Wilson Bull., 97(3), 1985, pp. 306–318

AN AERODYNAMIC BASIS FOR SELECTING TRANSMITTER LOADS IN BIRDS

DONALD F. CACCAMISE AND ROBERT S. HEDIN

With the development of small radio transmitters, the study of animal movements under natural conditions has expanded dramatically. For most large species (>200 g), the effects of carrying a transmitter can be minimized by adjusting the size of the transmitter package. For small animals the ratio of transmitter weight to body weight is difficult to control, however, because of limitations in the size of transmitters and batteries. For flying animals aerodynamic requirements make the size of the transmitter package particularly important. An informal standard appears to have emerged for flying animals of limiting the size of the transmitter package to ≤5% of body mass. This loading is recommended widely and is adopted commonly (Cochran 1980), although the rationale for selecting 5% as the upper limit is not discussed in the literature.

Transmitters used on small birds consist of 3 basic components: (1) transmitter and antenna, (2) battery, and (3) packaging (potting material plus harness or adhesive). The weight of the transmitter and packaging can be reduced only very little, but together they generally weigh much less than the battery. Battery size can be varied; however, smaller batteries provide shorter useful field lives. In most applications involving birds, when the battery is exhausted, the radio is lost and the experiment is terminated. It is expensive (labor and capital) to equip birds with transmitters, and there are scientific benefits in maximizing the length of the observation period on individual subjects.

Another important concern is the effect of the transmitter on overall energy balance and behavior of the subject. Energetic costs of powered locomotion increase with additional weight, and in flight the increase can be substantial. Increases in energy demand are likely to influence behavior. Estimates of the added transportation costs of transmitters can be helpful in selecting transmitters of appropriate size and may also aid in interpreting behavioral responses of experimental subjects. A method is needed to select transmitter size according to both the flying ability of experimental subjects and the energetic cost of transport. Such an approach would greatly increase the efficiency of telemetry studies on birds.

For reasons we will explain below, transmitter weights based on a fixed percentage of body weight (e.g., 5%) affect flight characteristics of large birds more than those of small birds (Tucker 1977). Also, use of a fixed percentage of body weight provides no easy method of estimating the

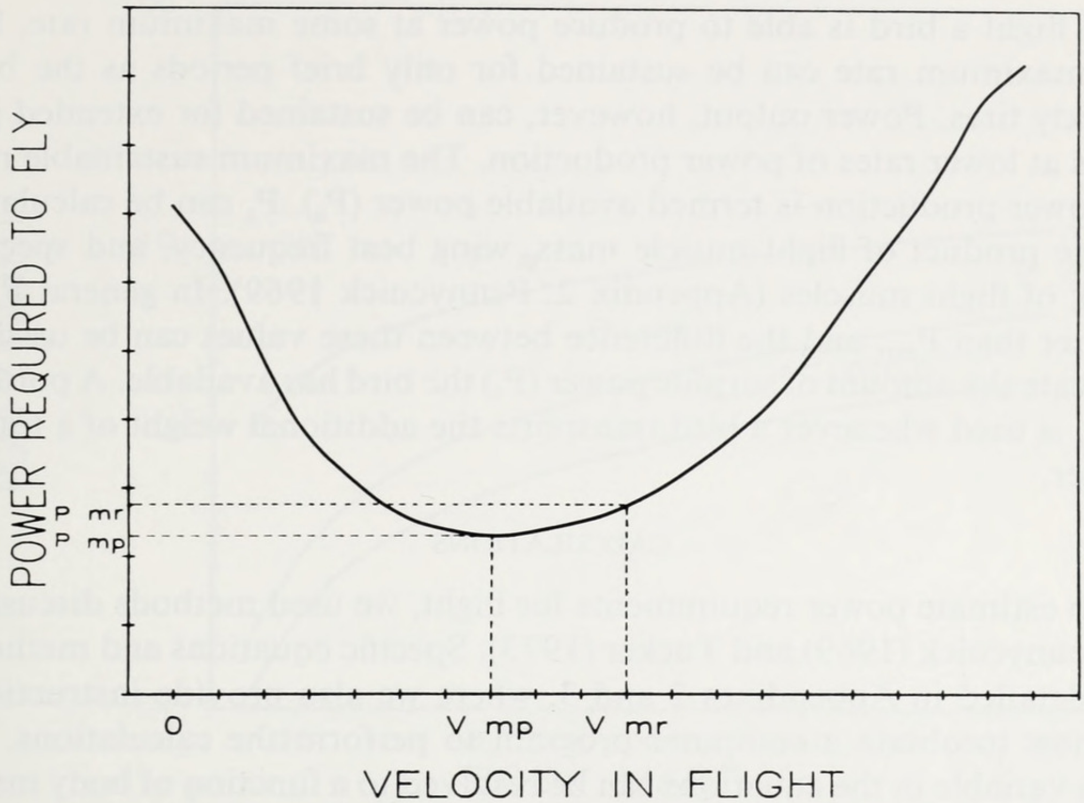

FIG. 1. The solid line represents the generalized relationship between flight velocity and power requirements for flight. The upper and right broken lines illustrate the relationship between V_{mr} and P_{mr}. V_{mp} is the velocity requiring the minimum amount of power (P_{mp}) necessary to fly in level flight (after Pennycuick 1969).

energetic cost of transporting the transmitter. We have developed a method to select transmitter weights based on flight characteristics. As the method is based on power requirements for flight, estimates of the added cost of transportation due to the transmitter can be made. We provide a general method based solely on body mass and indicate how estimates can be refined for individual species by taking simple measurements of wing morphology and wing beat frequencies.

BIRD FLIGHT

The power required for a bird to fly varies with flight velocity. At very low velocities (e.g., hovering) power requirements are very high, at intermediate velocities power requirements are low, and at high velocities power requirements are again high (Fig. 1). Within the range of intermediate velocities for any species, there is a particular velocity at which the bird can fly most efficiently; that is, it can travel the greatest distance per unit of energy expended (Pennycuick 1969). This is termed the veocity of maximum range (V_{mr}) (Appendix 1). Power required to fly at V_{mr} is P_{mr}.

In flight a bird is able to produce power at some maximum rate, but the maximum rate can be sustained for only brief periods as the bird quickly tires. Power output, however, can be sustained for extended periods at lower rates of power production. The maximum sustainable rate of power production is termed available power (P_a). P_a can be calculated as the product of flight muscle mass, wing beat frequency, and specific work of flight muscles (Appendix 2, Pennycuick 1969). In general P_a is greater than P_{mr}, and the difference between these values can be used to indicate the amount of surplus power (P_s) the bird has available. A portion of P_s is used whenever a bird transports the additional weight of a transmitter.

CALCULATIONS

To estimate power requirements for flight, we used methods discussed in Pennycuick (1969) and Tucker (1973). Specific equations and methods are detailed in Appendixes 2 and 3, where we also provide instructions on how to obtain a computer program to perform the calculations. As each variable in the equations can be resolved to a function of body mass, we performed our calculations using these allometric relationships. Such relationships reduce the variation among a large number of individuals to a single value. Therefore, the results of our calculations using allometric relationships represent estimates for dimensionally "average birds." These are useful for demonstrating general relationships, but estimates for any specific species can be greatly improved by taking several simple measurements (Appendix 3).

Body mass of small birds generally shows considerable diurnal and seasonal variation resulting primarily from changes in fat accumulation. In our calculations we wanted to be sure of developing conservative estimates for flight abilities in order to minimize the chance of overloading any bird. We began by defining base mass (m_b) as a minimum level representing birds having empty stomachs and little fat. For a given species, certain characteristics such as wing size, mass of flight muscle, and wing beat frequency remain relatively constant irrespective of changes in body mass. Calculations for these values were based on m_b (Appendix 2).

For small birds, changes in body mass due to fat accumulation can exceed 50% of m_b (e.g., Odum et al. 1961). Adjusting m_b to reflect possible increases in fat accumulation assures conservative estimates of flight abilities. We calculated an adjusted body mass by increasing m_b by 50%. The adjusted mass ($m_a = 1.5m_b$) was used in all calculations except those involving morphological relationships (see above and Appendix 3). In working with individual species, size of the adjustment can be changed

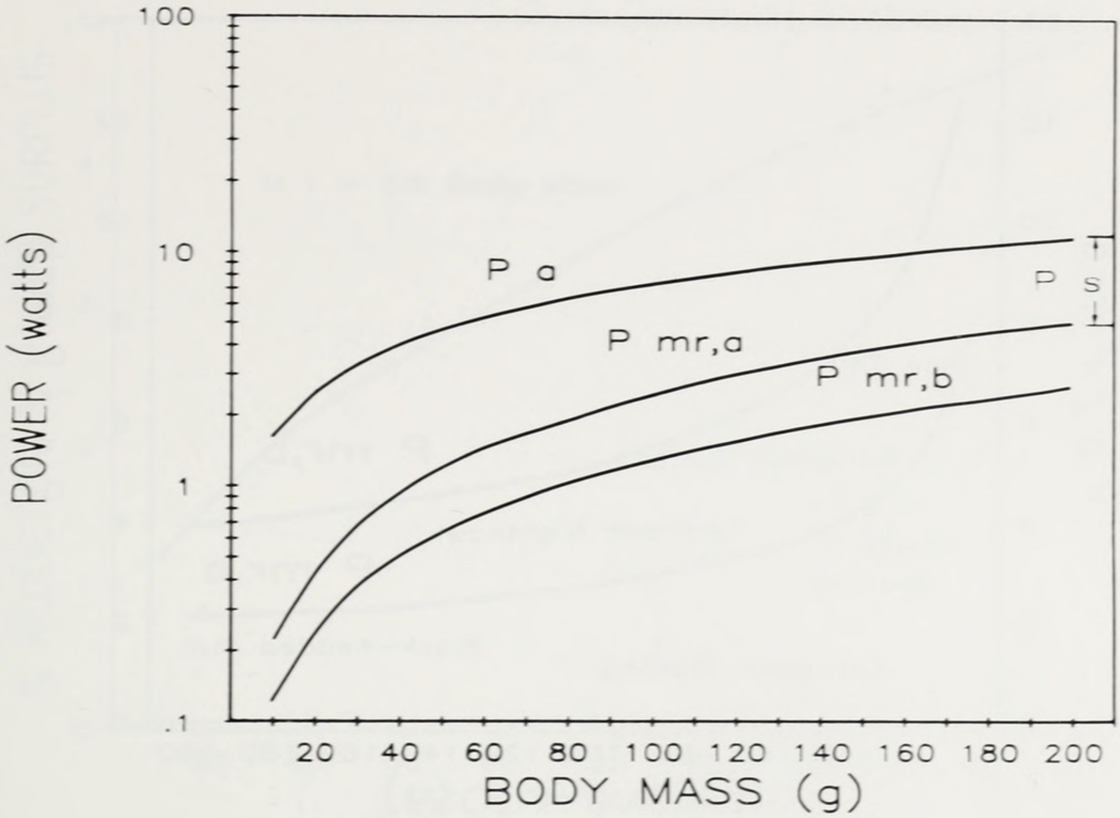

FIG. 2. The top line represents the total power available (P_a) for flight in relation to body mass. The bottom 2 lines are the power required to fly at V_{mr} for birds at base mass ($P_{mr,b}$) and adjusted mass ($P_{mr,a}$). Each relationship increases with mass, but $P_{mr,b}$ and $P_{mr,a}$ increase more rapidly. Thus, P_a and $P_{mr,b}$ converge at about 4645 g. S = surplus power.

to reflect the expected range of variation in m_b that would normally occur during the experiment.

Because power requirements vary with flight velocity, it was necessary to select a single velocity on which to base calculations. Hovering flight and flight at very slow speeds are based on unique aerodynamic relationships, so we excluded these from consideration (Pennycuick 1969). It has been suggested (Schnell and Hellack 1979) that birds most often fly at or below their most efficient speed. We, therefore, selected V_{mr} as the basis for all calculations.

In flight a bird produces drag in proportion to the size of its frontal area. Attachment of a transmitter increases drag by increasing frontal area. We included a function in the model to account for increased frontal area resulting from the transmitter (Appendix 2, equation 6). The effect increases with transmitter mass. This again provides for conservative estimates of flight capabilities.

RATIONALE

Larger birds are able to produce more power than smaller ones, so P_a is an increasing function with body mass (Fig. 2). Similarly, power re-

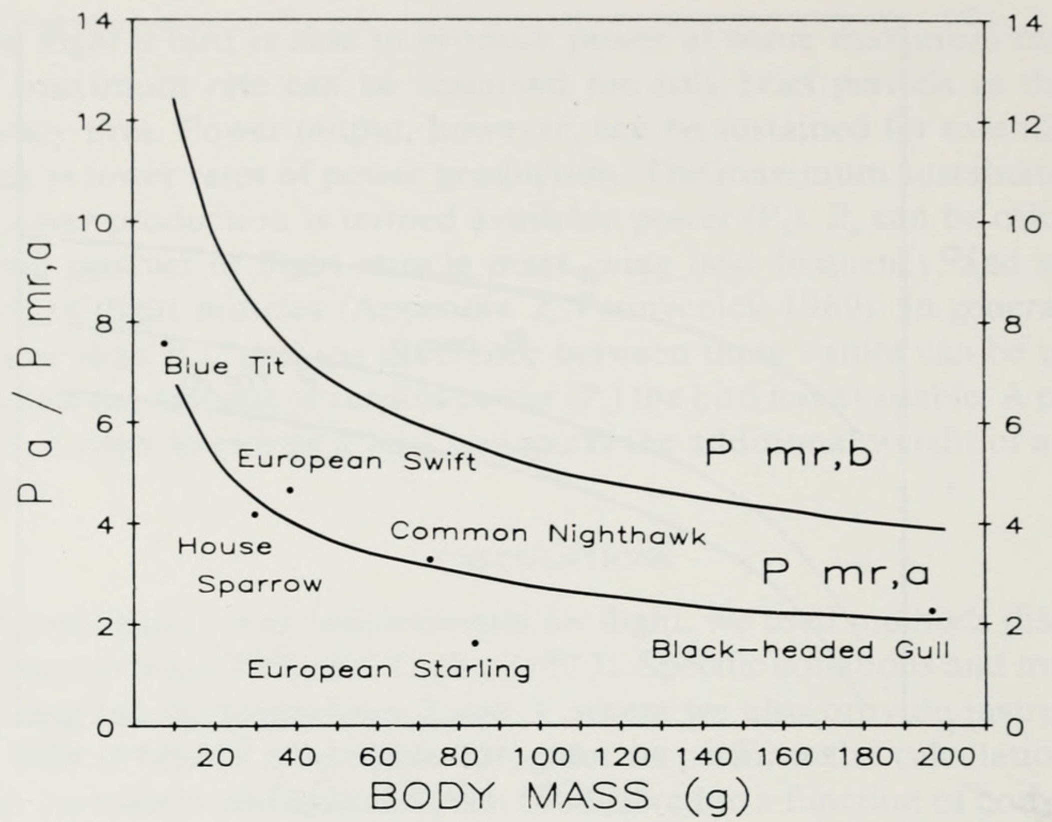

FIG. 3. The ratio of surplus power (P_s) to power required to fly at V_{mr} ($P_{mr,a}$). The upper line represents birds at base mass (m_b) and the lower line adjusted mass (m_a). This ratio provides a relative measure of the amount of surplus power available according to body mass and illustrates that small birds can carry much larger loads relative to their body mass than large birds. Measurements for the illustrated species come from Caccamise 1974 (Common Nighthawk, *Chordeiles minor*) and Greenewalt 1962 (Blue tit, *Parus caeruleus*; European Swift, *Apus apus*; House Sparrow, *Passer domesticus*; European Starling, *Sturnus vulgaris*; Black-headed Gull, *Larus ridibundus*).

quired to fly at the most efficient speed ($P_{mr,b}$), while lower than P_a, also increases with body size. The power curve using adjusted mass ($P_{mr,a}$) is identical to that using m_b, except it is elevated. This indicates increased power requirements when a bird is heavier (Fig. 2). In our calculations, the difference between amount of power needed to fly at V_{mr} ($P_{mr,a}$) and amount of power available (P_a) is termed surplus power (P_s). It is represented by the magnitude of the difference between the two curves (Fig. 2).

As $P_{mr,b}$ increases faster than P_a, these are convergent functions, and they eventually meet. This point represents the largest dimensionally average bird that can fly continuously at V_{mr}. Our estimates indicate that this would happen at a base mass of 4645 g. A dimensionally average bird of this size would have no surplus power when traveling at V_{mr} (i.e., $P_s = 0$). It would not be able to carry any additional weight without producing power at rates greater than P_a. While power could be produced for short intervals at such rates, sustained powered flight would not be

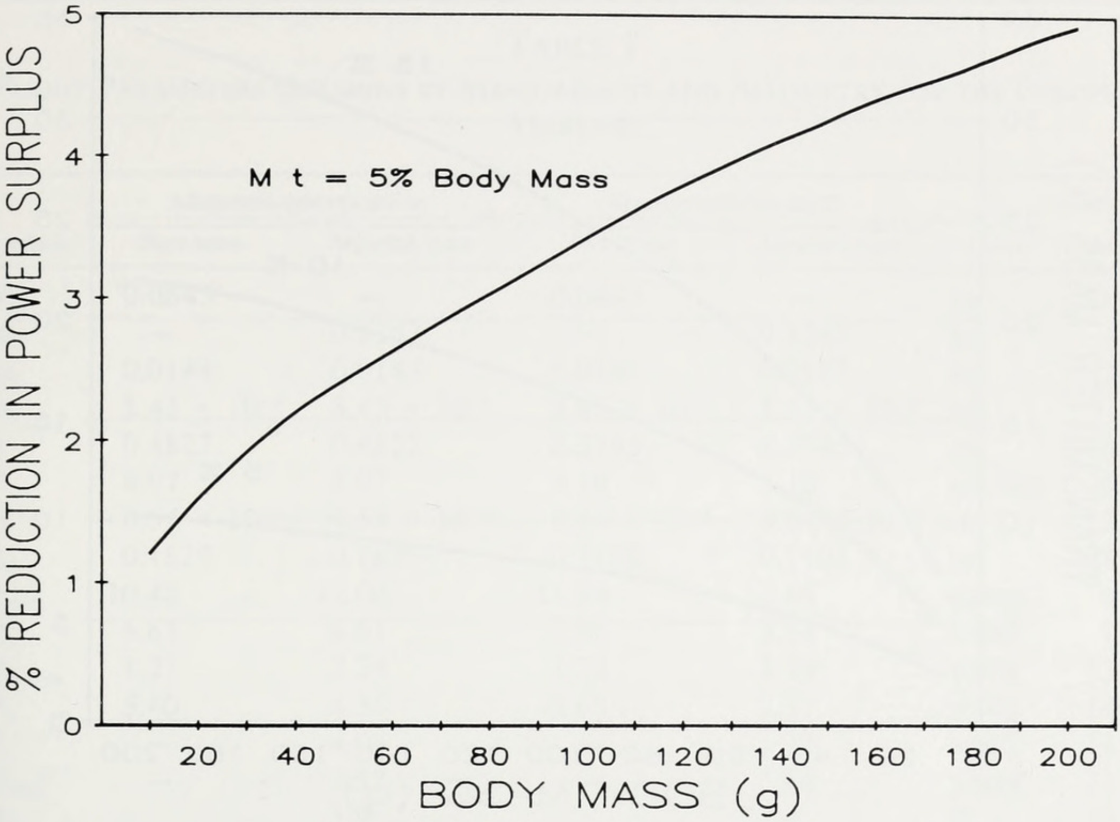

FIG. 4. Percent reduction in P_s according to body size (m_b) when transmitter is 5% of body mass. Selection of transmitter size using a single percentage of body size results in relatively greater reductions in power surplus for large birds than for small birds.

possible at velocities as high as V_{mr}. By comparison, P_a for small birds is much greater than $P_{mr,b}$, so surplus power is relatively large (Fig. 2).

The relative difference in P_s between large and small birds is the result of scaling effects. For example, differences in mass between large and small birds are relatively greater than differences in external dimensions. This is illustrated by the relationship between wing span and mass (Appendix 2, equation 4) where wing span increases with mass to the 0.33 power.

The ratio of $P_a/P_{mr,a}$ provides a means to evaluate the relative magnitude of P_s (Fig. 3). For example, species in the 20–30 g range can produce sufficient power to transport loads several times their body mass and still remain below P_a. As body mass increases, the power ratio declines until P_a and $P_{mr,b}$ are equal (body mass = 4645 g) when the power ratio equals 1 and power surplus equals 0.

P_a is determined using morphological characteristics, so it is constant for an individual bird with fixed dimensions or for a species if we use average dimensions. The effect of adding a load in the form of a transmitter is to increase the amount of power required to fly at a given speed (including V_{mr}). The additional power requirements reduce P_s because $P_{mr,a}$

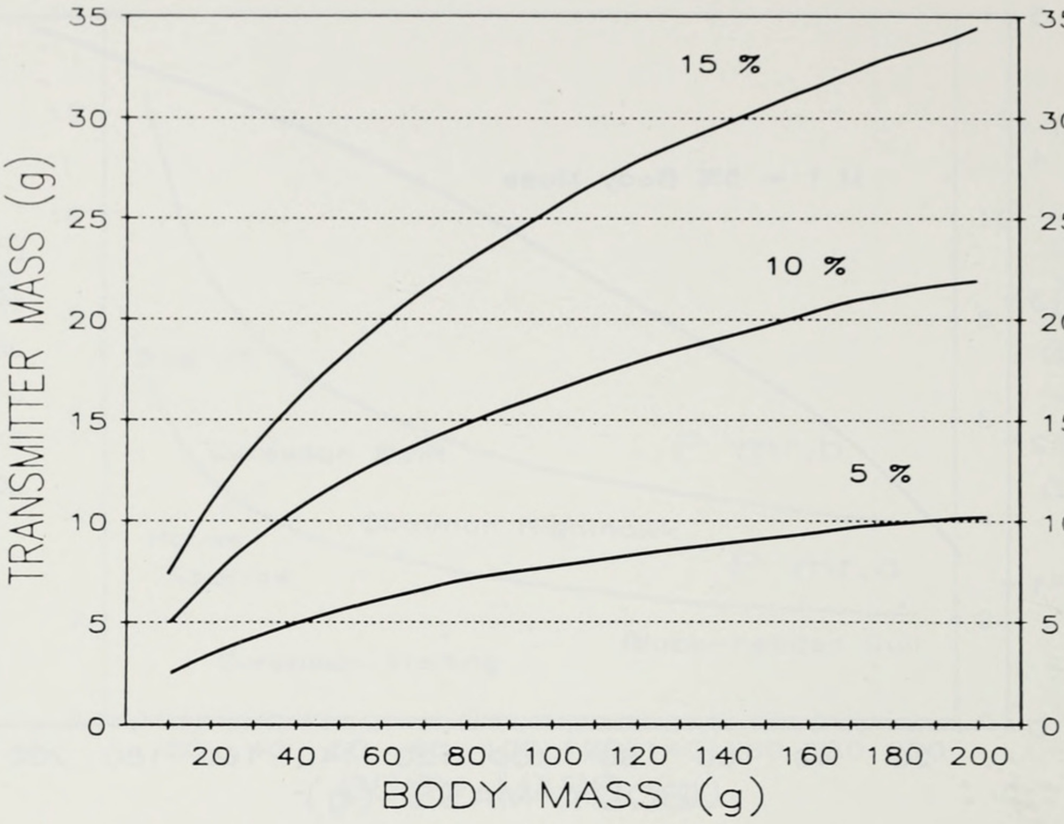

FIG. 5. The 3 lines represent the relationship between body mass (g) and transmitter mass (g) resulting in 5%, 10%, and 15% reductions in power surplus. These relationships can be used to select transmitter size according to the predicted decrease in power surplus caused by the added load. While these values represent good estimates for "average" birds, estimates can be improved for individual species by calculating values based on several simple measurements of wing morphology and flight characteristics (Appendix 3).

is elevated to a new higher level. As power required for flight is proportional to mass, adding to body mass by a fixed proportion will increase power requirements the same relative amount irrespective of body size. Therefore adding a transmitter weighing a fixed percentage of body mass increases power requirements the same proportionate amount for any sized bird (ignoring the slight effect of added transmitter drag). For example, equipping a 50-g bird with a 2.5-g (5% of body mass) transmitter will increase $P_{mr,a}$ by 7.7%. Likewise a 10-g transmitter on a 200-g bird will also increase $P_{mr,a}$ by about 7.7%.

A bird's ability to carry additional weight is determined by the resulting proportionate decline in P_s. Because P_s decreases with increasing body mass, adding a load as a fixed percentage of body mass reduces P_s relatively more for large birds than for smaller ones (Fig. 4). This results in relatively conservative loadings for small birds and liberal loadings for large birds. The use of a fixed percentage of body mass, therefore, does not result in a uniform effect over a range of body sizes.

For a bird of any given mass, it is possible to determine the transmitter

TABLE 1
FLIGHT PARAMETERS OBTAINED BY MEASUREMENT AND ALLOMETRY FOR THE EUROPEAN STARLING

Symbols	Allometric determination: Base mass	Allometric determination: Adjusted mass	Measurement (in part)[a]: Base mass	Measurement (in part)[a]: Adjusted mass	Units	Equation or source[b]
m_b	0.0845	—	0.0845	—	kg	G
m_a	—	0.1267	—	0.1267	kg	—
m_f	0.0144	0.0144	0.0185	0.0185	kg	2, G
m_t	8.45×10^{-3}	8.45×10^{-3}	8.45×10^{-3}	8.45×10^{-3}	kg	—
b	0.4827	0.4827	0.3745	0.3745	m	4, G
f	8.07	8.07	5.10	5.10	no./sec	5, G
A	6.54×10^{-4}	8.54×10^{-4}	6.54×10^{-4}	8.54×10^{-4}	m^2	3, T
S_d	0.1829	0.1829	0.1101	0.1101	m^2	8
V_{mr}	10.48	12.00	11.89	13.63	m/sec	9
P_a	6.61	6.61	5.38	5.38	watts	7
$P_{mr,b\|a}$	1.21	2.24	1.72	3.19	watts	13
P_s	5.40	4.36	3.65	2.17	watts	14
P_s'	—	4.04	—	1.72	watts	14
$P_{mr,a}'$	—	2.57	—	3.66	watts	13
R_p		5.9		12.4	%	15

[a] Measurements from the literature were used where available, otherwise parameters were determined allometrically as indicated.
[b] Allometric equations are referred to by numbers corresponding to equations in Appendix 2. Literature sources are referred to by letters: G = Greenewalt 1962, T = Tucker 1973.

mass that will result in any particular reduction in P_s. We performed this process over a series of body sizes and for reductions in power surplus of 5, 10, and 15% (Fig. 5). The curves increase rapidly over the smaller body sizes but quickly level off. This results from the relatively large P_s of small birds as opposed to large ones. Thus, for a given reduction in surplus power, a small bird can carry a greater proportion of its body weight than a large bird. For example, allowing a 15% reduction in P_s, a 20-g bird can carry a transmitter weighing over 50% of its body mass, while a 200-g bird can carry only 8% (Fig. 5).

Fig. 5 can be used to estimate the relative cost of transporting a transmitter by any bird weighing less than 200 g. The initial step is to decide the amount of reduction in surplus power that is appropriate for the particular experiment. As an initial guideline, the values represented in Fig. 4 indicate levels of reduction that result from the generally accepted loading of 5% of body mass. For example, an 80-g European Starling (*Sturnus vulgaris*) carrying a 4-g transmitter (5% of m_b) (Fig. 4) would give up only about 3.2% of its surplus power. Starlings are able to carry much heavier loads with no apparent effect on travel between foraging and roosting sites, as we have had them carry transmitters equal to about

8% of m_b (m_b = 80 g, m_t package = 6.5 g) for as long as 133 days (Caccamise et al. 1983). If it is decided that a 5% reduction in P_s is acceptable, then in Fig. 5 at a body mass of 80 g, the 5% line corresponds to a transmitter mass of 6.8 g.

These values are only approximations, as the relationships shown were determined allometrically for average-size birds. Values that better represent individual species can be calculated using equations provided in Appendix 2. Accuracy of the generalized relationships for individual species depends on how closely the flight characteristics of each particular species approach average values. In Fig. 3, the points represent values calculated from actual measurements of birds obtained from the literature, while the lines were determined entirely from allometric equations. Some species were quite close to predicted values while others were not.

In Table 1 we compare pertinent flight parameters for the European Starling obtained by measurement and allometry. In Fig. 3 the starling is not close to the line representing "average" birds. Therefore, this species illustrates the process of calculation as well as sources of variation between measured and allometric values. The greatest differences are in overestimates of wing span and flapping rate by the allometric equations. The overall result is that P_a is lower and $P_{mr,b,\ and\ a}$ are higher. This leads to an underestimate of the transmitter effects by the allometric equations.

CONCLUSIONS

The aerodynamics of bird flight are certainly too complicated to be interpreted in terms of a single measure like P_s. There are yet many factors that are only poorly understood. For instance, the large P_s of small birds indicates that they can carry several times their body weight while maintaining $P_{mr,a'}$ below P_a, but there is no way to predict the importance of such a large surplus in their normal activities. A large P_s probably contributes to specialized skills such as take-offs, landings, and general maneuverability. Also, how and where the transmitter is attached are important, as changes in the center of gravity will affect flight characteristics. Although P_s does provide a method to estimate a bird's ability to transport additional weight, its relationship to other aspects of flight awaits further research. Notwithstanding its shortcomings, this method seems to be a suitable approach for estimating the impact of a transmitter on power requirements for flight, and is likely to provide a better basis for determining transmitter size than methods used in the past.

SUMMARY

An accepted practice in radio telemetry studies is to limit transmitter size to 5% of body mass irrespective of bird size. This approach is unsatisfactory because it (1) ignores aero-

dynamic relationships indicating that small birds can carry loads equaling a larger proportion of their body mass than large birds, and (2) fails to provide an estimate of energetic costs of transporting the transmitter. We developed a method to select transmitter mass based on estimates of power requirements for flight and total power available for flight. We provide a general method based only on body mass, but we also show how estimates can be improved for individual species by taking several simple measurements.

A minimum value for body mass is selected considering factors affecting weight such as annual cycle. This is the base mass and is used to calculate the maximum sustainable rate of flight power (power available). Next, power requirements for flight are calculated. As power requirements vary with flight velocity, a single velocity must be selected: we use the most efficient velocity. To assure conservative estimates of a bird's ability to carry a transmitter, base mass is adjusted upwards by a percentage approximating the normal range in body mass. Adjusted mass is used to estimate the power required to fly at the most efficient velocity. The difference between power available for flight and the power required to fly at the most efficient velocity is surplus power. Adding a transmitter increases power requirements. We evaluate a bird's ability to carry a transmitter by calculating the reduction in surplus power caused by transmitters of various sizes.

Power surplus is proportionately greater for small birds than large birds, so basing transmitter size on a fixed percentage of body mass results in conservative loadings for small birds and liberal loadings for large birds. Our method allows an investigator to select transmitter size according to the reduction in power surplus that is considered appropriate for the experimental conditions, and at the same time it provides an estimate of the energetic cost of transporting the added mass of the transmitter.

ACKNOWLEDGMENTS

A portion of this work was done while DFC was on a sabbatical visit at the Department of Fishery and Wildlife Biology, Colorado State University. Sincerest gratitude is extended to R. Cook and other faculty members who made the stay enjoyable and rewarding. We are grateful to M. May, R. Ryder, and two referees (M. Fuller and J. Champion) for valuable comments on the manuscript. This is New Jersey Agricultural Experiment Station Publication No. 0-08230-02-85, supported by State funds and USDA Regional Research Funds.

LITERATURE CITED

Caccamise, D. F. 1974. Competitive relationships of the Common and Lesser Nighthawks. Condor 76:1–20.

———, L. A. Lyon, and J. Fischl. 1983. Seasonal patterns in roosting flocks of starlings and Common Grackles. Condor 85:474–481.

Cochran, W. W. 1980. Wildlife telemetry. Pp. 507–520 *in* Wildlife management techniques manual (S. D. Schemnitz, ed.). The Wildlife Society, Washington, D.C.

Greenewalt, C. H. 1962. Dimensional relationships for flying animals. Smithson. Misc. Collect. 144:1–40.

Odum, E. P., C. E. Connell, and H. L. Stoddard. 1961. Flight energy and estimated flight ranges of some migratory birds. Auk 78:515–527.

Pennycuick, C. J. 1969. The mechanisms of bird migration. Ibis 111:525–556.

Schnell, G. D. and J. J. Hellack. 1979. Bird flight in nature: optimized or a compromise? Am. Nat. 113:53–66.

Tucker, V. A. 1973. Bird metabolism during flight: evaluation of a theory. J. Exp. Biol. 58:689–709.

———. 1977. Scaling and avian flight. Pp. 497–509 *in* Scale effects in animal locomotion, (T. J. Pedley, ed.). Academic Press, New York, New York.

DEPT. ENTOMOLOGY AND ECONOMIC ZOOLOGY, COOK COLLEGE, NEW JERSEY AGRICULTURAL EXPERIMENT STATION, RUTGERS UNIV., NEW BRUNSWICK, NEW JERSEY 08903. ACCEPTED 23 MAR. 1985.

APPENDIX 1

SYMBOLS AND CONSTANTS USED IN CALCULATIONS

Symbol	Definitions and units
$'$	Indicates that transmitter effect has been included in the calculation.
A	Equivalent flat-plate area—the area of a flat plate yielding a drag equivalent to that produced by the frontal area of the bird (m^2).
A′	Equivalent flat-plate area of the bird plus that of the transmitter (m^2).
A_t	Equivalent flat-plate area of the transmitter (m^2).
b	Wing span from tip of one wing to tip of other (m).
f	Flapping frequency (no./sec).
m_a	Adjusted mass of bird—in our examples this equals base mass plus 50% (kg). The value can be changed to reflect range in body mass expected for any given species.
m_a'	Adjusted mass of bird plus mass of transmitter (kg).
m_b	Base mass of bird assuming minimum fat reserves, empty crop and stomach, and no transmitter (kg).
m_f	Mass of flight muscles (kg).
m_t	Mass of transmitter (kg).
p	Air density at sea level (1.18 kg/m^3). We used sea level for our calculations but this should be changed to reflect the elevation where the bird will be carrying the transmitter.
P_a	Available power (watts)—maximum sustainable rate of power output in flight.
P_i	Induced power (watts)—power needed to overcome force of gravity.
$P_{mr,a}$	Power maximum range (watts)—power required to fly at the most efficient velocity (greatest distance per unit of energy consumed) for birds at adjusted mass.
P_o	Profile power (watts)—power required to overcome profile drag of the wing as it moves through the air.
P_p	Parasite power (watts)—power required to overcome resistance of the body moving through air.
P_s	Surplus power (watts)—the difference between amount of power required to fly at V_{mr} ($P_{mr,a}$) and total amount of power available (P_a).
R_p	Proportionate reduction in surplus power caused by added costs of transporting a transmitter.
Q	Specific work of flight muscles (57 joules/kg).
S_d	Wing disk area—the circular area through which the flapping wings travel (m^2).
V_{mr}	Velocity maximum range (m/sec).

APPENDIX 2
EQUATIONS USED IN CALCULATIONS

Number	Equation	Explanation (source)
1	$W = mg$	Where m equals any mass (kg) and g is acceleration of gravity (9.81 m/sec^2).
2	$m_f = 0.17m_b$	(Pennycuick 1969)
3	$A = 0.00334m_a^{0.660}$	(Tucker 1973)
4	$b = 1.1m_b^{0.3333}$	(Tucker 1973)
5	$f = 3.816/b^{1.029}$	(derived using data in Greenewalt 1962)
6	$A_t = 0.00334m_t^{0.660}$	Flat-plate area where m_t is in kg (Tucker 1973)
7	$P_a = m_f Qf$	(Pennycuick 1969)
8	$S_d = 0.785b^2$	(Tucker 1973)
9	$V_{mr} = 1.13\left(\frac{(9.81m)^{0.5}}{p^{0.5}A^{0.25}S_d^{0.25}}\right)$	(Pennycuick 1973)
10	$P_i = \frac{2(9.81m)^2}{3.14159pb^2RV_{mr}}$	where $R = 0.7$ (Tucker 1973)
11	$P_p = \frac{pAV^3}{2}$	(Tucker 1973)
12	$P_o = 1.8m_a^{-0.16667}V_{mr}^{-0.5}(P_i + P_p)$	(Tucker 1973)
13	$P_{mr,a} = P_i + P_p + P_o$	(Tucker 1973)
14	$P_s = P_a - P_{mr,a}$	
15	$R_p = \frac{P_{mr,a}' - P_{mr,a}}{P_s}$	

APPENDIX 3

METHODS USED TO PERFORM CALCULATIONS FOR INDIVIDUAL SPECIES[a]

1. Determine m_b, remembering to consider age, stage of the annual cycle (e.g., premigratory), and other factors that might affect weight of the bird. This should represent a minimum normal mass. Then calculate m_a using an adjustment (% m_b) reflecting the expected range in body mass that would normally occur during the study. In our examples we used 50%.
2. Determine mass of flight muscles (m_f), wingspan (b), and flap frequency (f). This is best accomplished by direct measurement of individual species, but allometric equations (2, 4, and 5 respectively) can be used. Mass should be m_b.
3. Calculate P_a (equation 7).
4. Determine appropriate air density (p) for elevation where your experimental subjects will live, and then calculate the following: A, S_d, and V_{mr} (equations 3, 8, and 9). Mass should be m_a both here and in step 5.
5. Using equations 10–12, calculate P_i, P_p, and P_o; then combining these in equation 13, calculate $P_{mr,a}$.
6. Surplus power can now be calculated (equation 12).
7. Determine the mass, and calculate (equation 6) the equivalent flat-plate area of the transmitter. Calculate A′ as (A + A_t).
8. Calculate m_a' by adding the mass of the transmitter to m_a.
9. Using A′ and m_a' repeat steps 4–5 to calculate the same values, but including the effects of the transmitter.
10. Using equation 13, calculate the proportional reduction in surplus power caused by the transmitter (equation 15).

[a] A computer program that will perform all necessary calculations is available from the first author. To obtain a copy of the program, send a formatted (IBM-PC compatible, DOS 2.0), 5.25 in. floppy disk to Donald F. Caccamise, Dept. Entomology and Economic Zoology, Rutgers University, New Brunswick, New Jersey 08903.