

Metabolic Adaptation to Climate  
and Distribution of the Raccoon  
*Procyon lotor* and Other Procyonidae

JOHN N. MUGAAS,  
JOHN SEIDENSTICKER,  
and  
KATHLEEN P. MAHLKE-JOHNSON

## SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

*Smithsonian Contributions to Anthropology*  
*Smithsonian Contributions to Astrophysics*  
*Smithsonian Contributions to Botany*  
*Smithsonian Contributions to the Earth Sciences*  
*Smithsonian Contributions to the Marine Sciences*  
*Smithsonian Contributions to Paleobiology*  
*Smithsonian Contributions to Zoology*  
*Smithsonian Folklife Studies*  
*Smithsonian Studies in Air and Space*  
*Smithsonian Studies in History and Technology*

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs<sup>2</sup> submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

Robert McC. Adams  
Secretary  
Smithsonian Institution

Metabolic Adaptation to Climate  
and Distribution of the Raccoon  
*Procyon lotor* and Other Procyonidae

*John N. Mugaas, John Seidensticker,  
and Kathleen P. Mahlke-Johnson*



SMITHSONIAN INSTITUTION PRESS

Washington, D.C.

1993

## ABSTRACT

Mugaas, J.N., J. Seidensticker, and K. Mahlke-Johnson. Metabolic Adaptation to Climate and Distribution of the Raccoon *Procyon lotor* and Other Procyonidae. *Smithsonian Contributions to Zoology*, number 542, 34 pages, 8 figures, 12 tables, 1993.—Although the family Procyonidae is largely a Neotropical group, the North American raccoon, *Procyon lotor*, is more versatile in its use of climate, and it is found in nearly every habitat from Panama to 60°N in Canada. We hypothesized that most contemporary procyonids have remained in tropic and subtropic climates because they have retained the metabolic characteristics of their warm-adapted ancestors, whereas *Procyon lotor* evolved a different set of adaptations that have enabled it to generalize its use of habitats and climates. To test this hypothesis we compared *Procyon lotor* with several other procyonids (*Bassariscus astutus*, *Nasua nasua*, *Nasua narica*, *Procyon cancrivorus*, and *Potos flavus*) with respect to (1) basal metabolic rate ( $\dot{H}_b$ ), (2) minimum wet thermal conductance ( $C_{mw}$ ), (3) diversity of diet ( $D_d$ ), (4) intrinsic rate of natural increase ( $r_{max}$ ), and, where possible, (5) capacity for evaporative cooling ( $E_c$ ). We measured basal and thermoregulatory metabolism, evaporative water loss, and body temperature of both sexes of *Procyon lotor* from north central Virginia, in summer and winter. Metabolic data for other procyonids were from literature, as were dietary and reproductive data for all species.

*Procyon lotor* differed from other procyonids in all five variables. (1) *Procyon lotor*'s mass specific  $\dot{H}_b$  (0.46 mL O<sub>2</sub>·g<sup>-1</sup>·h<sup>-1</sup>) was 1.45 to 1.86 times greater than values for other procyonids. (2) Because of its annual molt, *Procyon lotor*'s  $C_{mw}$  was about 49% higher in summer than winter, 0.0256 and 0.0172 mL O<sub>2</sub>·g<sup>-1</sup>·h<sup>-1</sup>·°C<sup>-1</sup>, respectively. The ratio of measured to predicted  $C_{mw}$  for *Procyon lotor* in winter (1.15) was similar to values calculated for *Potos flavus* (1.02) and *Procyon cancrivorus* (1.25). Values for other procyonids were higher than this, but less than the value for *Procyon lotor* (1.76) in summer. On a mass specific basis, *Bassariscus astutus* had the lowest  $C_{mw}$  with a ratio of 0.85. (3) *Procyon lotor* utilized three times as many food categories as *Procyon cancrivorus*, *Nasua nasua*, and *Bassariscus astutus*; about two times as many as *Nasua narica*; and nine times as many as *Potos flavus*. (4) Intrinsic rate of natural increase correlated positively with  $\dot{H}_b$ . *Procyon lotor* had the highest  $r_{max}$  (2.52 of expected) and *Potos flavus* the lowest (0.48 of expected). The other procyonids examined also had low  $\dot{H}_b$ , but their  $r_{max}$ 's were higher than predicted (1.11–1.32 of expected). Early age of first female reproduction, fairly large litter size, long life span, high-quality diet, and, in one case, female social organization all compensated for low  $\dot{H}_b$  and elevated  $r_{max}$ . (5) Although data on the capacity for evaporative cooling were incomplete, this variable appeared to be best developed in *Procyon lotor* and *Bassariscus astutus*, the two species that have been most successful at including temperate climates in their distributions.

These five variables are functionally interrelated, and have co-evolved in each species to form a unique adaptive unit that regulates body temperature and energy balance throughout each annual cycle. The first four variables were converted into normalized dimensionless numbers, which were used to derive a composite score that represented each species' adaptive unit. *Procyon lotor* had the highest composite score (1.47) and *Potos flavus* the lowest (0.39). Scores for the other procyonids were intermediate to these extremes (0.64–0.79). There was a positive correlation between the number of climates a species occupies and the magnitude of its composite score. Linear regression of this relationship indicated that 89% of the variance in climatic distribution was attributed to the composite scores. Differences in metabolic adaptation, therefore, have played a role in delimiting climatic distribution of these species.

It was clear that *Procyon lotor* differed from the other procyonids with respect to thermoregulatory ability, diet, and reproductive potential. These differences have enabled it to become a highly successful climate generalist, and its evolution of an  $\dot{H}_b$  that is higher than the procyonid norm appears to be the cornerstone of its success.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

---

### Library of Congress Cataloging-in-Publication Data

Mugaas, John N.

Metabolic adaptation to climate and distribution of the raccoon *Procyon lotor* and other Procyonidae / John N. Mugaas,

John Seidensticker, and Kathleen P. Mahlke-Johnson.

p. cm.—(Smithsonian contributions to zoology ; no. 542)

Includes bibliographical references (p. ).

1. Raccoons—Metabolism—Climatic factors. 2. Procyonidae—Metabolism—Climatic factors. 3. Raccoons—Geographical distribution. 4. Procyonidae—Geographical distribution. I. Seidensticker, John. II. Mahlke-Johnson, Kathleen. III. Title. IV. Series.

QL1.S54 no. 542 [QL737.C26] 591 s-dc20 [599.74'443'04542] 93-3119

© The paper used in this publication meets the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials z39.48—1984.

# Contents

	<i>Page</i>
Introduction . . . . .	1
Defining the Problem . . . . .	1
Procyonid Origins . . . . .	1
Typical Procyonids . . . . .	2
The Atypical Procyonid . . . . .	3
The Hypothesis . . . . .	4
Hypothesis Testing . . . . .	4
Adaptive Significance of the Variables . . . . .	4
Basal Metabolic Rate and Intrinsic Rate of Natural Increase . . . . .	4
Minimum Thermal Conductance . . . . .	4
Capacity for Evaporative Cooling . . . . .	5
Diet . . . . .	5
Experimental Design and Summary . . . . .	5
Acknowledgments . . . . .	5
Materials and Methods . . . . .	6
Live-trapping . . . . .	6
Metabolic Studies . . . . .	6
Basal and Thermoregulatory Metabolism . . . . .	6
Evaporative Water Loss . . . . .	7
Body Temperature . . . . .	7
Calibrations . . . . .	7
Calorimeter . . . . .	7
Body Temperature Transmitters . . . . .	8
Statistical Methods . . . . .	8
Estimating Intrinsic Rate of Natural Increase . . . . .	8
Comparison of Adaptive Units . . . . .	8
Results . . . . .	8
Body Mass . . . . .	8
Basal Metabolic Rate . . . . .	9
Minimum Thermal Conductance . . . . .	9
Evaporative Water Loss . . . . .	11
Thermoregulation at Low Temperatures . . . . .	12
Body Temperature . . . . .	12
Summer . . . . .	14
Winter . . . . .	14
Thermoregulation at High Temperatures . . . . .	16
Body Temperature . . . . .	16
Summer . . . . .	16
Winter . . . . .	16
Daily Cycle of Body Temperature . . . . .	16
Discussion . . . . .	16
Basal Metabolic Rate . . . . .	16
Background . . . . .	16
Captive versus Wild Raccoons . . . . .	17
Seasonal Metabolism of Raccoons . . . . .	17
Comparison of <i>Procyon lotor</i> with Other Procyonids . . . . .	17

Influence of Diet on Basal Metabolism . . . . .	18
Background . . . . .	18
Food Habits of Procyonids . . . . .	18
Food Habits and Basal Metabolism . . . . .	19
Summary . . . . .	19
Basal Metabolism and Intrinsic Rate of Natural Increase . . . . .	19
Background . . . . .	19
<i>Procyon lotor</i> . . . . .	19
<i>Bassariscus astutus</i> . . . . .	19
<i>Nasua narica</i> . . . . .	19
<i>Nasua nasua</i> . . . . .	20
<i>Procyon cancrivorus</i> . . . . .	20
<i>Potos flavus</i> . . . . .	20
Summary . . . . .	20
Basal Metabolism and Climatic Distribution . . . . .	21
<i>Procyon lotor</i> . . . . .	21
Other Procyonids . . . . .	21
Minimum Thermal Conductance . . . . .	21
Background . . . . .	21
Effect of Molt on Thermal Conductance . . . . .	21
Comparison of Thermal Conductances . . . . .	22
<i>Procyon lotor</i> versus Tropical Procyonids . . . . .	22
<i>Bassariscus astutus</i> . . . . .	22
Thermoregulation and Use of Stored Fat at Low Temperatures . . . . .	22
Background . . . . .	22
Thermoregulation . . . . .	22
Stored Fat . . . . .	23
Thermal Model of the Raccoon and Its Den . . . . .	23
Metabolic Advantage of the Den . . . . .	23
Thermoregulation at High Temperatures . . . . .	24
Background . . . . .	24
Comparison of Procyonid Responses to Heat Stress . . . . .	24
<i>Potos flavus</i> . . . . .	24
<i>Nasua nasua</i> and <i>Nasua narica</i> . . . . .	24
<i>Bassariscus astutus</i> . . . . .	24
<i>Procyon lotor</i> . . . . .	24
<i>Procyon cancrivorus</i> . . . . .	24
Summary . . . . .	24
Composite Scores of Adaptive Units and Geographic Distribution . . . . .	25
Evolution of Metabolic Adaptations . . . . .	26
Evolution of Low Basal Metabolic Rate . . . . .	26
Evolution of High Basal Metabolic Rate . . . . .	27
Summary . . . . .	28
Appendix: List of Symbols . . . . .	29
Literature Cited . . . . .	30

# Metabolic Adaptation to Climate and Distribution of the Raccoon *Procyon lotor* and Other Procyonidae

*John N. Mugaas, John Seidensticker,  
and Kathleen P. Mahlke-Johnson*

## Introduction

### DEFINING THE PROBLEM

#### *Procyonid Origins*

The major carnivore radiations took place about 40 million years before present (MYBP) in the late Eocene and early Oligocene (Ewer, 1973:363; Wayne et al., 1989). Between 30 and 40 MYBP, a progenitor split into the ursid and procyonid lineages, which evolved into present-day bears, pandas, and raccoons (Wayne et al., 1989). The taxonomic relatedness of pandas to bears and raccoons has been tested extensively and a number of authors have summarized current thinking on the problem (Martin, 1989; Wayne et al., 1989; Wozencraft, 1989a, 1989b; Decker and Wozencraft, 1991). Davis (1964:322–327) and others (Leone and Wiens, 1956; Todd and Pressman, 1968; Sarich, 1976; O'Brien et al., 1985) place the giant panda, *Ailuropoda melanoleuca*, with the ursids. The taxonomic status of the red panda, *Ailurus fulgens*, appears to be less certain. Some current investigations align the red panda with bears (Segall, 1943; Todd and Pressman, 1968; Hunt, 1974; Ginsburg, 1982; Wozencraft, 1984:56–110; 1989a), whereas others place them intermediate to procyonids and bears (Wurster and Benirschke, 1968; Sarich, 1976; O'Brien et al., 1985), or in close relationship to the giant panda (Tagle et al., 1986).

The procyonid radiation took place in North America and produced forms that were mostly arboreal and omnivorous (Eisenberg, 1981:122; Martin, 1989). The center of this

diversification occurred in Middle America (Baskin, 1982; Webb, 1985b) during the Miocene (Darlington, 1963:367; Webb, 1985b). Fossil procyonids from the late Miocene are represented in Florida, California, Texas, Nebraska, Kansas, and South Dakota (Baskin, 1982; Martin, 1989) and include such genera as *Bassariscus*, *Arctonasua*, *Cyonasua*, *Paranasua*, *Nasua*, and *Procyon* (Baskin, 1982; Webb, 1985b). During the Miocene procyonids underwent a modest radiation within tropical and subtropical climates of North America's central and middle latitudes. *Cyonasua*, which has close affinities to *Arctonasua* (Baskin, 1982), appears in tropical South America in the late Miocene and immigrated there either by rafting across the Bolivar Trough or by island-hopping through the Antilles archipelagoes (Marshall et al., 1982; Marshall, 1988). Thus, procyonids were found on both continents prior to formation of the Panamanian land bridge (Darlington, 1963:367, 395; Marshall et al., 1982; Marshall, 1988). Origins of *Bassaricyon* and *Potos* are obscure but probably occurred in tropical rainforests of Middle America (Baskin, 1982; Webb, 1985b). A subsequent Pleistocene dispersal carried several modern genera (Table 1) across the Panamanian land bridge into South America (Webb, 1985b). *Bassariscus* and *Bassaricyon* represent the most primitive genera in Procyoninae and Potosinae subfamilies, respectively (Table 1; Wozencraft, 1989a; Decker and Wozencraft, 1991).

In the early Tertiary, mid-latitudes of North America were much warmer than they are now, but not fully tropical, and temperate deciduous forests, associated with strongly seasonal climates, occurred only in the far north (Barghoorn, 1953; Colbert, 1953; Darlington, 1963:589, 590). Major climatic deteriorations, with their attendant cooling of northern continents, occurred during the Eo-Oligocene transition, in the middle Miocene, at the end of the Miocene, and at about 3 MYBP (late Pliocene). This last deterioration corresponds with closure of the Panamanian isthmus (Berggren, 1982; Webb,

---

*John N. Mugaas, Department of Physiology, Division of Functional Biology, West Virginia School of Osteopathic Medicine, Lewisburg, West Virginia 24901. John Seidensticker and Kathleen P. Mahlke-Johnson, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008.*

TABLE 1.—Classification of recent Procyonidae after Wozencraft (1989a) and Decker and Wozencraft (1991). Information in parenthesis indicates general geographic distribution (modified from Kortlucke and Ramirez-Pulido (1982) and Poglayen-Neuwall (1975)): S.A. = South America; C.A. = Central America; M. = Mexico; U.S. = United States; C. = Canada. Lower case letters preceding geographic areas signify north (n), south (s), and west (w).

---

Order CARNIVORA Bowdich, 1821  
 Suborder CANIFORMIA Kretzoi, 1945  
 Family PROCYONIDAE Gray, 1825  
 Subfamily POTOSINAE Trouessart, 1904  
 Genus *Potos* E. Geoffroy and G. Cuvier, 1795  
*P. flavus* (S.A., C.A., M.)  
 Genus *Bassaricyon* Allen, 1876  
*B. alleni*\* (S.A.)  
*B. beddardi*\* (S.A.)  
*B. gabpii*\* (nS.A., C.A.)  
*B. lasius*\* (C.A.)  
*B. pauli*\* (C.A.)  
 Subfamily PROCYONINAE Gray, 1825  
 Genus *Bassariscus* Coues, 1887  
*B. astutus* (M., wU.S.)  
*B. sumichrasti* (C.A., M.)  
 Genus *Nasua* Storr, 1780  
*N. narica*† (nS.A., C.A., M., swU.S.)  
*N. nasua*† (S.A., sC.A.)  
 Genus *Nasua* Hollister, 1915  
*N. olivacea* (S.A.)  
 Genus *Procyon* Storr, 1780  
*P. cancrivorus* (S.A., sC.A.)  
*P. gloveralleni*‡ (Barbados)  
*P. insularis*‡ (Maria Madre Is., Maria Magdalene Is.)  
*P. lotor*‡ (C.A., M., U.S., sC.)  
*P. maynardi*‡ (Bahamas, New Providence Is.)  
*P. minor*‡ (Guadeloupe Is.)  
*P. pygmaeus*‡ (M., Quintana Roo, Cozumel Is.)

---

\*The several named forms of *Bassaricyon* are a single species, *Bassaricyon gabpii* (Wozencraft, 1989a).

†These are considered conspecific in some current taxonomies (Kortlucke and Ramirez-Pulido, 1982); however, the scheme followed here maintains them as separate species (Decker, 1991).

‡Several named forms of *Procyon* are a single species, *Procyon lotor* (Wozencraft, 1989a).

1985a). Climatic deterioration went on at an accelerating rate during the late Tertiary, with glacial conditions developing at the poles by the mid-Pliocene (Barghoorn, 1953). Therefore, throughout the Tertiary, as continents cooled, northern climate zones moved toward the tropics (Barghoorn, 1953; Colbert, 1953; Darlington, 1963:589, 590, 594, 595; Webb, 1985a).

During the late Miocene, late Pliocene, and Pleistocene, the Bering land bridge between North America and Asia formed periodically, offering an avenue for dispersal between northern continents (Darlington, 1963:366; Webb, 1985a). However, by the late Tertiary, northern continents had cooled to the extent that climate, with its attendant sharply defined vegetative zones, became the major factor limiting dispersal by this route (Darlington, 1963:366; Webb, 1985a). Those Holarctic mam-

mals that did cross the Bering land bridge in the late Tertiary were "cold-adapted" species associated with relatively cool, but not alpine, climates (Darlington, 1963:366; Ewer, 1973:369). Among carnivores this included some canids, ursids, mustelids, and felids (Darlington, 1963:393-395, 397; Webb, 1985a). Procyonids, however, did not cross the Bering land bridge into Asia, and Ewer (1973:369) ascribes this to their being an "essentially tropical group." Miocene radiation of procyonids occurred at a time when two of the four major climatic deteriorations (middle and late Miocene) were taking place (Webb, 1985a, 1985b). These deteriorations had the effect of cooling the middle latitudes to the extent that temperate forest forms began to appear in mid-latitude floras, along with a rapid influx of herbaceous plants (Barghoorn, 1953). The procyonid radiation did not penetrate beyond these climatically changing middle latitudes, which implies that these animals were "warm-adapted," and were, therefore, physiologically excluded from reaching the Bering land bridge. Today, three of the six genera and over half of the 18 species that comprise Procyonidae (Table 1; Wozencraft, 1989b) remain confined to tropical regions of North and South America (Hall and Kelson, 1959:878-897; Poglayen-Neuwall, 1975; Kortlucke and Ramirez-Pulido, 1982; Nowak and Paradiso, 1983:977-985).

#### Typical Procyonids

McNab (1988a) contends that basal metabolism is a highly plastic character in evolution, and he has amply shown that ecologically uniform species are more apt to share common metabolic rates than taxonomically allied species from drastically different environments (McNab, 1984a, 1986a, 1986b, 1988a). Procyonids represent a taxonomically allied group that shared a common ecological situation for millions of years; consequently, members of this family might be expected to show some uniformity in their  $\dot{H}_b$ . Basal and thermoregulatory metabolism of several procyonids have been measured: kinkajou, *Potos flavus* (Müller and Kulzer, 1977; McNab, 1978a; Müller and Rost, 1983), coatis, *Nasua nasua* (Chevallard-Hugot et al., 1980; Mugaas et al., in prep.), and *Nasua narica* (Scholander et al., 1950c; Mugaas et al., in prep.), ringtail, *Bassariscus astutus* (Chevalier, 1985), and crab-eating raccoon, *Procyon cancrivorus* (Scholander et al., 1950c). In general, these species have  $\dot{H}_b$ 's that are 40%-80% of the values predicted for them by the Kleiber (1961:206) equation. Lower than predicted  $\dot{H}_b$  is viewed as an energy-saving adaptation for procyonids living in relatively stable tropical climates (Müller and Kulzer, 1977; Chevallard-Hugot et al., 1980; Müller and Rost, 1983). This implies that lower than predicted  $\dot{H}_b$  is a general procyonid condition and that it represents a characteristic that evolved in response to the family's long association with tropical and subtropical forest environments.





FIGURE 1.—North American raccoon, *Procyon lotor*.

### *The Atypical Procyonid*

Although most procyonids are found in only tropical to subtropical climates, the North American raccoon, *Procyon lotor*, (Figure 1) has a much broader distribution that extends from tropical Panama (8°N) to southern Canada. In Alberta, Canada, its range reaches the edge of the Hudsonian Life Zone at 60°N (for distribution maps see Hall and Kelson, 1959:878–897, and Poglayen-Neuwall, 1975). Range extensions and an increase in numbers have been noted in Canada and in parts of

the United States since the 19th century (Lotze and Anderson, 1979; Kaufmann, 1982; Nowak and Paradiso, 1983:977–985). Thus, *Procyon lotor* is more complex ecologically than other procyonids, particularly when one takes into account its highly generalized food habits (Hamilton, 1936; Stuewer, 1943; Stains, 1956:39–51; Greenwood, 1981) and the wide range of habitat types (forest, prairie, desert, mountain, coastal marsh, freshwater marsh) and climates (tropical to north temperate) in which it is successful (Whitney and Underwood, 1952:1; Hall and Kelson, 1959:885; Lotze and Anderson, 1979; Kaufmann,

1982). On this basis it is clear that *Procyon lotor* has deviated from the typical procyonid portrait and has become the consummate generalist of the Procyonidae.

### *The Hypothesis*

Our general hypothesis was that whereas most contemporary procyonids have retained the metabolic characteristics of their warm-adapted ancestors, *Procyon lotor* possesses a different set of adaptations, which either evolved as characteristics unique to this species or were acquired from its ancestral stock. In either case, its unique adaptations have given *Procyon lotor* the physiological flexibility to generalize its use of habitats and climates and expand its geographic distribution to a much greater extent than other procyonids.

### *Hypothesis Testing*

We tested our hypothesis by comparing *Procyon lotor* with several other procyonids (*Bassariscus astutus*, *Nasua nasua*, *Nasua narica*, *Procyon cancrivorus*, and *Potos flavus*) on the basis of their (1) basal metabolic rate ( $\dot{H}_b$ ), (2) minimum wet thermal conductance ( $C_{mw}$ ), (3) diversity of diet ( $D_d$ ), (4) intrinsic rate of natural increase ( $r_{max}$ ), and, when data were available, (5) capacity for evaporative cooling ( $E_c$ ). In a genetic sense each one of these variables is a complex adaptive characteristic, expression of which is determined by the interaction of several genes (Prosser, 1986:110–165). Experience has shown that a given species will express each one of these variables in a specific manner that is relevant to its mass, physiology, behavior, and environmental circumstance. Thus, different expressions of these variables may represent specific climatic adaptations (Prosser, 1986:16) that have been selected-for by evolutionary process. Because these variables are interrelated with respect to regulation of body temperature and energy balance, they have co-evolved in each species to form an adaptive unit. For each species, measured and calculated values for the first four variables were converted into dimensionless numbers and used to derive a composite score that represented its adaptive unit. Climatic distributions of these species were then compared relative to their composite scores.

### ADAPTIVE SIGNIFICANCE OF THE VARIABLES

#### *Basal Metabolic Rate and Intrinsic Rate of Natural Increase*

Basal metabolic rate represents the minimum energy required by an animal to maintain basic homeostasis (Lusk, 1917:141; Kleiber, 1932, 1961:251; Benedict, 1938; Brody, 1945:59; Robbins, 1983:105–111). For mammals,  $\dot{H}_b$  appears to be determined by complex interactions between their body size (Kleiber, 1932, 1961:206; Benedict, 1938; Brody, 1945:368–374; Hemmingsen, 1960:15–36; McNab, 1983b;

Calder, 1987), the climate in which they live (Scholander et al., 1950c; McNab and Morrison, 1963; Hulbert and Dawson, 1974; Shkolnik and Schmidt-Nielsen, 1976; McNab, 1979a; Vogel, 1980), their food habits (McNab, 1978a, 1978b, 1980a, 1983a, 1984a, 1986a, 1986b, 1988a, 1989), and their circadian period (Aschoff and Pohl, 1970; Prothero, 1984). Some species have higher mass-specific  $\dot{H}_b$  than others, and this variation appears to be tied to ecological circumstances rather than taxonomic affinities (McNab, 1988a, 1989). Basal metabolic rate is important ecologically because it serves as a measure of a species' minimum "obligatory" energy requirement, and under many circumstances, it represents the largest energy demand associated with a daily energy budget (King, 1974:38–55; McNab, 1980a; Mugaas and King, 1981:37–40). Recently it also has been implicated as a permissive factor with respect to  $r_{max}$  of mammals (Hennemann, 1983; Lillegraven et al., 1987; Nicoll and Thompson, 1987; Thompson, 1987) via its direct effect on their rates of development and fecundity (McNab, 1980a, 1983a, 1986b; Hennemann, 1983; Schmitz and Lavigne, 1984; Glazier, 1985a, 1985b). The implication of this latter point is that those species with higher  $\dot{H}_b$ 's also have faster rates of development and greater fecundity and hence enjoy the competitive advantage of a higher  $r_{max}$ . Basal metabolism is, therefore, "a highly plastic character in the course of evolution" (McNab, 1988a:25) that has a profound influence on each species' life history.

#### *Minimum Thermal Conductance*

Whole-body resistance to passive heat transfer is equal to tissue resistance plus coat resistance. Within limits, these resistances can be altered; tissue resistance can be varied by changes in blood flow, whereas coat resistance can be changed by piloerection, molt, and behavior. When whole-body resistance is maximized (maximum tissue and coat resistances), passive heat transfer is minimized. The inverse of resistance is conductance; therefore, maximum whole-body resistance is the inverse of minimum thermal conductance ( $C_m$ ). Minimum thermal conductance is readily derived from metabolic chamber data, and it is commonly used to describe an animal's capacity to minimize passive heat transfer. Minimum thermal conductance interacts with  $\dot{H}_b$  and body mass to set the maximum temperature differential a mammal can maintain without increasing its basal level of heat production. The low temperature in this differential is the lower critical temperature ( $T_{lc}$ ).

Mass-specific  $C_m$  for mammals is negatively correlated with body mass (McNab and Morrison, 1963; Herreid and Kessel, 1967; McNab, 1970, 1979b; Bradley and Deavers, 1980; Aschoff, 1981), and for any given mass its magnitude is 52% higher during the active, rather than the inactive, phase of the daily cycle (Aschoff, 1981). However, some mammals have  $C_m$ 's that are higher or lower than would be predicted for them on the basis of body mass and circadian phase. Seasonal

variation in  $C_m$  (higher values during summer than winter) has been reported for many northern mammals that experience large annual variations in air temperature (Scholander et al., 1950a; Irving et al., 1955; Hart, 1956, 1957; Irving, 1972:165). Some tropical mammals with very thin fur coats, and others with nearly hairless bodies, have high  $C_m$ 's (McNab, 1984a), as do burrowing mammals (McNab, 1966, 1979b, 1984a) and the kit fox, *Vulpes macrotis* (Golightly and Ohmart, 1983). Some small mammals with low basal metabolic rates tend to have lower than predicted  $C_m$ 's: small marsupials (McNab, 1978a), heteromyid rodents (McNab, 1979a), several ant eaters (McNab, 1984a), the arctic hare, *Lepus arcticus* (Wang et al., 1973), the ringtail, *Bassariscus astutus* (Chevalier, 1985), and the fennec, *Fennecus zerda* (Noll-Banholzer, 1979). Thus, in spite of its mass dependence,  $C_m$  also has been modified during the course of evolution by selective factors in the environment and by the animal's own metabolic characteristics.

#### Capacity for Evaporative Cooling

Latent heat loss occurs as a result of evaporation from the respiratory tract and through the skin, and except under conditions of heat stress, it "is a liability in thermal and osmotic homeostasis" (Calder and King, 1974:302).  $E_c$ , defined as the ratio of evaporative heat lost to metabolic heat produced, can be used to quantify thermoregulatory effectiveness of evaporative cooling and to make comparisons of heat tolerance between species. Thermoregulatory effectiveness of latent heat loss is not just a function of the rate of evaporative water loss but also of the rate of metabolic heat production (Lasiewski and Seymour, 1972). For example, a low metabolic rate minimizes endogenous heat load and thus conserves water, whereas the opposite is true of high metabolic rates (Lasiewski and Seymour, 1972). Some mammals that live in arid regions have evolved low metabolic rates and thus capitalize on this relationship to reduce their thermoregulatory water requirement (McNab and Morrison, 1963; McNab, 1966; MacMillen and Lee, 1970; Noll-Banholzer, 1979). What is evident, therefore, is that an animal's capacity for increasing latent heat loss must evolve together with its  $\dot{H}_b$  and  $C_m$  in response to specific environmental demands.

#### Diet

McNab (1986a, 1988a, 1989) demonstrated that, for mammals, departures of  $\dot{H}_b$  from the Kleiber (1961:206) "norm" are highly correlated with diet and independent of phylogenetic relationships. McNab's analysis indicates that for mammals that feed on invertebrates, those species with body mass less than 100 g have  $\dot{H}_b$ 's that are equal to or greater than values predicted by the Kleiber equation, whereas those with body mass greater than 100 g have metabolic rates that are lower than predicted. Grazers, vertebrate eaters, nut eaters, and terrestrial frugivores also have  $\dot{H}_b$ 's that are equal to or greater than

predicted, whereas insectivorous bats, arboreal folivores, arboreal frugivores, and terrestrial folivores all have rates that are lower than predicted. McNab (1986a) found animals with mixed diets harder to categorize, but in general he predicted that their  $\dot{H}_b$ 's would be related to (1) a food item that is constantly available throughout the year, (2) a food item that is most available during the worst conditions of the year, or (3) a mix of foods available during the worst time of the year. Although these correlations do not establish cause and effect between food habits and  $\dot{H}_b$ , McNab's analysis does make it clear that the relationship between these variables has very real consequences for an animal's physiology, ecology, and evolution.

#### EXPERIMENTAL DESIGN AND SUMMARY

In this investigation we measured basal and thermoregulatory metabolism, evaporative water loss, and body temperature of raccoons from north central Virginia. Measurements were conducted on both sexes in summer and winter to determine how season and sex influenced these variables. We then compared the data for this widely distributed generalist with data from literature for its ecologically more restricted relatives. Dietary data for all species were taken from literature, as were reproductive data for calculation of  $r_{max}$ .

Our analysis demonstrated clear differences between *Procyon lotor* and other procyonids with respect to  $\dot{H}_b$ ,  $C_{mw}$ ,  $D_d$ , and  $r_{max}$ . The composite score calculated from these variables for *Procyon lotor* was much higher than those derived for other species, and there was a positive correlation between the number of climates a species occupies and the magnitude of its composite score. Data on evaporative water loss, although not complete for all species, suggested that tropical and subtropical procyonids have less capacity for evaporative cooling than *Procyon lotor* or *Bassariscus astutus*. It was clear, therefore, that with respect to its thermal physiology, *Procyon lotor* differed markedly from other procyonids, and we contend that these differences have allowed this species to become a highly successful climate generalist and to expand its distribution into many different habitats and climates. Our analysis also suggested that the cornerstone of *Procyon lotor*'s success as a climate generalist is its  $\dot{H}_b$ , which is higher than the procyonid norm.

#### ACKNOWLEDGMENTS

The authors would like to thank John Eisenberg and Devra Kleiman for their support and encouragement throughout the study. This investigation was supported by research grants from the West Virginia School of Osteopathic Medicine (WVSOM), and Friends of the National Zoo (FONZ). Logistic support was provided by the National Zoological Park's Conservation and Research Center (CRC), and the departments of Mammalogy and Zoological Research. Our ability to

conduct physiological research at CRC was made possible by the thoughtful support and encouragement provided by Chris Wemmer. His excellent staff at CRC, especially Jack Williams, Junior Allison, and Red McDaniel, were very helpful in providing hospitality and logistical support to the senior author and his family during their various visits to the Center. The assistance of several people at the National Zoo also is gratefully acknowledged: Mitch Bush and Lyndsay Phillips not only provided veterinary support throughout the investigation, but also performed surgical procedures required to implant temperature-sensitive radio transmitters in several raccoons; Olav Oftedal made his laboratory available to us at various times and loaned us equipment to use at CRC; Miles Roberts and his staff provided care for our captive raccoons in the Department of Zoological Research during various parts of the investigation. Greg Sanders and Ken Halama, supported by FONZ assistantships, cared for our captive raccoons at CRC, provided assistance in the laboratory whenever needed, and were an invaluable source of aid. Their friendship and help is gratefully acknowledged. Ellen Broudy and Andy Meyer, supported by WVSOM and a student work study grant, respectively, provided assistance in the laboratory. David Brown, John Eisenberg, Mary Etta Hight, Brian McNab, Steve Thompson, and W. Chris Wozencraft critically reviewed various phases of the manuscript and provided many helpful suggestions. We deeply appreciate the work of Jean B. McConville, whose beneficial editorial suggestions helped us improve several early versions of the manuscript. We also gratefully acknowledge Diane M. Tyler, our editor at the Smithsonian Institution Press, whose expertise helped us mold the manuscript into its final form. Jill Mellon and Sriyanie Miththalapa, supported by FONZ traineeships, assisted in measuring the daily cycle of body temperature in raccoons. The Virginia Commission of Game and Inland Fisheries gave us permission to use wild-caught raccoons in this project.

## Materials and Methods

### LIVE-TRAPPING

Raccoons were caught from May 1980 through December 1984 on a trapping grid of 30 to 35 stations (one or two "live traps" per station) that covered about one-third of the National Zoological Park's Conservation and Research Center (CRC) near Front Royal, Virginia (Seidensticker et al., 1988; Hallett et al., 1991). Animals were trapped during 10 consecutive days each month, and in this five-year interval 407 raccoons were captured and marked with tattoos and ear tags. All captured animals were individualized with respect to age, reproductive status, physical condition, parasite load, and mass and body dimensions. These data characterized the structure and dynamics of the raccoon population at CRC and provided information

on the annual cycle of fattening for raccoons in north central Virginia.

Animals used for metabolic measurements were captured at CRC about 1.5 km south of the trapping grid and thus were genetically representative of the area. Six males were captured and measured during the summer of 1983. These animals were kept isolated for a week before being measured and were released later that summer at the site of their capture. The other seven animals used in our study were from the collection of the National Zoological Park and all of them had their origins at CRC.

## METABOLIC STUDIES

### *Basal and Thermoregulatory Metabolism*

Metabolic measurements, conducted at CRC, were carried out on eight males during July and August 1983, on four females and three males from November 1983 through March 1984, and on four females during June and July 1984.

Raccoons were housed throughout the study such that they were constantly exposed to a natural cycle of temperature and photoperiod. Weather records for the Front Royal area indicate that average temperatures are around  $-0.5^{\circ}\text{C}$  in January and  $23.3^{\circ}\text{C}$  in July (Crockett, 1972). Light:dark (L:D) periods for the latitude of CRC ( $48^{\circ}55'\text{N}$ ; United States Department of the Interior Geological Survey, 1972), calculated from duration of daylight tables (List, 1971:506-512), were 14.9:9.1 and 9.4:14.6 hours L:D for summer and winter solstices, respectively, and 12.2:11.8 hours L:D for vernal and autumnal equinoxes.

Our animals were fed a measured amount of food daily, and they usually ate most of what was provided. Occasionally these animals would eat very little or none of their ration, and on some days they would eat all that was given to them. We fed them either feline diet (ground horse meat) or canned mackerel (Star-kist<sup>®\*</sup>) along with high-protein dog chow (Purina<sup>®</sup>). When available, fresh fruit also was added to their diet. Water was always provided ad libitum.

Measurements were conducted during the raccoons' daily inactive period (sunrise to sunset) in both summer and winter. Oxygen consumption was measured in a flow-through metabolism chamber at  $5^{\circ}\text{C}$  intervals from  $-10^{\circ}\text{C}$  to  $35^{\circ}\text{C}$ . Animals were held at each temperature until the lowest rate of oxygen consumption had been obtained and maintained for at least 15 minutes. During each determination, oxygen consumption was monitored for 30 minutes to one hour beyond a suspected minimum value to see if an even lower reading could be obtained. Raccoons attained minimum levels of oxygen consumption more quickly at warm ( $>10^{\circ}\text{C}$ ) than at cold

\*The use of product brand names in this publication is not intended as an endorsement of the products by the Smithsonian Institution.

temperatures. Depending on the temperature, therefore, each measurement took from two to five hours to complete. On days when two measurements could be completed, the second trial was always at a temperature 10°C warmer than the first.

The metabolism chamber was constructed from galvanized sheet metal (77.5 × 45.5 × 51.0 cm = 180 liters) and was painted black inside. Within the chamber, the animal was held in a cage (71 × 39 × 33 cm) constructed from turkey wire that also was painted black. This cage prevented the raccoons from coming into contact with the walls of the chamber, yet it was large enough to allow them to stand and freely move about. The bottom of the cage was 11 cm above the chamber floor, which was covered to a depth of one cm with mineral oil to trap urine and feces.

During measurements, the metabolism chamber was placed in a controlled-temperature cabinet (modified Montgomery Ward model 8969 freezer). Air temperature ( $T_a$ ) in the metabolism chamber was regulated with a Yellow Springs Instrument model 74 temperature controller.  $T_a$  was controlled to ±1.0°C at temperatures below freezing, and to ±0.5°C at temperatures above freezing. The chamber air and wall temperatures were recorded continuously (Linseis model LS-64 recorder) during each experiment, and, except during temperature changes, they were always within 0.5°C of each other.

Columns of Drierite® and Ascarite® removed water vapor and carbon dioxide, respectively, from air entering and leaving the chamber. Dry carbon-dioxide-free room air was pumped into the chamber (Gilman model 13152 pressure/vacuum pump) at a rate of 3.0 L/min (Gilmont model K3203-20 flow meter). Downstream from the chemical absorbents, an aliquot (0.1 L/min) of dry carbon-dioxide-free air was drawn off the chamber exhaust line and analyzed for oxygen content (Applied Electrochemistry model S-3A oxygen analyzer, model 22M analysis cell, and model R-1 flow control). All gas values were corrected to standard temperature and pressure for dry gas. Oxygen consumption was calculated from the difference in oxygen content between inlet and outlet air using Eq. 8 of Depocas and Hart (1957).

Each raccoon was fasted for at least 12 hours before oxygen consumption measurements began. At the start and end of each metabolic trial the animal was weighed to the nearest 10 g (Doctors Infant Scale, Detecto Scales, Inc., Brooklyn, N.Y., U.S.A.). The body mass used in calculating minimum oxygen consumption and evaporative water loss was estimated from timed extrapolations of the difference between starting and ending weights, and the time at which these variables were measured.

#### *Evaporative Water Loss*

During metabolic measurements at temperatures above freezing, evaporative water loss was determined gravimetrically. Upstream from the chemical columns, an aliquot of air

(0.1 L/min) was drawn off the exhaust line and diverted for a timed interval through a series of preweighed (0.1 mg) U-tubes containing Drierite®. The aliquot then passed through a second series of U-tubes containing Ascarite® before entering the oxygen analysis system. Evaporative water loss was calculated using Eq. 1

$$\dot{E} = (m_w \cdot \dot{V}_e) / (\dot{V}_a \cdot t \cdot m) \quad \text{Eq. 1}$$

where  $\dot{E}$  is evaporative water loss ( $\text{mg} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ),  $m_w$  is mass of water collected (mg),  $\dot{V}_e$  is rate of air flow into the chamber (3.0 L/min),  $\dot{V}_a$  is rate of air flow through the U-tubes (0.1 L/min),  $t$  is length of the timed interval (h), and  $m$  is the estimated mass of the raccoon at the time of sampling (g).

#### *Body Temperature*

Veterinarians at the National Zoological Park surgically implanted calibrated temperature-sensitive radio transmitters (Telonics, Inc., Mesa, AZ, U.S.A.) into abdominal cavities of two female and two male raccoons. Transmitter pulse periods were monitored with a digital processor (Telonics TDP-2) coupled to a receiver (Telonics TR-2-164/166). During some metabolic measurements, body temperatures of these animals were recorded to the nearest 0.1°C at 30-minute intervals. The daily cycle of body temperature of these raccoons also was measured once a month.

#### CALIBRATIONS

##### *Calorimeter*

At the conclusion of these experiments, the accuracy of our calorimetry apparatus was tested by burning an ethanol lamp in the metabolism chamber. During these tests a CO<sub>2</sub> analyzer was incorporated into the system (Beckman, LB-2). Results demonstrated that we measured 84% of the oxygen consumed by the lamp as well as 84% of the water and CO<sub>2</sub> it produced; standard deviation = ±2.6, ±5.0, and ±3.6, respectively (n = 27). Average respiratory quotient (RQ) calculated from these data was 0.657 ± 0.008 (n = 27), which is 99.5% of that predicted (0.66). McNab (1988b) reports that the accuracy of open-flow indirect calorimetry systems, such as ours, depends on the rate of air flow through the animal chamber. If flow rates are too low, there is inadequate mixing of air within the chamber, and the rate of oxygen consumption, as calculated from the difference in oxygen content of air flowing into and out of the chamber (Depocas and Hart, 1957), is underestimated. At some critical rate of air flow, which is unique to each combination of chamber and animal, this situation changes such that measured rates of oxygen consumption become independent of any further increase in flow rate (McNab, 1988b). In recent tests of our system, where we burned the ethanol lamp at a variety of chamber flow rates, the efficiency

of measurement increased linearly as flow rate increased, and the critical rate of air flow was about 6.7 L/min. This appeared to explain why a flow rate of 3.0 L/min underestimated oxygen consumption of the ethanol lamp.

Our earlier tests of the efficiency of our system indicated that although we underestimated actual oxygen consumption of the ethanol lamp, we did so with a fair degree of precision; probably because flow rates were closely controlled. During our metabolic measurements, chamber flow rates also were closely controlled at 3.0 L/min, and we believe, therefore, that these measurements also were carried out with a high degree of precision. Consequently, all measured values of oxygen consumption and water production were considered to be 84% of their actual value and were adjusted to 100% before being included in this report.

#### *Body Temperature Transmitters*

The calibration of all temperature-sensitive radio transmitters drifted over time. Transmitters were calibrated before they were surgically implanted and again after they were removed from the animals. Although the drift of each transmitter was unique, it was also linear (S. Tomkiewicz, Telonics, Inc., pers. com.). All body temperature measurements were corrected from timed extrapolations of the difference between starting and ending calibrations.

#### STATISTICAL METHODS

Values of oxygen consumption, evaporative water loss, and body temperature were plotted as a function of chamber air temperature. Linear regressions of oxygen consumption at temperatures below the thermoneutral zone ( $T_n$ ), and evaporative water loss at temperatures above freezing, were determined with the SAS (1982) GLM procedure. Lower critical temperature ( $T_{lc}$ ) was determined graphically from intersection of the line representing  $\dot{H}_b$  and the regression line representing oxygen consumption below  $T_n$ . Slopes and intercepts of regression lines, as well as other mean values, were compared with *t*-tests (Statistical Analysis System, 1982; Ott, 1984:138–175). Unless indicated otherwise, data are expressed as mean  $\pm$  standard deviation (s.d.).

#### ESTIMATING INTRINSIC RATE OF NATURAL INCREASE

We employed the method first described by Cole (1954) to calculate  $r_{max}$ :

$$1 = e^{-r_{max}} + b \cdot e^{-r_{max}(a)} - b \cdot e^{-r_{max}(n+1)} \quad \text{Eq. 2}$$

where *a* is potential age of females first producing young, *b* is potential annual birth rate of female young, and *n* is potential age of females producing their final young. After life-history

data were substituted into Eq. 2,  $r_{max}$  was determined by trial and error substitution (Hennemann, 1983).

Because  $r_{max}$  represents the genetically fixed, physiologically determined maximum possible rate of increase, data on earliest possible age of female reproduction, highest possible birth rate of female young, and longest possible female reproductive life span were used for *a*, *b*, and *n*, respectively. Calculated values, therefore, represent physiologically possible, not ecologically possible, intrinsic rates of increase (Hennemann, 1983, 1984; Hayssen, 1984; McNab, 1984b). Values of *n* were derived from longevity records for captive animals, and as these were all large values of similar duration (14–16 years), they had very little effect on  $r_{max}$ . All species considered have one litter per year, and because their sex ratios at birth are about 50:50, variation in *b* was due to differences in litter size. Therefore, age of first reproduction and litter size had the greatest effect on  $r_{max}$ . Intrinsic rate of increase scales to body mass (Fenchel, 1974), and we removed this effect by comparing each calculated  $r_{max}$  with the value expected ( $r_{maxe}$ ) on the basis of body mass (Hennemann, 1983).

#### COMPARISON OF ADAPTIVE UNITS

Dimensionless numbers for each of the four variables used in calculating composite scores were derived as follows. Ratios of measured to predicted values were used for basal metabolism ( $H_{br}$ ) and minimum wet thermal conductance ( $C_{mwr}$ ). Thermoregulatory ability at low temperatures is closely related to the ratio  $H_{br}/C_{mwr}$  (McNab, 1966). This ratio was used, therefore, to gauge each species' cold tolerance. For  $D_d$  we used the ratio of food categories actually used by a species to the total number of food categories taken by all species tested ( $D_{dr}$ ). The ratio of calculated to expected intrinsic rates of natural increase was used to derive  $r_{maxr}$ . Composite scores were calculated as

$$\text{Composite score} = [(H_{br}/C_{mwr}) + D_{dr} + r_{maxr}] / 3 \quad \text{Eq. 3}$$

The correlation between number of climates these species occupy and their composite scores was tested by linear regression.

#### Results

##### BODY MASS

According to monthly live-trapping records, the body mass of free-ranging female raccoons increased from 3.6  $\pm$  0.6 kg during summer to 5.6  $\pm$  0.8 kg in early winter, and the mass of free-ranging males increased from 4.0  $\pm$  0.5 to 6.7  $\pm$  0.9 kg during the same interval. These seasonal changes in body mass were due to fluctuations in the amount of body fat and represent a mechanism for storing energy during fall for use in winter. In summer, captive and trapped male and captive female raccoons had the same body mass (4.73  $\pm$  0.61, 4.41  $\pm$  0.70, and 4.67

$\pm 0.88$  kg, respectively, Table 2). Mass of captive females did not change between seasons, whereas captive males were heavier in winter than summer ( $p < 0.005$ ; Table 2). This seasonal change in mass of our captive males was of a much smaller magnitude (0.6 kg) than that observed for wild males

(2.7 kg). During winter, captive males ( $5.34 \pm 1.39$  kg) were heavier than captive females ( $4.49 \pm 0.98$  kg;  $p < 0.005$ ; Table 2). Thus, our captive animals maintained a body mass throughout the year that was intermediate to the range of values found for wild raccoons in the same area.

TABLE 2.—Body mass in kg and basal metabolism ( $\text{mL O}_2 \cdot \text{kg}^{-0.75} \cdot \text{h}^{-1}$ ) of *Procyon lotor* in summer and winter (s.d. = standard deviation and  $n$  = number of observations).

Season and sex	Body mass, $\pm$ s.d., (n)			Basal metabolism, $\pm$ s.d., (n)		
Summer						
Trapped male	4.41	$\pm 0.70$	(52)	780	$\pm 112$	(20)
Captive male	4.73	$\pm 0.61$	(22)	680	$\pm 102$	(8)
Captive female	4.67	$\pm 0.88$	(41)	618	$\pm 92$	(13)
Winter						
Captive male	5.34	$\pm 1.39$	(31)	704	$\pm 81$	(19)
Captive female	4.49	$\pm 0.98$	(42)	667	$\pm 139$	(25)

#### BASAL METABOLIC RATE

$$C_{mw} = \dot{H}_r / (T_b - T_a) \quad \text{Eq. 4}$$

$$C_{md} = (\dot{H}_r - \dot{E}_{eq}) / (T_b - T_a) \quad \text{Eq. 5}$$

Within thermoneutrality,  $\dot{H}_b$  ( $\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) was  $0.54 \pm 0.09$  for trapped males in summer,  $0.46 \pm 0.07$  for captive males in summer,  $0.42 \pm 0.07$  for captive females in summer,  $0.47 \pm 0.06$  for captive males in winter, and  $0.46 \pm 0.10$  for captive females in winter (Figures 2, 3). Ratios of these measured values to those predicted by the Kleiber (1932, 1961:206) equation are 1.28, 1.12, 1.02, 1.17, and 1.09, respectively. To minimize the effect of body size (Mellen, 1963) and to facilitate comparisons between sexes and seasons and between captive and trapped animals, basal metabolism also was calculated as a function of metabolic body size ( $\text{mL O}_2 \cdot \text{kg}^{-0.75} \cdot \text{h}^{-1}$ ; Table 2). Based on this analysis, trapped summer males had a higher basal metabolism than captive males ( $p < 0.025$ ) or females ( $p < 0.005$ ) in either season (Table 2). There was no difference in basal metabolism between captive males and females in either summer or winter, and there was no seasonal difference in their basal metabolic rates (Table 2).

#### MINIMUM THERMAL CONDUCTANCE

Minimum wet and dry thermal conductances were calculated using Eqs. 4 and 5

where  $C_{mw}$  is wet and  $C_{md}$  is dry conductance ( $\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$ );  $\dot{H}_r$  is the lowest resting metabolic rate measured at each temperature ( $\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ );  $\dot{E}_{eq}$  is oxygen equivalent for heat lost by evaporation [ $\dot{E}_{eq} = \text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} = \dot{E} \cdot \lambda / \gamma$ , where  $\dot{E}$  is evaporative water loss ( $\text{mg} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ),  $\lambda$  is heat of vaporization for water (2.43 J/mg), and  $\gamma$  is heat equivalent for oxygen (20.097 J/mL)];  $T_b$  is body temperature ( $^\circ\text{C}$ ); and  $T_a$  is chamber air temperature ( $^\circ\text{C}$ ). Only data from animals equipped with temperature-sensitive radio transmitters were used for these calculations.

$C_{mw}$  was calculated for each season from metabolic measurements made at all air temperatures below  $T_{lc}$  (Table 3). Because evaporative water loss was not measured at temperatures below freezing,  $C_{md}$  was calculated only from metabolic determinations made at air temperatures between  $T_{lc}$  and  $0^\circ\text{C}$ . There was no difference between males and females in summer for either  $C_{mw}$  or  $C_{md}$  ( $\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$ ). Data for each sex were combined to give a summer average of  $0.0256 \pm 0.0028$

TABLE 3.—Minimum wet and dry thermal conductances ( $\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$ ) of *Procyon lotor* in summer and winter. Means of values were calculated from equations 3 and 4 (s.d. = standard deviation and  $n$  = number of observations).

Season and sex	Thermal conductance					
	Wet	$\pm$ s.d.	(n)	Dry	$\pm$ s.d.	(n)
Summer						
Captive, both sexes	0.0256	$\pm 0.0028$	(18)	0.0246	$\pm 0.0019$	(12)
Winter						
Captive, female	0.0172	$\pm 0.0023$	(10)	0.0161	$\pm 0.0027$	(6)

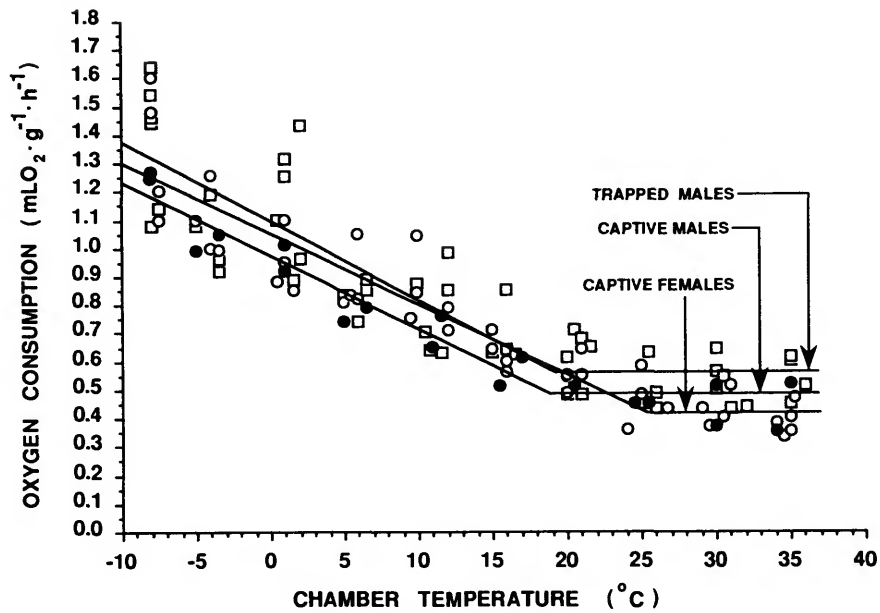


FIGURE 2.—Relationship between oxygen consumption and chamber air temperature for raccoons in summer: captive females, open circles; captive males, closed circles; trapped males, open squares. Sloping lines represent regressions of oxygen consumption on chamber air temperature, and horizontal lines, basal metabolism.

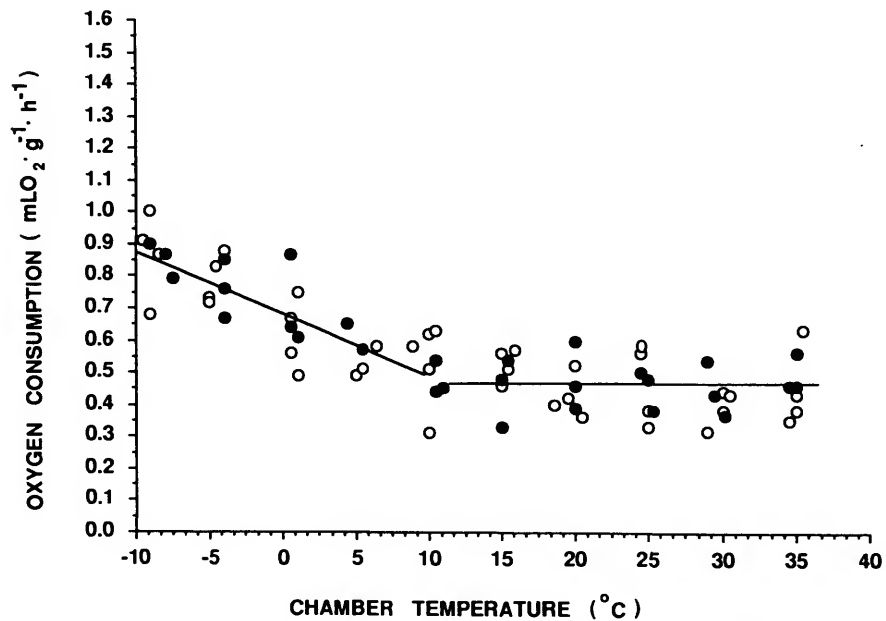


FIGURE 3.—Relationship between oxygen consumption and chamber air temperature for raccoons in winter: captive females, open circles; captive males, closed circles. Solid sloping line represents regression of oxygen consumption on chamber air temperature for males and females, and the horizontal line, basal metabolism for males and females.



for  $C_{mw}$ , and  $0.0246 \pm 0.0019$  for  $C_{md}$  (Table 3). These summer conductances were 49% higher ( $p < 0.005$ ) than those calculated for winter females ( $0.0172 \pm 0.0023$ , and  $0.0161 \pm 0.0027$  for  $C_{mw}$  and  $C_{md}$ , respectively; Table 3).  $C_{mw}$  and  $C_{md}$  were not different from each other in either summer or winter, which indicated that in both seasons evaporative water loss contributed very little to heat dissipation at temperatures below  $T_n$ . Comparisons of thermal conductances calculated on the basis of metabolic body size (Mellen, 1963) gave the same results.

#### EVAPORATIVE WATER LOSS

Evaporative water loss increased as chamber temperature increased in both summer and winter (Figures 4, 5). In summer, the pattern of increase was different for females and males. Polynomial regressions for trapped and captive males produced equations that describe a concave relationship between  $T_a$  and evaporative water loss, whereas the equation for females describes a sigmoid curve (Table 4; Figure 4). For females, water loss increased rapidly at temperatures above 25°C (Figure 4). The intercepts and coefficients of the  $X$ ,  $X^2$ , and  $X^3$  terms of the polynomial regression equations (Table 4) were compared (t-tests) to determine if they differed from each other.

The coefficients in the equation for trapped males differed from those for captive females in the  $X^2$  ( $p < 0.05$ ) and  $X^3$  ( $p < 0.025$ ) terms. The intercept and coefficients of the equation for captive males, however, were not different from those for either captive females or trapped males. Although this lack of difference is understandable in the case of trapped males, where the shape of the two curves is similar (concave), it is not so clear for the sigmoid curve of captive females (Figure 4). Perhaps the lack of difference in this case is simply due to the small number of observations available for captive males ( $n = 10$ ; Table 4). Nonetheless, in summer at 35°C, both captive and trapped males relied less on evaporative cooling than did captive females (Figure 4).

In winter, males and females had similar rates of evaporative water loss across the full range of temperatures tested (Figure 5). Therefore, data for both sexes were combined. The intercept and coefficients of this equation (Table 4) did not differ from those for summer females, but they did differ from those in the regression for trapped males in the  $X^2$  ( $p < 0.05$ ) and  $X^3$  ( $p < 0.025$ ) terms. As was the case for females in summer, rates of water loss for winter animals increased most rapidly at temperatures above 25°C (Figure 5).

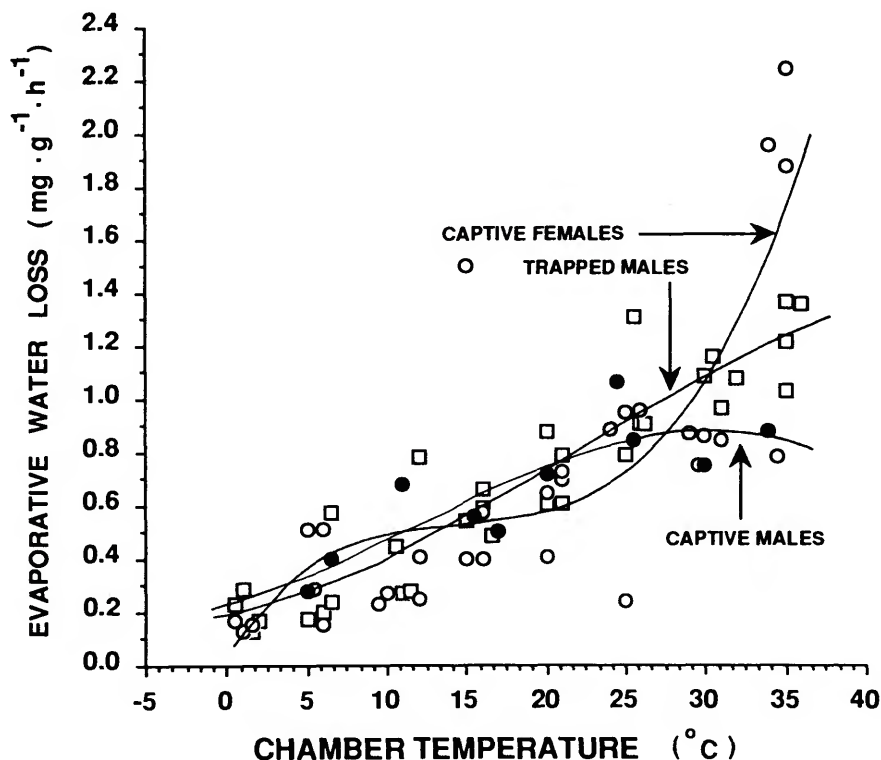


FIGURE 4.—Relationship between evaporative water loss and chamber air temperature for raccoons in summer: captive females, open circles; captive males, closed circles; trapped males, open squares. Lines represent polynomial regressions of evaporative water loss on chamber air temperature.

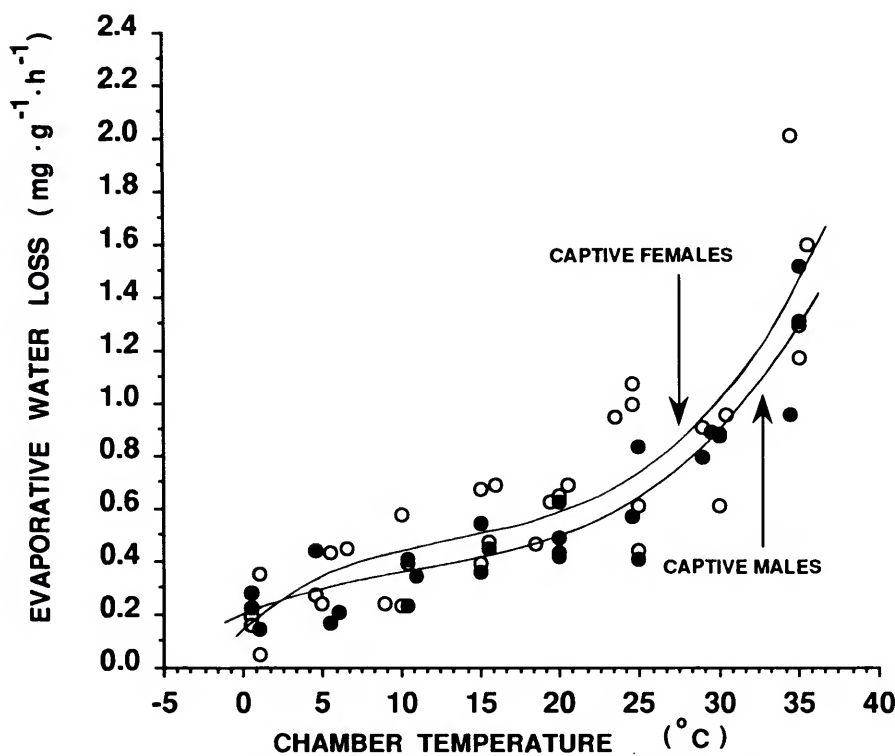


FIGURE 5.—Relationship between evaporative water loss and chamber air temperature for raccoons in winter: captive females, open circles; captive males, closed circles. Lines represent polynomial regressions of evaporative water loss on chamber air temperature.

TABLE 4.—Polynomial regression equations describing evaporative water loss ( $\text{mg} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) of *Procyon lotor* in summer and winter ( $X$  = chamber temperature ( $^{\circ}\text{C}$ ),  $Y$  = evaporative water loss,  $n$  = number of observations,  $R^2$  = coefficient of determination, and  $\text{SEE}$  = standard error of estimate).

Season and sex	Equation	(n)	$R^2$
Summer			
Trapped male	$Y = 0.1899 + 0.0114 \cdot X + 0.0011 \cdot X^2 - 0.00002 \cdot X^3$	(32)	0.86
SEE	0.0885 0.0223 0.0015 0.00003		
Captive male	$Y = 0.2174 + 0.0192 \cdot X + 0.0009 \cdot X^2 - 0.00003 \cdot X^3$	(10)	0.73
SEE	0.3983 0.0834 0.0048 0.00008		
Captive female	$Y = 0.0127 + 0.0943 \cdot X - 0.0060 \cdot X^2 + 0.00013 \cdot X^3$	(31)	0.64
SEE	0.2218 0.0547 0.0036 0.00006		
Winter			
Captive, both sexes	$Y = 0.1550 + 0.0426 \cdot X - 0.0025 \cdot X^2 + 0.00006 \cdot X^3$	(57)	0.80
SEE	0.0734 0.0192 0.0013 0.00002		

## THERMOREGULATION AT LOW TEMPERATURES

### Body Temperature

Body temperatures in Figure 6 are those recorded during metabolic measurements from animals equipped with surgi-

cally implanted, temperature-sensitive radio transmitters. Each point was recorded during the lowest level of oxygen consumption at each  $T_a$ . In both summer and winter,  $T_b$ 's were lowest during metabolic measurements at  $T_a$ 's around  $T_{lc}$ . At  $T_a$ 's below  $T_{lc}$ ,  $T_b$ 's increased (Figure 6), which is an unusual

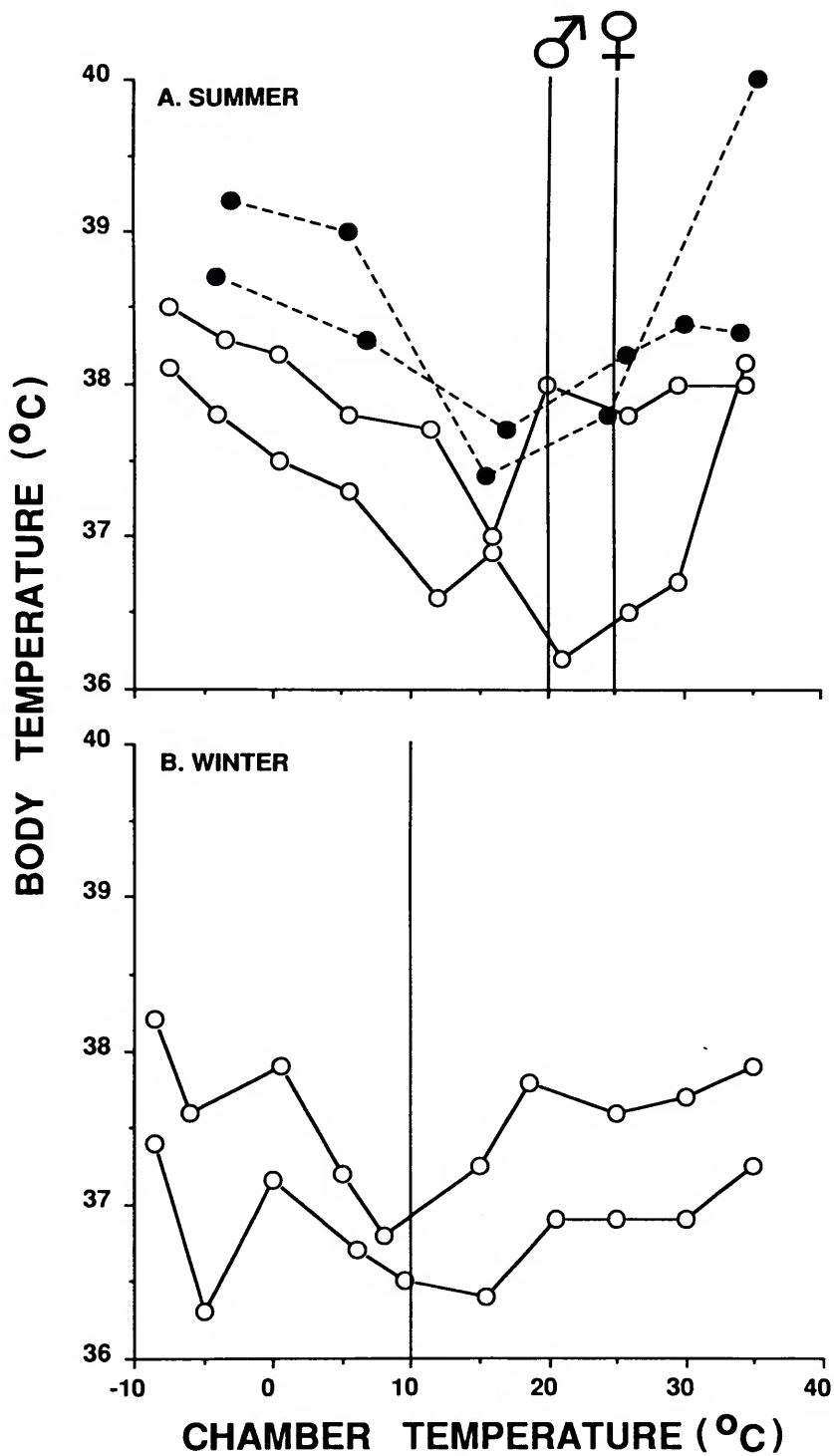


FIGURE 6.—Relationship between body temperature and chamber air temperature in summer (panel A), and winter (panel B); captive females, open circles and solid lines; captive males, solid circles and dashed lines. Solid vertical lines represent lower critical temperatures.

TABLE 5.—Regression equations describing oxygen consumption ( $\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) of *Procyon lotor* at temperatures below their lower critical temperature ( $I = x$ -intercept ( $^{\circ}\text{C}$ ),  $n$  = number of observations,  $R^2$  = coefficient of determination, SEE = standard error of estimate for the  $y$ -intercept ( $a$ ) and slope ( $b$ ),  $X$  = chamber temperature ( $^{\circ}\text{C}$ ), and  $Y$  = oxygen consumption).

Season and sex	Equation	(n)	$R^2$	SEE		$I$
				a	b	
Summer						
Trapped male	$Y = 1.09 - 0.0281 \cdot X$	(30)	0.64	0.0353	0.0040	38.8
Captive male	$Y = 0.97 - 0.0258 \cdot X$	(12)	0.91	0.0235	0.0025	37.6
Captive female	$Y = 1.04 - 0.0251 \cdot X$	(29)	0.78	0.0288	0.0026	41.1
Winter						
Captive, both sexes	$Y = 0.68 - 0.0193 \cdot X$	(36)	0.68	0.0157	0.0023	35.2

response. Under similar conditions, other procyonids either maintain a nearly constant  $T_b$  or allow it to fall slightly (Müller and Kulzer, 1977; Chevillard-Hugot et al., 1980; Müller and Rost, 1983; Chevalier, 1985). For our raccoons, confinement in the metabolism chamber at low temperatures must have stimulated a greater than necessary increase in metabolic rate such that heat production exceeded heat loss, which caused  $T_b$  to become elevated.

#### Summer

During summer,  $T_{lc}$  for male raccoons was  $20^{\circ}\text{C}$ , whereas for females it was  $25^{\circ}\text{C}$  (Figure 2). Regression equations calculated to describe oxygen consumption at  $T_a$ 's below  $T_{lc}$  are presented in Table 5. For three groups of summer animals, slopes of regressions are identical. This indicates that minimum conductances of these three groups were equivalent. Intercepts of these equations are different, which suggests a difference in metabolic cost of thermoregulation between these groups (Figure 2); captive males had a lower intercept than either trapped males ( $p < 0.005$ ) or captive females ( $p < 0.05$ ), but there was no difference in intercepts of captive females and trapped males. These regression equations, therefore, also were derived using values of oxygen consumption expressed in terms of metabolic body mass (Mellen, 1963). Relationships between intercepts of these equations are different than those for regressions in Table 5. Intercept for females was intermediate to, and not different from, those of the two groups of males. However, captive males still had a lower intercept than trapped males ( $p < 0.025$ ). Thus, in summer, thermoregulatory metabolism was less expensive for captive than for trapped males, and in spite of a  $5^{\circ}\text{C}$  difference in their  $T_{lc}$ 's (Figure 2), captive males and females had similar thermoregulatory costs.

Regression lines for three groups of animals in summer extrapolate to zero metabolism at values equivalent to, or greater than, normal  $T_b$ ;  $38.8^{\circ}\text{C}$  for trapped males,  $37.6^{\circ}\text{C}$  for captive males, and  $41.1^{\circ}\text{C}$  for captive females (Table 5). Thus, all three groups had minimized thermal conductance at  $T_a$ 's below  $T_{lc}$  (Scholander et al., 1950b; McNab, 1980b). Minimum wet thermal conductance calculated for raccoons in summer

with Eq. 4 (Table 3) is numerically similar to these "slope" values (Table 5), and it was, therefore, considered to be the best estimate of  $C_{mw}$  for *Procyon lotor* during that season ( $0.0256 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot ^{\circ}\text{C}^{-1}$ ).

#### Winter

During winter  $T_{lc}$  for both sexes decreased to  $11^{\circ}\text{C}$  (Figure 3). Regression equations of thermoregulatory metabolism for males and females in winter are not different from each other in either slope or intercept. These data, therefore, were combined into a single equation (Table 5). Slope and intercept of this equation are both lower ( $p < 0.005$  and  $p < 0.05$ , respectively) than those for summer animals (Table 5). Identical results were obtained from comparisons using regressions derived from oxygen consumption expressed in terms of metabolic body mass (Mellen, 1963). Thermoregulatory costs at any temperature below  $20^{\circ}\text{C}$  were lower for winter than summer animals (Figures 2, 3).

The regression line for *Procyon lotor* in winter (Table 5) extrapolates to zero metabolism at  $35.2^{\circ}\text{C}$ , which is below normal  $T_b$  (Figures 6, 7). This suggests that not all raccoons measured in winter minimized thermoregulatory metabolism or conductances at  $T_a$ 's below  $T_{lc}$  (Scholander et al., 1950b; McNab, 1980b). To assess this possibility, data for these animals were divided into three groups: (A) females with radio transmitters, (B) females without radio transmitters, and (C) males (Table 6). Regression equations of metabolism below  $T_{lc}$

TABLE 6.—Regression equations describing oxygen consumption ( $\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) of *Procyon lotor* at temperatures below their lower critical temperature in winter (A = females with radio transmitters, B = females without radio transmitters, C = males,  $I = x$ -intercept ( $^{\circ}\text{C}$ ),  $n$  = number of observations,  $R^2$  = coefficient of determination,  $X$  = chamber temperature ( $^{\circ}\text{C}$ ), and  $Y$  = oxygen consumption).

Group	Equation	(n)	$R^2$	$I$
A	$Y = 0.63 - 0.0158 \cdot X$	(10)	0.66	40.1
B	$Y = 0.72 - 0.0226 \cdot X$	(11)	0.71	32.1
C	$Y = 0.69 - 0.0200 \cdot X$	(15)	0.79	34.7

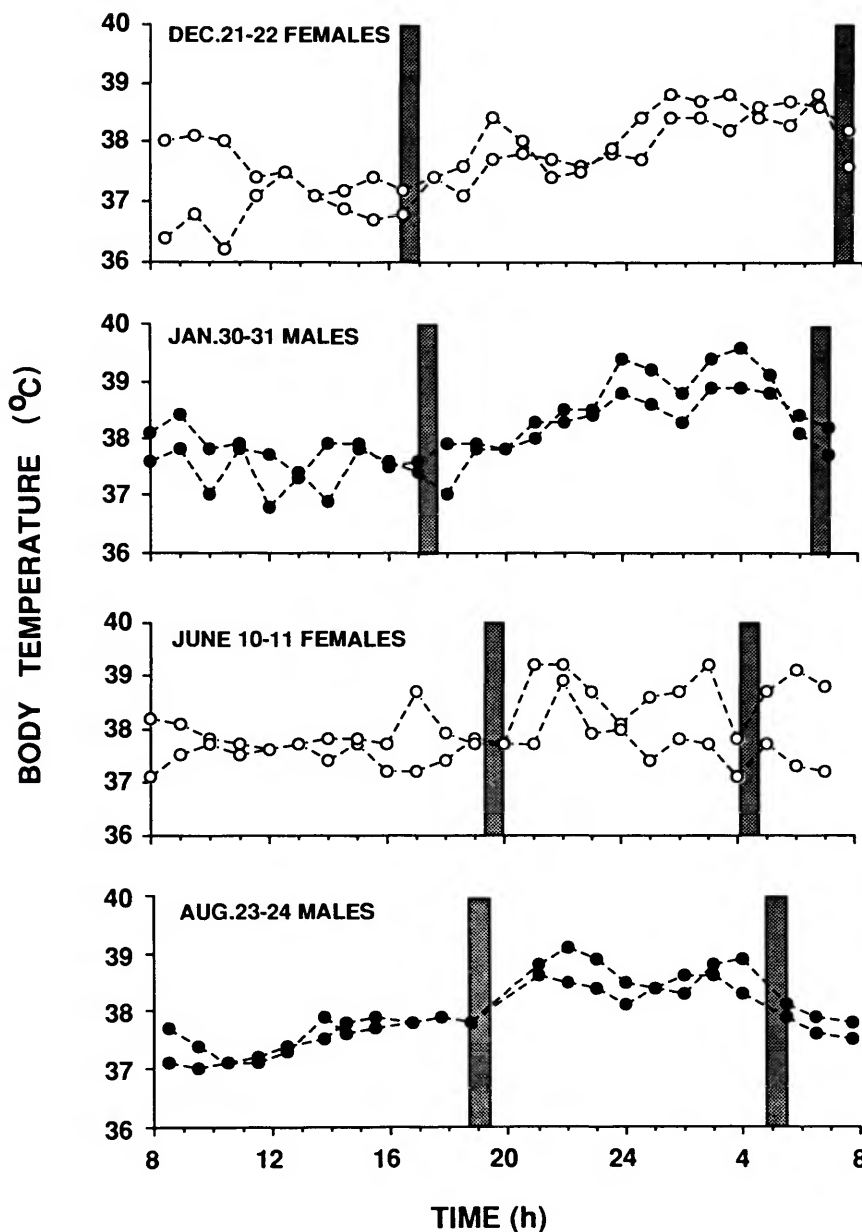


FIGURE 7.—Relationship between body temperature and time of day at various months of the year: captive females, open circles; captive males, closed circles. Vertical cross-hatched areas represent civil twilight.

were derived for each group, and based on extrapolated  $T_b$ 's at zero metabolism, only the two females with implanted radio transmitters (group A) minimized thermoregulatory metabolism and conductance. Had animals in groups B and C also minimized their thermal conductances, while retaining their measured metabolic rates, their rates of heat production would

have been disproportionately higher than their rates of heat loss. Equation 4 predicts that under these conditions their body temperatures would have been elevated to 42.0°C and 40.4°C, respectively. Thus, in order to avoid such a large increase in body temperature, animals in groups B and C increased their thermal conductances in preference to lowering their metabolic

rates. The regression equation of thermoregulatory metabolism for all winter animals (Table 5), therefore, overestimates minimum metabolic cost of temperature regulation below  $T_{lc}$ , and its slope underestimates  $C_{mw}$ . Consequently, the best estimate of  $C_{mw}$  for *Procyon lotor* in winter is the value calculated for group A animals with Eq. 4 ( $0.0172 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$ ; Table 3), and the minimum cost of thermoregulatory metabolism at any  $T_a$  below  $T_{lc}$  is best estimated by substituting this value into Eq. 4 and solving for  $\dot{H}_r$ .

## THERMOREGULATION AT HIGH TEMPERATURES

### Body Temperature

In both summer and winter,  $T_b$ 's increased during metabolic measurements at  $T_a$ 's above  $T_{lc}$  (Figure 6). This response also was seen during metabolic measurements conducted on other procyonids (Müller and Kulzer, 1977; Chevillard-Hugot et al., 1980; Müller and Rost, 1983; Chevalier, 1985).

### Summer

During summer our data suggested that the upper critical temperature ( $T_{uc}$ ) was higher than  $35^\circ\text{C}$ . The lowest rates of oxygen consumption at  $T_a = 35^\circ\text{C}$  occurred after 1.5 to 2.5 hours of exposure to that temperature. Prolonged exposure to this temperature in summer did not make animals restless, and their rate of oxygen consumption was very stable throughout each measurement. Body temperature responses at  $T_a = 35^\circ\text{C}$  were recorded from two males and two females that had implanted radio transmitters. With the exception of one male,  $T_b$ 's were maintained near  $38^\circ\text{C}$  (Figure 6). The one exception (a male) maintained its  $T_b$  at  $39.3^\circ\text{C}$ . At  $T_a = 35^\circ\text{C}$ , summer males had rates of evaporative water loss that were lower than those of summer females (Figure 4). At this temperature, males dissipated  $35\% \pm 6\%$  and females  $56\% \pm 18\%$  of their metabolic heat via evaporative water loss. Thus, at  $T_a = 35^\circ\text{C}$ , males must have utilized modes of heat transfer other than evaporative cooling (convective and conductive heat transfer) to a greater extent than females.

### Winter

Body temperature, evaporative water loss, and metabolic data indicated that, in winter,  $T_{uc}$  was very close to  $35^\circ\text{C}$ . In winter, the lowest level of oxygen consumption was recorded during the first hour after the chamber had reached  $T_a = 35^\circ\text{C}$ . Unlike summer, animals became restless after the first hour at  $35^\circ\text{C}$ , at which point their oxygen consumption increased and showed a high degree of variability. Body temperature responses at  $35^\circ\text{C}$  were recorded from both females that had implanted radio transmitters. In one case,  $T_b$  rose from  $37.9^\circ\text{C}$  at the end of the first hour to  $40.5^\circ\text{C}$  by the end of the second hour, and as it did not show signs of leveling off, we terminated

the experiment. We exposed that same animal to  $T_a = 35^\circ\text{C}$  one other time during winter. In that instance, its  $T_b$  rose to  $40.0^\circ\text{C}$  during the first 30 minutes and was maintained at that level for three hours with no apparent distress. The other female elevated its  $T_b$  from  $37.3^\circ\text{C}$  to  $39.0^\circ\text{C}$  during the second hour at  $T_a = 35^\circ\text{C}$  and maintained its  $T_b$  at that level for two hours. Thus, during winter, prolonged exposure to  $T_a = 35^\circ\text{C}$  stimulated more of an increase in  $T_b$  than it did in summer. During winter, both males and females increased evaporative water loss at  $T_a = 35^\circ\text{C}$  (Figure 5) but only to the extent that they dissipated  $35\% \pm 10\%$  of their metabolic heat production. Thus, even in winter, convective and conductive heat transfers were still the most important modes of heat loss at this temperature.

## DAILY CYCLE OF BODY TEMPERATURE

The daily cycle of raccoon  $T_b$ 's during summer and winter are presented in Figure 7. In general,  $T_b$ 's showed a marked circadian cycle in phase with photoperiod.  $T_b$ 's rose above  $38^\circ\text{C}$  for several hours each night but remained below  $38^\circ\text{C}$  during daytime. During summer, with the exception of one female whose record was not typical (Figure 7),  $T_b$ 's rose above  $38^\circ\text{C}$  shortly after sunset, whereas in winter  $T_b$ 's did not rise above  $38^\circ\text{C}$  until several hours after sunset. Once  $T_b$  was elevated it usually remained so until just before or after sunrise (Figure 7). During summer,  $T_b$  was above  $38^\circ\text{C}$  for 85% or more of the time between sunset and sunrise (87% for the female with the typical body temperature pattern, and 85% and 98% for males), whereas in winter it was elevated for only 47%–78% of the time between sunset and sunrise (47% and 61% for females, and 67% and 78% for males). During night,  $T_b$  would oscillate between  $38^\circ\text{C}$  and about  $39^\circ\text{C}$ , such that two peak values occurred. These peak values presumably corresponded to two periods of heightened nighttime activity. During summer, one of these peaks occurred before and the other after 24:00 hours, whereas in winter both peaks occurred after 24:00 hours. With the exception of one female in winter (Figure 7), the lowest  $T_b$  of the day for both sexes was near  $37^\circ\text{C}$ , and this typically occurred during daytime (Figure 7).

## Discussion

### BASAL METABOLIC RATE

#### Background

Basal metabolism represents the minimum energy required by a mammal to maintain endothermy and basic homeostasis (Lusk, 1917:141; Kleiber, 1932, 1961:251; Benedict, 1938: 191–215; Brody, 1945:59; Robbins, 1983:105–111). Mammals with lower than predicted  $\dot{H}_b$  maintain endothermy and enjoy its attendant advantages at a discount, whereas others, with rates that are higher than predicted, pay a premium

(Calder, 1987). Such variation in  $\dot{H}_b$  appears to be tied to ecological circumstances rather than taxonomic affinities (Vogel, 1980; McNab, 1986a, 1988a, 1989), and depending on environmental conditions, each rate provides an individual with various advantages and limitations. During the course of evolution, therefore, each species'  $\dot{H}_b$  evolves to provide it with the best match between its energy requirements for continuous endothermy, its food supply, and the thermal characteristics of its environment.

#### Captive versus Wild Raccoons

Male raccoons trapped in summer had higher  $\dot{H}_b$ 's than our captive animals in any season (Table 2). The higher rate of metabolism of these trapped males could have been due to the stress of captivity or to the fact that "wild" animals actually may have higher metabolic rates than those that have adjusted to captivity. If the latter is true, then our data for captive animals underestimated the actual energy cost of maintenance metabolism for *Procyon lotor* in the wild. At present, we have no way of determining which of these alternatives is true.

#### Seasonal Metabolism of Raccoons

In some temperate-zone mammals,  $\dot{H}_b$  is elevated in winter, which presumably increases their "cold-hardiness." Conversely, lower summer metabolism is considered to be a mechanism that reduces the potential for heat stress. Such seasonal variation in  $\dot{H}_b$  has been found in several species: collard peccary, *Tayassu tajacu* (Zervanos, 1975); antelope jackrabbit, *Lepus alleni* (Hinds, 1977); desert cottontail, *Sylvilagus audubonii* (Hinds, 1973); and, perhaps, cold-acclimatized rat, *Rattus norvegicus* (Hart and Heroux, 1963). Unlike these species, our captive raccoons showed no seasonal variation in  $\dot{H}_b$  (Table 2). Instead, raccoons achieved "cold-hardiness" in winter and reduced their potential for heat stress in summer with a large seasonal change in thermal conductance (Table 3).

#### Comparison of *Procyon lotor* with Other Procyonids

*Procyon lotor* has a much higher mass-specific  $\dot{H}_b$  than other procyonids (Table 7). To quantify the magnitude of this difference, we compared the measured value for *Procyon lotor*

TABLE 7.—Metabolic characteristics of several procyonid species.

Species	Body mass (g)	Basal <sup>a</sup> metabolism		Minimum <sup>b</sup> conductance		T <sub>b</sub> <sup>c</sup>		T <sub>n</sub> <sup>d</sup>		References
		Meas	H <sub>br</sub>	Meas	C <sub>mwr</sub>	α	ρ	T <sub>lc</sub>	T <sub>uc</sub>	
<i>Bassariscus astutus</i>	865	0.43	0.68	0.0288 <sup>e</sup>	0.85	37.6	23	35.5		Chevalier (1985)
<i>Procyon cancrivorus</i>	1160	0.40	0.69	0.0368 <sup>e</sup>	1.25			26		Scholander et al. (1950b,c)
<i>Potos flavus</i>	2030	0.36	0.51							McNab (1978a)
<i>Potos flavus</i>	2400	0.32	0.65			38.1	36.0	23	30	Müller and Kulzer (1977)
<i>Potos flavus</i>	2600	0.34	0.71	0.0200 <sup>f</sup>	1.02			23	33	Müller and Rost (1983)
<i>Nasua nasua</i>	3850	0.26	0.60	0.0200 <sup>f</sup>	1.24	38.3	36.4	25	33	Chevillard-Hugot et al. (1980)
<i>Nasua nasua</i>	4847	0.33	0.79	0.0238 <sup>e</sup>	1.65	39.1	37.9	30	35	Mugaas et al. (in prep.)
<i>Nasua narica</i>	5554	0.25	0.62	0.0208 <sup>e</sup>	1.55	38.9	37.4	25	35	
<i>Nasua narica</i>	4150	0.42	1.20	0.0341 <sup>e</sup>	2.20					Scholander et al. (1950b,c)
				0.0224 <sup>g</sup>	1.45					
<i>Procyon lotor</i>										This study
Summer										
Trapped male	4400	0.54	1.28					20		
Captive male	4790	0.46	1.07	0.0256 <sup>f</sup>	1.77	38.4	37.5	20		
Captive female	4670	0.42	1.02	0.0256 <sup>f</sup>	1.79	38.2	37.6	25		
Winter										
Captive male	5340	0.47	1.17			38.6	37.6	11		
Captive female	4490	0.46	1.10	0.0172 <sup>f</sup>	1.15	38.3	37.3	11		

<sup>a</sup> Meas is measured basal metabolism (mL O<sub>2</sub>·g<sup>-1</sup>·h<sup>-1</sup>). H<sub>br</sub> is the ratio of measured to predicted basal metabolism where the predicted value is calculated from  $\dot{H}_b = 3.42 \cdot m^{-0.25}$  (Kleiber, 1932, 1961:206) and m is body mass in grams.

<sup>b</sup> Meas is measured minimum thermal conductance (mL O<sub>2</sub>·g<sup>-1</sup>·h<sup>-1</sup>·°C<sup>-1</sup>). C<sub>mwr</sub> is the ratio of measured to predicted minimum thermal conductance where the predicted value is calculated from C<sub>m</sub> = 1.0·m<sup>-0.5</sup> (McNab and Morrison, 1963; Herreid and Kessel, 1967), and m is body mass in grams.

<sup>c</sup> T<sub>b</sub> is body temperature during the active (α) and rest (ρ) phases of the daily cycle (°C).

<sup>d</sup> T<sub>n</sub> is the thermoneutral zone as defined by the lower (T<sub>lc</sub>) and upper (T<sub>uc</sub>) critical temperatures (°C).

<sup>e</sup> Conductance calculated as the slope of the line describing oxygen consumption at temperatures below the lower critical temperature.

<sup>f</sup> Conductance calculated from C<sub>mwr</sub> =  $\dot{H}_r / (T_b - T_2)$ , where  $\dot{H}_r$  is resting metabolic rate at temperatures below T<sub>lc</sub>, and other symbols are as described elsewhere.

<sup>g</sup> Inactive-phase thermal conductance: estimated from Scholander et al. (1950b), assuming that active-phase thermal conductance is 52% higher than values determined during the inactive phase (Aschoff, 1981).

with one calculated for it from a mass-specific least-squares regression equation (Eq. 6;  $R^2 = 0.78$ ) derived from data for those procyonids with lower than predicted  $\dot{H}_b$ : *Potos flavus*, *Procyon cancrivorus*, *Nasua nasua*, *Nasua narica*, and *Bassariscus astutus* (Table 7).

$$\dot{H}_b = 2.39 \cdot m^{0.25} \quad \text{Eq. 6}$$

$\dot{H}_b$  in Eq. 6 is basal metabolism ( $\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) and  $m$  is body mass (g). Measured values of  $\dot{H}_b$  for *Procyon lotor* were 1.45 to 1.86 times greater than those predicted for it by Eq. 6 (Table 8).

#### Influence of Diet on Basal Metabolism

BACKGROUND.—With respect to  $\dot{H}_b$ , McNab (1986a:1) maintains that “the influence of climate is confounded with the influence of food habits,” and that departures from the Kleiber (1961) “norm” are best correlated with diet. Although this does appear to be the case for diet specialists, the analysis is not so clear-cut for omnivorous species (McNab, 1986a). His analysis also indicates that an animal’s “behavior” (i.e., whether it is terrestrial, arboreal, subterranean, aquatic, etc.), secondarily modifies the influence of food habits on  $\dot{H}_b$ . For example,

TABLE 8.—Basal metabolism ( $\text{mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ) of *Procyon lotor* as predicted by Eq. 6 ( $\dot{H}_b = 2.39 \cdot m^{0.25}$ ). Body masses, used to calculate predicted values, and measured values were taken from Table 7.

Season and sex	Predicted	Measured/Predicted
Summer		
Trapped male	0.29	1.86
Captive male	0.29	1.59
Captive female	0.29	1.45
Winter		
Captive male	0.28	1.68
Captive female	0.29	1.59

terrestrial frugivores have  $\dot{H}_b$ 's that are very near predicted values, whereas arboreal frugivores have rates that are much lower than predicted (McNab, 1986a).

FOOD HABITS OF PROCYONIDS.—Food habits of six procyonids for which metabolic data are available are presented in Table 9. All six species clearly have mixed diets. Compared to other species, *Procyon lotor* is highly catholic in its diet, taking food from almost twice as many categories as *Nasua narica*, three times as many as *Procyon cancrivorus*, *Nasua nasua*, and *Bassariscus astutus*, and nine times as many as *Potos flavus*.

TABLE 9.—Food habits of some Procyonids. References for foods were as follows: *Potos flavus*, *Procyon cancrivorus*, and *Nasua nasua* taken from Bisbal (1986); *Nasua narica* taken from Kaufmann (1962:182–198); *Bassariscus astutus* taken from Martin et al. (1951), Taylor (1954), Wood (1954), Towell and Teer (1977), and Trapp (1978); *Procyon lotor* taken from Hamilton (1936), Stuewer (1943:218–220), Stains (1956:39–51), and Greenwood (1981). Symbols represent either qualitative ( $\equiv$ ) or quantitative (+,†) assessments of feeding habits:  $\equiv$  indicates that the animal was observed eating the food; + and † represent volume and frequency, respectively, of food utilization. No attempt was made to account for seasonal variation in the use of these foods.  
 + <20% by volume when found. † 1%–19% frequency of occurrence.  
 ++ >20% by volume when found. †† 20%–50% frequency of occurrence.  
 ††† >50% frequency of occurrence.

Food	<i>Potos flavus</i>	<i>Procyon cancrivorus</i>	<i>Nasua nasua</i>	<i>Nasua narica</i>	<i>Bassariscus astutus</i>	<i>Procyon lotor</i>
Mammalia			+ †	$\equiv$	++ †††	++ ††
Aves					++ †	+ ††
Birds' eggs						†††
Reptilia		+ †	+ †††	$\equiv$	+ †	+ †
Amphibia		+ †		$\equiv$		+ †
Pices		++ ††				++ ††
Insecta	++ †	+ †††	++ †††	$\equiv$	+ ††	++ ††
Arachnida			++ †††	$\equiv$	+ †	+ †
Chilopoda			++ †††			
Diplopoda				$\equiv$		+ †
Crustacea		++ †††		$\equiv$		++ †††
Mollusca		+ ††		$\equiv$		+ ††
Annelida				$\equiv$		+ †
Nuts						++ ††
Grains						++ ††
Buds						+ †
Fruit	++ †††		++	$\equiv$	††	++ †††
Leaves						+ †
Grass						+ †



For those species for which food habit data are quantified, we used Eisenberg's (1981:247–251) substrate/feeding matrix method, where "substrate" is analogous to McNab's (1986a) "behavior," to construct the following feeding categories that are based on the major food groups utilized by each species (Table 9).

1. *Potos flavus*: (1) arboreal/frugivore, insectivore.
2. *Procyon cancrivorus*: (1) semiaquatic/crustacevore, molluscivore, insectivore, piscivore, carnivore.
3. *Nasua nasua*: (1) terrestrial/insectivore, arachnidivore, carnivore, frugivore.
4. *Bassariscus astutus*: (1) terrestrial/carnivore, insectivore, frugivore.
5. *Procyon lotor*: (1) terrestrial/carnivore, granivore, frugivore, insectivore; and (2) semiaquatic/crustacevore, molluscivore, insectivore, piscivore, carnivore.

**FOOD HABITS AND BASAL METABOLISM.**—The most important foods in the diet of *Procyon lotor* are vertebrates, nuts, seeds, and fruits (Table 9). These are the same foods that are eaten by those dietary specialists that have  $\dot{H}_b$ 's equivalent to, or higher than, values predicted for them by the Kleiber equation (McNab, 1986a). The most important foods in the diets of *Potos flavus*, *Procyon cancrivorus*, and *Nasua nasua* are invertebrates and fruit (Table 9), and these foods are eaten by dietary specialists that have lower than predicted  $\dot{H}_b$ 's (McNab, 1986a). Major foods in the diet of *Bassariscus astutus* are terrestrial vertebrates, insects, and fruit (Table 9). Dietary specialists that eat terrestrial vertebrates have higher than predicted  $\dot{H}_b$ 's, whereas those that feed on insects have  $\dot{H}_b$ 's that are lower than predicted (McNab, 1986a). Year-round utilization of vertebrates by *Bassariscus astutus* suggests that it also should have a metabolic rate that is equivalent to or higher than predicted, rather than lower (McNab, 1986a). However, perhaps year-round inclusion of insects in its diet (Martin et al., 1951; Taylor, 1954; Wood, 1954; Toweill and Teer, 1977; Trapp, 1978), plus water- and energy-conserving advantages of a low metabolic rate, each exert a stronger selective influence on  $\dot{H}_b$  than do vertebrates in its diet.

**SUMMARY.**—The basal metabolic rate of these procyonids does appear to be influenced by diet. But, it is apparent from this family's evolutionary history and tropical origins that climate also has had a profound influence on its member's metabolism. The history of the family and the data presented here (Table 7) suggest that lower than predicted  $\dot{H}_b$  is a feature that evolved very early as the primary metabolic adjustment to a tropical climate. From this perspective, it could be argued that climate would have been the major selective force determining  $\dot{H}_b$ , whereas food habits would have had a secondary influence.

#### *Basal Metabolism and Intrinsic Rate of Natural Increase*

**BACKGROUND.**—McNab (1980a) suggested that if food is not restricted during an animal's reproductive period, the factor

that will limit growth and reproduction will be the rate at which energy can be used in growth and development. Under these conditions, an increase in  $\dot{H}_b$  would actually increase  $r_{\max}$  because it would provide a higher rate of biosynthesis, a faster growth rate, and a shorter generation time. Hennemann (1983) tested McNab's (1980a) premise and found a significant correlation between  $r_{\max}$  and metabolic rate, independent of body size, for 44 mammal species. A low correlation coefficient for this relationship, however, indicated to him (Hennemann, 1983) that factors such as (1) food supply, (2) thermal characteristics of the environment, and (3) brain size also contribute toward shaping a species' reproductive potential, particularly when these factors strongly influence rates of biosynthesis or growth or for some reason alter generation time. Results of our estimates of  $r_{\max}$  for procyonids are presented in Table 10.

*Procyon lotor.*—This species had the highest  $\dot{H}_b$  and  $D_b$ , and also had the highest  $r_{\max}$  (1.34; Table 10). Such a high  $r_{\max}$  may infer that this trait evolved under conditions where food and temperature were not limiting to reproduction. Under these conditions selection could have favored those reproductive characteristics sensitive to a higher  $\dot{H}_b$  (biosynthesis, growth, and generation time; McNab, 1980a). *Procyon lotor*'s high reproductive potential is due to its early age of first female reproduction and its large litter size, characteristics that may reflect metabolically driven increases in both biosynthesis and growth.

*Bassariscus astutus.*—This species has a low  $\dot{H}_b$  but an  $r_{\max}$  that was 124% of expected (Table 10). This suggests that  $r_{\max}$  evolved under conditions where food and temperature were not limiting to reproduction. Reduced litter size should restrict this species' reproductive potential and may be a reflection of its low  $\dot{H}_b$ . The factor that is responsible for increasing its reproductive potential, however, is its early age of first female reproduction. *Bassariscus astutus* is the smallest of these procyonids, and even though it has a low  $\dot{H}_b$ , its small mass may contribute to its ability to reach adult size and sexual maturity in its first year. The high quality of its diet (a high proportion of small vertebrates; Table 9) also may be a factor that is permissive to early female reproduction. Thus, small body size and diet may be factors that have allowed this species to evolve a higher than expected reproductive potential in spite of its low  $\dot{H}_b$ .

*Nasua narica.*—This species is one of the largest procyonids (Table 7), and it possesses characteristics that should limit its reproductive potential: lower than predicted  $\dot{H}_b$  (Table 7), a relatively low-quality diet (Kaufmann, 1962:182–198; Table 9), and delayed time of first reproduction (Table 10). In spite of this, *Nasua narica* has a higher than expected  $r_{\max}$  (111% of predicted; Table 10). The life history feature that enhances *Nasua narica*'s reproductive potential, and increases  $r_{\max}$  beyond expected, is its large litter size. In this species females live in bands. Each year just before their young are born these bands break up, and each female seeks out a den for herself and

TABLE 10.—Intrinsic rate of natural increase ( $r_{\max}$ ) of several procyonids. (a = potential age of females producing first young; b = potential annual birth rate of female young (= average litter size/2; average litter size was calculated from the published range of litter sizes for each species); n = potential age of females producing their final young;  $r_{\max e}$  = intrinsic rate of natural increase expected from body mass (Hennemann, 1983);  $r_{\max r}$  = ratio of calculated to expected intrinsic rate of natural increase ( $r_{\max}/r_{\max e}$ .)

Species	Body mass (g)	a	b	n	$r_{\max}$	$r_{\max e}^*$	$r_{\max r}^\dagger$	References
<i>Procyon lotor</i>	4940	0.83	2.25	16	1.34	0.53	2.52	Dunn and Chapman (1983); Eisenberg (1981:489); Kaufmann (1987); Lotze and Anderson (1979); Nowak and Paradiso (1983:981); Sanderson (1987); Stains (1956:28–31); This study
<i>Bassariscus astutus</i>	900	0.83	1.50	14	1.02	0.82	1.24	Kaufmann (1982, 1987); Nowak and Paradiso (1983:979, 980); Poglayen-Neuwall and Poglayen-Neuwall (1980); Poglayen-Neuwall and Towell (1988); Russell (1983)
<i>Nasua narica</i>	3900	2.50	2.25	14	0.62	0.56	1.11	Kaufmann (1982, 1987); Nowak and Paradiso (1983:983); Sanderson (1983)
<i>Nasua nasua</i>	3850							Chevillard-Hugot et al. (1980)
<i>Procyon cancrivorus</i>	1160	0.83	1.50	15	1.02‡	0.77	1.32	Crandall (1964:312); Poglayen-Neuwall (1987)
		1.75			0.65‡		0.84	
<i>Potos flavus</i>	2490	1.75	0.50	12	0.30	0.63	0.48	Ford and Hoffmann (1988); Nowak and Paradiso (1983:984)
<i>Bassaricyon gabbii</i>	1600	1.75	0.50	15	0.32	0.71	0.45	Eisenberg (1981:489); Nowak and Paradiso (1983:985)

\*  $r_{\max e} = 4.9 \cdot m^{0.2622}$ , where m is body mass in grams.

† Regression of  $r_{\max}$  on body mass (m). Assume  $r_{\max} = 1.02$  for *Procyon cancrivorus*:  $r_{\max} = 0.00005 \cdot m + 0.623$ ;  $R = 0.19$ ;  $R^2 = 0.03$ . Regression of  $r_{\max r}$  (Table 10) on  $H_{br}$  (Table 7); assume *Nasua nasua* has the same  $r_{\max r}$  as *Nasua narica*:  $r_{\max r} = 3.35 \cdot H_{br} - 1.11$ ;  $R = 0.93$ ;  $R^2 = 0.86$ .

‡ Estimate based on females reproducing in their first (a = 0.83) or second (a = 1.75) year.

her litter. Once the young are able to leave the den (approximately five weeks), bands reform. In this situation, females not only care for their own young but also for those of other females in the band (Kaufmann, 1962:157–159, 1982, 1987; Russell, 1983). This social structure may contribute to this species' ability to produce large litters and in this way increase its reproductive potential.

*Nasua nasua*.—Unfortunately, there is not enough reproductive data to allow calculation of  $r_{\max}$  for *Nasua nasua* (Table 10), therefore, it is not possible to compare the reproductive potential of this South American coati with its North American relative, *Nasua narica*. Given its low  $\dot{H}_b$  and relatively low-quality diet of fruit and terrestrial invertebrates (Table 9), however,  $r_{\max}$  of *Nasua nasua* may be very similar to that of *Nasua narica*.

*Procyon cancrivorus*.—The age of first female reproduction for *Procyon cancrivorus* has not been reported. However, if one assumes females can reproduce in their first year,  $r_{\max}$  for *Procyon cancrivorus* would be 1.02 (132% of expected; Table 10). If, on the other hand, first female reproduction is delayed until the second year,  $r_{\max}$  would be 0.65 (84% of predicted; Table 10). *Procyon cancrivorus* has a low  $\dot{H}_b$ , reduced litter size, and small body mass. Its low  $\dot{H}_b$  may limit litter size, but as with *Bassariscus astutus*, the quality of its diet (a high percentage of small vertebrates; Table 9) and its small body size may make it possible for females to reproduce in their first year and thus increase the species' reproductive potential. This

reasoning would argue that *Procyon cancrivorus* probably enjoys higher, rather than lower, than expected  $r_{\max}$ .

*Potos flavus*.—In addition to a low  $\dot{H}_b$ , this species possesses other characteristics that limit its reproductive potential: low-quality diet, delayed reproduction, and birth of a single young each year. Because there does not appear to be any other feature of its life history that can counteract the influence of these factors,  $r_{\max}$  in *Potos flavus* has evolved to be only 48% of expected (0.30; Table 10). Its close relative, the olingo, *Bassaricyon gabbii*, appears to share the same condition (Table 10).

SUMMARY.—This brief survey illustrates that, with the exception of *Potos flavus*, procyonids tend to have values of  $r_{\max}$  that are higher than those predicted for them on the basis of mass (Table 10). Regression analysis indicates that, within the family, body mass accounts for only a small amount (3%) of the variation in  $r_{\max}$ , whereas the positive slope of the correlation between  $r_{\max r}$  and  $H_{br}$  ( $R = 0.93$ ) suggests that low metabolism has a limiting effect on  $r_{\max}$  (see Table 10, footnote f). The implication here is that low  $\dot{H}_b$  would be associated with a lower rate of biosynthesis, a slower growth rate, and a longer generation time. Procyonids with low  $\dot{H}_b$  but higher than expected  $r_{\max}$  must possess other traits that serve to offset the effects of low metabolism. Our survey indicates that the following features compensate for low  $\dot{H}_b$  and help increase  $r_{\max}$ : (1) a high-quality diet may make biosynthesis and growth more efficient, thus optimizing the time element associated

with each of these processes; (2) larger litter sizes and cooperation in care of the young may increase survivorship in spite of a slower growth rate; and (3) an early age of first reproduction, a long reproductive life span, and moderate-size litters (two to four young) may in the long run add as many individuals to the population as a shortened generation time. Our survey also suggests that, at the other extreme, factors such as a low-quality diet, reduced litter size, absence of cooperative care of the young, delayed age of first reproduction, and shortened reproductive life span all serve to decrease  $r_{\max}$ . Thus, it is obvious that diet, litter size, social structure, reproductive strategy, and reproductive life span can operate synergistically with  $\dot{H}_b$  to magnify its influence on  $r_{\max}$  (as with *Procyon lotor* and *Potos flavus*), or they can function in opposition to  $\dot{H}_b$  to change the direction of its influence on  $r_{\max}$  (as with *Bassariscus astutus*, *Procyon cancrivorus*, *Nasua narica*, and perhaps *Nasua nasua*).

#### Basal Metabolism and Climatic Distribution

*Procyon lotor*.—The evolution of a higher  $\dot{H}_b$  (Tables 7, 8) may have been the physiological cornerstone that enabled *Procyon lotor* to break out of the mold being exploited by other procyonids and to generalize its use of habitats and climates. Once this basic physiological change was in place, selection for appropriate alterations in thermal conductance, capacity for evaporative cooling, diversity of diet, and energy storage would have provided this species with the suite of adaptations needed to extend its distribution into other habitats and climates. Support for this concept follows from the fact that high levels of  $\dot{H}_b$  are associated with (1) cold-hardiness in mammals that live in cold-temperate and arctic climates (Scholander et al., 1950c; Irving et al., 1955; Irving, 1972:115, 116; Shield, 1972; Vogel, 1980; Golightly and Ohmart, 1983); (2) the ability to utilize a wide variety of food resources and to occupy a large number of different environments and habitats (McNab, 1980a); and (3) a high intrinsic rate of natural increase (McNab, 1980a; Hennemann, 1983; Lillegraven et al., 1987; Nicoll and Thompson, 1987; Thompson, 1987).

OTHER PROCYONIDS.—Other procyonids (*Potos flavus*, *Procyon cancrivorus*, *Nasua narica*, and *Nasua nasua*) have lower than predicted  $\dot{H}_b$ 's (Table 7), a characteristic that is considered to be an energy-saving adaptation for those that live in relatively stable tropical and subtropical habitats (Müller and Kulzer, 1977; Chevillard-Hugot et al., 1980; Müller and Rost, 1983). However, *Bassariscus astutus* is found in tropical, subtropical, and temperate climates. This species is found from tropical Mexico to temperate regions of the western United States (Kaufmann, 1982, 1987; Nowak and Paradiso, 1983:979). In the northern part of its distribution, *Bassariscus astutus* lives in habitats that are unstable (arid regions), that are low in productivity, and that characteristically have marked seasonal changes in temperature. Its lower than predicted  $\dot{H}_b$  could be an important water-conserving adaptation at times when temperatures are high (McNab and Morrison, 1963;

McNab, 1966; MacMillen and Lee, 1970; Noll-Banholzer, 1979) and an important energy-conserving mechanism when cold weather may limit food availability and hunting time (Scholander et al., 1950c; Wang et al., 1973). As will be seen later, *Bassariscus astutus* is unique among procyonids with lower than predicted  $\dot{H}_b$ 's in that it also has a lower than predicted  $C_{\text{mw}}$  (Table 7). This allows it to use less energy than expected for thermoregulation at low temperatures. Another species with a similar set of adaptations (lower than predicted  $\dot{H}_b$  and  $C_{\text{mw}}$ ) is the arctic hare, *Lepus arcticus* (Wang et al., 1973), which lives in one of the coldest and least-productive regions on earth. Wang et al. (1973) suggest that this combination of adaptations allows *Lepus arcticus* to better match its energy requirements to the low productivity of its environment. A similar relationship may hold for *Bassariscus astutus*, particularly in colder arid portions of its distribution, and may be the reason that it, but not other procyonids with low  $\dot{H}_b$ 's, has been able to inhabit temperate climates.

#### MINIMUM THERMAL CONDUCTANCE

##### Background

Thermal conductance is a measure of the ease with which heat is passively transferred to or from a body through its tissues and pelt. Within  $T_n$ , a mammal is able to vary its thermal conductance over a wide range of values by changing heat transfer characteristics of both of these layers. Minimum thermal conductance occurs when total heat transfer through these layers is reduced to its lowest possible rate. This minimum value, which is the reciprocal of maximum resistance, occurs, theoretically, but not always practically (see McNab, 1988b), at the animal's  $T_{lc}$  and is best estimated under standard conditions in a metabolism chamber (McNab, 1980b; Aschoff, 1981). Minimum thermal conductance scales to body mass (McNab and Morrison, 1963; Herreid and Kessel, 1967; McNab, 1970, 1979b; Bradley and Deavers, 1980; Aschoff, 1981). Therefore, to make comparisons between species of various sizes, we scaled out body mass by expressing  $C_{\text{mw}}$  as the ratio of measured to predicted values ( $C_{\text{mw}r}$ ; Table 7). These ratios were used to make comparisons of heat-transfer characteristics between species that occupy different habitats or climates.

##### Effect of Molt on Thermal Conductance

In summer,  $T_{lc}$ 's of male and female *Procyon lotor* (Figure 2) were very similar to those of other procyonids (22°C–26°C; Table 7). In winter,  $T_{lc}$  of both sexes shifted downward to 11°C (Figure 3). This seasonal shift in  $T_{lc}$  occurred as the result of a seasonal change in minimum thermal conductance (Table 3). For many northern mammals, a seasonal change in thermal conductance is partly mediated via cyclic changes in the insulative quality of their pelt (Scholander et al., 1950a; Irving et al., 1955; Hart, 1956, 1957; Irving, 1972:165).

*Procyon lotor* begins to shed its heavy winter coat about the time its young are born. Molt progresses through summer and by late August the new coat is complete (Stuewer, 1942). During its summer molt, *Procyon lotor*'s  $C_{mw}$  increased by about 49% over the value for female raccoons in winter (Table 3). In summer, therefore, it had the highest mass specific  $C_{mw}$  of those procyonids considered ( $C_{mwr} = 1.77$  and  $1.79$ ; Table 7). An increase in thermal conductance facilitates passive heat loss for temperate and arctic species, and this serves as an important thermoregulatory adaptation during warm summer months (Scholander et al., 1950c; Irving et al., 1955; Hart, 1956, 1957; Irving, 1972:165). This adaptation is particularly important to those temperate- and arctic-zone species (including raccoons) whose  $\dot{H}_b$ 's do not decrease during summer (Irving et al., 1955). From August on, the fur of *Procyon lotor* becomes increasingly longer and heavier, with peak, or prime, condition occurring in late fall and early winter (Stuewer, 1942). Minimum conductance of our captive raccoons was lowest in winter ( $C_{mwr} = 1.15$ ) when their pelts were in prime condition (Tables 3, 7). Because "primeness" of raccoon pelts varies geographically, thicker pelts being associated with colder climates (Goldman, 1950:21; Whitney and Underwood, 1952:24-41), the degree of seasonal change in  $C_{mw}$  must also vary geographically.

The only other procyonid for which a seasonal molt has been described is *Bassariscus astutus*. Molt in this species extends from late summer to late fall (Toweill and Toweill, 1978). How molt effects thermal conductance in *Bassariscus astutus* is not known because metabolic data for this species (Table 7) apparently were collected only when their pelts were in prime condition (Chevalier, 1985).

Goldman (1950:20) reports that *Procyon cancrivorus* does not have a seasonal molt. Like other tropical procyonids, *Procyon cancrivorus* lives in an environment that has the following characteristics: high even temperatures throughout the year (1°C–13°C difference in monthly mean temperature), a greater range in temperature between day and night than in mean monthly temperature throughout the year, uniform lengths of day and night, seasonal variation in rainfall, and lowest temperatures during the rainy season(s) (Kendeigh, 1961:340). In such a stable environment there would be no advantage to a sharply defined seasonal molt cycle that could place an animal in thermoregulatory jeopardy by increasing its thermal conductance. This would be particularly true for animals like tropical procyonids that have lower than predicted  $\dot{H}_b$ 's but that maintain typical eutherian body temperatures (Table 7). Consequently, molt in all tropical procyonids may either be prolonged or continuous. This is a feature of their biology that needs to be examined in more detail.

#### Comparison of Thermal Conductances

*Procyon lotor* VERSUS TROPICAL PROCYONIDS.— $C_{mwr}$  for *Procyon lotor* in winter was 1.15, which is similar to the values for *Potos flavus* and *Procyon cancrivorus*, 1.02 and 1.25,

respectively (Table 7). These two tropical species, therefore, have  $C_{mw}$ 's that are similar on a mass specific basis to the value for *Procyon lotor* in winter. However, at their  $T_{lc}$ 's, the thermal gradient sustained by these tropical animals is only about 11°C, whereas for *Procyon lotor* in winter it was 26.5°C. Examination of Eq. 4 with respect to these thermal gradients suggests that tropical procyonids achieve such low  $C_{mw}$ 's by virtue of their lower than predicted  $\dot{H}_b$ 's rather than by having pelts that are exceptionally good insulators. In fact, the insulation afforded by the pelts of these tropical procyonids is about the same as that of the 50 g arctic lemming, *Dicrostonyx groenlandicus rubricatus*, whose coat has an insulative value that is about half that of the hare, *Lepus americanus*, red fox, *Vulpes fulva alascensis*, and pine martin, *Martes americana*, animals comparable in size to these procyonids (Scholander et al., 1950a). Therefore, pelts of these tropical procyonids do not have the same insulative value as the prime winter coat of *Procyon lotor*.

*Nasua narica* and *Nasua nasua* have tropical and subtropical distributions and they are the only procyonids that are diurnal (Kaufmann, 1962:103-105, 1982, 1987). Because they are active during the day they experience a more extreme thermal environment (higher  $T_a$ 's and solar radiation) than their nocturnal cousins. Values of  $C_{mwr}$  for *Nasua narica* (1.45 and 1.55) and *Nasua nasua* (1.24 and 1.65) are higher than those for *Procyon cancrivorus* or *Potos flavus* (Table 7). Thus, these coatis have higher mass specific  $C_{mw}$ 's than their nocturnal tropical cousins. A high  $C_{mw}$  reduces the cost of thermoregulation in hot environments because it increases an animal's ability to lose excess heat passively. The higher  $C_{mw}$ 's of these coatis serve as an adaptation that contributes to the success of their diurnal life style as well as their ability to expand their habitat use to areas with less thermal stability, such as oak and pine woodlands and deserts.

*Bassariscus astutus*.—This species has the lowest mass specific  $C_{mw}$  of these procyonids ( $C_{mwr} = 0.85$ ; Table 7), which indicates that its pelt has a greater insulative value than the coats of *Potos flavus*, *Procyon cancrivorus*, *Nasua nasua*, or *Nasua narica*. This, coupled with a lower than predicted  $\dot{H}_b$ , allows *Bassariscus astutus* to maintain  $T_b$  with less energy expenditure than is possible for any other procyonid of comparable size; and this combination of adaptations provides *Bassariscus astutus* with a distinct energy advantage in environments that have low productivity (Wang et al., 1973). The evolution of a pelt that provides better insulation must be considered an important contributing factor for the spread of this species into desert regions of the western United States.

#### THERMOREGULATION AND USE OF STORED FAT AT LOW TEMPERATURES

##### Background

THERMOREGULATION.—At temperatures below a mammal's  $T_n$ , heat loss exceeds  $\dot{H}_b$ . To maintain  $T_b$  under these

conditions, metabolic rate must be increased (Eq. 4). *Procyon lotor* in summer during its annual molt (Table 5; Figure 2), *Bassariscus astutus* (Chevalier, 1985), *Nasua nasua* (Chevallard-Hugot et al., 1980; Mugaas et al., in prep.), *Nasua narica* (Scholander et al., 1950b; Mugaas et al., in prep.), and *Potos flavus* (Müller and Kulzer, 1977; Müller and Rost, 1983) all are able to elevate their metabolic rates by 130% above basal when they are exposed to  $T_a = 0^\circ\text{C}$ . *Procyon cancrivorus* responds to  $0^\circ\text{C}$  with an increase in metabolic rate of 257% above basal (Scholander et al., 1950b). All animals listed have about the same  $T_{ic}$  and  $T_b$ , so the temperature differential producing this response is about the same for each species. Metabolic ability to defend body temperature against low ambient temperatures, therefore, is well developed in these procyonids. Such large increases in metabolic rate are energetically expensive, and if these animals were routinely exposed to  $T_a = 0^\circ\text{C}$ , it would be difficult for them to acquire enough food each day to maintain endothermy. Raccoons in winter pelage, however, need only elevate their metabolic rate by 47% above basal to maintain endothermy at  $T_a = 0^\circ\text{C}$  (Table 5; Figure 3). Each year at the completion of its molt, the raccoon's highly insulative pelt is renewed. This lowers their  $T_{ic}$  by  $9^\circ\text{C}$  to  $15^\circ\text{C}$  below that measured for them in summer (Figure 3) and decreases their cost of thermoregulation at low temperatures. The increased insulative capacity of their pelt is one of the primary adaptations that has allowed *Procyon lotor* to extend its distribution into cold climates.

**STORED FAT.**—Cyclic fattening is an integral and important part of a raccoon's annual cycle (Mugaas and Seidensticker, ms); however, it has not been reported for other procyonids. During winter in parts of the United States and Canada, raccoons are confined to their dens for variable periods of time (days to months) depending on the severity of the weather (Stuewer, 1943:223–225; Whitney and Underwood, 1952: 108–116; Sharp and Sharp, 1956; Mech et al., 1968; Schneider et al., 1971). During this confinement, they do not hibernate but rather enter a state of "dormancy" and become inactive. While dormant they remain endothermic ( $T_b > 35^\circ\text{C}$ ; Thorkelson, 1972:87–90) and derive most of their energy requirement from fat reserves accumulated during fall. The rate at which fat stores are consumed during winter dormancy depends on the thermoregulatory requirement imposed on them by local weather conditions, the insulative quality of their pelt, and any advantage they may gain by seeking shelter in a den.

#### *Thermal Model of the Raccoon and Its Den*

Heat transfer between an animal and its environment is a function of the interaction of its body temperature and thermal conductance with various environmental variables (air temperature, wind speed, vapor pressure, and thermal radiation). When a raccoon is outside its den, its thermal conductance ( $C_{mw}$ ) is the only barrier to heat transfer with the external environment. However, when it enters a tree den, a raccoon imposes two other thermal barriers between itself and the

external environment: (1) conductance of the air space between its fur and the den's walls ( $C_a$ ) and (2) conductance of the den's walls ( $C_d$ ; Thorkelson, 1972:59–63; Thorkelson and Maxwell, 1974). Thorkelson and Maxwell (1974) modeled heat transfer of a simulated raccoon (a water-filled aluminum cylinder equipped with a heater and covered with a raccoon pelt) in a closed tree den. In their system, 65% of resistance to heat flux was attributable to the pelt, whereas the remainder (35%) was due to  $C_a$  and  $C_d$ . Because resistance is the inverse of conductance, and resistances for the raccoon and its den are arranged in series, we can estimate total conductance ( $C_t$ ) of this system with Eq. 7.

$$1/C_t = 1/C_{mw} + 1/C_a + 1/C_d \quad \text{Eq. 7}$$

Minimum thermal conductance  $C_{mw}$  for raccoons in winter was  $0.0172 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$  (Table 3). Based on Thorkelson and Maxwell's (1974) model we let  $1/C_{mw} = 0.65(1/C_t) = 1/0.0172 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$ , and  $1/C_a + 1/C_d = 0.35(1/C_t)$ . Substituting these values into Eq. 7 and solving for  $C_t$  yields  $0.0112 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \cdot ^\circ\text{C}^{-1}$ , a value that is 35% lower than that of the animal alone. Substituting this value and the value for basal metabolism of winter raccoons ( $0.47 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ; Table 7) into Eq. 4 and solving for  $(T_b - T_a)$  yields a new temperature differential of  $42^\circ\text{C}$ . Therefore, by using tree dens, raccoons in north central Virginia, with  $T_b = 37^\circ\text{C}$  (Figure 7), could effectively reduce their  $T_{ic}$  from  $11^\circ\text{C}$  to  $-5^\circ\text{C}$  and markedly reduce their metabolic cost of thermoregulation.

#### *Metabolic Advantage of the Den*

Given prevailing winter temperatures in north central Virginia (see "Materials and Methods"), adult raccoons in that area should be able to sustain endothermy most of the time they are in their dens by simply maintaining  $H_b$ . Depending on the mass of their stored fat, they could remain in their dens for several weeks without eating (Mugaas and Seidensticker, ms). The thermal advantage of a den could be further enhanced during colder temperatures if two or more raccoons occupied it at the same time and huddled together, and/or if these animals could reduce  $C_{mw}$  even more by lowering  $T_b$  and cooling their extremities. Although we do not have any data to verify the second mechanism, there are many accounts in natural history literature that document raccoons occupying dens together (Lotze and Anderson, 1979). This habit could be particularly important for the young of the year and may be one reason why they often continue to den with their mothers during winter (Lotze and Anderson, 1979; Seidensticker et al., 1988). Raccoons that live in colder climates, such as Minnesota, undoubtedly obtain the same advantage from a den as Virginia animals, but because of their greater body mass, longer fur, and potentially lower  $C_{mw}$ ,  $T_{ic}$  of a Minnesota raccoon in a den could be even lower than what we calculated for Virginia raccoons. Therefore, when they are in their dens, raccoons living in very cold climates also may be able to maintain homeothermy with a basal level of metabolism.

## THERMOREGULATION AT HIGH TEMPERATURES

*Background*

In hot environments mammals depend on behavior to minimize their thermal load (escape to shaded or cooler microclimates, use posture and orientation to wind and sun, restrict activity, become nocturnal, etc.) and on evaporative water loss to rid themselves of excess heat. With regard to evaporative heat loss, Calder and King (1974:326) arbitrarily subdivided the response to various  $T_a$ 's as follows: "(1) cool temperatures at which water loss should be minimized, both to reduce heat loss and as an adaptation to terrestriality; (2) an intermediate temperature range wherein evaporation is gradually increased as dry heat losses are proportionately reduced with smaller thermal gradients; and (3) warm to hot temperatures at which evaporation must be actively increased to dispose of metabolic and exogenous heat loads." Some mammals are able to thermoregulate very well at high ambient temperatures via panting or sweating, whereas others have a very limited capacity. Hence, there is no general approach to calculating evaporative water loss under these conditions (Campbell, 1977:85). However, the ratio of evaporative heat lost to metabolic heat produced can be used to quantify a species' capacity for evaporative cooling and to make comparisons between species.

*Comparison of Procyonid Responses to Heat Stress*

*Potos flavus*.—This species lives in Neotropical forests of Central and South America. It is nocturnal, arboreal in habit, and appears to be the most heat-sensitive of these procyonids. Its  $T_{uc}$  is at 30°C to 33°C (Table 7; Müller and Kulzer, 1977; Müller and Rost, 1983). It begins to pant at about 30°C, but its efforts at evaporative cooling are very ineffective. At 33°C *Potos flavus* can dissipate 33% of its metabolic heat via evaporative water loss, but at 35°C the efficiency of this mechanism falls to 20% (Müller and Rost, 1983). Consequently, when exposed to  $T_a$ 's above 33°C, any kind of excitement causes its  $T_b$  to rise rapidly in an uncontrolled manner (Müller and Kulzer, 1977; Müller and Rost, 1983). These animals rely on their nocturnal and arboreal habits to keep them out of situations that could lead to hyperthermia (Müller and Kulzer, 1977; Müller and Rost, 1983).

*Nasua nasua* and *Nasua narica*.—*Nasua nasua* is abundant in tropical and subtropical South America, whereas *Nasua narica* occupies the same climates in North America from southern Arizona and New Mexico south through Panama and on into Colombia and Ecuador (Hall and Kelson, 1959:892; Ewer, 1973:391, 392; Poglayen-Neuwall, 1975). Both coatis are diurnal and forage primarily on the ground (Kaufmann, 1962:185-188, 1987; Poglayen-Neuwall, 1975; Nowak and Paradiso, 1983:982), consequently they are exposed to a more severe thermal environment while active (higher  $T_a$ 's and solar

radiation) than are nocturnal procyonids. Both coatis are more heat-tolerant than *Potos flavus*; their  $T_{uc}$ 's are higher (33°C-35°C; Table 7), they can tolerate  $T_a$ 's of 35°C without raising their  $T_b$ 's (Chevallard-Hugot et al., 1980; Mugaas et al., in prep.), and they have a greater capacity for evaporative cooling than *Potos flavus* (Mugaas et al., in prep.). The greater heat tolerance of these coatis is compatible with their diurnal habits and widespread distribution in a variety of forest habitats in both tropical and subtropical areas of the western hemisphere.

*Bassariscus astutus*.—In addition to living in Neotropical forests of Mexico, *Bassariscus astutus* also flourishes in hot arid climates, and it has extended its range much farther north than *Nasua narica* (Hall and Kelson, 1959:881, 892; Poglayen-Neuwall, 1975; Kaufmann, 1982). Its  $T_{uc}$  is higher (35.5°C; Table 7) than that of *Potos flavus*, but it is comparable to those of *Nasua nasua* and *Nasua narica*. Its capacity for evaporative cooling is well developed; at 40°C *Bassariscus astutus* is able to dissipate 100% of its resting metabolic heat via evaporative water loss, and at 45°C it is able to dissipate 172% (Chevalier, 1985). In spite of its great capacity for evaporative cooling, this species is nocturnal, a habit that, along with its low  $\dot{H}_b$ , should allow it to keep thermoregulatory water requirements to a minimum.

*Procyon lotor*.—Our data suggested that  $T_{uc}$  for *Procyon lotor* in winter was comparable to that for *Bassariscus astutus* (35°C), and that in summer it was even higher. When exposed to temperatures near the upper end of its  $T_b$ , *Procyon lotor* increased the gradient for passive heat loss with a controlled rise in  $T_b$  (Figure 6). In summer its capacity for passive heat loss was enhanced by the molt of its heavy winter fur. *Procyon lotor*'s capacity for evaporative cooling also appeared to be well developed, although our animals were not heated to the point that evaporative cooling was fully expressed (Figures 4, 5). However, *Procyon lotor* is nocturnal, and this may allow it to eliminate, or at least reduce, the need for evaporative cooling, even in hot climates. Thus, *Procyon lotor* appears to be well equipped physiologically and behaviorally to cope with thermal demands of hot environments in its distribution.

*Procyon cancrivorus*.—Unfortunately, data for the crab-eating raccoon are not complete enough at high temperatures to include it in this survey.

**SUMMARY.**—This comparison demonstrates that capacity for evaporative cooling, tolerance of an elevated  $T_b$  to enhance passive heat loss, and behavioral avoidance of thermal stress are the primary methods used by procyonids to thermoregulate at high temperatures. *Procyon lotor* and *Bassariscus astutus*, whose distributions extend into temperate regions, have developed these abilities to a greater extent than other procyonids. *Potos flavus*, whose distribution is confined to lowland tropical forests, has the least ability in this regard. *Nasua nasua* and *Nasua narica* appear to have thermoregulatory abilities that are intermediate to those of *Bassariscus astutus* and *Potos flavus*. This suggests that ancestral pro-

TABLE 11.—Distribution by climate of selected procyonid species.

Species	Tropics	Subtropics	Mild* temperate	Cold+ temperate
<i>Procyon lotor</i>	+	+	+	+
<i>Bassariscus astutus</i>	+	+	+	
<i>Nasua nasua</i>	+	+		
<i>Nasua narica</i>	+	+		
<i>Procyon cancrivorus</i>	+	+		
<i>Potos flavus</i>	+			

\* Extends from the subtropics north to the northern limit of *Bassariscus astutus*' distribution (Hall and Kelson, 1959:881), which approximates the 10°C isotherm for average annual temperature in the United States (Kincer, 1941).

† Extends northward from the 10°C isotherm for average annual temperature in the United States.

cyonids may have had poor to modest ability to thermoregulate at high temperatures, a condition that would have limited their ability to leave the thermal stability afforded by tropical forests. Dispersal into temperate climates, therefore, required not only increased cold tolerance but also selective enhancement of those mechanisms used in thermoregulation at high temperatures.

COMPOSITE SCORES OF ADAPTIVE UNITS AND GEOGRAPHIC DISTRIBUTION

In Table 11, procyonid species are arranged in descending order with respect to the number of major climates that are included in their geographic distributions (Hall and Kelson, 1959:878-897; Poglayen-Neuwall, 1975; Kortlucke and Ramirez-Pulido, 1982; Nowak and Paradiso, 1983:977-985). Composite scores ranged from a high of 1.47 for *Procyon lotor* to a low of 0.39 for *Potos flavus*, whereas *Nasua nasua*, *Nasua narica*, *Procyon cancrivorus*, and *Bassariscus astutus* had intermediate values ranging from 0.64 to 0.79 (Table 12). Figure 8 demonstrates that there is a direct relationship between the number of climates these species occupy and their composite scores. Regression analysis ( $Y = 2.68 \cdot X + 0.24$ ; where Y is number of climates, and X is composite score) demonstrates a high degree of correlation between these variables ( $R = 0.94$ ) and indicates that 89% of the variance in distribution can be explained by composite scores. The various combinations of adaptations expressed by these species do, therefore, play a role in delimiting their climatic (latitudinal) distributions.

*Procyon lotor*'s normalized scores were higher in all categories than those of other procyonids. *Procyon lotor*, therefore, possesses those traits that have allowed it to become the premier climate generalist of the procyonid family. As an adaptive unit, these traits provide *Procyon lotor* with the physiological and behavioral flexibility required to take full advantage of a wide range of climates and habitats, and its distribution verifies that it has done so. Even so, it is probably not fair to assume that this species represents a perfect

physiological match with climate over its entire distribution. *Procyon lotor* is, in many respects, still a forest-dwelling species, and its ability to expand its distribution into other habitats such as prairie and desert may well be due, in part, to its use of behavior to take advantage of favorable microclimates in otherwise hostile environments (Bartholomew, 1958, 1987). This feature of *Procyon lotor*'s biology needs to be further examined.

All five species with low  $\dot{H}_b$ 's have composite scores less than 1.0 (Table 12; Figure 8). Four of these five, *Nasua nasua*, *Nasua narica*, *Procyon cancrivorus*, and *Potos flavus*, have  $H_{br}/C_{mwr}$  ratios that are 0.6 or less, which indicates they are the least cold-tolerant procyonids (McNab, 1966). These four species also are confined to either tropic, or tropic and subtropic climates (Table 11). This suggests that these species share a common thermoregulatory adaptation that represents a specialization to these climates. Attendant with this adaptation, however, is a high cost of thermoregulation at temperatures below their  $T_{lc}$ , and this must be an important

TABLE 12.—Normalized and composite scores for selected procyonids. ( $H_{br}$  = ratio of measured to predicted basal metabolism (Table 7),  $C_{mwr}$  = ratio of measured to predicted minimum thermal conductance (Table 7),  $D_{dr}$  = ratio of food categories actually utilized by each species to total food categories eaten by all six species (calculated from Table 9),  $r_{maxr}$  = ratio of calculated to expected  $r_{max}$  (Table 10).)

Species	Normalized scores			Composite* score
	$H_{br}/C_{mwr}$	$D_{dr}$	$r_{maxr}$	
<i>Procyon lotor</i>	0.95	0.95	2.52	1.47
<i>Bassariscus astutus</i>	0.80	0.33	1.24	0.79
<i>Nasua nasua</i>	0.48	0.33	1.11†	0.64
<i>Nasua nasua</i>	0.48	0.33	1.11†	0.64
<i>Nasua narica</i>	0.40	0.53	1.11	0.68
<i>Procyon cancrivorus</i>	0.55	0.33	1.32	0.73
<i>Potos flavus</i>	0.60	0.11	0.48	0.39

\* Composite score =  $[(H_{br}/C_{mwr}) + D_{dr} + r_{maxr}]/3$ .

† Value calculated for *Nasua narica* (Table 10) and used with the assumption that it must be similar to the value for *Nasua nasua*.

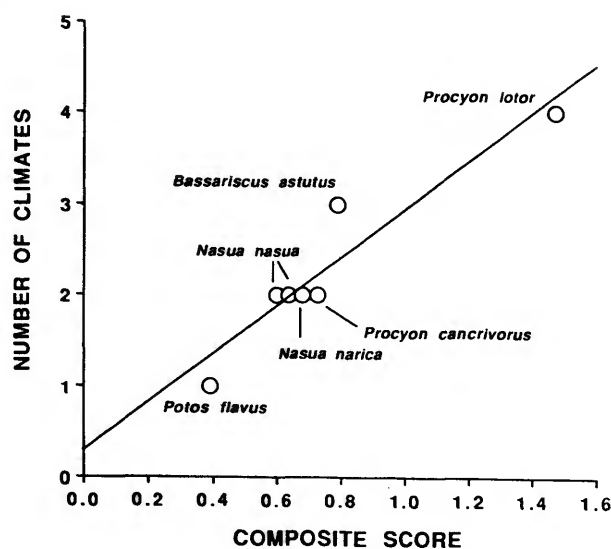


FIGURE 8.—Relationship between number of climates in which a species is found and its composite score. Symbols for *Nasua nasua* overlap at coordinates (0.64, 2). Solid line represents linear regression of climates (Y) on composite scores (X):  $Y = 2.68 \cdot X + 0.24$ ;  $R = 0.94$ .

factor in limiting their distributions to tropic and subtropical climates. Differences in their distributions within these climates, therefore, must hinge more on differences in their  $D_{dr}$  and  $r_{maxr}$  values than on differences in their  $H_{br}/C_{mwr}$  ratios. This is supported by the fact that *Potos flavus*, which has the lowest  $D_{dr}$  and  $r_{maxr}$  values, is confined to a single climate, whereas *Nasua nasua*, *Nasua narica*, and *Procyon cancrivorus* each possess larger  $D_{dr}$  and  $r_{maxr}$  values and are found in two climates. Thus, *Potos flavus*, with its highly specialized diet and low reproductive potential, is the most ecologically specialized of these procyonids, and its distribution is limited to the single climate that can provide its requirements. *Nasua nasua*, *Nasua narica*, and *Procyon cancrivorus* are less specialized and thus show more ecological flexibility in their distributions.

*Bassariscus astutus*, the other species with low  $H_{br}$ , is found in three climates, which indicates that it has greater ecological flexibility than *Nasua nasua*, *Nasua narica*, or *Procyon cancrivorus*.  $D_{dr}$  and  $r_{maxr}$  are comparable for these four species (Table 12). This suggests that the greater ecological flexibility of *Bassariscus astutus* is derived largely from its greater cold tolerance. *Bassariscus astutus* has a more insulative pelt than these other procyonids ( $C_{mwr} = 0.85$ ; Table 7), so its  $H_{br}/C_{mwr}$  ratio is higher (0.80; Table 12). This, and its greater capacity for evaporative cooling (Chevalier, 1985), allows *Bassariscus astutus* to take advantage of a wider range of thermal environments than these other species. However, even with its higher  $H_{br}/C_{mwr}$  ratio, the composite score for *Bassariscus*

*astutus* is not much different than those for *Nasua nasua*, *Nasua narica*, and *Procyon cancrivorus* (Table 12). Consequently, *Bassariscus astutus* is found in more climates than would be predicted for it on the basis of its composite score (Figure 8). This suggests that either the  $H_{br}/C_{mwr}$  ratio carries greater weight in determining distribution than is reflected in this analysis, or as has been described for some other species (Bartholomew, 1958, 1987), *Bassariscus astutus* may extend its distribution farther than expected via use of its behavior. In either case, for procyonids with low  $H_{br}$ , *Bassariscus astutus* represents the pinnacle of adaptation for climate generalization.

## EVOLUTION OF METABOLIC ADAPTATIONS

### Evolution of Low Basal Metabolic Rate

A radiation of frugivorous and omnivorous Procyoninae (Table 1) occurred in the middle and late Miocene of North America. It included origins of such terrestrial genera as *Cyonasua*, *Nasua*, and *Procyon* (Webb, 1985b). The earliest procyonid genus to find its way to South America was *Cyonasua*, an omnivorous carnivore that presumably split, along with its sister genus *Arctonasua*, from a common North American ancestor (Baskin, 1982; Webb, 1985b). *Cyonasua*, about the size of present-day raccoons, was adapted to a wide range of habitats and was probably comparable to modern raccoons with respect to the breadth of its feeding habits (Webb, 1985b; Marshall, 1988). Because North American *Arctonasua* was about the same size as *Cyonasua* (Webb, 1985b) and shared a number of characters with it (Baskin, 1982), we speculate that it also may have had similar habits and occupied similar climates and habitats. *Bassariscus*, another member of Procyoninae, had an even earlier origin in tropical North America (Webb, 1985b). The origin of the small arboreal forms *Potos* and *Bassaricyon* (subfamily Potosinae) is obscure but is thought to have occurred in the rainforests of Central America (Webb, 1985b). What were the metabolic capabilities of these early procyonids? We do not know, but for several million years, from middle to late Miocene, procyonids lived in tropical and subtropical forests of Central and North America (Webb, 1985b; Marshall, 1988). Then, in the Pleistocene, several modern forms crossed the Panamanian land bridge into similar habitats and climates in South America; but none of them appear to have spread far enough northward to have crossed the Bering land bridge.

Several million years exposure to a tropical environment, with its continuous high temperatures and modest range of thermal extremes, would have favored selection of metabolic and thermoregulatory traits that would minimize energy requirements: a lower than predicted basal metabolic rate, a prolonged or continuous molt resulting in very little annual change in minimum thermal conductance, and a modest capacity for evaporative cooling. In addition, we would expect selection to have favored a diverse diet, good reproductive



potential, and behavioral flexibility to utilize a variety of habitats within these climates. Our analysis has shown that such characteristics are the norm for extant members of this family living in tropical and subtropical climates, and we speculate that these traits also were common to early procyonids and served to restrict them to these climates. Our speculation is supported by the fact that their known fossil history from the Miocene is confined to geographic areas that had tropical and subtropical climates.

Later on, during Pleistocene glaciations, tropical and subtropical forests shrank, savannas expanded, and temperate climate was pushed toward equatorial regions. The opposite occurred during interglacial periods (Raven and Axelrod, 1975; Webb, 1977, 1978; Marshall, 1988). Consequently, mid-latitudes experienced alternating periods of temperate and tropical, or at least subtropical, climate change. Selection of characteristics that would have adapted a species with low  $\dot{H}_b$  to temperate as well as tropic or subtropic climates could have occurred in mid-latitudes at the temperate edge of these tropical advances and retreats. Our analysis indicates that, for this purpose, selection would have favored lower than predicted thermal conductance, seasonal molt, increased capacity for evaporative cooling, increased tolerance of elevated  $T_b$ , increased flexibility of thermoregulatory behavior, food habits that provided for year-round access to a high-quality diet in all three climates, and a higher than predicted  $r_{max}$ .

*Bassariscus astutus* is the only species with low  $\dot{H}_b$  that has all these characteristics, and it is the only one of them that has added temperate climate to its distribution (Table 11). This suggests that *Bassariscus astutus* is a species that evolved away from the norm for procyonids with low  $\dot{H}_b$ , toward characteristics that allowed it to become more of a climate generalist. *Potos flavus*, with its dietary specialization, low tolerance to high temperatures, and arboreal mode of existence, has become a highly specialized species totally dependent on tropical forests for its survival. As such, it also represents a species that has evolved away from the procyonid norm and portrays the extreme in climate specialization. Olingos, *Bassaricyon gabbii* (Table 1), may be similar to *Potos flavus* in this respect (see also Table 10). This suggests that of the extant procyonids, *Nasua nasua*, *Nasua narica*, and *Procyon cancrivorus* have retained metabolic and behavioral characteristics that are closest to those of their Miocene ancestors.

#### *Evolution of High Basal Metabolic Rate*

Between the time that *Cyonasua* appeared and the Panamanian land bridge was established in the upper Pliocene (4 to 5 million years ago), northern climates continued their gradual cooling. This, along with ongoing elevation of the continents and continuous modification of their mountain ranges, served to shrink the tropical forest and create pockets of climatic instability within it and on its edges (Darlington, 1963:578–

596; Marshall, 1988). In areas of instability, selection would have favored traits that provided for a broader range of thermal tolerance: higher  $\dot{H}_b$ , improved insulative quality of pelt, a more sharply defined molt cycle, improved capacity for evaporative cooling, greater  $D_a$ , and higher  $r_{max}$ . Consequently, by the upper Pliocene, two metabolically distinct groups of procyonids could have been established: those species with low  $\dot{H}_b$  living in climatically stable forests and those with higher  $\dot{H}_b$  living in unstable tropical, subtropical, and perhaps temperate climates.

*Procyon lotor* is the only extant procyonid with high  $\dot{H}_b$ . *Procyon cancrivorus* is its congeneric counterpart in Central and South America (Table 1), and the two species are sympatric in Panama and Costa Rica. However, in terms of its metabolism, thermal conductance, molt, diversity of diet,  $r_{max}$ , and climatic distribution, *Procyon cancrivorus* shares more in common with other procyonids than it does with *Procyon lotor* (Tables 7, 11, 12; Figure 8). This suggests that metabolically *Procyon lotor* portrays a divergent line of this genus that arose as the result of a series of mutations that gave rise to different metabolic characteristics. This view is in keeping with a recent phylogenetic analysis of this family that shows the genus *Procyon* to be highly derived (Decker and Wozencraft, 1991). Consequently, it would be instructive and would add to our knowledge of the evolution of climatic adaptation to know more about the genetic relatedness of these two species as well as their historical relationship.

Genus *Procyon* appears in the fossil record (Hemphillian and Blancan ages; Baskin, 1982) prior to Pleistocene glaciations. During the Pleistocene, there were four different glacial advances and retreats in a relatively short time period (the first appearing little more than a million years ago; Darlington, 1963:578–596; Webb, 1985a; Marshall, 1988). Glacial retreats created pulses of time during which subtropic and temperate climates advanced toward the poles into areas with large seasonal differences in light/dark cycles, whereas glacial advances pushed these climates southward into areas having smaller seasonal differences in light/dark cycles (Raven and Axelrod, 1975; Webb, 1977, 1978; Marshall, 1988). Those members of the genus *Procyon* caught in these wide latitudinal fluctuations would have experienced conditions favorable to continued selection for characteristics conducive to physiologic adaptation to a wide range of climatic conditions. *Procyon lotor* is the only member of its genus to have survived this selective process, and as we have seen, it does possess traits that adapt it to a wide range of climatic conditions. Primary among these is its higher  $\dot{H}_b$ , which provides it with advantages not shared with other procyonids (see earlier discussion). Three other adaptations also have had a profound influence on *Procyon lotor*'s ability to generalize its use of climate: (1) the increased insulative quality of its pelt coupled with its sharply defined molt cycle, which allows for a large annual change in thermal conductance; (2) its annual cycle of fat storage; and (3) a diverse high-quality diet. The first two of these adaptations

required evolution of neuroendocrine pathways capable of responding to time-dependent environmental cues such as changing day length, changing temperature, etc. Such conditions would have been available as selective stimuli in high-latitude forests and savannas of interglacial periods. *Procyon lotor*'s elevated basal metabolic rate would have increased its overall energy requirement, and it makes good intuitive sense, therefore, that evolution during the Pleistocene also would have favored selection of a diverse diet containing many items of high nutritive value.

#### SUMMARY

Our analysis has illustrated that within Procyonidae there are two distinct modes of metabolic adaptation to climate. One is typified by those species with low  $\dot{H}_b$ 's (*Bassariscus astutus*, *Nasua nasua*, *Nasua narica*, *Procyon cancrivorus*, and *Potos flavus*), and the other by *Procyon lotor* with its higher  $\dot{H}_b$ . Those with low  $\dot{H}_b$ 's have more restricted geographic distributions, and, with the exception of *Bassariscus astutus*, they are all confined to tropical and subtropical areas. The fossil history of this family indicates that it had its origins in tropical forests of North and Central America. This indicates that those

procyonids whose distributions are still primarily restricted to tropical forests share many of the metabolic adaptations characteristic of their ancestors. We speculate, therefore, that ancestral procyonids had a lower than predicted  $\dot{H}_b$ , a pelt with modest to poor insulative quality, good thermogenic ability but poor heat tolerance, modest to poor capacity for evaporative cooling, no well-defined molt cycle, no cyclic period of fattening, nocturnal habits, and a modestly diverse diet of high-enough quality to provide for an average reproductive potential. Although this pedigree contributed to the success of this family in tropical and subtropical forests, it limited the ability of its members to expand their distributions into cooler, less stable climates. Viewed in this perspective, *Procyon lotor*'s high basal metabolic rate, extraordinarily diverse diet, well-defined cyclic changes in fat content and thermal conductance, high level of heat tolerance, high capacity for evaporative cooling, and high reproductive potential all stand out in sharp contrast to the condition described for other procyonids. This suggests that the North American raccoon represents culmination of a divergent evolutionary event that has given this species the ability to break out of the old procyonid mold and carry the family into new habitats and climates.

# Appendix

## List of Symbols

$a$	potential age of females first producing young
$b$	potential annual birth rate of female young
$C_a$	conductance of air
$C_d$	conductance of den walls
$C_m$	minimum thermal conductance
$C_{md}$	minimum dry thermal conductance
$C_{mw}$	minimum wet thermal conductance
$C_{mwr}$	ratio of measured to predicted minimum wet thermal conductance
$C_t$	total conductance
$D_d$	diversity of diet
$D_{dr}$	ratio of food categories actually used by a species to the total number of food categories taken by all species tested
$\dot{E}$	evaporative water loss
$E_c$	ratio of evaporative heat lost to metabolic heat produced
$\dot{E}_{eq}$	oxygen equivalent for heat lost by evaporation
$\dot{H}_b$	basal metabolic rate
$\dot{H}_r$	lowest resting metabolic rate at each temperature
$H_{br}$	ratio of measured to predicted basal metabolic rate
$m$	mass of animal
$m_w$	mass of water
$n$	potential age of females producing their final young
$r_{max}$	intrinsic rate of natural increase
$r_{maxe}$	expected intrinsic rate of natural increase
$r_{maxr}$	ratio of calculated to expected intrinsic rate of natural increase
RQ	respiratory quotient
$T_a$	chamber air temperature
$T_b$	body temperature
$T_{lc}$	lower critical temperature
$T_n$	thermoneutral zone
$T_{uc}$	upper critical temperature
$t$	time
$\dot{V}_a$	rate of air flow through U-tubes
$\dot{V}_e$	rate of air flow into metabolism chamber
$\alpha$	active phase of the daily cycle
$\gamma$	heat equivalent of oxygen
$\lambda$	heat of vaporization of water
$\rho$	rest phase of the daily cycle

## Literature Cited

- Aschoff, Jürgen  
1981. Thermal Conductance in Mammals and Birds: Its Dependence on Body Size and Circadian Phase. *Comparative Biochemistry and Physiology*, 69A:611-619, 3 figures, 2 tables.
- Aschoff, J., and H. Pohl  
1970. Rhythmic Variations in Energy Metabolism. *Federation Proceedings*, 29:1541-1552, 18 figures.
- Barghoorn, Elso S.  
1953. Evidence of Climatic Change in the Geologic Record of Plant Life. In Harlow Shapley, editor, *Climatic Change, Evidence, Causes, and Effects*, pages 235-248, 3 figures, 1 table. Cambridge: Harvard University Press.
- Bartholomew, George A.  
1958. The Role of Physiology in the Distribution of Terrestrial Vertebrates. In Carl L. Hubbs, editor, *Zoogeography. American Association for the Advancement of Science*, 51: 81-95. Washington, D.C.  
1987. Interspecific Comparison as a Tool for Ecological Physiologists. In Martin E. Feder, Albert F. Bennett, Warren W. Burggren, and Raymond B. Huey, editors, *New Directions in Ecological Physiology*, pages 11-37, 1 figure. Cambridge: Cambridge University Press.
- Baskin, Jon Alan  
1982. Tertiary Procyoninae (Mammalia: Carnivora) of North America. *Journal of Vertebrate Paleontology*, 2:71-93, 14 figures, 5 tables.
- Benedict, Francis G.  
1938. Vital Energetics. *Carnegie Institution of Washington*, 503: viii + 215 pages, 46 figures, 4 tables.
- Berggren, William A.  
1982. Role of Ocean Gateways in Climatic Change. In *Climate in Earth History, Studies in Geophysics*, pages 118-125, 4 figures. Washington, D.C.: National Academy Press.
- Bisbal, Francisco J.  
1986. Food Habits of Some Neotropical Carnivores in Venezuela (Mammalia, Carnivora). *Mammalia*, 50:329-339, 1 figure, 2 tables, 2 appendices.
- Bradley, S. Robert, and Daniel R. Deavers  
1980. A Re-examination of the Relationship between Thermal Conductance and Body Weight in Mammals. *Comparative Biochemistry and Physiology*, 65A:465-476, 6 figures, 6 tables.
- Brody, Samuel  
1945. *Bioenergetics and Growth*. xii + 1023 pages, 377 figures, 86 tables, 11 appendices. New York: Reinhold Publishing Corporation.
- Calder, William A., III  
1987. Scaling Energetics of Homeothermic Vertebrates: An Operational Allometry. *Annual Review of Physiology*, 49:107-120, 1 figure, 1 table.
- Calder, William A., and James R. King  
1974. Thermal and Caloric Relations of Birds. In Donald S. Farner and James R. King, editors, *Avian Biology*, 4:259-413, 34 figures, 17 tables. New York: Academic Press.
- Campbell, Gaylon S.  
1977. *An Introduction to Environmental Biophysics*. xv + 159 pages, 55 figures, 14 tables. New York: Springer-Verlag.
- Chevalier, C.D.  
1985. Thermoregulation in Desert-adapted Ringtail Cats (*Bassariscus astutus*). [Abstract.] *American Zoologist*, 25:58A.
- Chevillard-Hugot, Marie-Christine, E.F. Müller, and E. Kulzer  
1980. Oxygen Consumption, Body Temperature and Heart Rate in the Coati (*Nasua nasua*). *Comparative Biochemistry and Physiology*, 65A:305-309, 6 figures, 2 tables.
- Colbert, Edwin H.  
1953. The Record of Climatic Changes as Revealed by Vertebrate Paleocology. In Harlow Shapley, editor, *Climatic Change, Evidence, Causes, and Effects*, pages 249-271. Cambridge: Harvard University Press.
- Cole, Lamont C.  
1954. The Population Consequences of Life History Phenomena. *The Quarterly Review of Biology*, 29:103-137, 10 figures.
- Crandall, Lee S.  
1964. *The Management of Wild Mammals in Captivity*. xv + 469 pages, 10 tables, 11 plates. Chicago: The University of Chicago Press.
- Crockett, Curtis W.  
1972. Climatological Summaries for Selected Stations in Virginia. *Water Resources Research Center*, 53. Virginia Polytechnic Institute and State University, Blacksburg, Virginia.
- Darlington, Philip J., Jr.  
1963. *Zoogeography: The Geographical Distribution of Animals*. xiii + 675 pages, 80 figures, 21 tables, frontispiece. New York: John Wiley and Sons, Incorporated.
- Davis, D. Dwight  
1964. The Giant Panda: A Morphological Study of Evolutionary Mechanisms. *Fieldiana: Zoology Memoirs*, 3: 339 pages, 159 figures, 25 tables.
- Decker, Denise M.  
1991. Systematics of the Coatis Genus *Nasua* (Mammalia: Procyonidae). *Proceedings of the Biological Society of Washington*, 104:370-386, 3 figures, 3 tables, 2 appendices.
- Decker, Denise M., and W. Chris Wozencraft  
1991. Phylogenetic Analysis of Recent Procyonid Genera. *Journal of Mammalogy*, 72:42-55, 2 figures, 2 appendices.
- Depocas, Florent, and J. Sanford Hart  
1957. Use of the Pauling Oxygen Analyzer for Measurement of Oxygen Consumption of Animals in Open-Circuit Systems and in a Short-Lag, Closed-Circuit Apparatus. *Journal of Applied Physiology*, 10:388-392, 3 figures, 1 table.
- Dunn, J.P., and J.A. Chapman  
1983. Reproduction, Physiological Responses, Age Structure, and Food Habits of Raccoon in Maryland, USA. *Zeitschrift für Säugetierkunde*, 48:161-175, 6 figures, 7 tables.
- Eisenberg, John F.  
1981. *The Mammalian Radiations*. xx + 610 pages, 157 figures, 61 tables, 6 appendices. Chicago: The University of Chicago Press.
- Ewer, R.F.  
1973. *The Carnivores*. xv + 494 pages, 79 figures, 22 tables. Ithaca: Cornell University Press.
- Fenchel, Tom  
1974. Intrinsic Rate of Natural Increase: The Relationship with Body Size. *Oecologia* (Berlin), 14:317-326, 3 figures, 1 table.
- Ford, Linda S., and Robert S. Hoffmann  
1988. *Potos flavus*. *Mammalian Species*, 321:1-9, 3 figures.
- Ginsburg, Léonard  
1982. Sur la position systématique du petit Panda, *Ailurus fulgens* (Carnivora, Mammalia). *Geobios* (Lyon), Mémoire Spécial,

- 6:247-258, 12 figures.
- Glazier, Douglas S.  
1985a. Relationship between Metabolic Rate and Energy Expenditure for Lactation in *Peromyscus*. *Comparative Biochemistry and Physiology*, 80A:587-590, 1 table.  
1985b. Energetics of Litter Size in Five Species of *Peromyscus* with Generalizations for Other Mammals. *Journal of Mammalogy*, 66:629-642, 1 figure, 6 tables.
- Goldman, Edward A.  
1950. The Raccoons of North and Middle America. *North American Fauna*, 60:1-153, 1 figure, 22 plates.
- Golightly, Richard T., Jr., and Robert D. Ohmart  
1983. Metabolism and Body Temperature of Two Desert Canids: Coyotes and Kit Foxes. *Journal of Mammalogy*, 64:624-635, 7 figures.
- Greenwood, Raymond J.  
1981. Foods of Prairie Raccoons during the Waterfowl Nesting Season. *Journal of Wildlife Management*, 45:754-760, 2 tables.
- Hall, E. Raymond, and Keith R. Kelson  
1959. *The Mammals of North America*. xxx + 1083 pages, 553 figures, 500 maps, 1 addendum. New York: Ronald Hall Press Company.
- Hallett, James G., Margaret A. O'Connell, Gregory D. Sanders, and John Seidensticker  
1991. Comparison of Population Estimators for Medium-sized Mammals. *Journal of Wildlife Management*, 55:81-93.
- Hamilton, W.J., Jr.  
1936. The Food and Breeding Habits of the Raccoon. *Journal of Science*, 36:131-140, 1 chart, 1 plate.
- Hart, J.S.  
1956. Seasonal Changes in Insulation of the Fur. *Canadian Journal of Zoology*, 34:53-57, 2 figures, 1 table.  
1957. Climatic and Temperature Induced Changes in the Energetics of Homeotherms. *Revue Canadienne de Biologie*, 16:133-174, 12 figures, 2 tables.
- Hart, J.S., and O. Heroux  
1963. Seasonal Acclimatization in Wild Rats (*Ratus norvegicus*). *Canadian Journal of Zoology*, 41:711-716, 3 figures.
- Hayssen, V.  
1984. Basal Metabolic Rate and the Intrinsic Rate of Increase: An Empirical and Theoretical Reexamination. *Oecologia* (Berlin), 64:419-424, 2 figures.
- Hemmingsen, Axel M.  
1960. Energy Metabolism as Related to Body Size and Respiratory Surfaces, and Its Evolution. *Reports of the Steno Memorial Hospital and the Nordisk Insulinlaboratorium*, 9:1-110, 12 figures.
- Hennemann, Willard W., III  
1983. Relationship among Body Mass, Metabolic Rate and the Intrinsic Rate of Natural Increase in Mammals. *Oecologia* (Berlin), 56:104-108, 1 figure, 1 appendix.  
1984. Commentary. *Oecologia* (Berlin), 64:421-423, 2 figures.
- Herreid, Clyde F., II, and Brina Kessel  
1967. Thermal Conductance in Birds and Mammals. *Comparative Biochemistry and Physiology*, 21:405-414, 2 figures, 2 tables.
- Hinds, David S.  
1973. Acclimatization of Thermoregulation in the Desert Cottontail, *Sylvilagus audubonii*. *Journal of Mammalogy*, 54:708-728, 5 figures, 3 tables.  
1977. Acclimatization of Thermoregulation in Desert-Inhabiting Jackrabbits (*Lepus alleni* and *Lepus californicus*). *Ecology*, 58:246-264, 10 figures, 4 tables.
- Hulbert, A.J., and T.J. Dawson  
1974. Standard Metabolism and Body Temperature of Perameloid Marsupials from Different Environments. *Comparative Biochemistry and Physiology*, 47A:583-590, 2 figures, 2 tables.
- Hunt, Robert M., Jr.  
1974. The Auditory Bulla in Carnivora: An Anatomical Basis for Reappraisal of Carnivore Evolution. *Journal of Morphology*, 143:21-76, 42 figures, 13 plates.
- Irving, Laurence  
1972. *Arctic Life of Birds and Mammals Including Man*. Zoophysiology and Ecology, 2: xi + 192 pages, 59 figures, 22 tables. New York: Springer-Verlag.
- Irving, Laurence, Hildur Krog, and Mildred Monson  
1955. The Metabolism of Some Alaskan Animals in Winter and Summer. *Physiological Zoology*, 28:173-185, 15 figures, 1 table.
- Kaufmann, John H.  
1962. Ecology and Social Behavior of the Coati, *Nasua narica* on Barro Colorado Island, Panama. *University of California Publications in Zoology*, 60:95-222, 20 figures, 13 tables, 16 plates.  
1982. Raccoon and Allies. In J.A. Chapman and G.A. Feldhamer, editors, *Wild Mammals of North America: Biology, Management, and Economics*, pages 567-585, 2 figures. Baltimore: Johns Hopkins University Press.  
1987. Ringtail and Coati. In Milan Novak, James A. Baker, Martyn E. Obbard, and Bruce Malloch, editors, *Wild Furbearer Management and Conservation in North America*, pages 500-508, 9 figures, 1 table. Ontario: Ministry of Natural Resources.
- Kendeigh, S. Charles  
1961. *Animal Ecology*. x + 468 pages, 203 figures, 61 tables. Englewood Cliffs, New Jersey: Prentice-Hall, Incorporated.
- Kincer, J.B.  
1941. Climate and Weather Data for the United States. In Gove Hambidge, editor, *Climate and Man, Yearbook of Agriculture*, pages 685-747, 46 maps. Washington, D.C.: United States Government Printing Office.
- King, James R.  
1974. Seasonal Allocation of Time and Energy Resources in Birds. In Raymond A. Paynter, Jr., editor, *Avian Energetics*. *Nuttall Ornithological Club*, 15:4-85, 4 figures, 9 tables. Cambridge.
- Kleiber, Max  
1932. Body Size and Metabolism. *Hilgardia*, 6:315-353, 1 figure, 11 tables.  
1961. *The Fire of Life*. xxii + 454 pages, 65 figures, 78 tables, 28 appendices. New York: John Wiley and Sons, Incorporated.
- Kortlucke, S., and J. Ramirez-Pulido  
1982. Family Procyonidae. In James H. Honacki, Kenneth E. Kinman, and James W. Koepl, editors, *Mammal Species of the World*, pages 252-255. Lawrence, Kansas: Allen Press, Incorporated.
- Lasiewski, Robert C., and Roger S. Seymour  
1972. Thermoregulatory Responses to Heat Stress in Four Species of Birds Weighing Approximately 40 Grams. *Physiological Zoology*, 45: 106-118, 6 figures, 1 table.
- Leone, Charles A., and Alvin L. Wiens  
1956. Comparative Serology of Carnivores. *Journal of Mammalogy*, 37:11-23, 2 figures, 4 tables.
- Lillegraven, Jason A., Steven D. Thompson, Brian K. McNab, and James L. Patton  
1987. The Origin of Eutherian Mammals. *Biological Journal of the Linnean Society* (London), 32:281-336, 10 figures.
- List, Robert J.  
1971. Smithsonian Meteorological Tables, Sixth Edition. *Smithsonian Miscellaneous Collections*, 114: xi + 527 pages, 174 tables.
- Lotze, Joerg-Henner, and Sydney Anderson  
1979. *Procyon lotor*. *Mammalian Species*, 119:1-8, 4 figures.
- Lusk, Graham  
1917. *The Elements of the Science of Nutrition*. 641 pages, 28 figures, 149 tables, 1 appendix. Philadelphia: W.B. Saunders Company.

- MacMillen, Richard E., and Anthony K. Lee  
1970. Energy Metabolism and Pulmocutaneous Water Loss of Australian Hopping Mice. *Comparative Biochemistry and Physiology*, 35: 355-369, 5 figures, 3 tables.
- Marshall, Larry G.  
1988. Land Mammals and the Great American Interchange. *American Scientist*, 76:380-388, 7 figures.
- Marshall, Larry G., S. David Webb, J. John Sepkoski, Jr., and David M. Raup  
1982. Mammalian Evolution and the Great American Interchange. *Science*, 215:1351-1357, 3 figures, 1 table.
- Martin, Alexander C., Herbert S. Zim, and Arnold L. Nelson  
1951. *American Wildlife and Plants*. x + 500 pages. New York: McGraw-Hill Book Company, Incorporated.
- Martin, Larry D.  
1989. Fossil History of the Terrestrial Carnivora. In John L. Gittleman, editor, *Carnivore Behavior, Ecology, and Evolution*, pages 536-568, 10 figures. Ithaca: Cornell University Press.
- McNab, Brian K.  
1966. The Metabolism of Fossorial Rodents: A Study of Convergence. *Ecology*, 47:712-733, 19 figures, 5 tables.  
1970. Body Weight and the Energetics of Temperature Regulation. *Journal of Experimental Biology*, 53:329-348, 9 figures, 3 tables, table of symbols.  
1978a. The Comparative Energetics of Neotropical Marsupials. *Journal of Comparative Physiology*, 125:115-128, 14 figures, 3 tables.  
1978b. Energetics of Arboreal Folivores: Physiological Problems and Ecological Consequences of Feeding on an Ubiquitous Food Supply. In G.G. Montgomery, editor, *The Ecology of Arboreal Folivores*, pages 153-162, 10 figures, 3 tables. Washington, D.C.: Smithsonian Institution Press.  
1979a. Climatic Adaptation in the Energetics of Heteromyid Rodents. *Comparative Biochemistry and Physiology*, 62A:813-820, 6 figures.  
1979b. The Influence of Body Size on the Energetics and Distribution of Fossorial and Burrowing Mammals. *Ecology*, 60:1010-1021, 12 figures, 1 table.  
1980a. Food Habits, Energetics, and the Population Biology of Mammals. *The American Naturalist*, 116:106-124, 9 figures, 1 table.  
1980b. On Estimating Thermal Conductance in Endotherms. *Physiological Zoology*, 53:145-156, 5 figures, 1 table.  
1983a. Ecological and Behavioral Consequences of Adaptation to Various Food Resources. In J.F. Eisenberg and D.G. Kleiman, editors, *Advances in the Study of Mammalian Behavior*. *American Society of Mammalogists*, special publication, 7:664-697, 12 figures, 2 tables.  
1983b. Energetics, Body Size, and the Limits to Endothermy. *Journal of Zoology, London*, 199:1-29, 16 figures.  
1984a. Physiological Convergence amongst Ant-Eating and Termite-Eating Mammals. *Journal of Zoology, London*, 203:485-510, 19 figures, 2 tables.  
1984b. Commentary. *Oecologia* (Berlin), 64:423-424.  
1986a. The Influence of Food Habits on the Energetics of Eutherian Mammals. *Ecological Monographs*, 56:1-19, 6 figures, 2 tables, 1 appendix.  
1986b. Food Habits, Energetics, and the Reproduction of Marsupials. *Journal of Zoology, London*, 208:595-614, 10 figures, 1 table.  
1988a. Complications Inherent in Scaling the Basal Rate of Metabolism in Mammals. *The Quarterly Review of Biology*, 63:25-54, 6 figures, 4 tables.  
1988b. Energy Conservation in a Tree-Kangaroo (*Dendrolagus matschiei*) and the Red Panda (*Ailurus fulgens*). *Physiological Zoology*, 61:280-292, 9 figures.  
1989. Basal Rate of Metabolism, Body Size, and Food Habits in the Order Carnivora. In John L. Gittleman, editor, *Carnivore Behavior, Ecology, and Evolution*, pages 335-354, 3 figures, 1 table. Ithaca: Cornell University Press.
- McNab, Brian K., and Peter Morrison  
1963. Body Temperature and Metabolism in Subspecies of *Peromyscus* from Arid and Mesic Environments. *Ecological Monographs*, 33:63-82, 26 figures, 7 tables.
- Mech, L. David, Donald M. Barnes, and John R. Tester  
1968. Seasonal Weight Changes, Mortality, and Population Structure of Raccoons in Minnesota. *Journal of Mammalogy*, 49:63-73, 2 figures, 3 tables.
- Mellen, William J.  
1963. Body Size and Metabolic Rate in the Domestic Fowl. *Agricultural Science Review*, Fall:20-26, and 49, 1 figure.
- Mugaas, John N., and James R. King  
1981. Annual Variation of Daily Energy Expenditure by the Black-billed Magpie: A Study of Thermal and Behavioral Energetics. *Studies in Avian Biology*, 5: viii + 78 pages, 14 figures, 18 tables, list of symbols, 1 appendix.
- Mugaas, John N., and John Seidensticker  
Ms. Geographic Variation of Lean Body Mass, and a Model of Its Effect on the Capacity of the Raccoon to Fatten and Fast.
- Mugaas, John N., John Seidensticker, and Paul Cook  
In prep. Basal and Thermoregulatory Metabolism of the Coatis *Nasua nasua* and *Nasua narica* (Carnivora: Procyonidae).
- Müller, E., and E. Kulzer  
1977. Body Temperature and Oxygen Uptake in the Kinkajou (*Potos flavus*, Schreber), a Nocturnal Tropical Carnivore. *Archives Internationales de Physiologie et de Biochimie*, 86:153-163, 5 figures, 1 table.
- Müller, E.F., and H. Rost  
1983. Respiratory Frequency, Total Evaporative Water Loss and Heart Rate in the Kinkajou (*Potos flavus* Schreber). *Zeitschrift für Säugetierkunde*, 48:217-226, 8 figures, 2 tables.
- Nicoll, M.E., and Steven D. Thompson  
1987. Basal Metabolic Rates and Energetics of Reproduction in Therian Mammals: Marsupials and Placentals Compared. *Symposium of the Zoological Society of London*, 57:7-27, 4 figures, 3 tables.
- Noll-Banholzer, Ursel  
1979. Body Temperature, Oxygen Consumption, Evaporative Water Loss and Heart Rate in the Fennec. *Comparative Biochemistry and Physiology*, 62A:585-592, 6 figures, 5 tables.
- Nowak, Ronald M., and John L. Paradiso  
1983. *Walker's Mammals of the World*. Fourth edition, lxxxvi + 1362 pages. Baltimore: The Johns Hopkins University Press.
- O'Brien, Stephen J., William G. Nash, David E. Wildt, Mitchell E. Bush, and Raoul E. Benveniste  
1985. A Molecular Solution to the Riddle of the Giant Panda's Phylogeny. *Nature*, 317:140-144, 4 figures.
- Ott, Lyman  
1984. *An Introduction to Statistical Methods and Data Analysis*. Second edition, xi + 775 pages, 118 figures, 169 tables, 1 appendix. Boston: Duxbury Press.
- Poglayen-Neuwall, I.  
1975. Procyonids and Pandas. In Rudolf Altevoigt, Renate Angermann, Heinrich Dathe, Bernhard Grzimek, Konrad Herter, Detlef Müller-Using, Urs Rahm, and Erich Thenius, editors, *Mammals 111. Grzimek's Animal Life Encyclopedia*, 12:90-116, 14 figures, 5 plates. New York: Van Nostrand and Reinhold Company.  
1987. Management and Breeding of the Ringtail or Cacomistle *Bassariscus astutus* in Captivity. *International Zoo Yearbook*, 26:276-280, 1 table.
- Poglayen-Neuwall, I., and Ingeborg Poglayen-Neuwall  
1980. Gestation Period and Parturition of the Ringtail *Bassariscus astutus*

- (Liechtenstein, 1830). *Zeitschrift für Säugetierkunde*, 45:73–81, 1 figure.
- Poglayen-Neuwall, Ivo, and Dale E. Toweill  
1988. *Bassariscus astutus*. *Mammalian Species*, 327:1–8, 4 figures.
- Prosser, C. Ladd  
1986. *Adaptational Biology: Molecules to Organisms*. vii + 784 pages, 226 figures, 22 tables. New York: John Wiley and Sons, Incorporated.
- Prothero, John  
1984. Scaling of Standard Energy Metabolism in Mammals, I: Neglect of Circadian Rhythms. *Journal of Theoretical Biology*, 106:1–8, 2 tables.
- Raven, Peter H., and Daniel I. Axelrod  
1975. History of the Flora and Fauna of Latin America. *American Scientist*, 63:420–429, 10 figures.
- Robbins, Charles T.  
1983. *Wildlife Feeding and Nutrition*. xvi + 343 pages, 97 figures, 56 tables. New York: Academic Press.
- Russell, James K.  
1983. Altruism in Coati Bands: Nepotism or Reciprocity? In Samuel K. Wasser, editor, *Social Behavior of Female Vertebrates*, pages 263–290, 8 figures, 3 tables. New York: Academic Press.
- Sanderson, G.C.  
1983. *Procyon lotor* (Mapache, Raccoon). In Daniel H. Janzen, editor, *Costa Rican Natural History*, pages 485–488, 1 figure. Chicago: The University of Chicago Press.  
1987. Raccoon. In Milan Novak, James A. Baker, Martyn E. Obbard, and Bruce Malloch, editors, *Wild Furbearer Management and Conservation in North America*, pages 486–499, 10 figures, 4 tables. Ontario: Ministry of Natural Resources.
- Sarich, V.M.  
1976. Transferrin. *Transactions of the Zoological Society of London*, 33:165–171.
- Schmitz, O.J., and D.M. Lavigne  
1984. Intrinsic Rate of Increase, Body Size, and Specific Metabolic Rate in Marine Mammals. *Oecologia* (Berlin), 62:305–309, 2 figures, 2 appendices.
- Schneider, Dean G., L. David Mech, and John R. Tester  
1971. Movements of Female Raccoons and Their Young as Determined by Radio-Tracking. *Animal Behavior Monograph*, 4:1–43, 11 figures, 6 tables.
- Scholander, P.F., Vladimir Walters, Raymond Hock, and Laurence Irving  
1950a. Body Insulation of Some Arctic and Tropical Mammals and Birds. *Biological Bulletin*, 99:225–236, 6 figures.  
1950b. Heat Regulation in Some Arctic and Tropical Mammals and Birds. *Biological Bulletin*, 99:237–258, 11 figures, 2 tables.  
1950c. Adaptation to Cold in Arctic and Tropical Mammals and Birds in Relation to Body Temperature, Insulation, and Basal Metabolic Rate. *Biological Bulletin*, 99:259–271, 3 figures, 3 tables.
- Segall, Walter  
1943. The Auditory Region of the Arctoid Carnivores. *Zoological Series of Field Museum of Natural History*, 29:33–59, 4 figures.
- Seidensticker, John, A.J.T. Johnsingh, Rebecca Ross, Greg Sanders, and Maryla B. Webb  
1988. Raccoons and Rabies in Appalachian Mountain Hollows. *National Geographic Research*, 4:359–370, 4 figures, 7 tables.
- Sharp, Ward M., and Louise H. Sharp  
1956. Nocturnal Movements and Behavior of Wild Raccoons at a Winter Feeding Station. *Journal of Mammalogy*, 37:170–177, 2 figures.
- Shield, John  
1972. Acclimation and Energy Metabolism of the Dingo, *Canis dingo* and the Coyote, *Canis latrans*. *Journal of Zoology, London*, 168:483–501, 3 figures, 9 tables.
- Shkolnik, Amiram, and Knut Schmidt-Nielsen  
1976. Temperature Regulation in Hedgehogs from Temperate and Desert Environments. *Physiological Zoology*, 49:56–64, 4 figures, 1 table.
- Stains, Howard J.  
1956. The Raccoon in Kansas, Natural History, Management, and Economic Importance. *University of Kansas Museum of Natural History and State Biological Survey of Kansas Miscellaneous Publication*, 10: iv + 76 pages, 14 figures, 19 tables, 4 plates.
- Statistical Analysis System (SAS)  
1982. *A User's Guide: Statistics*. Raleigh: SAS Institute, Incorporated.
- Stuewer, Frederick W.  
1942. Studies of Molting and Priming of Fur of the Eastern Raccoon. *Journal of Mammalogy*, 23:399–404, 3 figures, 1 table.  
1943. Raccoons: Their Habits and Management in Michigan. *Ecological Monographs*, 13:203–257, 55 figures, 16 tables.
- Tagle, D.A., M.M. Miyamoto, M. Goodman, O. Hofmann, G. Braunitzer, R. Göltenboth, and H. Jalanka  
1986. Hemoglobin of Pandas: Phylogenetic Relationships of Carnivores as Ascertained with Protein Sequence Data. *Naturwissenschaften*, 73:512–514, 2 figures.
- Taylor, Walter P.  
1954. Food Habits and Notes on Life History of the Ring-tailed Cat in Texas. *Journal of Mammalogy*, 35:55–63, 1 table.
- Thompson, S.D.  
1987. Body Size, Duration of Parental Care, and the Intrinsic Rate of Natural Increase in Eutherian and Metatherian Mammals. *Oecologia* (Berlin), 71:201–209, 2 figures, 3 tables, 1 appendix.
- Thorkelson, Jeffrey  
1972. Design and Testing of a Heat Transfer Model of a Raccoon (*Procyon lotor*) in a Closed Tree Den. xvii + 95 pages, 35 figures, 16 tables, 3 appendices. Doctoral dissertation, Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis.
- Thorkelson, Jeffrey, and Robert K. Maxwell  
1974. Design and Testing of a Heat Transfer Model of a Raccoon (*Procyon lotor*) in a Closed Tree Den. *Ecology*, 55:29–39, 6 figures, 3 tables.
- Todd, Neil B., and Suzanne R. Pressman  
1968. The Karyotype of the Lesser Panda (*Ailurus fulgens*) and General Remarks on the Phylogeny and Affinities of the Panda. *Carneige Genetics Newsletter*, 5:105–108, 2 figures.
- Toweill, Dale E., and James G. Teer  
1977. Food Habits of Ringtails in the Edwards Plateau Region of Texas. *Journal of Mammalogy*, 58:660–663, 1 table.
- Toweill, Dale E., and Deyanne B. Toweill  
1978. Growth and Development of Captive Ringtails (*Bassariscus astutus flavus*). *Carnivore*, 1:46–53, 3 figures, 2 tables.
- Trapp, Gene R.  
1978. Comparative Behavioral Ecology of the Ringtail and Gray Fox in Southwestern Utah. *Carnivore*, 1:3–32, 10 figures, 13 tables, 1 appendix.
- United States Department of the Interior Geological Survey  
1972. *Front Royal Quadrangle N3852.5-W7807.517.5*. AMS 5361 1 NW-Series V034.
- Vogel, Peter  
1980. Metabolic Levels and Biological Strategies in Shrews. In Knut Schmidt-Nielsen, Liana Bolis, and C. Richard Taylor, editors, *Comparative Physiology: Primitive Mammals*, pages 170–180, 2 figures, 1 table. Cambridge: Cambridge University Press.
- Wang, Lawrence C.H., Douglas L. Jones, Robert A. MacArthur, and William A. Fuller  
1973. Adaptation to Cold: Energy Metabolism in an Atypical Lagomorph,

- the Arctic Hare (*Lepus arcticus*). *Canadian Journal of Zoology*, 51:841-846, 1 figure, 2 tables.
- Wayne, Robert K., Raoul E. Benveniste, Dianne N. Janczewski, and Stephen J. O'Brien  
 1989. Molecular and Biochemical Evolution of the Carnivora. In John L. Gittleman, editor, *Carnivore Behavior, Ecology, and Evolution*, pages 465-494, 5 figures, 2 tables. Ithaca: Cornell University Press.
- Webb, S. David  
 1977. A History of Savanna Vertebrates in the New World, Part I: North America. *Annual Review of Ecology and Systematics*, 8:355-380, 2 figures.  
 1978. A History of Savanna Vertebrates in the New World, Part II: South America and the Great Interchange. *Annual Review of Ecology and Systematics*, 9:393-426, 1 table.  
 1985a. Main Pathways of Mammalian Diversification in North America. In F.G. Stehli and S.D. Webb, editors, *The Great American Biotic Interchange*, pages 201-217, 1 figure, 1 table. New York: Plenum Publishing.  
 1985b. Late Cenozoic Mammal Dispersals between the Americas. In F.G. Stehli and S.D. Webb, editors, *The Great American Biotic Interchange*, pages 357-386, 3 figures, 1 table. New York: Plenum Publishing.
- Whitney, Leon F., and Acil B. Underwood  
 1952. *The Raccoon*. vi + 177 pages, 2 tables, 8 plates. Orange, Connecticut: Practical Science Publishing Company.
- Wood, John E.  
 1954. Food Habits of Furbearers of the Upland Post Oak Region in Texas. *Journal of Mammalogy*, 35:406-414, 2 tables.
- Wozencraft, W. Chris  
 1984. A Phylogenetic Reappraisal of the Viverridae and Its Relationship to Other Carnivora. Two volumes, xxviii + 1023 pages, 22 figures, 81 tables, 34 plates, 9 appendices. Doctoral dissertation, Department of Systematics and Ecology, University of Kansas, Lawrence.  
 1989a. The Phylogeny of the Recent Carnivora. In John L. Gittleman, editor, *Carnivore Behavior, Ecology, and Evolution*, pages 495-535, 2 figures, 2 tables, 1 appendix. Ithaca: Cornell University Press.  
 1989b. Appendix: Classification of the Recent Carnivora. In John L. Gittleman, editor, *Carnivore Behavior, Ecology, and Evolution*, pages 569-593. Ithaca: Cornell University Press.
- Wurster, D.H., and K. Benirschke  
 1968. Comparative Cytogenetic Studies in the Order Carnivora. *Chromosoma* (Berlin), 24:336-382, 34 figures, 1 table.
- Zervanos, Stam M.  
 1975. Seasonal Effects of Temperature on the Respiratory Metabolism of the Collared Peccary (*Tayassu tajacu*). *Comparative Biochemistry and Physiology*, 50A:365-371, 6 figures.







## REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

**Manuscripts** intended for series publication receive substantive review (conducted by their originating Smithsonian museums or offices) and are submitted to the Smithsonian Institution Press with Form SI-36, which must show the approval of the appropriate authority designated by the sponsoring organizational unit. Requests for special treatment—use of color, foldouts, case-bound covers, etc.—require, on the same form, the added approval of the sponsoring authority.

**Review** of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of manuscripts and art.

**Copy** must be prepared on typewriter or word processor, double-spaced, on one side of standard white bond paper (not erasable), with 1<sup>1</sup>/<sub>4</sub>" margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

**Front matter** (preceding the text) should include: **title page** with only title and author and no other information; **abstract page** with author, title, series, etc., following the established format; **table of contents** with indents reflecting the hierarchy of heads in the paper; also, **foreword** and/or **preface**, if appropriate.

**First page** of text should carry the title and author at the top of the page; **second page** should have only the author's name and professional mailing address, to be used as an unnumbered footnote on the first page of printed text.

**Center heads** of whatever level should be typed with initial caps of major words, with extra space above and below the head, but no other preparation (such as all caps or underline, except for the underline necessary for generic and specific epithets). Run-in paragraph heads should use period/dashes or colons as necessary.

**Tabulations** within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or numbered table captions.

**Formal tables** (numbered, with captions, boxheads, stubs, rules) should be submitted as carefully typed, double-spaced copy separate from the text; they will be typeset unless otherwise requested. If camera-copy use is anticipated, do not draw rules on manuscript copy.

**Taxonomic keys** in natural history papers should use the aligned-couplet form for zoology and may use the multi-level indent form for botany. If cross referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

**Synonymy** in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

**Text-reference system** (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones, 1910:122)" or "...Jones (1910:122)." If bibliographic footnotes are

required, use the short form (author, brief title, page) with the full citation in the bibliography.

**Footnotes**, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

**Bibliography**, depending upon use, is termed "Literature Cited," "References," or "Bibliography." Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume (number):page: "10(2):5-9." For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

**Legends** for illustrations must be submitted at the end of the manuscript, with as many legends typed, double-spaced, to a page as convenient.

**Illustrations** must be submitted as original art (not copies) accompanying, but separate from, the manuscript. Guidelines for preparing art may be secured from the Series Section, SI Press. All types of illustrations (photographs, line drawings, maps, etc.) may be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively as they will appear in the monograph. If several illustrations are treated as components of a single composite figure, they should be designated by lowercase italic letters on the illustration; also, in the legend and in text references the italic letters (underlined in copy) should be used: "Figure 9b." Illustrations that are intended to follow the printed text may be termed **Plates**, and any components should be similarly lettered and referenced: "Plate 9b." Keys to any symbols within an illustration should appear on the art rather than in the legend.

**Some points of style:** Do not use periods after such abbreviations as "mm, ft, USNM, NNE." Spell out numbers "one" through "nine" in expository text, but use digits in all other cases if possible. Use of the metric system of measurement is preferable; where use of the English system is unavoidable, supply metric equivalents in parentheses. Use the decimal system for precise measurements and relationships, common fractions for approximations. Use day/month/year sequence for dates: "9 April 1976." For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc. Omit space between initials of a personal name: "J.B. Jones."

**Arrange and paginate sequentially every sheet of manuscript** in the following order: (1) title page, (2) abstract, (3) contents, (4) foreword and/or preface, (5) text, (6) appendices, (7) notes section, (8) glossary, (9) bibliography, (10) legends, (11) tables. Index copy may be submitted at page proof stage, but plans for an index should be indicated when the manuscript is submitted.

