*Erithacus rubecula*	16.3	1.51	17	3
D2**	*Erithacus rubecula*	16.3	1.45	13	5
D3**	*Regulus regulus*	5.6	0.41	55	0.2
E	*Dendroica striata*	19.0	1.02	13	5
F	*Melospiza melodia*	21.9	1.53	20	2
H	*Oenanthe oenanthe*	31.0	3.82	30[a]	0.9
I	*Oenanthe oenanthe*	34.5	2.45	30[a]	0.9
J	*Hylocichla ustulata*	32.0	5.47	33	0.7
K	*Columba livia*	254	20.4	9[b]	10
L	*Columba livia*	384	22.0	9	10

*Letters refer to Figure 1 in Raveling and Lefebvre (1967), where the original references were given. Estimates cited by Dolnik and Blumenthal (1964) are excluded from this table, but are discussed in the text.
**Estimate not used by Raveling and Lefebvre, but given in the sources quoted by them.

[a]Conservative guess.
[b]Not given in the original paper, but calculated from the data therein.

errors in most or all of the measurements. The most general systematic error is that the measurements on small birds were uncorrected for water-loss (whereas the measurements on pigeons were corrected): hence we would expect the data to overestimate the power consumption of small birds (and hence underestimate n). On the other hand, independent measurements by Tucker (1966) of the metabolism of a budgerigar flying in a wind-tunnel gave values much higher than those in Table 1. Russian work on small birds (reviewed by Dolnik and Blumenthal 1964) has also given estimates spread over a wide range. It is not yet clear whether the discrepancies between different measurements represent experimental errors, interspecific differences, or variations in the performance of the same species under different conditions. Thus, on experimental grounds, the value which should be adopted for n is still in doubt.

On theoretical grounds, Raveling and Lefebvre's theory is open to serious objections. It is based on empirical physiological rules (Brody 1945, Hemmingsen 1960) which apply also to men and horses; however, horses do not fly, and even man finds it difficult (Wilkie 1959). The power required for flight is a function of the aerodynamic properties of the bird, and it is hard to understand why it should be proportional to basal metabolism, which is a function of its physiology and thermal insulation. Flight may be

"hard work" for a turkey, but it is not necessarily *equally* "hard work" for a kinglet.

Consider a swan weighing 10 kg. On Raveling and Lefebvre's theory, its power consumption in flight should be 170 times that of a warbler weighing 10 g. Yet its flight muscles weigh 1,000 times more (Greenewalt 1962). Are its muscles really six times less powerful? Assuming that the swan flies 2.5 times faster, its lift-drag ratio must, on their theory, be 15 times that of the warbler. Are its wings really 15 times more efficient?

For a large bird such as a swan, flight must indeed be "hard work," in the sense that the power required is a large multiple of the resting metabolism; yet swans are long-distance migrants. How do they supply their muscles with oxygen? How do they keep cool? How do they conserve water? These are interesting physiological questions, and they should not be dismissed as trivial.

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