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INSULATION, RADIATION, AND CONVECTION IN SMALL ARCTIC MAMMALS

MARK A. CHAPPELL

ABSTRACT.—The insulation (I), skin area (A_s), surface area (A), effective surface area for radiant energy exchange (A_{ee}), and convection coefficient (h_c) were determined for six species of small arctic mammals. Measurements were made under steady-state conditions using pelt-covered, internally heated Wood's metal casts of the animals. Surface areas of the animals studied depended primarily on body mass; shape was of lesser importance. The latter finding was an artifact of different fur lengths—the elongate species studied (weasels) had short fur, whereas more compact animals (lemmings) had much longer coats which greatly increased their diameters and therefore areas. Insulation in blackbody radiation conditions depended primarily on pelage depth but also to some extent on the density of hair growth. Measured values of A_{ee} were approximately equal to values of A . Convection coefficients varied directly with wind velocity and inversely with body diameter. Nusselt Number-Reynolds Number plots of convection data revealed that convection from the animals was approximately the same as that from similar-sized cylinders, and that shape and pelage characteristics were not important in determining h_c .

Animals living in stressful thermal environments often possess morphological, physiological, or behavioral adaptations that help them regulate rates of energy exchange. However, the significance of any one adaptation should be assessed in perspective with all pathways of energy flow between animal and environment. The total energy budget approach to ecology (Bakken, 1976; Heller and Gates, 1971; Porter and Gates, 1969; Robinson et al., 1976) provides a framework for evaluating the importance of the various energy-exchange pathways for any organism and environment.

Both physical and biological parameters must be quantified in order to calculate the energy budget. Four of the most important physical parameters are the insulation of the integument (i), the surface area of the intact, fur-bearing animal (A), the effective surface area for emission and absorption of radiation (A_{ee}), and the coefficient of convection (h_c). These are difficult to measure accurately, because they may vary with the animal's size, shape, posture, and (in birds and mammals) the complexities of the plumage or pelage. Recently, several groups have examined heat flow from spheres, cylinders, and other geometrical shapes (Wathen et al., 1971, 1973; Mitchell, 1976). A method for use with actual animal shapes was presented by Heller (1972), who measured the A , A_{ee} , and h_c of four chipmunk species using heated, fur-covered metal models. However, all of these species were of conventional shape (not unusually elongated or compact) and had approximately equivalent sizes and fur lengths. Additional data are desirable from animals of diverse shapes, sizes, and pelage thicknesses in order to evaluate the effects of these variables on A_{ee} and h_c , and for comparison with the data from simple geometrical shapes.

The study described here utilized the heated-model technique to describe the I , A , A_{ee} , and h_c of six species of small arctic mammals varying in size from 3 to 150 g, in pelage depth from 2.5 to 11 mm, and in shape from extremely elongate (weasels) to almost spherical (lemmings). The parameters were measured primarily from animals cast in standing postures, but values were also obtained from a few specimens cast in a curled resting position.

MATERIALS AND METHODS

Animals.—Six species of small mammals from the North Slope region of Alaska were used in this study: two short-tailed weasels (*Mustela erminea*); three least weasels (*Mustela nivalis*);

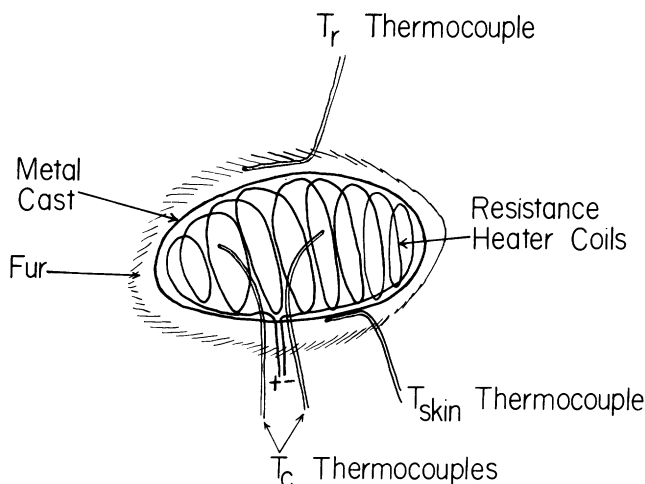


FIG. 1.—Schematic cross section of typical cast, showing placement of heater coils and thermocouple positions for measurements of skin temperature, T_r , and T_c (Note: thermocouple diameter highly exaggerated).

four varying lemmings (*Dicrostonyx torquatus*); six brown lemmings (*Lemmus sibiricus*); one tundra vole (*Microtus oeconomus*); and two masked shrews (*Sorex cinereus*). All were captured in the wild except for three of the *Lemmus*; several had been maintained in captivity for varying periods.

This study utilized pelt-covered, internally heated Wood's alloy casts of the animals. These allowed many measurements to be made in thermal steady-state conditions. The methods used for construction of these models resembled those of Heller (1972) and Morrison and Tietz (1957). Because the thermal conductivity of Wood's alloy is relatively low, the heating coils were distributed as evenly as possible within the cast, so as to minimize the possibility of unequal heat distribution (Fig. 1).

Surface areas.—The total surface areas (A) and skin areas (A_s) of the casts were obtained by the method described by Birkebak (1966) and Heller (1972). Casts were assumed to consist of a variety of geometrical shapes, the areas of which were summed. Circumferences of sections were obtained by circling them with fine threads and measuring their lengths to the nearest 1.0 mm. For measurements of A_s the threads were wrapped tightly against the skin; for measurements of A they were wrapped carefully around the pelage, depressing it as little as possible. This method measures only skin surfaces available for heat transfer; appressed areas, such as folds of skin between legs and body, are not included. Areas of the thin lower leg sections were not included, because they are very small relative to total surface area and are probably unimportant to the total energy balance of the animals. Curled animals were measured as modified hemispheres (lemmings) or flattened discs (weasels), as by Brown and Lasiewski (1972).

The A_{ee} was estimated from vacuum chamber measurements of heat loss rates (Tibbals et al., 1964) and fur surface and chamber wall temperatures. In a vacuum, heat loss occurs by radiant exchange alone, and the rate is described by the equation:

$$q_r = A_{ee} \epsilon \sigma (T_r^4 - T_w^4) \quad (1)$$

where q_r = rate of heat loss, ϵ = pelt emissivity, σ is the Stefan-Boltzmann constant (5.67×10^{-5} kW m⁻² °K⁻⁴), T_r = radiating surface temperature of the pelt (K), and T_w = inside wall temperature of the chamber (K). The emissivity for long-wave radiation (wavelength 5–22 nm) of animal surfaces is usually close to unity (Birkebak, 1966; Bartlett and Gates, 1967). Fur, however, is partially transparent to longwave infrared (Cena and Monteith, 1975; Walsberg et al., 1978), and hence the actual emission temperature can be defined as an integrated value obtained from the fur depth-temperature profile (W. P. Porter, pers. comm.). For this experiment T_r was defined as

the average temperature at a depth of 2 mm below the surface of the fur. This is a typical extinction depth for long-wave radiation in animal pelts (Cena and Monteith, 1975).

To calculate A_{ee} , the unknowns in equation 1 (q_r , T_r , and T_w) were obtained as described in Heller (1972), except that T_r was measured below the actual surface. To minimize measurement inaccuracies due to conduction of heat away from the tips of thermocouples, each T_r thermocouple was situated so that at least 1.5 cm of its length was within the fur (Fig. 1). During measurements, the temperature of the vacuum chamber containing the model was maintained constant, within the range of 15 to 26°C.

Three to six separate measurements of A_{ee} were made for each model, moving thermocouples slightly each time to compensate for possible errors caused by thermocouple placements at incorrect depths or areas or poor thermal contact between pelt and cast. All measurements from each cast were averaged to obtain the final A_{ee} value.

Fur depth and cast diameters.—Thickness of the fur on the casts was measured by inserting a thin needle through the pelage, marking the depth of penetration with a pen, and measuring the marked length on a ruler to the nearest 0.5 mm. Five to 10 measurements along the back, flanks, and belly were averaged for each cast. Diameters of casts, from fur surface to fur surface, were determined to the nearest 1.0 mm through the center of the torso. For curled animals, the height and diameter of the curl were recorded.

Convection coefficients.—A cast losing heat by convection also loses heat by radiation. The rate of heat loss (in a blackbody environment) can be described as:

$$\text{power in} = A_{ee} \epsilon \sigma (T_r^4 - T_w^4) + h_c A (T_r - T_a) \quad (2)$$

where h_c is the convection coefficient ($\text{kW m}^{-2} \text{ } ^\circ\text{K}^{-1}$) and T_a is air temperature (K). Because A_{ee} was usually similar to A , these two areas were set equal to A for calculations of emitted radiation. The unknowns in equation (2) were obtained in a wind tunnel as by Heller (1972), but at higher air velocities (0.85 to 7.5 m s^{-1}). Turbulence in the wind tunnel was small at the utilized air velocities (as checked by observing undisturbed flow of thin smoke trails). Thermocouples measuring T_r were placed as in Fig. 1. For measurements in the absence of forced convection the end of the tunnel was blocked and the fan turned off. Air velocity under these conditions was assumed to be about 0.1 m s^{-1} . Air and wall temperatures in the wind tunnel were kept within the 288 to 299°K range.

Measurements of h_c from each cast were obtained for at least five air velocities (0.1 to 7.5 m s^{-1}). Three to six determinations were made at each wind speed, with the T_r thermocouples moved between each reading, and the measurements were averaged to yield a final value.

Temperatures of the skin surface of casts were checked at low and high air velocities to test for uniform heat distribution within the casts. This was accomplished by inserting thermocouples through the fur to the skin-metal interface (Fig. 1). At high wind speeds, the high rate of heat loss could have led to intracast thermal gradients, which would result in inaccurate h_c values. However, the measured skin temperatures were almost always fairly uniform ($\pm 1.5^\circ\text{K}$) over the entire cast (except for the tip of the snout, which was normally 1–2°K cooler than elsewhere). Also, skin temperatures were usually within 1°K of internal cast temperature, but at high V ($>5.0 \text{ m s}^{-1}$) this difference occasionally increased to 2°K.

Insulation.—The insulation of pelts was derived from data obtained while measuring h_c in the absence of forced convection ($V \sim 0.1 \text{ m s}^{-1}$). Insulation (expressed as $\text{m}^2 \text{ } ^\circ\text{K} \text{ kW}^{-1}$) was calculated from power input, A , T_r , and cast temperature (T_c) at equilibrium, according to the equation:

$$I = A(T_c - T_r)/(\text{power in}) \quad (3)$$

Because heat transfer through fur is dependent on the radiant characteristics of the environment (Cena and Monteith, 1975), all measurements were made in blackbody conditions at T_a within the range of 16 to 26°C. This consistence allowed meaningful interspecific comparisons. A few measurements of I were computed for higher air velocities to determine the effects of wind on insulatory properties.

RESULTS AND DISCUSSION

Surface areas and insulation.—The total surface areas of furred casts, skin areas, effective surface areas for radiant energy exchange, and other parameters of the six small mammal species are given in Tables 1 and 2. As expected, the insulation (I) of

TABLE 1.—Energy exchange parameters. "W" in animal number indicates winter pelage; "M" and "F" stand for male and female; "C" indicates curled posture. Dimensions given under torso diameter are width (w) and height (h) of curl.

Animal	Live mass (g)	Torso diam. (m)	A_s (m ²)	A (m ²)	A_{ge} (m ²)	A_p/A	A_{ge}/A
<i>Mustela erminea</i>							
F1	131	0.040	0.0188	0.0274	0.0283	0.69	1.03
WF2	150	0.041	0.0192	0.0281	0.0270	0.68	0.96
<i>Mustela nivalis</i>							
M1	78	0.025	0.0105	0.0149	0.0146	0.70	0.98
F2	40	0.022	0.0086	0.0129	0.0132	0.67	1.02
CF3	40	0.063w, 0.026h	0.0067	0.0089	0.0097	0.75	1.09
<i>Dicrostonyx torquatus</i>							
W1	50	0.042	0.0083	0.0180	0.0175	0.46	0.97
W2	52	0.045	0.0080	0.0190	0.0177	0.42	0.93
CW3	60	0.078w, 0.039h	0.0070	0.0166	0.0153	0.42	0.92
S1	40	0.040	0.0075	0.0147	0.0150	0.51	1.02
<i>Lemmus sibiricus</i>							
1	33	0.035	0.0052	0.0106	0.0109	0.49	1.03
2	52	0.045	0.0092	0.0156	0.0142	0.59	0.91
W1	42	0.042	0.0070	0.0144	0.0148	0.49	1.03
W2	37	0.040	0.0064	0.0120	0.0131	0.53	1.09
Baby	6	0.020	0.0020	0.0038	0.0038	0.64	1.00
CW3	25	0.060w, 0.035h	0.0047	0.0106	0.0098	0.44	0.92
<i>Sorex cinereus</i>							
1	3.2	0.016	0.0017	0.0023	0.0026	0.73	1.14
2	3.7	0.020	0.0018	0.0027	0.0026	0.65	0.95
<i>Microtus oeconomus</i>							
A	41	0.033	0.0077	0.0119	0.0124	0.65	1.09

the pelt (under blackbody conditions) is strongly correlated with the thickness of the fur layer (Fig. 2). The data are best fit by the equation $I = 8.23 \times \text{fur thickness} + 20.48$ ($r^2 = 0.83$; $n = 18$). This equation also accurately predicts the pelt insulation of the white-tailed antelope ground squirrel (*Ammospermophilus leucurus*), a desert species that has an extremely short summer pelage (average fur depth 1.7 mm; unpublished observations). Some of the variance in the data on arctic mammals is probably due to differences in the fur density (number of hairs per unit skin area). For example, shrews have unusually dense pelages and are better insulated than weasels of similar fur thickness. Fluffing the fur to its maximum extent also increases I , to a greater extent in the long-furred lemmings than in species with shorter pelages. Porter and Gates (1969) estimated pelage insulation by dividing the conductivity of air into the thickness of the fur, assuming that fur insulation results from the trapping of a layer of still air. Empirical measurements of I from the present study are considerably lower than values predicted on the basis of Porter and Gates' formula (see also Birkebak, 1966; Walsberg et al., 1978). The discrepancy ranges from 30 to 80%, being smallest in densely furred animals such as shrews and largest in loosely furred animals like lemmings. Imperfect trapping of the layer of air (resulting in some circulation within the pelage), coupled with other factors such as conduction and radiation within and between individual hairs likely accounts for the difference (Birkebak, 1966).

The small number of insulation measurements taken in forced convection conditions indicate that I decreases somewhat as air velocity (V) increases. Animals with short fur (e.g., weasels) suffer less insulation loss at high V than do longer-furred

TABLE 2.—Insulation of $V = 0.1 \text{ m s}^{-1}$ and blackbody radiation conditions.

Animal	Mean fur depth (mm)	T_a (K)	T_w (K)	I ($\text{m}^{-2} \text{ }^\circ\text{KkW}^{-1}$)
<i>Mustela erminea</i>				
F1	5.0	23.6	23.7	55.8
WF2	6.0	18.8	19.0	72.6
<i>Mustela nivalis</i>				
M1	4.0	24.3	24.7	45.4
F2	3.5	24.6	24.4	38.4
CF3	3.4	19.0	19.2	34.9
<i>Dicrostonyx torquatus</i>				
W1	9.5	21.8	22.2	108.2 (124 fluffed)
W2	10.5	22.2	22.4	111.7 (136–140 fluffed)
CW3	8.5	19.4	19.7	83.8 (91 fluffed)
S1	6.5	21.8	22.0	77.5
<i>Lemmus sibiricus</i>				
1	4.0	23.4	23.5	61.4
2	5.5	22.6	22.2	88.6 (112 fluffed)
W1	10.0	22.9	22.6	97.0 (106 fluffed)
W2	9.5	23.0	22.9	96.3
Baby	5.0	22.9	22.7	61.4
CW3	8.0	21.0	20.9	74.0
<i>Sorex cinereus</i>				
1	3.3	23.7	23.6	55.8
2	3.5	19.4	19.3	60.7
<i>Microtus oeconomus</i>				
A	4.5	23.0	22.8	51.7 (61.4 fluffed)

species (e.g., lemmings). The amount of decrease in I as V shifts from 0.1 to 6.0 m s^{-1} ranges from about 25% (weasels) to 35% (lemmings). The relationship between I and V is plotted in Fig. 3, which indicates that I varies approximately as the square root of V . This observation is consistent with theoretical predictions (Davis and Birkebak, 1974) and with data from small birds (Robinson et al., 1976; Chappell, 1980). The change in I with V may be partly due to compaction of the fur layer from wind pressure; active piloerection will probably counteract this phenomenon to some extent in live animals.

Rather surprisingly, the surface areas of pelages (A) of the species measured in this study seem to depend primarily upon the animal's mass and are relatively independent of shape: a 40 g lemming has about the same A as a 40 g weasel, despite the extremely elongated shape of the latter. This is an artifact of the different fur lengths of the two species. Lemmings have much longer fur than weasels, which greatly increases their diameter and counteracts their compact shape (a 40 g lemming has almost twice the torso diameter and nearly three times the fur depth of a 40 g weasel). The skin area (A_s) of a weasel is substantially greater than that of a lemming of similar mass (Table 1; Brown and Lasiewski, 1972). As might be expected, the fur surface and skin areas of curled animals are considerably smaller than those of similarly sized animals in standing postures. The A values of the three curled casts averaged 30 to 40% smaller than A values for erect casts of the same species and size.

The A_{ee} of many organisms is generally smaller than the total surface area (lizards, Bartlett and Gates, 1967; spruce and fur branches, Tibbals et al., 1964; pine branches, Gates et al., 1965), presumably because an uneven black surface can radiate to itself

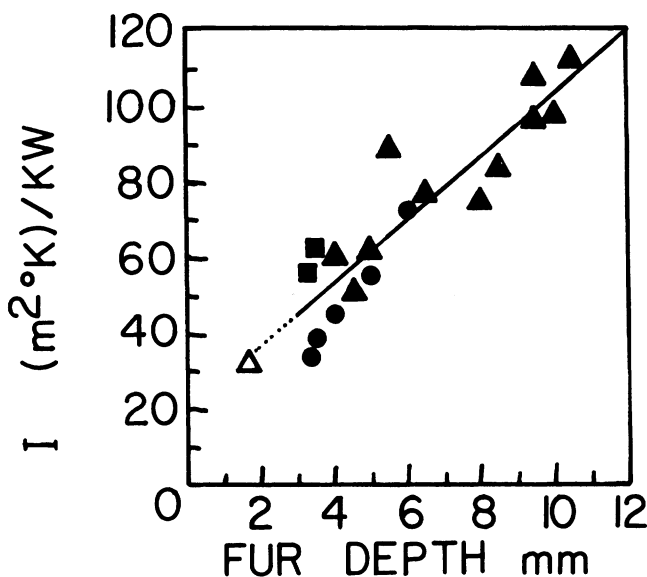


FIG. 2.—Relationship between insulation (I) in blackbody conditions with unstirred air ($V \sim 0.1 \text{ m s}^{-1}$), and fur depth. Data on antelope ground squirrels (open triangles) were not used in calculating the regression line. Circles = weasels, squares = shrews, dark triangles = lemmings and *Microtus*.

across concavities, as well as to its surroundings. As defined, it is physically impossible for A_{ee} to be larger than A . However, in Heller's (1972) study the measured A_{ee} was always slightly larger than A , and in this study A_{ee} occasionally exceeded A (Table 1). Heller believed this discrepancy reflected the difficulty of measuring total surface area accurately. It is also possible that the difference may result from the difficulty of obtaining accurate measurements of T_r , because the utilized T_r value was not integrated from the depth-temperature profile (as discussed above), or because of thermocouple conductivity. Even though thin (0.13 mm) thermocouples were used, conduction of heat away from the tips of the thermocouples may have caused slight errors. Thicker thermocouples (0.52 mm) were used initially, but invariably yielded A_{ee} values much larger than A measurements. Even the 0.13 mm wire gave unreliable results when only the measuring tip contacted the pelage. The placement procedure shown in Fig. 1 was developed to alleviate these problems by creating a large area of contact between thermocouple and fur. Despite some uncertainty about the precise A_{ee} values, results of this study indicate that the difference between A and A_{ee} is not large in small mammals. This is to be expected, because the geometries of the animals do not contain large concavities or areas of overlap that would lead to smaller $A:A_{ee}$ ratios (e.g., conifer branches; Tibbals et al., 1964). For most purposes, therefore, the value of A may be substituted for A_{ee} in energy budget calculations. The accuracy of this substitution will be improved if A is measured at average fur thickness rather than over the tips of the longest hairs.

Convection.—The rate of convective heat loss is related to air velocity, the temperature gradient between the fur surface and ambient air, and the thickness of the boundary layer adhering to the animal. Boundary layer thickness in turn depends on wind speed, animal size and shape, and surface texture characteristics. At a given air velocity, these complex relationships may be expressed as a constant, h_c ($\text{kW m}^{-2} \text{°K}^{-1}$). According to engineering theory, the h_c should vary as a power function of air

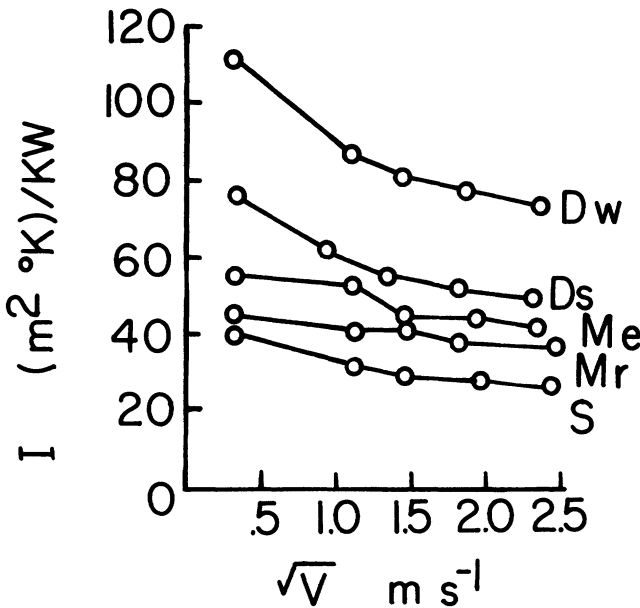


FIG. 3.—Relationship between insulation (I) and air velocity (V) under blackbody conditions for five representative casts. Dw = *Dicrostonyx* W2, Ds = *Dicrostonyx* S1, Me = *Mustela erminea* F1, Mr = *Mustela nivalis* M1, S = *Sorex* 1.

TABLE 3.—Convection data (r^2 in parentheses).

Animal	# data points	h_c as a function of V (kW m ⁻² °K ⁻¹)	Nu as a function of Re
<i>Mustela erminea</i>			
F1	5	0.00349V + .0025 (0.99)	0.175 Re ^{-.532} (0.97)
WF2	5	0.00272V + .0036 (0.99)	0.724 Re ^{-.363} (0.89)
<i>Mustela nivalis</i>			
M1	5	0.00397V + .0033 (0.99)	0.530 Re ^{-.395} (0.89)
F2	5	0.00473V + .0027 (0.91)	0.350 Re ^{-.459} (0.96)
CF3	9	0.00461V + .0057 (0.93)	0.140 Re ^{-.624} (0.98)
<i>Dicrostonyx torquatus</i>			
W1	5	0.00397V + .0032 (0.99)	0.458 Re ^{-.404} (0.96)
W2	5	0.00230V + .0037 (0.94)	0.268 Re ^{-.505} (0.98)
CW3	9	0.00328V + .0019 (0.90)	0.132 Re ^{-.594} (0.96)
S1	5	0.00341V + .0019 (0.98)	0.210 Re ^{-.495} (0.92)
<i>Lemmus sibiricus</i>			
1	5	0.00325V + .0031 (0.99)	0.385 Re ^{-.436} (0.94)
2	5	0.00435V + .0025 (0.99)	0.241 Re ^{-.521} (0.95)
W1	5	0.00336V + .0027 (0.99)	0.151 Re ^{-.551} (0.98)
W2	5	0.00364V + .0045 (0.93)	0.268 Re ^{-.505} (0.98)
Baby	5	0.00484V + .0047 (0.99)	0.495 Re ^{-.419} (0.90)
CW3	5	0.00269V + .0019 (0.95)	0.140 Re ^{-.549} (0.96)
<i>Sorex cinereus</i>			
1	5	0.00618V + .0082 (0.99)	0.639 Re ^{-.413} (0.96)
2	5	0.00550V + .0097 (0.98)	0.894 Re ^{-.387} (0.96)
<i>Microtus oeconomus</i>			
A	5	0.00450V + .0003 (0.96)	0.265 Re ^{-.508} (0.96)

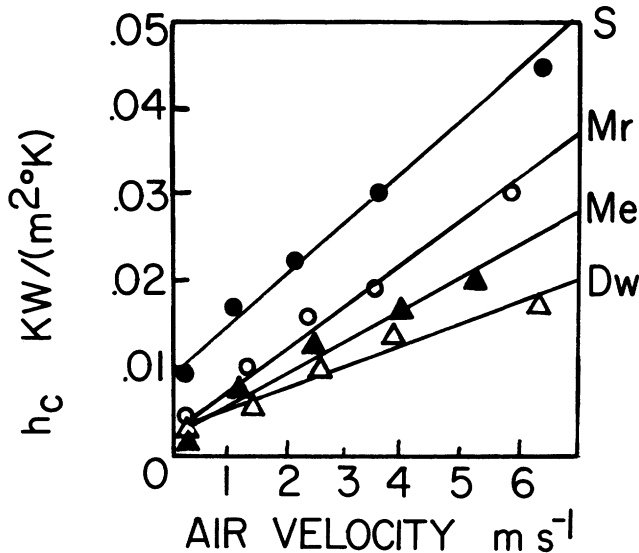


FIG. 4.—Relationship between the coefficient of convection (h_c) and air velocity (V) for four representative casts. Data points for each cast are shown as open or closed circle or triangle. Cast codes as in Fig. 3.

velocity and body diameter. Results from wind tunnel experiments with spheres and cylinders are in agreement with theory (Wathen et al., 1971, 1973; Mitchell, 1976). Robinson et al. (1976) have suggested that convective heat loss would be proportional to $V^{0.5}$. They and others (Gessaman, 1972; Chappell, 1980) have empirically demonstrated that heat loss is a function of $V^{0.5}$ in birds. Heller's (1972) values of h_c varied linearly with air velocity. Results from the present study are ambiguous. As expected, there is an inverse relationship between h_c and body diameter, but the data points are most reliably predicted by least-squares regressions of h_c on V (rather than on $V^{0.5}$), with the coefficients of determination (r^2) higher than 0.95 in most cases. These regressions are given in Table 3, and are plotted in Fig. 4 for four species of different sizes and shapes. Regressions of h_c on $V^{0.5}$ also yield good r^2 values, but the average (about 0.92–0.94) is slightly less than for the corresponding h_c versus V regressions. Conversion of the data to Nusselt and Reynolds numbers gives results consistent with the sphere-cylinder data and heat transfer theory. The Nusselt (Nu ; $= h_c D/k$) and Reynolds (Re ; $= \rho V D/\mu$) numbers are dimensionless values, useful because once the Nu - Re empirical relationship is established it can be used to predict h_c for any sized animal with similar surface geometry (Kreith, 1965). Values for k (thermal conductivity of air), ρ (density of air), and μ (viscosity of air) were obtained from Tracy et al. (1978). The regressions relating Nu to Re are also given in Table 3 (these regressions include the entire range of Re values for each animal). The Nu and Re values of 4 representative animals are plotted in Fig. 5, along with a theoretical curve for convection from an ideal cylinder. The data points fall out parallel to and below the cylinder curve, which is similar to the results obtained by Wathen et al. (1971, 1973) and Mitchell (1976). The Re - Nu relationships do not differ substantially among the species studied. This can be most easily appreciated from inspection of Fig. 5, which shows little dissimilarity in the curves for even the most differently shaped animals (weasels and lemmings). Thus, body shape does not seem to influence convective heat transfer

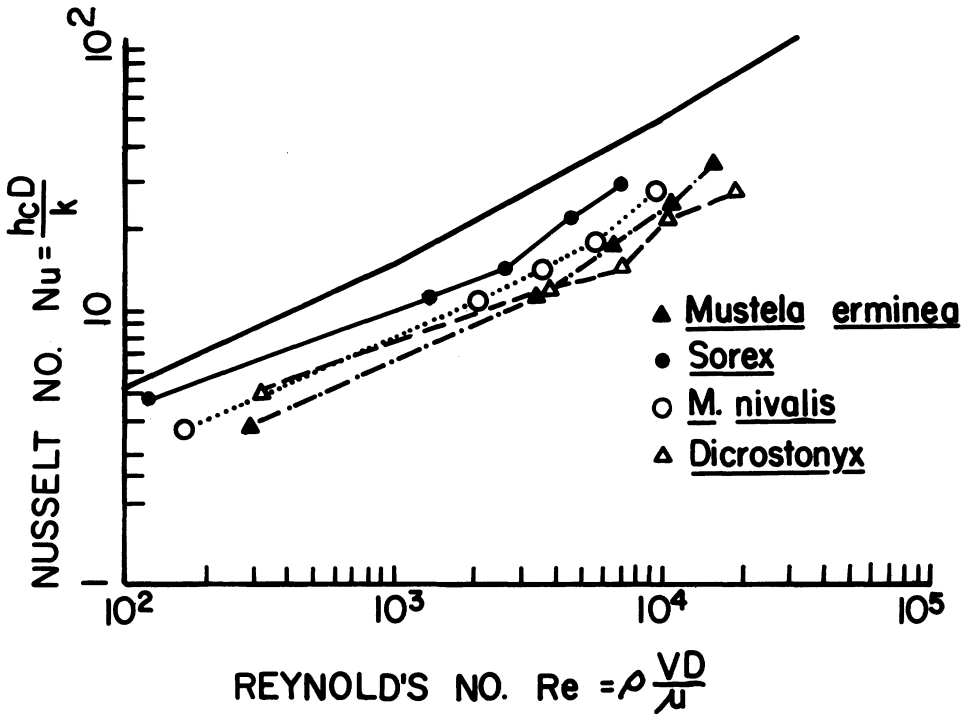


FIG. 5.—Nusselt-Reynolds plot for the same 4 casts as in Fig. 3.

strongly in these animals. Pelage characteristics also have little influence (except as they affect body diameter).

The observed linearity in the direct h_c versus V regressions may be more apparent than real. All of the points at high V fall out below the regression lines, and most points from moderate V (1.0–2.0 m s⁻¹) are slightly above the lines (Fig. 4). Because of the small number of sampled air velocities, overestimation of h_c at high V could distort and obscure a power curve or other nonlinear relationship. Such overestimates could have arisen from intracast temperature gradients (discussed above), although checks indicated that this phenomenon was not severe. If gradients existed, they would increase with the rate of heat loss and therefore would be largest at high V .

There appears to be no strong or consistent effect upon h_c from assuming a curled posture, although the number of samples is small. Of the three curled casts examined, one had h_c values almost equivalent to those of an erectly postured cast of the same species and size, one had h_c values slightly larger than those of an erect cast, and the third had h_c values slightly smaller than those of an erect cast. Apparently the heat conservation effect of curling is not a factor of decreasing convective heat loss per unit area, but is entirely due to decreased total surface area available for heat transfer to the environment.

In general, the results from these experiments on actual animal castings with natural pelages are in good agreement with data obtained from simple fur-covered geometrical shapes. For most biophysical modeling purposes, then, animal shapes can accurately be assumed to behave convectively as cylinders or spheres of appropriate dimensions. In natural environments, the instantaneous value of convective heat flow varies rapidly with fluctuations of air velocity and direction, as well as turbulence levels. Average h_c values are probably more meaningful than exact measurements, not only to

the biophysical ecologist but also to the animal itself, because it can only respond to some average heat flow (Porter and Gates, 1969; Mitchell, 1976). Hence, for small furred animals, time-consuming empirical determinations of h_c , while rigorous, are probably not necessary. Exceptions to this rule are possible for animals with unusual shapes or pelage configurations.

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