

## THE RELATIONSHIP OF THE EXTERNAL SURFACE AREA OF BIRDS TO SKIN SURFACE AREA AND BODY MASS

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### SUMMARY

Data from 12 bird species reveal that skin surface area averages 23% larger than the external surface area of the plumage. Use of skin surface area instead of the area of the external plumage surface may produce large errors in heat-transfer analyses.

### INTRODUCTION

Estimating the extent of an animal's exterior surface, and its interface with the environment, is of prime importance in thermal biology. Regardless of the mode of transfer, heat fluxes across an animal's surface are often calculated as intensive quantities (e.g.  $W/m^2$ ) and converted to values for a particular animal by multiplying by surface area. Thus, the accuracy of heat-transfer estimates may be directly proportional to the accuracy of surface area estimates. In studies of avian thermal biology, the skin surface area is frequently used in calculations (e.g. Veghte, 1964; Pohl, 1969; Drent & Stonehouse, 1971; Calder, 1974) and is commonly estimated using Meeh's (1879) formula with Rubner's (1883) constant of 10

$$S_{\text{skin}} = 10 M^{0.667}, \quad (1)$$

where  $S_{\text{skin}}$  is skin surface area beneath the feathers ( $\text{cm}^2$ ) and  $M$  is body mass (g). Though Rubner's constant of 10 was originally derived for domestic fowl, Drent & Stonehouse (1971) have verified this formula as a surprisingly good predictor of skin surface area in birds representing a variety of taxa and a weight range spanning three orders of magnitude. To a large degree, however, a bird's skin is not the surface directly in contact with the environment. With the exception of areas such as the feet and the beak, the environmental interface is generally the exterior surface of the plumage, and thus the relevance of skin surface area to many thermal studies of birds is questionable. In this report, we examine the relationships between the external surface area of the plumage ( $S_{\text{ext}}$ ), skin surface area, and body mass.

### METHODS

For this analysis, we define  $S_{\text{skin}}$  as only that skin surface beneath the feathers. This conforms with Rubner's (1902, cited in Drent & Stonehouse, 1971) original measure-

Table 1. *Surface areas (cm<sup>2</sup>)*

	Body weight (g)	$S_{\text{skin}}^*$	$S_{\text{ext}}^\dagger$	$\frac{S_{\text{skin}}}{S_{\text{ext}}}$	Beak surface area	Leg surface area $\ddagger$
<i>Columba livia</i>	649.1	700.0	598.0	1.17	7.4	47.8
<i>Zenaida macroura</i>	119.2	241.0	198.0	1.22	1.7	14.3
<i>Selasphorus rufus</i> §	3.8	—	16.7	—	—	—
<i>Empidonax traillii</i> §	13.2	—	48.7	—	—	—
<i>Turdus migratorius</i>	97.1	198.0	196.0	1.01	3.1	14.0
<i>Anthus spinoletta</i>	20.2	87.3	66.2	1.32	0.9	5.2
<i>Passer domesticus</i>	32.3	106.0	80.0	1.33	1.5	6.7
<i>Agelaius phoeniceus</i>	44.4	143.0	94.2	1.52	2.5	10.5
<i>Junco hyemalis</i>	19.4	75.5	66.7	1.13	0.7	5.3
<i>Zonotrichia leucophrys</i>	27.3	80.0	68.5	1.17	1.0	6.3

## Data from other studies

<i>Aptenodytes forsteri</i>	23510	—	6440
<i>Pica pica</i> ¶	172.7	—	244
<i>Corvus corax</i> **	860	835	1662

\* Area of skin beneath feathers; does not include that of the beak and non-feathered portions of the hind-limbs.

† Area of the external plumage surface; does not include that of the beak and non-feathered portions of the hind-limbs.

‡ Surface area of non-feathered portion of the hind-limbs.

§ Surface area was estimated geometrically.

|| Average of values for five individuals. Area was estimated by covering the external surface with paper of known mass per unit area and weighing the paper (Le Maho, 1976). See text for discussion.

¶ Average of values for male and female magpies. Surface area was estimated geometrically (Mugaas, 1976).

\*\* Body weight and  $S_{\text{ext}}$  are average values for five individuals;  $S_{\text{skin}}$  was measured on a single bird (Veghte, 1975). See text for discussion.

ments and excludes the relatively small surface areas of the beak (about 1% of  $S_{\text{skin}}$ ) and the non-feathered portions of the hind limbs (about 7% of  $S_{\text{skin}}$ ). Similarly,  $S_{\text{ext}}$  also excludes the beak and non-feathered portions of the hind limbs. The tail is ignored since it is considered to be of minor thermal significance.

For measurements of  $S_{\text{ext}}$ , an individual was frozen in a typical perching position with the wings folded and the neck retracted. The bird was then wrapped in a thin polyethylene film with care taken not to compress the plumage. The film was folded to conform to the bird's contours and taped in place or spot-fused with a soldering iron. This produced a thin mould of the bird's body from the head to the base of the tail, except for the beak and non-feathered portions of the legs. The mould was then cut into sections so that it could be pinned flat. Surface area was determined by tracing these sections onto paper of known mass per unit area and weighing the paper. The reproducibility of results obtained using this technique was tested by measuring  $S_{\text{ext}}$  five times for one House Sparrow (*Passer domesticus*).  $S_{\text{ext}}$  thus measured was  $78.9 \pm 2.02 \text{ cm}^2$  ( $\bar{x} \pm \text{s.d.}$ ), and the coefficient of variation was only 2.6%. The maximum estimate was 6.2% greater than the minimum. The accuracy of the polyethylene film method was supported by comparison with independent estimates obtained by geometrical approximation. The bird was assumed to resemble a prolate spheroid with a hemispherical head. Surface area was calculated using the appropriate equations of Hodgman (1960) and measured values for the diameter of the head, the length of

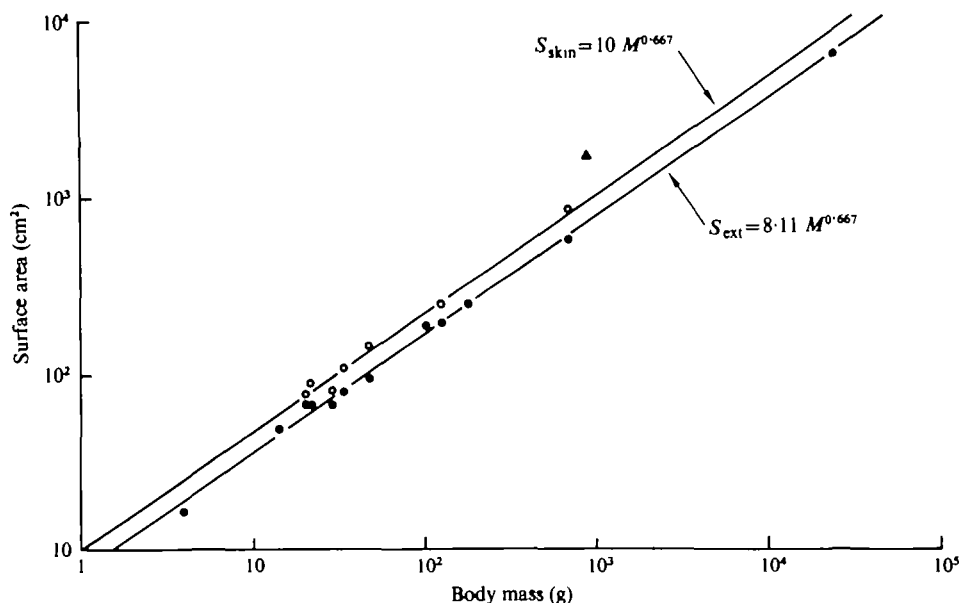


Fig. 1. The relation of the external surface area of the plumage ( $S_{\text{ext}}$ ) and the skin surface area beneath the plumage ( $S_{\text{skin}}$ ) to body mass. Filled circles represent data from Table 1 to which the line describing  $S_{\text{ext}}$  was fitted. Triangle shows Veghte's (1975) value for  $S_{\text{ext}}$  in Ravens, which was not used in calculations. Unfilled circles show values for  $S_{\text{skin}}$  measured in this study. Values for  $S_{\text{skin}}$  and  $S_{\text{ext}}$  are virtually identical in *Turdus migratorius* and are plotted as a single half-filled circle.

the body from midneck to the base of the tail, and the diameter of the body. Body diameter was taken as the average of the largest dorso-ventral width and the largest lateral width. Such geometrical estimates average 103% (range, 91–112%) of the values in Table 1 measured for eight species using polyethylene film. This type of geometrical approximation was also used to estimate  $S_{\text{ext}}$  for *Selasphorus rufus* and *Empidonax traillii* in this study and by Mugaas (1976) to estimate  $S_{\text{ext}}$  for *Pica pica*.

Skin surface area beneath the plumage was measured by coating the defeathered carcass with a silicon rubber sealant (Johnson, 1972). This sealant does not shrink and, after curing, resists stretching and can be peeled off the bird. The surface area of this mould of the bird's skin surface was then determined in the same manner as was that of the polyethylene film. The surface area of the beak was calculated separately from the rest of the body.

The silicon rubber technique is not practical for use on the digits and the tibiotarsal region because of their small diameter, and these surfaces were approximated as a set of elliptical cylinders. Area was computed using the appropriate equation of Hodgman (1960) and the length and maximum and minimum diameters of each element (measured to the nearest 0.1 mm).

#### RESULTS AND DISCUSSION

Table 1 gives results of complementary skin and external surface area measurements for eight species ranging in weight from 19.4 to 649 g. Surprisingly, the skin

surface area beneath the plumage ( $S_{\text{skin}}$ ) averages 23 % larger (range, 1–52 %) than the external plumage surface ( $S_{\text{ext}}$ ). These apparently paradoxical results are produced by the folding of the appendages and skin while the bird is perched. Prominent areas where this occurs include the patagium and the main body of the wing, the neck (which is retracted and curved), and the skin surfaces between the body wall and the fore- and hind limbs. The contributions of the beak and the non-feathered portions of the hind limbs to total skin surface area are small compared to the skin area beneath the feathers; the beak averages 1.2 % of  $S_{\text{skin}}$  (range, 0.7–1.6 %) and the non-feathered portions of the legs average 7.0 % (range, 5.9–7.9 %). Our skin surface measurements agree remarkably well with those predicted using the Meeh formula (Fig. 1). Measured  $S_{\text{skin}}$  values for eight species average 2.8 % below those predicted using equation (1); the greatest difference is 17.5 % in *Anthus*.

Few additional data are available on  $S_{\text{ext}}$  in birds (Table 1). Le Maho's (1976) value for Emperor Penguins (*Aptenodytes forsteri*) is not exactly comparable to the values for other species since it includes the feet and beak (Le Maho, 1977), but the surface area added by these structures is probably minor. Veghte's (1975) value for Ravens (*Corvus corax*), obtained by an optical method, is exceptional in that  $S_{\text{ext}}$  is estimated as larger than the measured or predicted  $S_{\text{skin}}$  ( $S_{\text{ext}} \approx 2 \times S_{\text{skin}}$ ). This relation differs so greatly from that obtained from the other 12 species that it was not used in allometric analyses. A least-squares regression of the logarithmically transformed data for the remaining 12 species in Table 1 (which span five orders of magnitude in body mass) yields the relation

$$\log S_{\text{ext}} = 0.667 \log M + \log 8.11, \quad (2)$$

where  $S_{\log Y, \log X} = 0.0397$  and  $r = 0.998$  (Fig. 1). This line parallels that describing the relation of skin surface area to body mass, with the line describing  $S_{\text{skin}}$  elevated 23 % above that describing  $S_{\text{ext}}$ . Thus, these allometric relations predict the same average increase of  $S_{\text{skin}}$  over  $S_{\text{ext}}$  as observed in the eight species in which both variables were measured. The 0.667 slope of equation (2) is that expected for the surface-area-to-weight relation of objects of similar geometry if specific gravity is constant, thus implying that birds in general are remarkably similar in their body configurations. Drent & Stonehouse (1971) suggested that 'penguins must be as far removed from the standard configuration as any bird'. However, the external surface area of *Aptenodytes* averages only 4 % below that predicted by equation (2) and 9 % below that predicted by a separate regression equation ( $\log S_{\text{ext}} = 0.667 \log M + \log 7.81$ ) computed by excluding *Aptenodytes* from the data base of equation (2).

The significance of these differences between  $S_{\text{skin}}$  and  $S_{\text{ext}}$  may be illustrated by a simple example. Calculation of the thermal radiation ( $R$ ) emitted by a bird requires knowledge of the surface emissivity ( $\epsilon$ ), the surface temperature ( $T$ ), and the surface area ( $S$ )

$$R = \sigma \epsilon T^4 S, \quad (3)$$

where  $\sigma$  is the Stephan-Boltzmann constant. Estimating the bird's surface area for radiative heat transfer using the Meeh formula would likely produce about a 23 % overestimate of  $S$  and thus an identical error in  $R$ . Under ecologically realistic conditions (i.e.  $0^\circ\text{C} < T < 50^\circ\text{C}$ ), this error in  $R$  is equal to that produced by a 15–17 °C overestimate of  $T$ .

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REFERENCES

- CALDER, W. A. (1974). Consequences of body size for avian energetics. In *Avian Energetics* (ed. R. A. Paynter), pp. 86-151. Nuttall Ornith. Club, Harvard University, Cambridge, Mass.
- DRENT, R. H. & STONEHOUSE, B. (1971). Thermoregulatory responses of the Peruvian Penguin, *Spheniscus humboldti*. *Comp. Biochem. Physiol.* **40 A**, 689-710.
- HODGMAN, C. D. (ed.) (1960). *Handbook of Chemistry and Physics*. Cleveland, Ohio: Chemical Rubber Publ. Co. 3481 p.
- JOHNSON, S. R. (1972). Thermal adaptation in North American Sturnidae. Ph.D. dissertation, University of British Columbia.
- LE MAHO, Y. (1977). The Emperor Penguin: a strategy to live and breed in the cold. *Am. Sci.* **65**, 680-693.
- LE MAHO, Y., DELCLITTE, P. & CHATONNET, J. (1976). Thermoregulation in fasting Emperor Penguins under natural conditions. *Am. J. Physiol.* **231**, 913-922.
- MEEH, K. (1879). Oberflächenmessungen des menschlichen Körpers. *Z. Biol.* **15**, 426-458.
- MUGAAS, J. N. (1976). Thermal energy exchange, microclimate analysis, and behavioral energetics of Black-billed Magpies, *Pica pica hudsonia*. Ph.D. dissertation, Washington State University.
- POHL, H. (1969). Some factors influencing the metabolic response to cold in birds. *Fedn. Proc.* **28**, 1059-1064.
- RUBNER, M. (1883). Über den Einfluss der Körpergrösse auf Stoff- und Kraftwechsel. *Z. Biol.* **19**, 535-562.
- RUBNER, M. (1902). *Die Gesetze des Energieverbrauchs bei der Ernährung*. Leipzig and Wien: F. Deuticke.
- VEGHTE, J. H. (1964). Thermal and metabolic responses of the Gray Jay to cold stress. *Physiol. Zool.* **37**, 316-328.
- VEGHTE, J. H. (1975). Thermal exchange between the Raven (*Corvus corax*) and its environment. Ph.D. dissertation, University of Michigan.

