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TEMPERATURE REGULATION IN SKUNKS (MEPHITIS MEPHITIS  
AND SPILOGALE PUTORIUS): RE-EXAMINATION OF  
METABOLISM AND BODY SIZE IN MUSTELIDS

BY

KATHY L. KNUDSEN

B.A. UNIVERSITY OF MONTANA, 1975

Presented in partial fulfillment of the requirements

for the degree of

Master of Arts

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1979

Approved by

  
Chairman, Board of Examiners

  
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Temperature Regulation in Skunks (Mephitis mephitis and Spilogale putorius): Re-examination of Metabolism and Body Size in Mustelids (47 pp.)

Director: Dr. Delbert L. Kilgore *DW*

Energy requirements of mammals are such that metabolism increases with increasing body size. While the metabolism of most species conforms rather closely to the values predicted from the interspecific relationship between metabolic rate and body mass, some phylogenetic groups of mammals deviate considerably from predicted values. One such group is the mustelid carnivores who in general have higher than expected metabolic rates. In fact, small mustelid species have metabolic rates up to 100% greater than predicted. The basis of such elevated rates is not known, however, most mustelids tend to have an elongate body form and therefore a high surface to volume ratio. Their high metabolic rates then might possibly result from an elevated rate of heat loss from this relatively large surface area. Some species of mustelids such as skunks (subfamily Mephitinae) do not have an elongate body form therefore may not exhibit this elevated metabolism.

Oxygen uptake, carbon dioxide production, evaporative water loss and body temperature were measured in 6 adult spotted skunks (Spilogale putorius) and 2 adult striped skunks (Mephitis mephitis) at various air temperatures ranging from 8 to 40°C and 4 to 36°C respectively, in 4°C intervals. From this data estimates of thermal conductance (heat loss) and net heat transfer were calculated.

Both species of skunks exhibit a normal mammalian pattern of thermoregulation although they differ somewhat from each other. Striped skunks have a rather broad thermoneutral zone between 17 and 28°C, while spotted skunks have a relatively narrow thermoneutral zone or a thermoneutral point at 33°C. The standard metabolic rates of striped skunks ( $0.266 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) and spotted skunks ( $0.426 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) are 28 and 36% respectively, lower than those rates predicted for mammals of the same body sizes. In addition, these rates are also lower than rates predicted for mustelids of the same body sizes. Both species of skunks have a significantly shorter and heavier body form than most of the other mustelidae. The significantly lower metabolic rates of the skunks in comparison to other mustelids suggests that body form may be an important determinant of the relationship between body size and metabolism in this group.

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## CHAPTER I

### INTRODUCTION

Total metabolic rate of mammals increases with increasing body size. This interspecific relationship between metabolic rate (M) and body mass (W) can be described by an equation in the form  $M = kW^b$ , where k and b are constants. The exponent b gives the rate at which metabolism changes with size. Brody (1945) empirically determined the value of b to be 0.73 while Kleiber (1975) found it to be 0.75. The difference between these values is too small to be statistically valid (Kleiber, 1975).

Why metabolic rate is related to the 3/4 power of body mass is not clear. Ultsch (1973) explains it in terms of the ability of an organism to obtain oxygen from its environment. McMahon (1973) proposed that elastic criteria are important in establishing limits on biological proportions and thus on metabolism. Another suggestion, by Blum (1977), involves considering the values of exponents in four or higher dimensional spaces. For example, in the third dimension the ratio of surface area to mass is 0.67 while in the fourth dimension the relationship is 0.75. It may not be necessary to consider surface to volume relationships in a hypothetical four-dimensional space, as an exponent of 0.75 can also be accounted for by a "folding" of surfaces in ordinary three-dimensional space (Derome, 1978). Kleiber (1975) points out that it is impossible for the exponent to be 1. If metabolic rate of mammals was directly proportional to body size (b = 1.0) small mammals would require fur up to 20 cm thick to maintain a normal body temperature, while large mammals would have surface temperatures above the boiling



point.

Rubner (1883 cited in Kleiber, 1975) proposed that the metabolic rate of homeotherms should be related to surface area since heat production equals heat lost through the surface. This "surface rule" assumes that the surface controlling the rate of metabolism increases as the square of a linear dimension. Therefore, metabolic rate should increase with the 0.67 or 2/3 power of body mass (Swan, 1974; Kleiber, 1975) which it clearly does not. Either the surface area of mammals increases more rapidly with increase in linear dimension as suggested by Derome (1978) or other factors influence metabolism besides surface area. Regardless, surface area is an important determinant of metabolic rate of homeotherms (James, 1970; Brown and Lasiewski, 1972; Swan, 1974; Derome, 1978).

While the metabolism of most species conforms rather closely to the values predicted from the interspecific relationship between metabolic rate and body mass, some phylogenetic groups of mammals have consistently higher or lower metabolic rates than predicted. The metabolic rates of Australian (Kinnear and Shield, 1975) and neotropical marsupials (McNab, 1978), for example, are 30 and 20% respectively, less than the predicted values. Lower than predicted rates also occur in heteromyid rodents (Tucker, 1965; Hudson and Rummel, 1966) and in geomyids (McNab, 1966). Packard (1968) noted that microtine rodents have elevated metabolic rates as exemplified by Microtus montanus, which has a metabolic rate 75% above the predicted value. In other phylogenetic groups, in particular the mustelid carnivores, the relationship between metabolic rate and body mass is not the same over a wide range of body

sizes. In a study on seven species of mustelids, Iversen (1972) found that the species under 1 kg had metabolic rates up to 100% greater than predicted while the species over 1 kg had metabolic rates only 20% higher than predicted. He concluded that a metabolic adjustment has occurred in the small mustelidae. Since the small mustelids studied by Iversen were all weasels, which have an elongate body form, it is possible that their high metabolic rates are due to their relatively high surface area. Surface area of elongate mustelids does in fact influence their metabolism (Brown and Lasiewski, 1972). The metabolic rates of cold-stressed long-tailed weasels (Mustela frenata) when compared with those of woodrats (genus Neotoma), which are more normally shaped mammals, are 50% to 100% higher. Weasels also have 15% more surface area than woodrats.

Iversen's conclusions concerning metabolism and body size in mustelids, especially that for small species, may well be biased by his inclusion of only small elongate weasels. More normally shaped small mustelids may not show the metabolic adjustments noted by Iversen (1972). The purpose of this study was two-fold: (1) to study thermoregulation in small and medium size mustelids (spotted skunks, Spilogale putorius and striped skunks, Mephitis mephitis which appear to have a more normal mammalian body shape and (2) to re-examine the relationship between metabolism and body size in mustelids.

## CHAPTER II

### MATERIALS AND METHODS

Experimental animals.--The descended adult striped and spotted skunks used in this study were purchased from commercial suppliers. The spotted skunks (4 males and 2 females) were collected in Hendry County, Florida; the striped skunks (2 males) were reared in captivity or field captured in southern Florida.

The skunks were caged individually in a room held at  $22 \pm 2^{\circ}\text{C}$  on a natural photoperiod and were provided with dry dog food and water ad libitum. This diet was regularly supplemented with freshly killed mice and meat scraps. They were held in captivity for several months before being used in the experiments.

Oxygen consumption.--Oxygen consumption of spotted skunks (mean body mass 0.624 kg; range 0.519 to 0.801) and striped skunks (mean body mass 5.667 kg; range 5.544 to 5.770) was measured at various air temperatures during July and August of 1976 and January and February of 1977, respectively. Food was withheld from spotted skunks for a minimum of 8 hours prior to determinations of oxygen uptake and 11 hours from the striped skunks so all animals were post-absorptive. To determine if there was a period of low or minimal metabolism, oxygen consumption in one individual of each species was measured for 24 hours (Appendix I; Tables A and B). Based on their 24-hour cycle of metabolism, all subsequent measurements of oxygen consumption of spotted skunks were made between 0700 and 1700 hours and between 1000 and 1900 hours on striped skunks.

Animals were weighed and placed in air-tight metabolic chambers of two sizes (0.23 x 0.24 x 0.35 m or 0.40 x 0.40 x 0.55 m). The chambers were equipped with gas ports and a silent running, low speed stirring fan and were painted flat-black on the interior to reduce infra-red reflectivity (Porter, 1969). The animals were suspended above a layer of mineral oil on a wire mesh platform and could be observed through a small glass window. The chambers were positioned within a constant temperature cabinet which was preset to the desired temperature. Animals were exposed to the experimental temperature for at least one hour before their oxygen consumption was measured. Air temperatures within chambers ( $T_a$ ) were continuously recorded with copper-constantan thermocouples connected to a multi-point potentiometric recorder (Honeywell Electronic 16). The thermocouples were calibrated with a mercury thermometer certified by the National Bureau of Standards (NBS). The systematic error of air temperatures within the respirometers did not exceed  $0.03^{\circ}\text{C}$  while the imprecision was 1% of any air temperature. The systematic error (accuracy) and imprecision of measurements are reported as recommended by Eisenhart (1968).

Air was drawn through the metabolic chamber and then through a drying column (Appendix II). Flow of dry air was measured with a Brooks flowmeter which had been calibrated with a NBS certified VOL-U-METER (Brooks, model 1058). Systematic error of flow volumes was  $9 \times 10^{-4}$ , while the imprecision (standard error/ $\text{ml min}^{-1} \times 100$ ) was less than 0.3% of any flow rate. Air flow was held constant during any given measurement of oxygen consumption but ranged from 1.9 to  $4.3 \text{ l min}^{-1}$  for the spotted skunks and from 6.8 to  $12.2 \text{ l min}^{-1}$  for the striped skunks. All

gas volumes were corrected to standard conditions of temperature and pressure. A sample of the effluent air was passed through a Beckman G2 paramagnetic oxygen analyzer (2% full scale). The analyzer was calibrated by varying the pressure within the cell and the calibration was frequently checked with a certified primary gas standard. Systematic error of oxygen concentration measurements was 0.04% O<sub>2</sub> while imprecision (standard error/%O<sub>2</sub> x 100) was 0.04% of any O<sub>2</sub> concentration.

The change in fractional oxygen concentration was monitored until a period of minimal, prolonged and constant oxygen consumption was obtained. It was assumed that the metabolic rate of the animal during these periods reflected resting rates since all of the animals were observed to be resting quietly. The fractional oxygen concentration varied by +0.04% or less during these periods which lasted for 10 minutes or more.

Spotted and striped skunks were exposed to experimental temperatures between 8 and 40°C and 4 and 36°C respectively, in approximately 4°C intervals. The oxygen consumption of skunks was measured at different temperatures on different days.

Carbon dioxide production.--Variations in fractional concentration of CO<sub>2</sub> in the effluent air were measured with a Beckman (model 864) infrared CO<sub>2</sub> analyzer. The analyzer was modified to include a linearizer circuit which yielded a linear readout of CO<sub>2</sub> concentrations between 0 and 2.5%. The analyzer was calibrated by 'bleeding' dry CO<sub>2</sub> into room air flowing through the metabolic chamber. The fractional concentration of CO<sub>2</sub> in the effluent air could then be calculated from the flow vol-

umes. Carbon dioxide production rates were calculated from the analyzer output during periods of minimal oxygen uptake.

Oxygen consumption and carbon dioxide production values were corrected for changes in the respiratory exchange ratio (R).

Evaporative water loss.--Evaporative water loss was measured gravimetrically during oxygen consumption experiments. Water vapor in the effluent air was collected in Drierite columns for periods of approximately six minutes when oxygen consumption was at a constant and minimal level. At the higher temperatures, heat tape was used to prevent condensation of water vapor from the effluent air in the tubing between the respirometer and collection column.

Body temperatures.--Body temperatures of skunks were recorded before and immediately after each measurement of oxygen consumption. A thermistor probe was inserted into the rectum to a depth of 8cm in spotted skunks and to 10cm in striped skunks. The thermistor probe was calibrated with a NBS certified mercury thermometer. The systematic error of these measurements does not exceed 0.03°C, while the imprecision does not exceed 0.6% of any temperature.

Statistical analysis.--A multiphase regression technique was used in the analysis of oxygen consumption and body temperature data to estimate the inflection point of a segmented line (Hudson, 1966; Johnson, 1968).

## CHAPTER III

### RESULTS

#### Spilogale putorius

Gas exchange in relation to ambient air temperature.--Oxygen consumption of spotted skunks is an inverse linear function of air temperature ( $T_a$ ) below about 33°C (Fig. 1), but increases with temperatures above this point. This species appears to have either an extremely narrow thermoneutral zone or a thermoneutral point (TNP). The air temperature at which metabolism is minimal is 33.18°C. The mean metabolic rate of this species at the TNP ( $\dot{V}_{O_2} = 0.426 \text{ ml O}_2 \text{ g}^{-1}\text{h}^{-1}$ ) is 36% lower than that predicted for a mammal with the same body mass from the equation of Morrison, Ryser and Dawe (1959);  $\dot{V}_{O_2} = 3.8 W^{0.73}$ , where  $\dot{V}_{O_2}$  is oxygen consumption ( $\text{ml O}_2 \text{ g}^{-1}\text{h}^{-1}$ ) and  $W$  is body mass in grams (Fig. 1).

The relationship between carbon dioxide production ( $\dot{V}_{CO_2}$ ) and air temperature (Appendix III, Table A), is similar to that between  $\dot{V}_{O_2}$  and  $T_a$ . The lowest  $\dot{V}_{CO_2}$  recorded was at an air temperature slightly below the TNP (31°C). The mean respiratory exchange ratio (R) computed from the  $\dot{V}_{O_2}$  and  $\dot{V}_{CO_2}$  data was 0.67 which is within the normal range of this ratio (Kleiber, 1975).

Evaporative water loss.--Total (combined respiratory and cutaneous) evaporative water loss of spotted skunks, expressed per ml  $O_2$  consumed, increases gradually with an increase in air temperature from 8 to 32°C (Fig. 2). The mean water loss at 32°C is 2.19 mg  $H_2O$ / ml  $O_2$ . Above 32°C water loss rises markedly and becomes more variable. The maximum

Figure 1: Relationship between weight specific oxygen consumption and air temperature in six adult Spilogale putorius. Lines were fitted with a multiphase regression technique (see Methods). The horizontal dotted line represents the oxygen consumption value predicted from the equation of Morrison et al. (1959) for a mammal with a body mass equal to the mean body mass of these skunks.



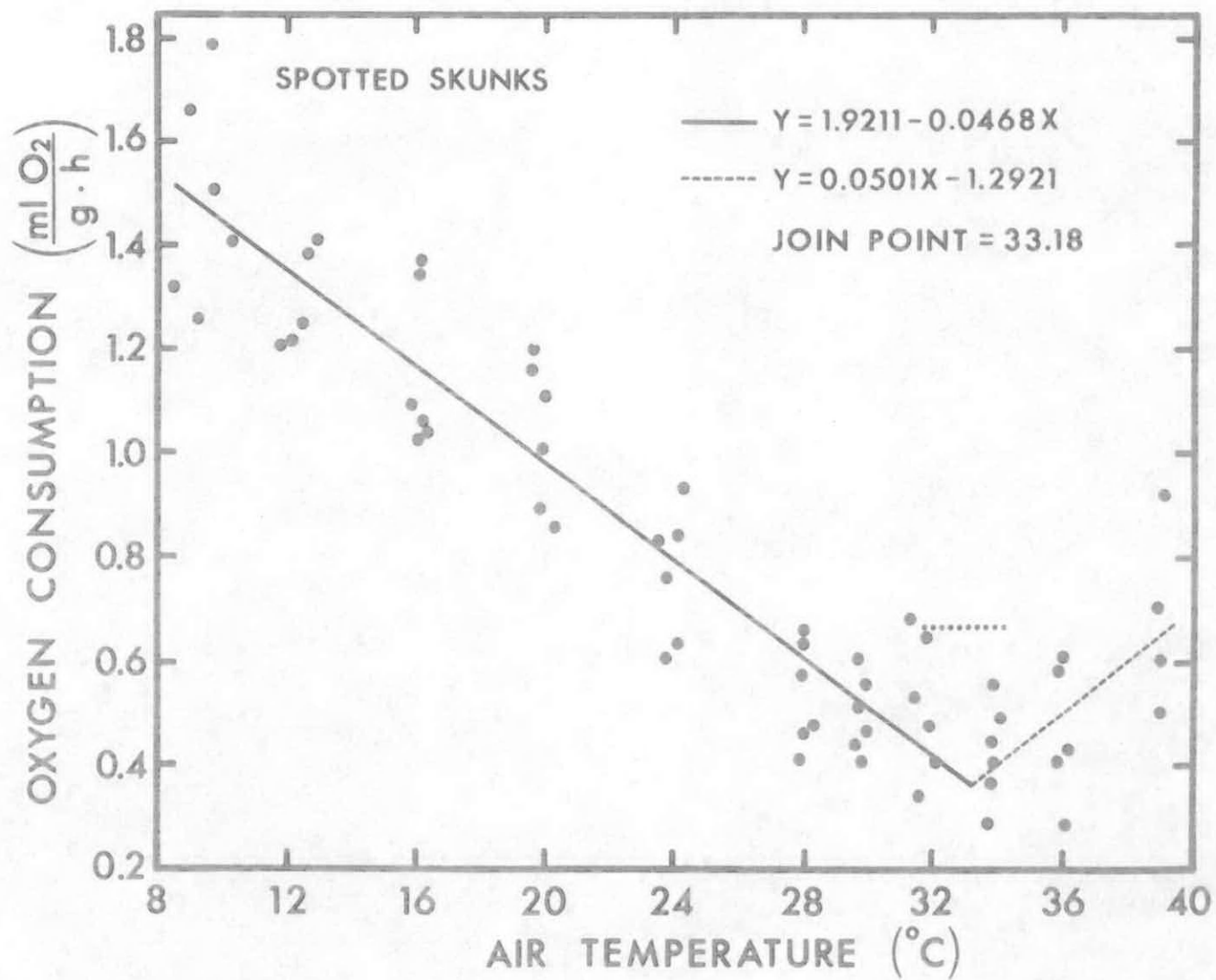
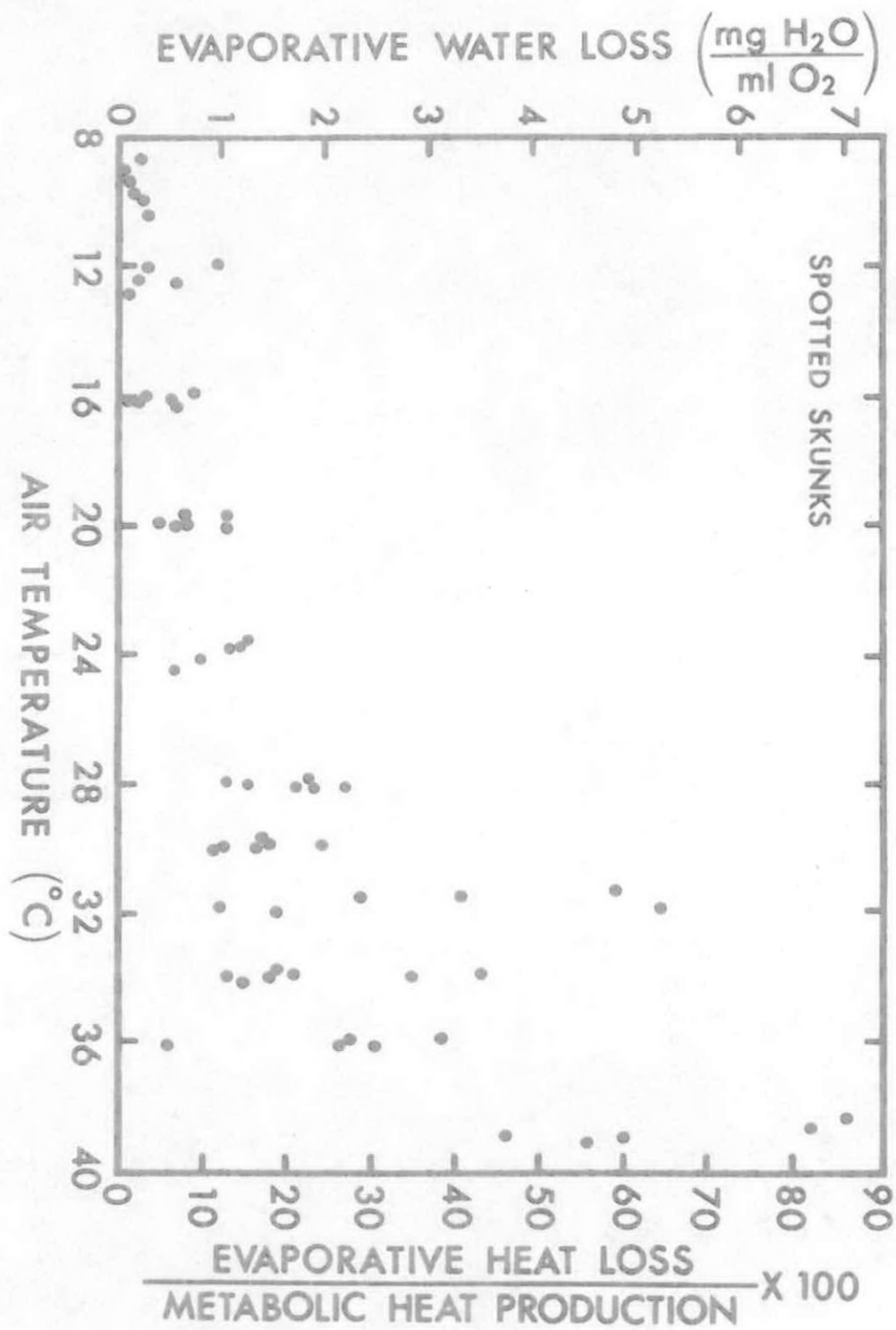


Figure 2: Evaporative water loss expressed per ml O<sub>2</sub> consumed and fraction of heat production lost by evaporation at various air temperatures of six adult Spilogale putorius. At 24 and 28°C quantity of water in incurrent air was calculated based on relative humidity and not measured.



water loss measured in this species was 6.66 mg H<sub>2</sub>O/ml O<sub>2</sub>.

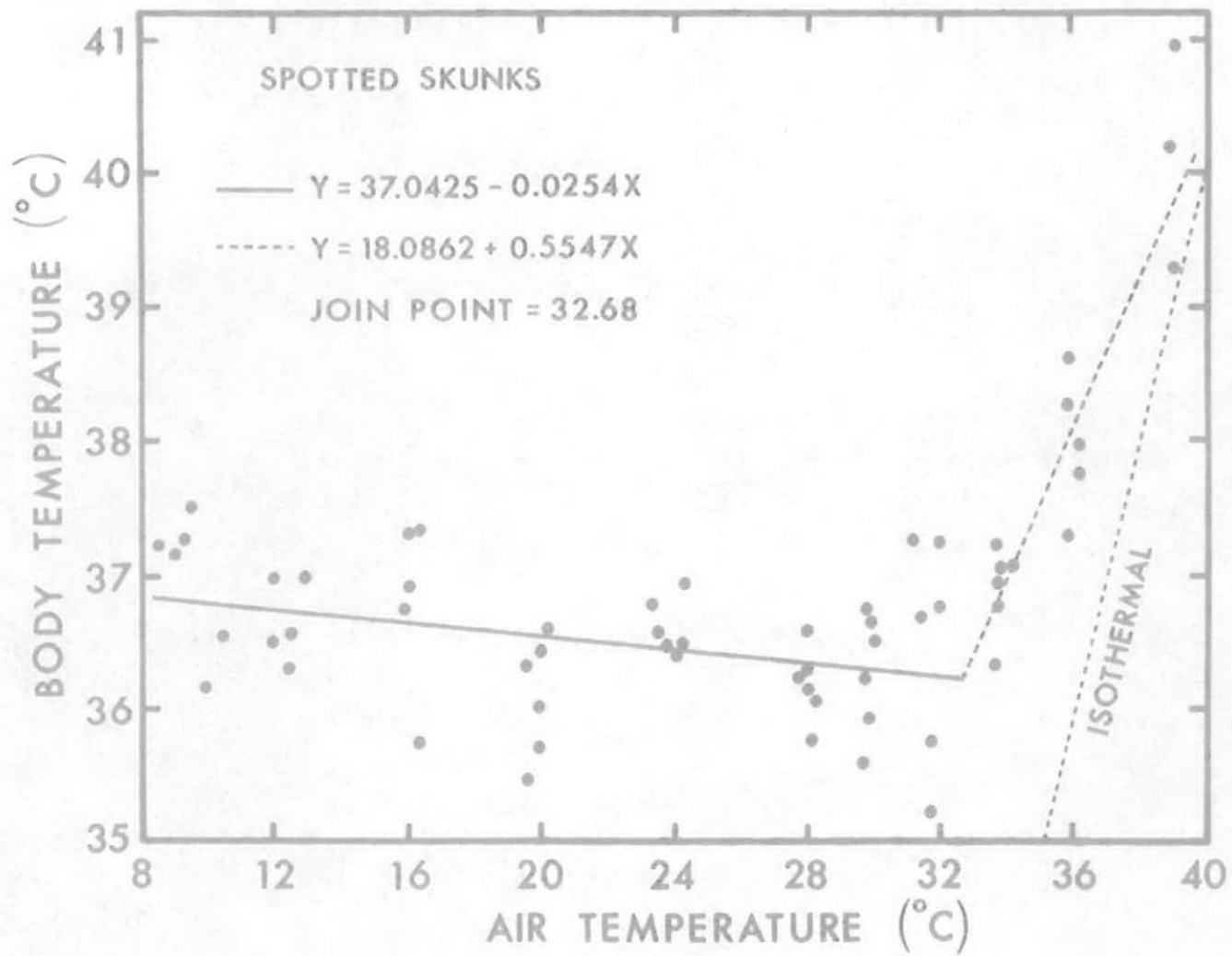
Heat loss by evaporation in spotted skunks represents only 2% of the metabolic heat production at 8°C (estimated from 0.58 cal/ mg H<sub>2</sub>O evaporated and 4.7 cal/ml O<sub>2</sub> consumed, but this fraction increases to 27% at 32°C (Fig. 2). The mean evaporative water loss at the highest air temperature (38°C) was 4.95 mg H<sub>2</sub>O/ml O<sub>2</sub> and represents 61% of the metabolic heat production of skunks at that temperature.

Body temperature.--Body temperatures (T<sub>b</sub>) of the spotted skunks following their exposure to various T<sub>a</sub>s remained fairly constant (varying between 35.2 and 37.5°C) at air temperatures below the TNP (Fig. 3). There is a tendency for body temperatures to decrease slightly as T<sub>a</sub> increases from 8 to 32°C. The slope of the least-squares regression line fitted to these data (Fig. 3) is significantly different from zero (P<0.05). Above 32°C body temperatures increased concomitantly with elevations in heat production (Figs. 1 and 3).

Body temperatures measured before the animals were placed in the metabolic chambers ranged from 35.7 to 39.4°C. The mean T<sub>b</sub> measured under these conditions was 37.3°C and differed significantly (P<.01) from the mean body temperatures recorded after exposure to air temperatures between 20 and 24°C (mean = 36.4°C).

Thermal conductance and dry heat transfer.--Thermal conductance of spotted skunks can be computed from the approximation of Fourier's Law of heat flow,  $MR = C (T_b - T_a)$  where MR is the metabolic rate (or  $\dot{V}_{O_2}$ ), C is the thermal conductance, T<sub>b</sub> is body temperature and T<sub>a</sub> is air

Figure 3: Body temperatures of six adult Spilogale putorius at various air temperatures. Lines were fitted with a multiphase regression technique (see Methods).



temperature. The minimal thermal conductance of spotted skunks (Appendix III, Table A) is  $0.21 \text{ cal g}^{-1}\text{h}^{-1}\text{C}^{-1}$ . Above the TNP conductance increases to a maximum of  $10.59 \text{ cal g}^{-1}\text{h}^{-1}\text{C}^{-1}$ . The minimal thermal conductance predicted from the equation of Herreid and Kessel (1967),  $C = 4.91W^{-0.505}$  where W is body mass in grams, for a mammal of the same body size (624 g) is  $0.19 \text{ cal g}^{-1}\text{h}^{-1}\text{C}^{-1}$ . The observed minimal value is 11% higher than that predicted.

Dry heat transfer (h) or dry conductance (Calder and Schmidt-Nielsen, 1967; Bligh and Johnson, 1973; Weathers and Schoenbaechler, 1976) is a measure of the facility with which heat is lost by non-evaporative means; that is by conduction, convection and radiation, and is dependent on the difference between body and air temperature. At air temperatures from 8 to  $32^{\circ}\text{C}$ , h of spotted skunks is relatively constant ( $0.26 \text{ cal g}^{-1}\text{h}^{-1}\text{C}^{-1}$ ), but above the TNP h increases to a mean value of  $1.3 \text{ cal g}^{-1}\text{h}^{-1}\text{C}^{-1}$  at  $39^{\circ}\text{C}$  (Fig. 4). However, the amount of heat lost by dry transfer at a particular air temperature ( $\text{cal g}^{-1}\text{h}^{-1}$ ) decreases with increasing temperature up to  $32^{\circ}\text{C}$  (Fig. 4). From 32 to  $39^{\circ}\text{C}$  dry heat loss remains relatively constant ( $1.46 \text{ cal g}^{-1}\text{h}^{-1}$ ).

### Mephitis mephitis

Gas exchange in relation to ambient air temperature.--In male striped skunks oxygen consumption increases with decreasing temperatures below  $17^{\circ}\text{C}$  but increases at air temperatures above  $29^{\circ}\text{C}$  (Fig. 5).

Unlike the spotted skunks, male striped skunks appear to have a relatively broad thermoneutral zone (TNZ); oxygen consumption was minimal at air temperatures from 17 to  $29^{\circ}\text{C}$  (Fig. 5). The mean metabolic

Figure 4: Dry heat transfer (h) from six adult Spilogale putorius at various air temperatures. The dry heat transfer coefficient is calculated as follows:

$$h = \frac{\text{rate of heat production} - \text{rate of heat loss by evaporation}}{(T_b - T_a) \cdot \text{body mass}}$$

Dry heat loss is h multiplied by  $(T_b - T_a)$ .



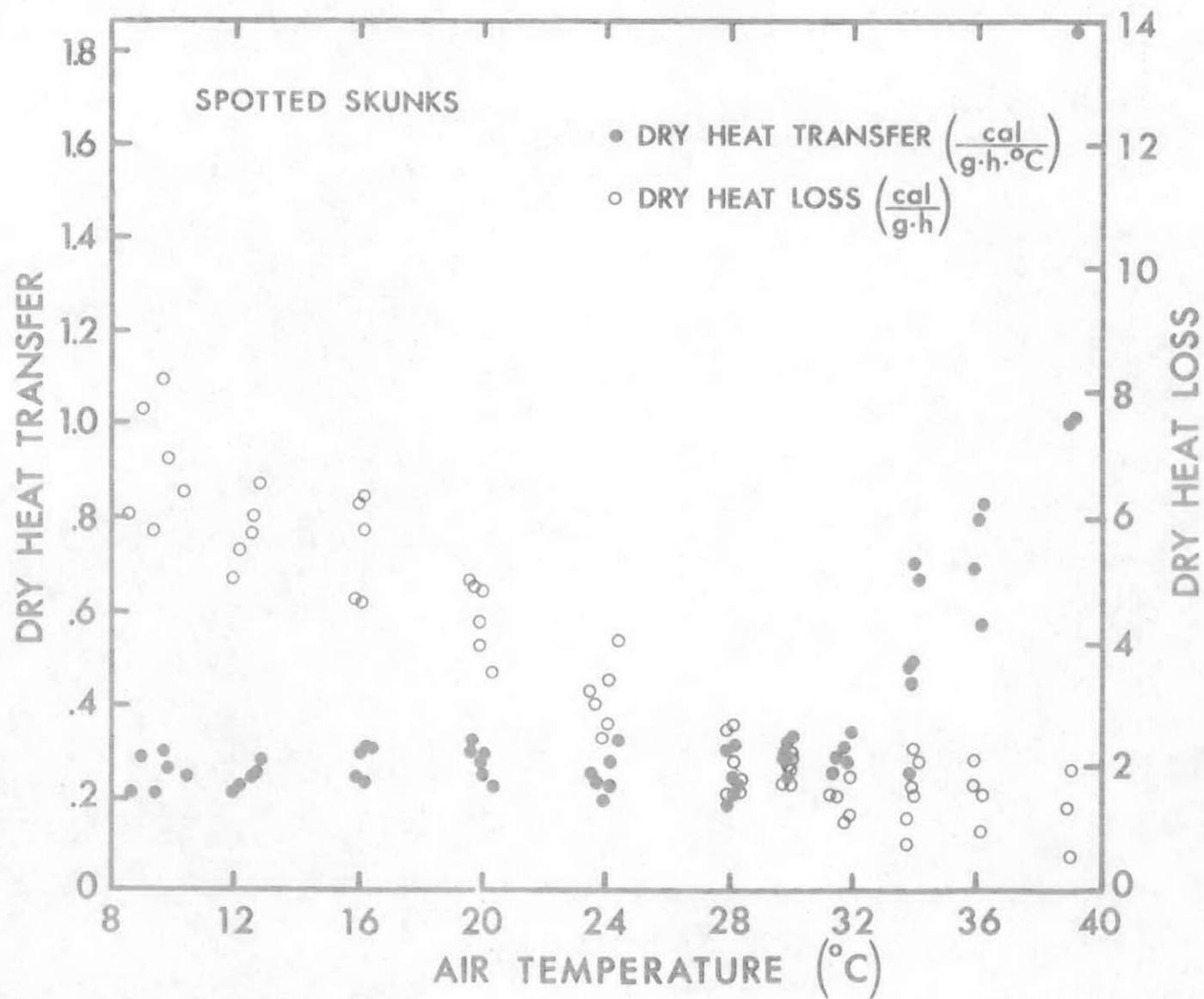
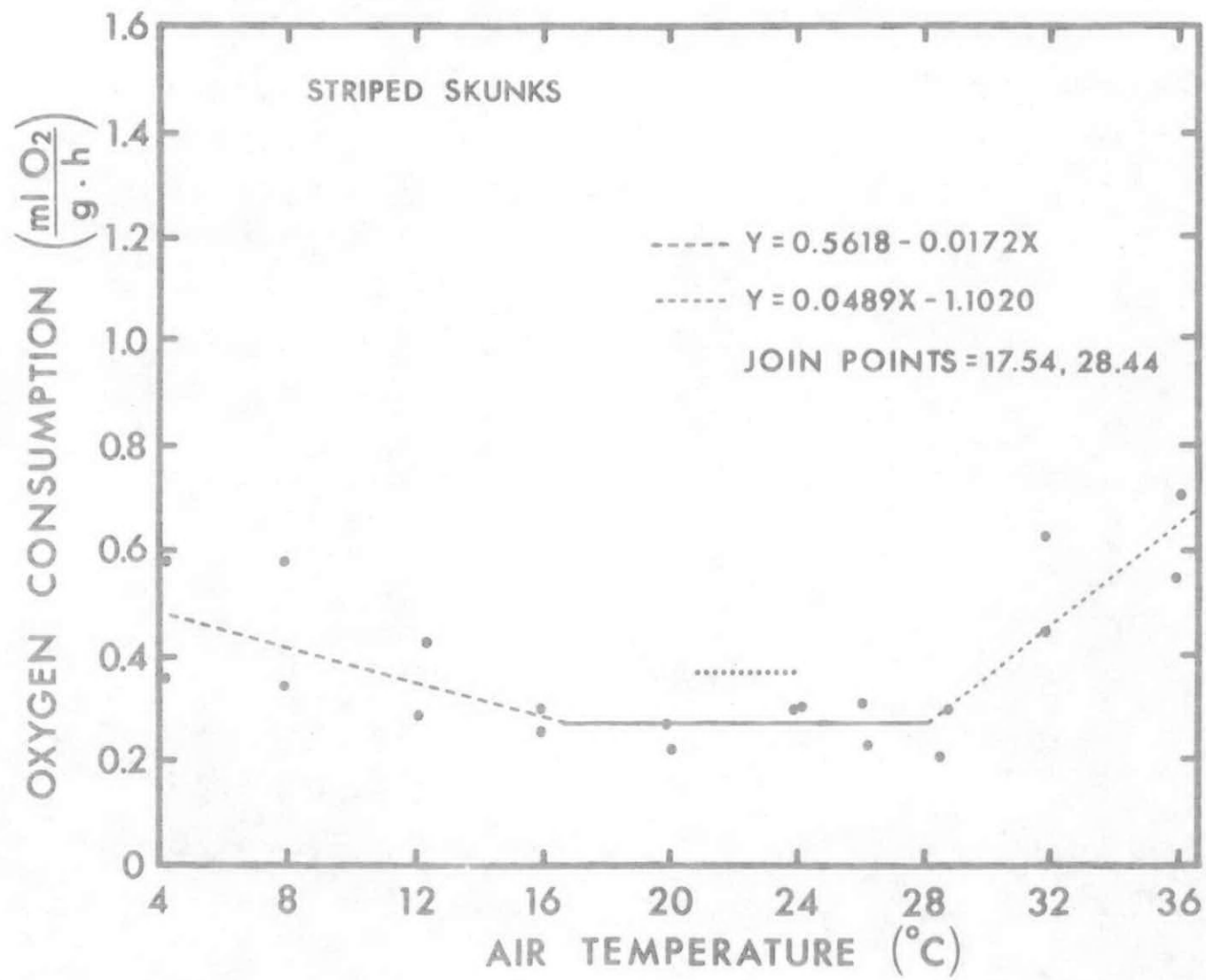


Figure 5: Relationship between weight specific oxygen consumption and air temperature in two adult Mephitis mephitis. Lines were fitted with a multiphase regression technique (see Methods). The horizontal dotted line represents the oxygen consumption value predicted from the equation of Morrison et al. (1959) for a mammal with a body mass equal to the mean body mass of these skunks.



rate of these skunks at the TNZ was  $0.266 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  which is 28% less than that predicted for mammals of the same body size (Morrison et al., 1959).

The relationship between  $\dot{V}_{\text{CO}_2}$  and  $T_a$  (Appendix III, Table B), is similar to the relationship between  $\dot{V}_{\text{O}_2}$  and  $T_a$ . The mean value of R was 0.70.

Evaporative water loss.--Total evaporative water loss in striped skunks, expressed per ml  $\text{O}_2$  consumed, tends to increase with an increase in  $T_a$ , but varies considerably between air temperatures of 20 and  $29^\circ\text{C}$  (Fig. 6). The mean water loss at air temperatures from 17 to  $29^\circ\text{C}$  (TNZ) is 1.21 mg  $\text{H}_2\text{O}/\text{ml O}_2$ . At the highest  $T_a$  these skunks were exposed to evaporative water loss was 3.12 mg  $\text{H}_2\text{O}/\text{ml O}_2$ .

Evaporative heat loss increases from only 5% of the metabolic heat production at  $4^\circ\text{C}$  to 38% at  $36^\circ\text{C}$  (estimated from 4.7 cal/ml  $\text{O}_2$  and 0.58 cal/mg  $\text{H}_2\text{O}$ ). At thermoneutrality evaporative heat loss accounted for 15% of the metabolic heat production (Fig. 6).

Body temperatures.--Body temperatures of striped skunks were fairly constant (varying between 35.8 and  $36.9^\circ\text{C}$ ) at temperatures below  $20^\circ\text{C}$  (Fig. 7). The slope of the least-squares regression line fitted to these data is not significantly different from zero ( $P > 0.05$ ). Above  $20^\circ\text{C}$  body temperatures increased with increase in  $T_a$  and was maximal ( $38.8^\circ\text{C}$ ) at a  $T_a$  of  $32^\circ\text{C}$ .

Body temperatures recorded before the animals were placed in metabolic chambers ranged from 35.8 to  $38.7^\circ\text{C}$ . The mean  $T_b$  under these conditions ( $36.7^\circ\text{C}$ ) was not significantly different ( $P > 0.10$ ) from body

Figure 6: Evaporative water loss expressed per ml O<sub>2</sub> consumed and fraction of heat production lost by evaporation at various air temperatures of two adult Mephitis mephitis.

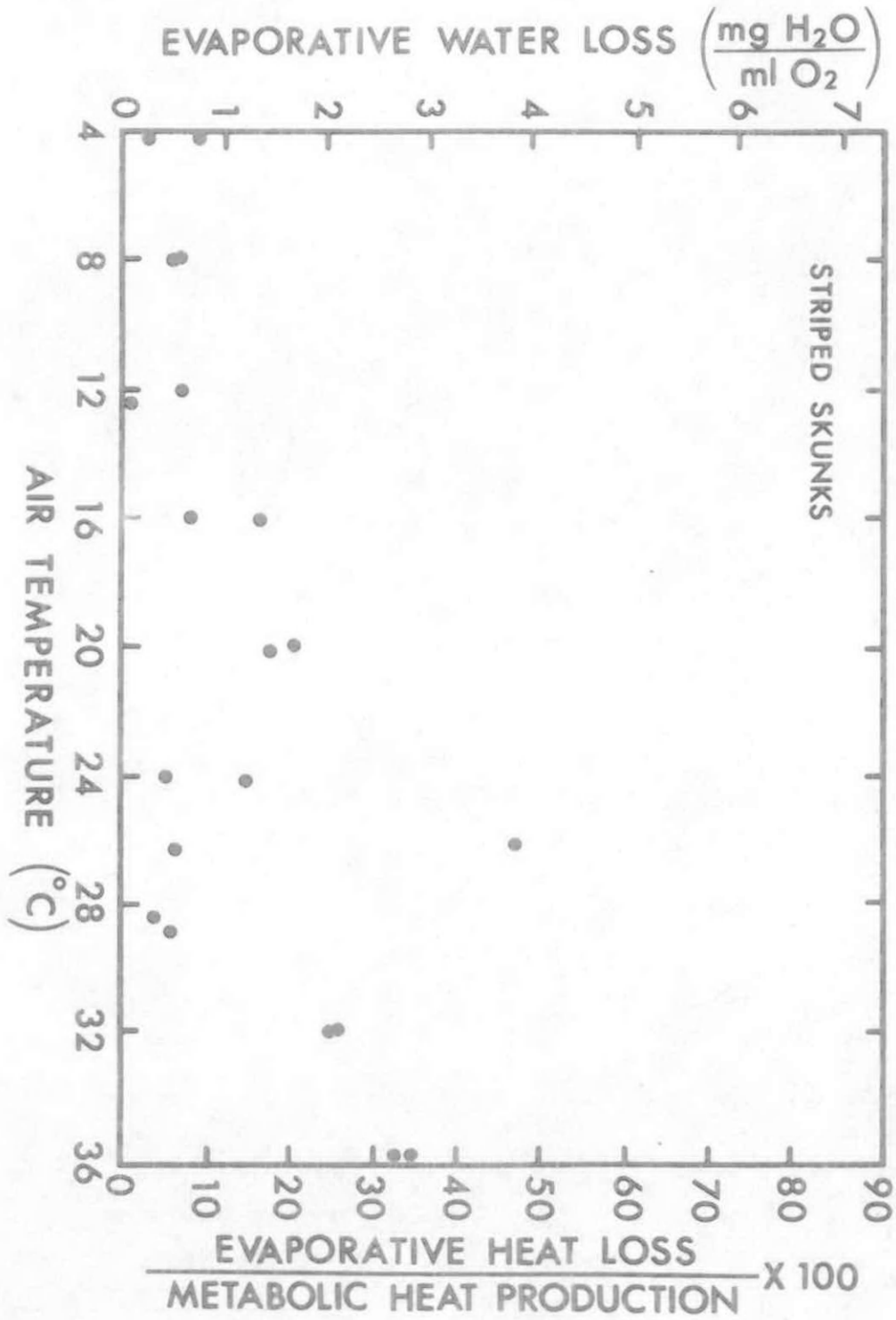
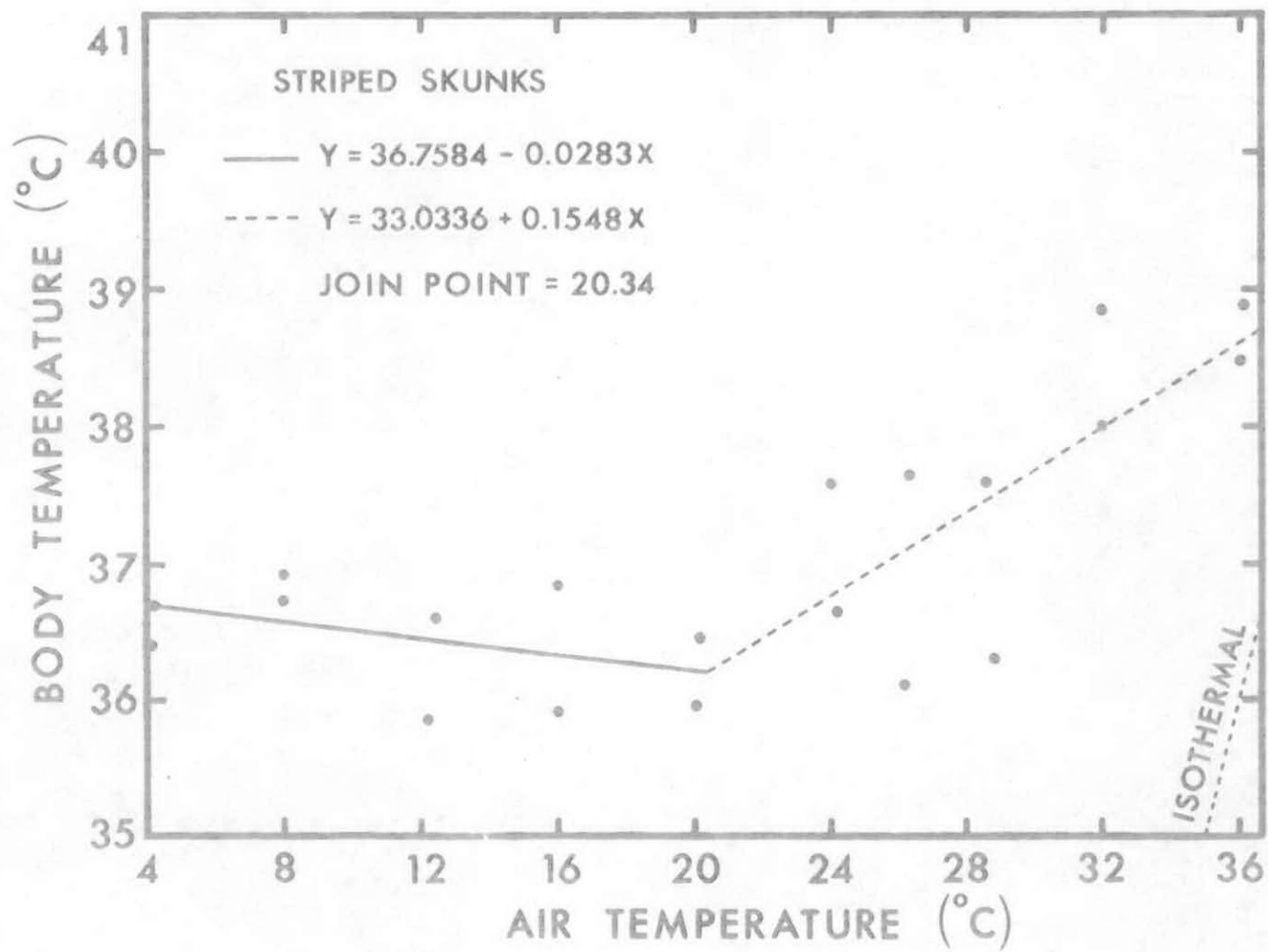


Figure 7: Body temperatures of two adult Mephitis mephitis at various air temperatures. Lines were fitted with a multiphase regression technique (see Methods).





temperatures recorded after metabolic rate determinations at 20 and 24°C (mean = 36.6°C).

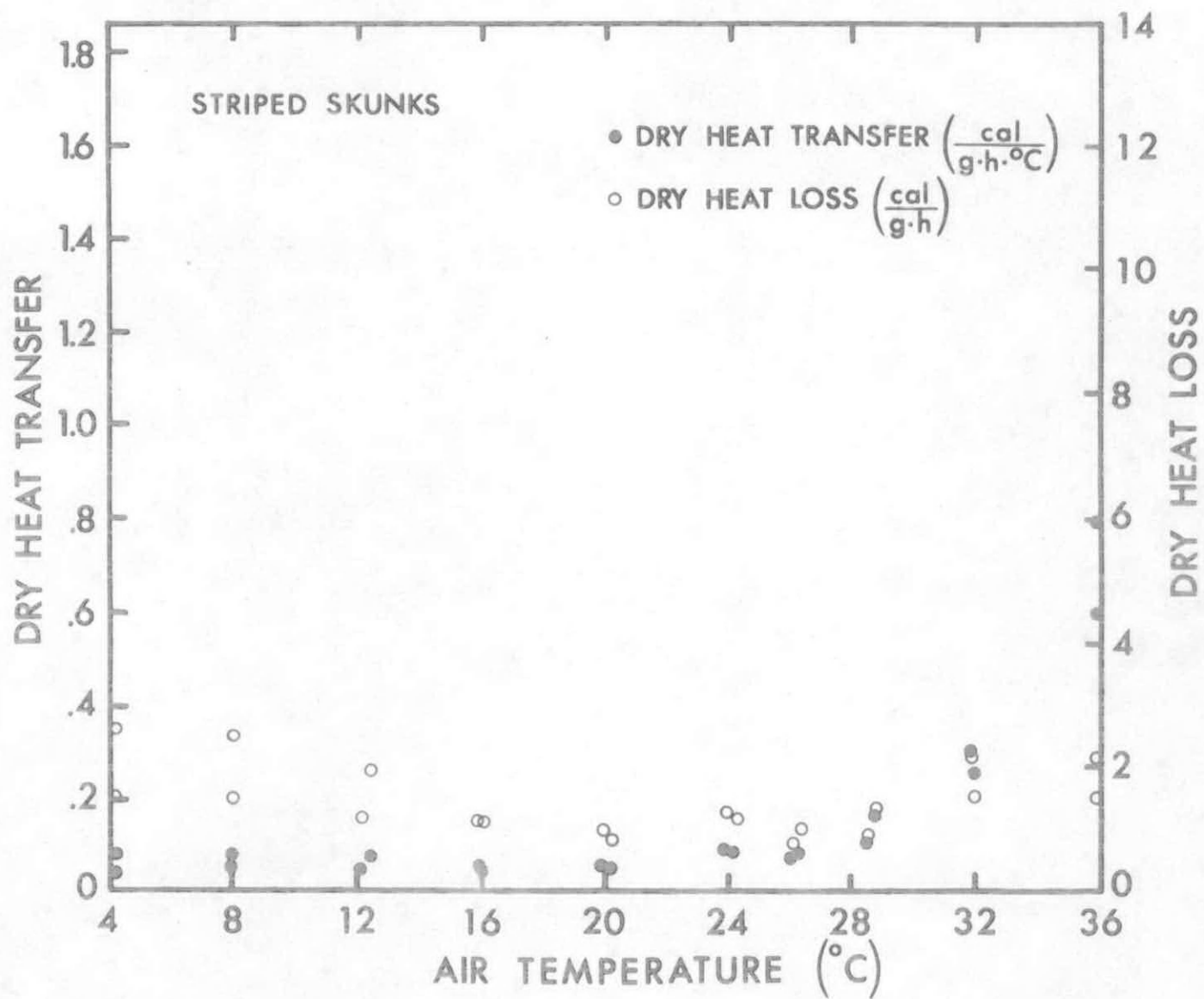
Thermal conductance and dry heat transfer.--Thermal conductances of male striped skunks (see above for the method of computation) remained quite constant from 4 to 20°C (Appendix III, Table B). The minimal computed conductance based on  $\dot{V}_{O_2}$  was 0.052 cal g<sup>-1</sup>h<sup>-1</sup>°C<sup>-1</sup> which is 16% less than that (0.0625 cal g<sup>-1</sup>h<sup>-1</sup>°C<sup>-1</sup>) predicted from the equation of Herreid and Kessel (1967). C values increased slightly from 20 to 28°C but rose sharply above 28°C to a mean of 1.14 cal g<sup>-1</sup>h<sup>-1</sup>°C<sup>-1</sup> at 36°C. Dry heat transfer (h) of male striped skunks (Fig. 8) is relatively constant from 4 to 20°C (0.063 cal g<sup>-1</sup>h<sup>-1</sup>°C<sup>-1</sup>). From 20 to 28°C h increases only slightly but above 28°C, h rises to a mean value of 0.710 cal g<sup>-1</sup>h<sup>-1</sup>°C<sup>-1</sup> at 36°C. Below 20°C a mean of 91% of the metabolic heat production is dissipated by dry heat transfer, while at the highest T<sub>a</sub> (36°C) only 62% of the metabolic heat is lost by non-evaporative transfers.

Dry heat loss (cal g<sup>-1</sup>h<sup>-1</sup>) decreases with increasing temperature up to about 20°C (Fig. 8). From 20 to 28°C dry heat loss was fairly constant but increased to a mean of 1.83 cal g<sup>-1</sup>h<sup>-1</sup> above 28°C.

Figure 8: Dry heat transfer from two adult Mephitis mephitis at various air temperatures. The dry heat transfer coefficient is calculated as follows:

$$h = \frac{\text{rate of heat production} - \text{rate of heat loss by evaporation}}{(T_b - T_a) \cdot \text{body mass}}$$

Dry heat loss is h multiplied by  $(T_b - T_a)$ .



## CHAPTER IV

### DISCUSSION

Spotted and striped skunks are able to maintain a nearly constant body temperature over a wide range of ambient air temperatures below thermoneutrality. The mean body temperature of striped skunks ( $36.7^{\circ}\text{C}$ ) recorded in this study is very close to that reported by Folk (1957) for the same species and at the same air temperature ( $36.4^{\circ}\text{C}$ ). The body temperatures of both species are similar to those of other mustelids. Folk (1977) noted resting body temperatures of  $36.6^{\circ}\text{C}$  for least weasels and  $38.0^{\circ}\text{C}$  for the wolverine.

The two species of skunks exhibit different patterns of thermoregulatory response to variations in air temperature. Male striped skunks have a relatively broad thermoneutral zone (TNZ) between 17 and  $28^{\circ}\text{C}$ , while the spotted skunks have a relatively narrow TNZ or a thermoneutral point (TNP) at  $33^{\circ}\text{C}$ . The pattern shown by the spotted skunks, that is, a narrow range of air temperature over which metabolism is minimal is not an uncommon thermoregulatory response. Similar patterns have been observed, for example, in the California pocket mouse (Tucker, 1965), the black-tailed prairie dog (Reinking et al., 1977) and the nine-banded armadillo (Johansen, 1961). MacMillen and Grubbs (1976) have recently formulated a hypothesis based on the relationship between metabolic water production and evaporative water loss at various air temperatures which might explain the significance of such a narrow TNZ or TNP. At low air temperatures metabolic water production of mammals (as a result of their high metabolic rates) exceeds, evaporative water loss. Therefore water independent mammals might be expected to show a maximal

increase in metabolic rate and therefore metabolic water production as air temperature decreases below thermoneutrality (MacMillen and Grubbs, 1976) and might expectably have a lower critical temperature (LCT) above that of water dependent mammals.

The relatively low ( $17^{\circ}\text{C}$ ) lower critical temperature and wider zone of thermal neutrality of the striped skunks relative to spotted skunks probably results from a combination of factors such as their larger body size, lower weight-specific thermal conductance, lower surface to volume ratio and better insulation (Hart, 1957, 1971; Kleiber, 1972; Prosser, 1973). The striped skunks had more dense and proportionally longer fur than the spotted skunks when their metabolic rates were measured and therefore differences in LCT and width of the TNZ might also have resulted from seasonal insulatory changes in the striped skunks.

The predicted standard metabolic rate (SMR) of mammals the size of spotted skunks is  $0.688 \text{ ml O}_2 \text{ g}^{-1}\text{h}^{-1}$  (Morrison et al., 1959). The observed SMR for this species was  $0.426 \text{ ml O}_2 \text{ g}^{-1}\text{h}^{-1}$ , or 36% lower than predicted. The observed SMR of the striped skunks ( $0.266 \text{ ml O}_2 \text{ g}^{-1}\text{h}^{-1}$ ) is likewise lower by about a third of that predicted ( $0.368 \text{ ml O}_2 \text{ g}^{-1}\text{h}^{-1}$ ) on a weight basis. While striped skunks held outside and deprived of food undergo a winter or carnivorean lethargy as evidenced by reduced body temperatures and activity (Mutch and Aleksuk, 1977) the low metabolic rates of the skunks in this study are not believed to be a result of such a winter lethargy. The striped skunks were maintained at an air temperature of  $22^{\circ}\text{C}$  and fed ad libitum all winter and maintained a normal body temperature throughout the study. Also lower than expected

metabolic rates were observed in spotted skunks and their oxygen consumption was measured during the summer. These data suggest that skunks and perhaps all the members of the subfamily Mephitinae may as a group have lower than expected metabolic rates similar to other phylogenetic groups of mammals such as those noted earlier.

The metabolic rates of spotted and striped skunks are also lower than those of other mustelids. Iversen (1972) formulated the following predictive equations for the metabolic rate of mustelids of various body sizes:

$$1 \text{ kg} \quad \text{MR(kcal/day)} = 95.8W(\text{kg})^{0.55} \quad (1)$$

$$1 \text{ kg} \quad \text{MR(kcal/day)} = 84.6W(\text{kg})^{0.78} \quad (2)$$

The SMR of the spotted skunks is 59% lower than predicted from equation (1), while the striped skunks have a metabolic rate 48% lower than predicted from Iversen's equation (2). It is apparent that skunks deviate considerably from these predictive models.

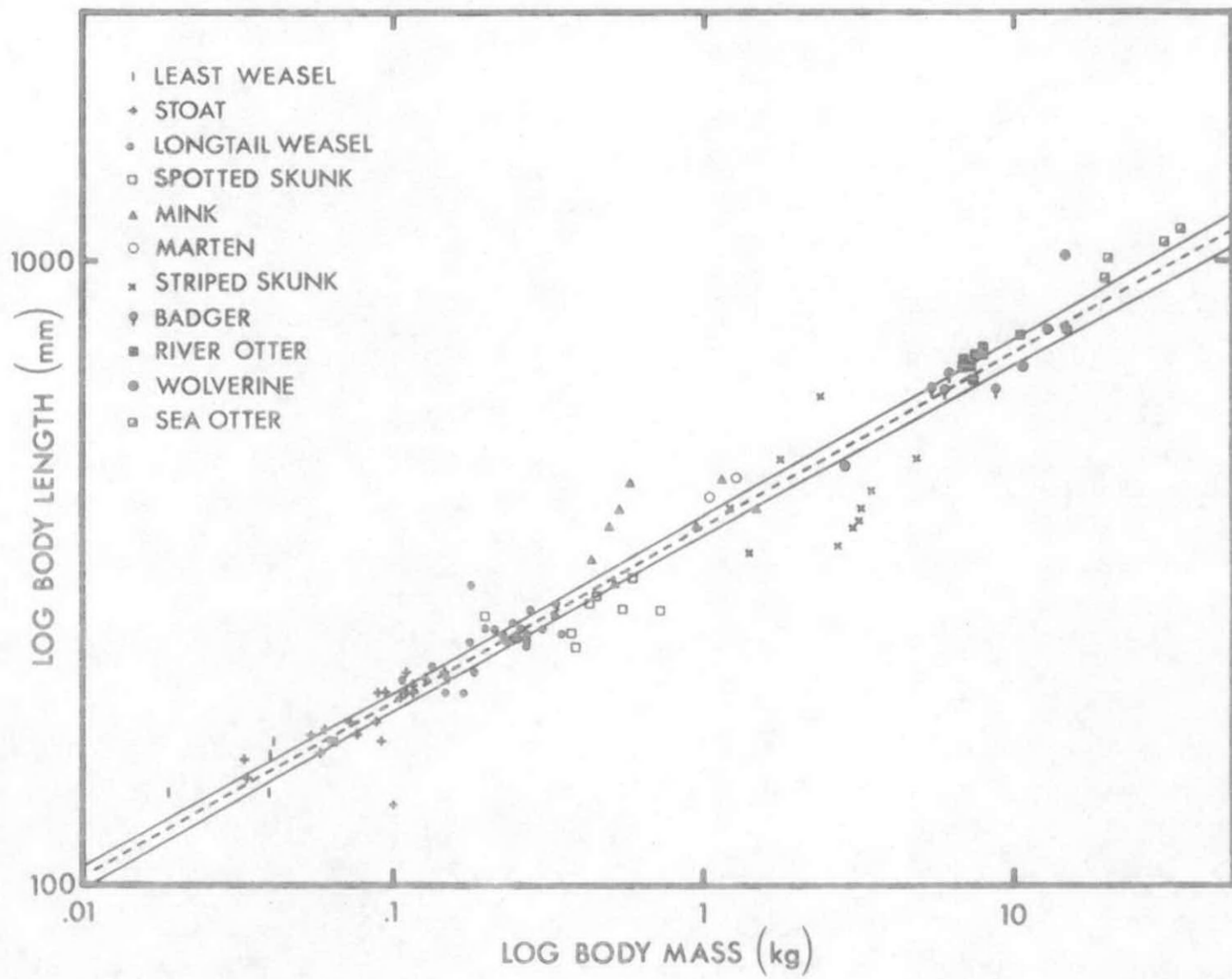
Iversen's models may not be an accurate representation of the metabolic rate of the mustelid family since the small mustelids he used were all weasels. Small weasels have metabolic rates up to 100% greater than those predicted from the standard mammalian curve. These extremely elevated metabolic rates of small weasels could possibly result from a number of factors including non-locomotory muscle activity, their high surface to volume ratio, high thermal conductances, etc. Murie (1961) found that differences in "nervous temperament" between two subspecies of Peromyscus maniculatus lead to consistently different rates of metabolism. In his study, Murie (1961) noted that coastal mice, as a group, spent a greater proportion of test time in an alert or nervous state and

had consistently higher rates of metabolism compared to mountain mice under the same conditions. Another possible reason for the elevated metabolism of weasels is that they have a high conductance probably due to their elongate body form and therefore greater surface area. The minimal conductance of long-tailed weasels is 50% greater than that predicted (Brown and Lasiewski, 1972) using the equation of Herreid and Kessel (1967). There are different body forms among the mustelidae (Fig. 9) and these appear to be an important determinant of the relationship between body size and metabolism in this group.

A plot of mean and individual body lengths of mustelids of various body masses (Fig. 9, Appendix IV) yields a relationship with a slope of 0.28 (95% confidence interval for the slope equals 0.27-0.29). This slope is significantly less than 0.33 ( $P < 0.05$ ) which is the slope one would expect if the larger species were geometrically similar to the smaller species. The lower slope indicates that the small weasels are proportionately longer than larger mustelids or vice versa. The elevated metabolic rates of small weasels reported by Iversen could therefore be a consequence of higher heat loss or conductance due to their relatively greater surface area. Spotted and striped skunks are below the 95% confidence limits fitted to the least-squares regression line (Fig. 9) and thus have a significantly shorter and heavier body form than most of the other mustelidae. The significantly lower weight-specific metabolic rate of the skunks in comparison to other mustelids is consistent with this finding. Even though other mustelids are outside the confidence limits established for the regression line in Figure 9, the pattern of deviation in relation to the line for skunks is statistically different

Figure 9: Relationship between  $\text{Log}_{10}$  body length and  $\text{Log}_{10}$  body mass of mustelids. Data are from the literature (Burt, 1946; Hall, 1946; Hall, 1951; Hall and Kelson, 1959; Southern, 1964; Banfield, 1974) or from museum specimens. The relationship between body length and body mass (kg) is described by the equation  $BL = 375.2W^{0.28}$ . The solid lines on either side of the least-squares regression line (dashed) are 95% confidence limits.





( $P < 0.005$ ), than that for the other mustelids combined (chi-square with contingency tables). That is, more skunks are below the line than above, whereas other mustelids are more evenly distributed above and below the line.

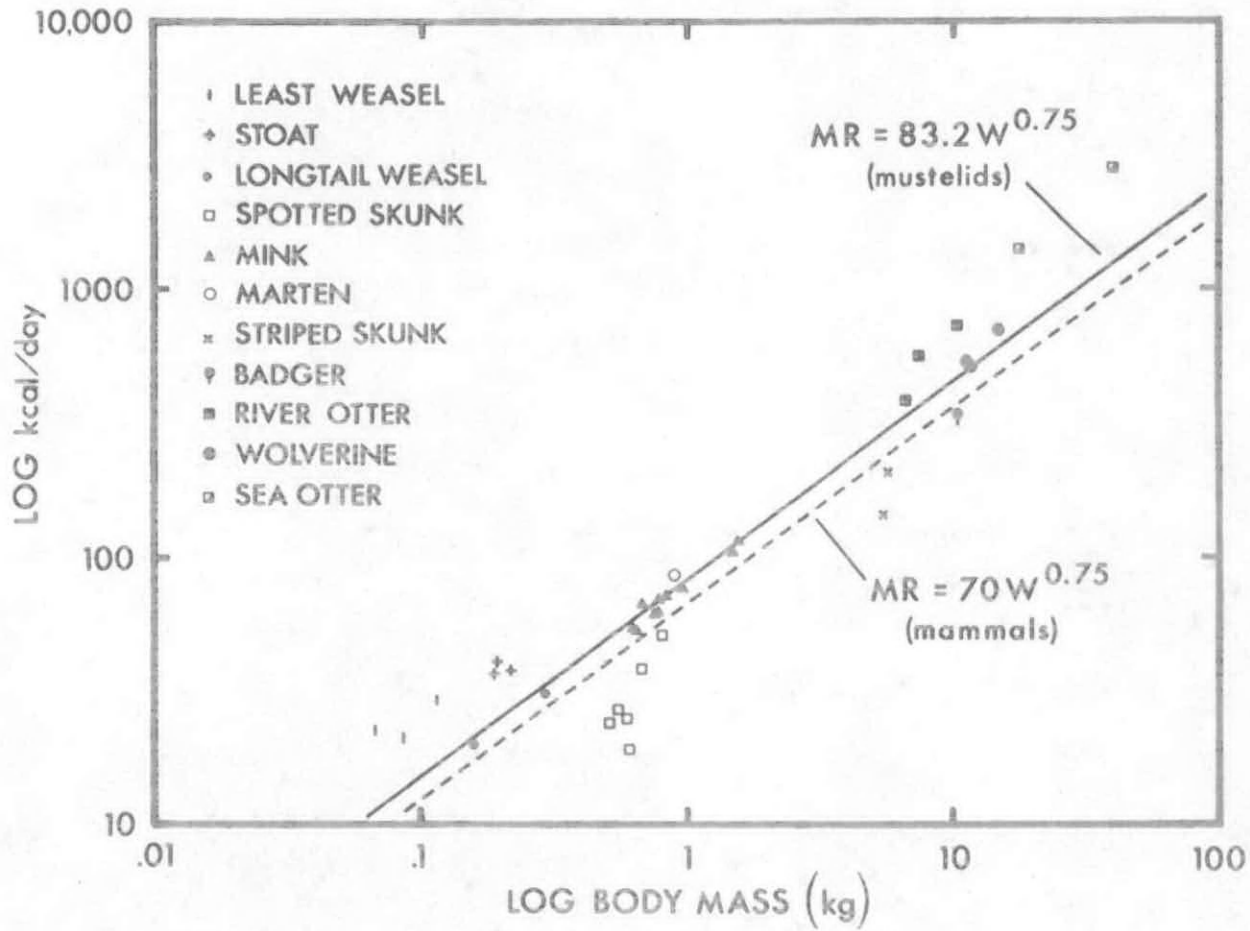
Minimal thermal conductance of these skunks is close to the standard values for mammals using the predictive equation of Herreid and Kessel (1967). Spotted skunks have an observed conductance that is only slightly higher (11%) than that predicted, while the conductance of striped skunks is only 16% lower. In contrast, the minimal thermal conductance of long-tailed weasels is 50% greater than that predicted. Brown and Lasiewski (1972) attribute the extremely high weight-specific conductance of these weasels to their large surface area, shorter pelage, and their inability to achieve a spherical resting posture. The striped skunks have a lower relative conductance when compared with that in spotted skunks due to their larger body size (Herreid and Kessel, 1967) and to seasonal differences in the insulative properties of their fur (Hart, 1971).

Since heat loss by evaporation, which is included in the minimal conductance values, is not actually heat conducted to the environment, dry heat transfer ( $h$ ) is a more accurate estimate of thermal conductance (Figs. 4 and 8). At low to moderate air temperatures the difference between dry heat transfer and minimal thermal conductance in these skunks is insignificant since heat loss by evaporation accounts for less than 5% of metabolic heat production at these temperatures. At extremely high air temperatures the difference between  $h$  and  $C$  is greater. The minimal value of  $h$  for spotted skunks is even closer to the predicted

thermal conductance value (Herreid and Kessel, 1967).

If the available data on the metabolic rates of mustelids from this study and from those of Farrell and Wood (1968), Brown and Lasiewski (1972), Iversen (1972) and Morrison et al., (1974), are combined (Fig. 10), the relationship between metabolic rate and body mass in this phylogenetic group of mammals is more similar to that in other groups of mammals or to mammals in general than previously suggested by Iversen (1972). The slope of the regression line fitted to these data is not significantly different from the standard mammalian values of 0.73 or 0.75, although the metabolic rate of mustelids in general is 16% higher than that in other mammals.

Figure 10: A double logarithmic plot of the relationship between metabolic rate and body mass in mustelids (solid line). The dashed line represents the relationship for all mammals (Kleiber, 1975).



## CHAPTER V

### SUMMARY

The metabolic rates of six spotted (Spilogale putorius) and two striped (Mephitis mephitis) skunks were measured at various air temperatures. Both species exhibit a normal mammalian pattern of thermoregulation in that metabolism increases with decreasing air temperatures below thermoneutrality and increases at air temperatures above thermoneutrality, although the patterns differ somewhat from each other. Spotted skunks have a relatively narrow thermoneutral zone or a thermoneutral point at 33°C, while striped skunks have a rather broad thermoneutral zone between 17 and 28°C. The relatively low (17°C) lower critical temperature (LCT) and wider zone of thermoneutrality of the striped skunks relative to the spotted skunks probably is the result of a combination of factors such as their larger body size, lower weight-specific thermal conductance, lower surface to volume ratio and better insulation.

While the metabolic rates of most mustelids are higher than those predicted for other mammals of the same body size, spotted and striped skunks have metabolic rates that are 36 and 28%, respectively, lower than predicted for other mammals. The significantly lower metabolic rates of skunks compared to other mustelids may be due to their atypical body form. Both species of skunks were found to have a significantly shorter and heavier body form than the other mustelid species which tend to be long and thin. The high metabolic rates of most mustelids possibly result from a high conductance due to their relatively high surface area.

**APPENDIX I**

TABLE A

24 hour cycle in oxygen consumption ( $\dot{V}_{O_2}$ ) in one adult male spotted skunk (mass = 0.74 kg,  $T_a = 22^\circ\text{C}$ , 19-20 July, 1976)

<u>Time</u>	$\dot{V}_{O_2}$ <u>ml O<sub>2</sub> min<sup>-1</sup></u>	$\dot{V}_{O_2}$ <u>ml O<sub>2</sub> g<sup>-1</sup>h<sup>-1</sup></u>
1200	6.711	.5516
1330	6.150	.5055
1400	6.136	.5043
1430	6.019	.4947
1500	6.014	.4943
1530	6.109	.5021
1600	8.425	.6722
1630	7.879	.6286
1700	8.061	.6432
1730	8.125	.6483
1810	8.202	.6544
1830	8.390	.6694
1900	8.311	.6631
1945	9.388	.7490
2000	9.101	.7261
2030	9.147	.7298
2100	9.958	.7945
0100	10.570	.8688
0130	9.383	.7712
0200	9.371	.7702



Table A (con't)

<u>Time</u>	$\dot{V}_{O_2}$ <u>ml O<sub>2</sub> min<sup>-1</sup></u>	$\dot{V}_{O_2}$ <u>ml O<sub>2</sub> g<sup>-1</sup>h<sup>-1</sup></u>
0230	10.542	.8665
0300	10.404	.8551
0330	11.671	.9593
0400	9.653	.7934
0500	9.666	.7945
0700	6.796	.5586
0800	6.292	.5172
1100	6.941	.5705

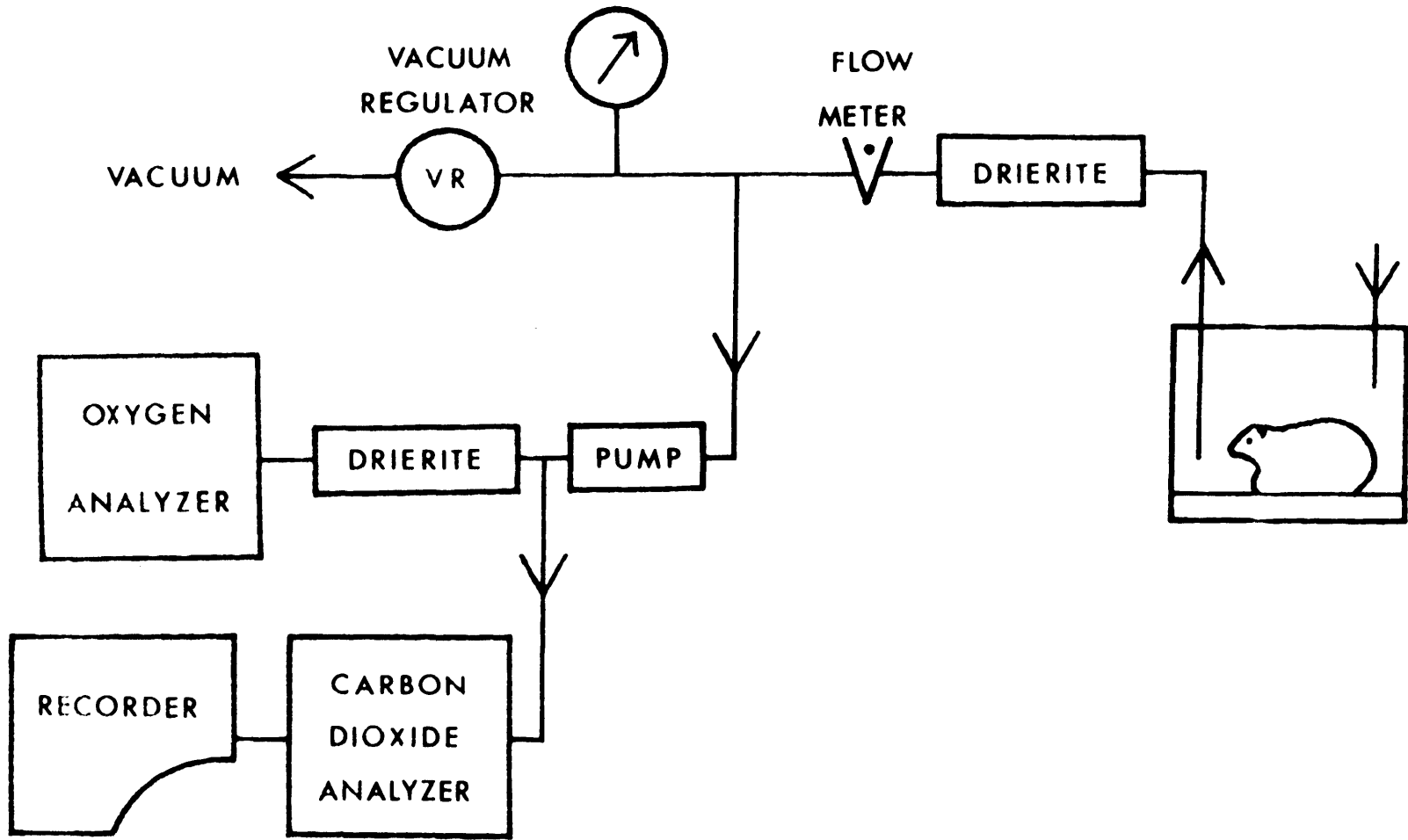
TABLE B

24 hour cycle in oxygen consumption ( $\dot{V}_{O_2}$ ) in one adult male striped skunk (mass = 5.751 kg,  $T_a = 22^\circ\text{C}$ , 28-29 December, 1976)

<u>Time</u>	$\dot{V}_{O_2}$ <u>ml <math>O_2</math> min<sup>-1</sup></u>	$\dot{V}_{O_2}$ <u>ml <math>O_2</math> g<sup>-1</sup> h<sup>-1</sup></u>
1200	22.507	.2348
1440	21.970	.2292
1530	20.871	.2177
1640	20.847	.2175
1840	25.024	.2611
1940	27.935	.2914
2040	27.400	.2859
2220	27.547	.2874
2340	26.304	.2744
2450	71.957	.7507
0300	26.331	.2747
0340	24.698	.2577
0430	28.063	.2928
0540	28.358	.2959
0730	25.100	.2619
1040	24.645	.2571

## APPENDIX II

**Flow system utilized for oxygen consumption  
and carbon dioxide measurements.**



**APPENDIX III**

TABLE A

Body temperature, oxygen consumption, carbon dioxide production, conductance and dry heat transfer at various ambient temperatures in six adult spotted skunks.

$T_a$	$T_b$	$\dot{V}_{O_2}$	$\dot{V}_{CO_2}$	C	h
$^{\circ}C$	$^{\circ}C$	ml $O_2$ $g^{-1}h^{-1}$	ml $CO_2$ $g^{-1}h^{-1}$	cal $g^{-1}h^{-1}^{\circ}C$	cal $g^{-1}h^{-1}^{\circ}C^{-1}$
8.67	37.23	1.320	.819	.2171	.2113
9.07	37.07	1.662	1.030	.2792	.2768
9.39	37.25	1.261	.819	.2129	.2079
9.68	37.50	1.781	1.026	.3008	.2955
9.81	36.16	1.509	.773	.2693	.2624
10.44	36.55	1.404	1.046	.2529	.2446
11.91	36.50	1.208	.703	.2308	.2039
12.02	36.97	1.213	.770	.2284	.2203
12.52	36.30	1.245	.752	.2463	.2415
12.64	36.57	1.375	.736	.2703	.2515
12.88	36.96	1.409	.846	.2750	.2712
15.93	36.74	1.097	.719	.2477	.2259
16.06	37.31	1.439	.644	.2984	.2924
16.11	37.31	1.027	.601	.2274	.2209
16.12	36.90	1.365	.757	.3088	.3051
16.31	35.73	1.333	.983	.3224	.3010
16.34		1.061	.770		
19.60	35.45	1.152	.810	.3417	.3151
19.61	36.32	1.200	.821	.3375	.2935
19.90	36.07	1.005	.646	.2923	.2676
19.90	35.71	.884	.633	.2627	.2498
20.00	36.41	1.112	.701	.3187	.2949
20.30	36.55	.851	.578	.2524	.2147
23.46	36.55	.832	.554	.2989	.2476
23.65	36.79	.760	.562	.2717	.2309
23.87	36.48	.607	.357	.2261	.1944
24.09	36.48	.640	.467	.2430	.2174
24.11	36.43	.841	.630	.3210	.2748
24.40	36.94	.934	.555	.3502	.3229
27.89	36.23	.418	.325	.2355	.1810
27.97	36.14	.636	.458	.3657	.3148
38.00	36.26	.661	.397	.3760	.3162
28.03	36.57	.573	.436	.3154	.2407
28.06	35.75	.470	.318	.2872	.2071

TABLE A (Con't)

$T_a$ °C	$T_b$ °C	$\dot{V}_{O_2}$ ml $O_2$ $g^{-1}h^{-1}$	$\dot{V}_{CO_2}$ ml $CO_2$ $g^{-1}h^{-1}$	C cal $g^{-1}h^{-1}oC^{-1}$	h cal $g^{-1}h^{-1}oC^{-1}$
28.20	36.06	.474	.351	.2834	.2232
29.74	36.12	.449	.292	.3309	.2721
29.78	36.72	.519	.335	.3516	.2897
29.81	36.52	.603	.304	.4225	.3189
29.83	35.57	.411	.225	.3365	.2898
29.91	35.92	.461	.251	.3605	.3201
29.95	36.63	.554	.248	.3896	.3233
31.32	37.25	.684	.320	.5419	.2475
31.48	36.68	.532	.241	.4080	.2843
31.70	35.22	.333	.278	.4446	.3148
31.84	35.75	.641	.304	.7703	.2727
31.94	37.23	.475	.289	.4221	.3429
32.05	36.75	.412	.306	.4122	
33.76	36.79	.285	.246	.4423	.2515
33.80	36.34	.370	.321	.6848	.4460
33.80	37.22	.436	.336	.5992	.4817
33.81	36.94	.408	.332	.6129	.4866
33.89	37.09	.559	.435	.8211	.7144
34.07	37.09	.498	.351	.7750	.6668
35.87	38.27	.583	.402	1.142	.6981
35.92	37.30	.403	.287	1.372	
35.97	38.60	.610	.514	1.090	.7938
36.11	37.73	.285	.234	.8267	.5764
36.16	37.96	.431	.291	1.125	.8245
38.92	40.21	.704	.558	2.569	1.019
38.96		.506	.400		
39.05	39.32	.609	.500	10.593	1.888
39.09	40.95	.919	.765	2.310	1.018

TABLE B

Body temperature, oxygen consumption, carbon dioxide production, conductance and dry heat transfer at various ambient temperatures in two adult striped skunks.

$T_a$	$T_b$	$\dot{V}_{O_2}$	$\dot{V}_{CO_2}$	C	h
$^{\circ}C$	$^{\circ}C$	ml $O_2$ $g^{-1}h^{-1}$	ml $CO_2$ $g^{-1}h^{-1}$	cal $g^{-1}h^{-1}^{\circ}C$	cal $g^{-1}h^{-1}^{\circ}C^{-1}$
4.02	36.39	.358	.219	.0522	.0476
4.19	36.66	.581	.366	.0841	.0819
7.87	36.72	.344	.312	.0559	.0522
7.91	36.90	.578	.388	.0935	.0876
12.05	35.84	.283	.249	.0559	.0523
12.38	36.59	.420	.283	.0813	.0813
15.94	35.89	.292	.155	.0686	.0578
15.96	36.81	.257	.176	.0578	.0536
19.91	35.94	.272	.247	.0799	.0636
20.06	36.44	.216	.152	.0620	.0511
23.93	37.57	.295	.177	.1015	.0957
24.13	36.64	.298	.164	.1119	.0956
26.03	36.07	.313	.210	.1466	.0781
26.24	37.63	.233	.175	.0964	.0904
28.44	37.59	.207	.160	.1062	.1030
28.78	36.28	.293	.183	.1838	.1741
31.83	38.84	.629	.415	.4216	.3133
31.86	37.99	.441	.298	.3379	.2486
35.95	38.44	.547	.378	1.037	.6093
36.03	38.68	.702	.486	1.245	.8114



#### APPENDIX IV

Body length and body mass of mustelids from the literature and from museum specimens. Superscripts refer to source of data. 1, museum specimens; 2, Banfield, 1974; 3, Southern, 1964; 4, Hall, 1946; 5, Burt, 1946; 6, Hall and Kelson, 1959; 7, Hall, 1951.

Mustela rixosa

Body length (mm)	Body mass (kg)
169	0.041 <sup>7</sup>
142	0.039
140	0.018 <sup>1</sup>
163	0.040

Mustela erminea

172	0.054 <sup>7</sup>
164	0.058
148	0.034
213	0.126 <sup>1</sup>
159	0.033
136	0.099
199	0.105
183	0.087
170	0.092
218	0.145
175	0.076
215	0.148
205	0.115
177	0.060
202	0.109
170	0.064
170	0.063
205	0.093
211	0.114
180	0.072
206	0.087
217	0.109

Mustela frenata

Body length (mm)	Body mass (kg)
256	0.207 <sup>7</sup>
250	0.276
222	0.131
250	0.243 <sup>1</sup>
276	0.272
249	0.221
260	0.297
244	0.172
305	0.175
268	0.333
257	0.250
246	0.266
249	0.247
279	0.331
260	0.193
205	0.165
206	0.143
244	0.234
245	0.268
221	0.180
254	0.345
266	0.240
245	0.230
212	0.105

Martes americana

420	1.040 <sup>1</sup>
445	1.274

Spilogale putorius

Body length (mm)	Body mass (kg)
290	0.452 <sup>1</sup>
277	0.541
279	0.410
270	0.194
238	0.380
306	0.584
274	0.705
252	0.368

Mephitis mephitis

485	4.800 <sup>1</sup>
400	1.205
430	3.236
396	3.200
605	2.333
480	1.750
348	2.695
373	3.000
335	1.400 <sup>4</sup>
380	3.180 <sup>5</sup>

Taxidea taxus

618	5.443 <sup>4</sup>
615	5.930
622	8.640 <sup>5</sup>
659	6.150 <sup>2</sup>

Gulo gulo

Body length (mm)	Body mass (kg)
473	2.860 <sup>1</sup>
769	14.800 <sup>2</sup>
678	10.600
770	12.950 <sup>5</sup>
1012	14.550 <sup>6</sup>

Mustela vison

Body length (mm)	Body mass (kg)
440	0.585
442	1.125
400	0.532
372	0.488
330	0.430
304	0.511
398	1.449
375	0.950

Lutra canadensis

702	7.750 <sup>2</sup>
680	7.200
703	7.780 <sup>4</sup>
680	6.960
694	6.820 <sup>5</sup>
691	7.730 <sup>6</sup>

Lutra lutra

754	10.300 <sup>3</sup>
650	7.400

Enhydra lutris

1070	30.000 <sup>2</sup>
934	19.700
1118	34.400
1016	19.700

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