

# SHORT COMMUNICATIONS

## BODY SIZE AND LONGEVITY IN BIRDS

STAN L. LINDSTEDT

AND

WILLIAM A. CALDER

The concept of physiological time was introduced by Hill (1950). He reasoned that as metabolic rate and longevity change with body size, time itself may be scaled. Hence, spans such as growth to maturity, gestation period and the time required for digestion transpire on a time scale dependent upon the body size of an animal. Since Hill's hypothesis, many of these rate variables have been examined in birds and mammals and related allometrically to their body size (Stahl 1962, Aschoff and Pohl 1970, Calder 1974).

These allometric or power function equations have the form:

$$Y = aM^b \quad (1)$$

where  $Y$  is some variable,  $M$  is body mass and the numerical values of  $a$  and  $b$  are derived empirically by fitting a least-squares regression line to a series of points (for details see Lasiewski and Dawson 1967). These equations have the more convenient form:

$$\log Y = \log a + b \log M \quad (2)$$

which is the expression of a straight line. We have analyzed the longevity of birds as a function of body mass to describe further the concept of physiological time.

Farner (1955) distinguished three expressions of longevity. *Potential longevity* is the maximum life span of an individual of a species under "optimal" conditions. As these conditions are largely undefined, much less controlled, zoo and aviary records may approach, but never reach these values. *Potential natural longevity* is the maximum life span of an individual in the wild under ideal natural conditions. We assume that the maximum survival records of banded birds approach these values. *Mean natural longevity* is defined as the mean age attained by individuals of a population at the time of death. As this is a mean value, incorporating external factors of predation and disease, it does not represent a species' physiological potential. In this report, therefore, we examine individual species longevity records in wild (banded) and captive birds as a function of body mass.

## METHODS AND MATERIALS

Maximum longevity was plotted against body mass for 152 wild and 58 captive individuals. Life spans for captive birds were obtained from zoo records and the *Biology Data Book* (Altman and Dittmer 1972). Bird banding records were the source of the maximum individual longevities for birds in the wild as published by Rydzewski (1962, 1963, 1973) and Kennard (1975). They recorded few body weights, so approximate weights for each species were obtained

from other sources (Groebels 1932, Wetherbee 1934, Stewart 1937, Graber and Graber 1962, Murray and Jehl 1964). A table of these data is available from the senior author. The method of least squares was used to obtain regressions of life span and body mass. With a sufficient span of body size from smallest to largest bird, variability in body mass for any one species incorporates an error which has insignificant effect on the regression slope (see Lasiewski and Calder 1971).

## RESULTS

Longevity of banded birds ranged from 4.08 to 38 years while body mass spanned five orders of magnitude (3.5 to 12,200 g). The relation of longevity to body mass in these animals is summarized in figure 1, and least squares regression equations are given in table 1. These equations show lifespan to be related to 0.18 to 0.26 power of body mass. For all groups of birds listed in table 1, the correlation coefficient between maximum longevity and body mass was significant at the 0.01 level.

Two equations relating longevity and body mass have been obtained for mammals (fig. 2) by Sacher (1959) and Günther and Guerra (1955). Unfortunately, longevity was not defined in either study and sample sizes were not given. The disparity between these equations for mammals is probably due to the difficulty of obtaining longevity data. As life span has the lowest frequency of all periodic events (heart rate has the highest known frequency), it is the least likely to be measured in a standardized fashion.

## DISCUSSION

C. H. Blake (pers. comm. to W. A. Calder) pointed out that some orders or families of birds seem to have characteristically long (i.e., Charadriiformes and Procellariiformes) or short (i.e., Paridae, Galliformes, and Troglodytidae) longevities for their size. Thus, the composite equations must be regarded as of limited applicability to any given species.

TABLE 1. Least squares regression equations for relation of longevity and body mass.<sup>a</sup>

Group	$t_{1s} = aM^b$	Standard error of		Sample size	Equation no.
		a	b		
All wild birds	$t_{1s} = 17.6M^{0.20}$	4.1	0.01	152	(3)
Wild passerines	$t_{1s} = 21.6M^{0.26}$	6.2	0.02	71	(4)
Wild nonpasserines	$t_{1s} = 16.6M^{0.18}$	4.0	0.02	81	(5)
Captive birds	$t_{1s} = 28.3M^{0.19}$	4.3	0.02	58	(6)

<sup>a</sup> Where  $t_{1s}$  is maximum longevity in years and  $M$  is body mass in kg.

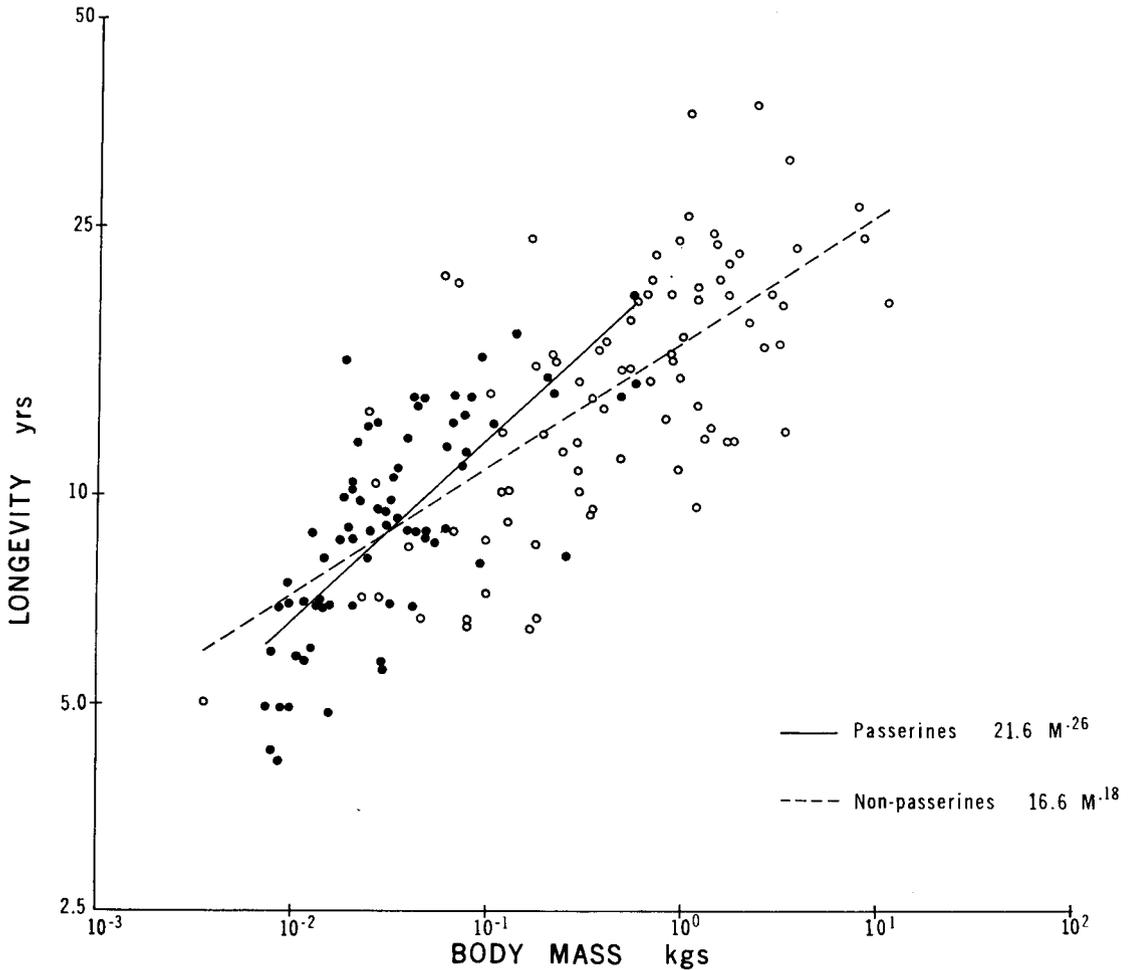


FIGURE 1. The relation of maximum longevity and body weight in wild birds, showing separate lines for passerine (solid circles) and nonpasserine (open circles) species.

If the error in this study is systematic there may be a bias against the longer-lived birds. Since large-scale banding programs have not been in operation much longer than one lifespan of a large bird species, there has been less opportunity to demonstrate longevity records for large-bodied species. Correspondingly, more records exist for small-bodied species. The effect of both of these sampling errors would be to decrease the slope of the regression lines which include large nonpasserine birds. To analyze this effect, we computed a regression line for the wild nonpasserine species including only those birds in the same size range as the passerine species (under 600 g). The slope of the line was 0.22 compared with 0.18 for the unselected data. We also tested for the effect of changing data points randomly (or including erroneous weights or records) by first increasing and then decreasing 20% of the data points by a factor of two. The 95% confidence limits of the new equations included the initial equation.

Stahl (1962) combined allometric equations to give nondimensional ratios or "criteria of similarity." For example, breath time (yrs) in mammals is equivalent to  $4.7 \times 10^{-5} M^{0.28}$  whereas pulse time (yrs) equals  $1.2 \times 10^{-5} M^{0.27}$ . Therefore, a ratio of breath to pulse time yields  $3.9 M^{0.01}$  and, as the residual mass ex-

ponent is quite small, it may be concluded that there are about 3.9 heartbeats per respiratory cycle in all mammals, regardless of size. Longevity in birds can be examined in the same manner.

Metabolic rate is proportional to about  $M^{0.75}$  and is expressed as energy expended per animal per unit time. Lasiewski and Dawson (1967) examined standard metabolism ( $\dot{H}$ ) in birds and found

$$\dot{H} = 6.25 M^{0.724} \quad (7)$$

for 35 passerine and

$$\dot{H} = 3.79 M^{0.723} \quad (8)$$

for 58 nonpasserine species ( $\dot{H}$  has been converted to watts,  $M$  is body mass in kg).

These exponents are similar to those describing metabolism in mammals (Kleiber 1961):

$$\dot{H} = 3.39 M^{0.75} \quad (9)$$

Exponents of approximately 0.75 are also reported for many poikilotherms (Hemmingsen 1950, Bartholomew and Tucker 1964, Kayser and Heusner 1964, Whitford and Hutchinson 1967). The energy use per kilogram of animal tissue per lifetime in birds then is:

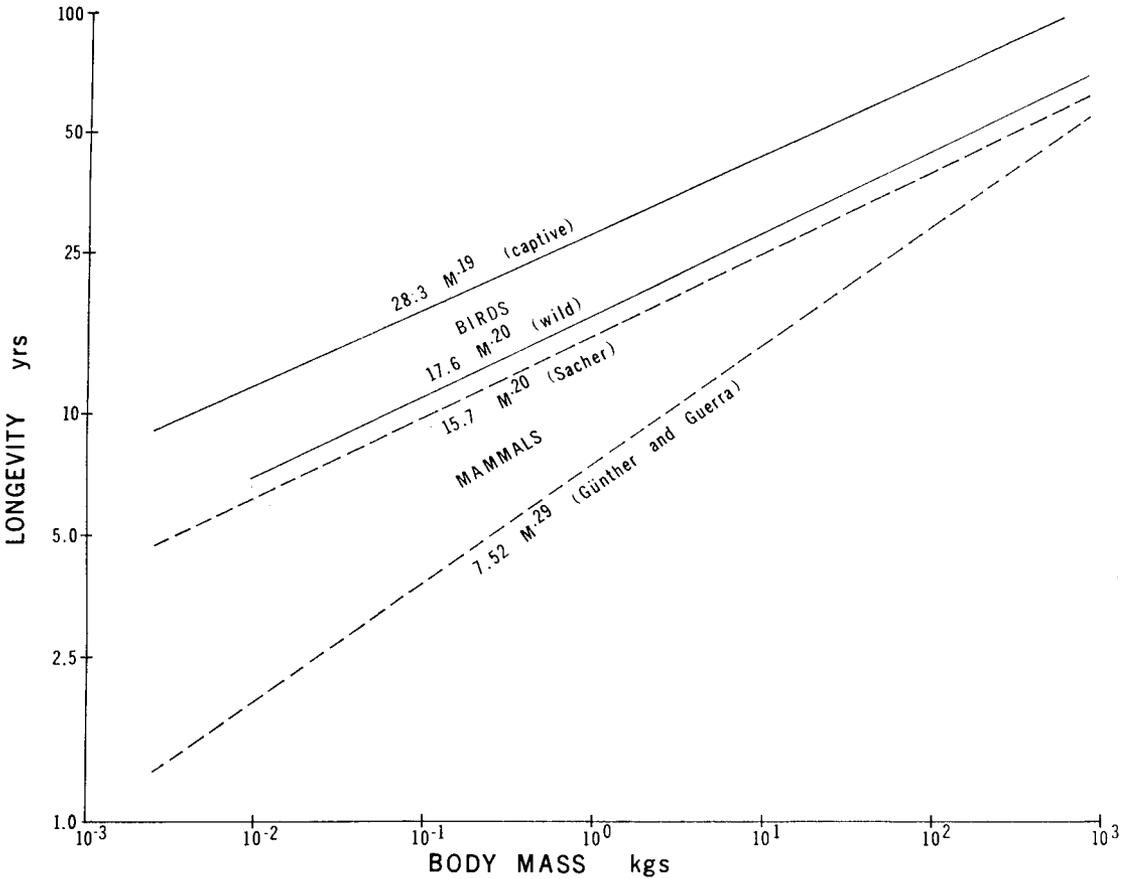


FIGURE 2. The relation of longevity and body weight in wild and captive birds compared with lines for mammals from equations by Günther and Guerra (1955) and Sacher (1959).

$$\frac{\dot{H}}{\text{body mass}} \times \text{longevity} = \frac{M^{0.75}}{M^1} \times M^{0.25} \text{ or } 0.20$$

Hence, energy requirement per unit body mass per lifetime appears to be independent of body size. For passerine birds, for example, we can substitute equations (4) and (7) in equation (10):

$$\frac{6.25 M^{0.72}}{1 M^{1.0}} \times 3.15 \times 10^7 \text{ sec/yr} \times 21.6 M^{0.25} = 4.25 \times 10^9 M^{0.02} \quad (11)$$

A passerine bird may thus be expected to burn about four million kilojoules per kilogram body mass per lifetime to support its basal metabolic functions.

The respiratory minute volume (*V<sub>e</sub>*) of birds has also been shown to vary approximately as the 0.75 power of body size (Lasiewski and Calder 1971):

$$V_e = 284 M^{0.77} \quad (12)$$

thus making the volume of air ventilated per gram body tissue per lifetime nearly constant for all birds as well. The heart rate (*f<sub>h</sub>*) and respiratory rate (*f<sub>r</sub>*) (Calder 1968) of birds are:

$$f_h = 155.8 M^{-0.23} \quad (13)$$

$$f_r = 17.2 M^{-0.31} \quad (14)$$

Consequently, the number of breaths or heartbeats

per lifetime of all birds is very nearly size-independent, as is the case for mammals (Stahl 1962).

These considerations of bird longevity verify Hill's (1950) suggestion that effective physiological time is scaled to body size. As more data become available (e.g., longevity records for large birds with longest lifespans) this relationship should be refined.

ACKNOWLEDGMENTS

This research was supported in part by a Society of Sigma Xi grant to S.L.L. and NSF Grant GB13249 to W.A.C. We are indebted to J. H. Kennard for supplying longevity data and C. H. Blake for critically analyzing the equations. C. R. Schwalbe, D. L. Lyon and N. M. Waser reviewed the manuscript.

LITERATURE CITED

ALTMAN, P. L., AND D. S. DITTMER (eds.). 1972. Biology data book. Fed. Am. Soc. Exp. Biol. Vol. I. Bethesda, Md.  
 ASCHOFF, I., AND H. POHL. 1970. Rhythmic variations in energy metabolism. Fed. Proc., Fed. Am. Soc. Exp. Biol. 29:1541-1552.  
 BARTHOLOMEW, G. A., AND V. A. TUCKER. 1964. Size, body temperature, thermal conductance, oxygen consumption and heart rate in Australian varanid lizards. Physiol. Zool. 37:341-354.  
 CALDER, W. A. 1968. Respiratory and heart rates of birds at rest. Condor 70:358-365.

- CALDER, W. A. 1974. Consequences of body size for avian energetics, p. 86–151. In R. A. Paynter Jr. [ed.], *Avian energetics*. Nuttall Ornith. Club.
- FARNER, D. S. 1955. Birdbanding in the study of population dynamics, p. 397–449. In A. Wolfson [ed.], *Recent studies in avian biology*. Univ. Illinois Press, Urbana.
- GRABER, R. R., AND J. W. GRABER. 1962. Weight characteristics of birds killed in nocturnal migration. *Wilson Bull.* 74:74–88.
- GROEBBELS, F. 1932. *Der Vogel*, Bd. I. Gebrüder Borntraeger, Berlin.
- GÜNTHER, B., AND E. GUERRA. 1955. Biological similarities. *Acta Physiol. Lat. Am.* 5:169–186.
- HEMMINGSEN, A. M. 1950. The relation of standard (basal) energy metabolism to total fresh weight of living organisms. *Rep. Steno Hosp. (Copenhagen)* 4:7–258.
- HILL, A. V. 1950. The dimensions of animals and their muscular dynamics. *Sci. Prog.* 38:209–230.
- KAYSER, C., AND A. HEUSNER. 1964. Étude comparative du métabolisme énergétique série animale. *J. Physiol. (Paris)* 56:489–524.
- KENNARD, J. H. 1975. Longevity records of North American birds. *Bird-Banding* 46:55–73.
- KLEIBER, M. 1961. *The fire of life*. Wiley, New York.
- LASIEWSKI, R. C., AND W. A. CALDER. 1971. A preliminary allometric analysis of respiratory variables in resting birds. *Respir. Physiol.* 11:152–166.
- LASIEWSKI, R. C., AND W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13–23.
- MURRAY, B. G., JR., AND J. R. JEHL, JR. 1964. Weights of autumn migrants from coastal New Jersey. *Bird-Banding* 35:253–263.
- RYDZEWSKI, W. 1962. Longevity of ringed birds. *The Ring* 33:147–152.
- RYDZEWSKI, W. 1963. Longevity records, II. *The Ring* 34:177–181.
- RYDZEWSKI, W. 1973. Longevity records. *The Ring* 44:7–10.
- SACHER, G. A. 1959. Relation of lifespan to brain weight and body weight in mammals, p. 115–141. In G. E. W. Wolstenholme and M. O'Connor [eds.], *The lifespan of animals*. Ciba Foundation Colloquia on Aging. Vol. 5. Little, Brown and Co., Boston.
- STAHL, W. R. 1962. Similarity and dimensional methods in biology. *Science* 137:205–212.
- STEWART, P. A. 1937. A preliminary list of bird weights. *Auk* 54:324–332.
- WETHERBEE, K. B. 1934. Some measurements and weights of live birds. *Bird-Banding* 5:55–64.
- WHITTFORD, W. G., AND V. H. HUTCHINSON. 1967. Body size and metabolic rate in salamanders. *Physiol. Zool.* 40:127–133.

*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721. Accepted for publication 26 May 1975.*

## USE OF BILATERAL SCRATCHING BEHAVIOR BY EMBERIZINES AND ICTERIDS

JON S. GREENLAW

The bilateral-scratch (or double-scratch) is an unusual foraging behavior employed by some emberizine finches and a few other kinds of birds in displacing litter, loose soil, or snow. Because of its potential taxonomic significance in Emberizinae, this behavior has received considerable recent attention (Harrison 1967, Gobeil 1968, Clark 1970, 1971, 1972, Enders 1970, Taylor 1970, Hailman 1973, 1974).

Except for the comparative treatments of bilateral scratching in two species of *Pipilo* (Davis 1957) and in two members of the *Zonotrichia*–*Junco* complex (Hailman 1974), little information is available on variation in the use of this behavior by emberizines. Since knowledge of variation in bilateral scratching is important for behavioral, evolutionary, and taxonomic reasons, I here undertake to consolidate information from my own observations and from the literature on this subject. Most of my own data are qualitative and concern bilateral scratching in certain northeastern American emberizines. I also collected quantitative data in 1967 and 1968 on seasonal change in the frequency of use of bilateral scratching by the Rufous-sided Towhee (*Pipilo erythrophthalmus*) in two New Jersey populations. Statements unaccompanied by a citation in the following text are based on my field notes.

This paper also documents the occurrence of bilateral scratching in the family Icteridae and discusses its use by two species of North American icterids.

## BILATERAL SCRATCHING IN THE EMBERIZINAE

*General characteristics.* The basic patterns of movement shared by all emberizines in bilateral scratching are a) simultaneous or nearly simultaneous use of both legs, and b) a double hop that results in a short displacement of the bird forward then backward to its original position. The forward hop is a preparatory action that provides momentum to the scratching bird and permits it to shift both feet forward under its body during the displacement to grasp the loose soil or litter near its head. The preparatory hop continues without pause into the rearward or power hop. During this latter phase, the bird recoils backward, pushing itself against the resistance of the substrate, simultaneously dislodging the soil or debris under its feet and thrusting it out behind as the legs are returned to a support position.

Davis (1957:134) reported that the Rufous-sided Towhee (western race, *P. e. megalonyx*) initiates its scratch with “a sharp backward thrust of both feet simultaneously” that displaces the bird rearward. This displacement is then corrected by a recovery or return hop. I have been unable to confirm this mode (backward then forward) of bilateral scratching in any emberizine that I have observed performing the behavior, including the towhee (eastern races, *erythrophthalmus* and *rileyi*).

*Variation in bilateral scratching.* The basic patterns of movement and the manner of use (e.g., stance, frequency of use) of bilateral scratching vary both within and among species. The nature of the substrate, gait, and alternate food supplies seem to be the most important factors influencing variation in this behavior.