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GEOGRAPHIC VARIATION OF LEAN BODY MASS AND A MODEL OF ITS EFFECT ON THE CAPACITY OF THE RACCOON TO FATTEN AND FAST

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John N. Mugaas and John Seidensticker[1]

ABSTRACT

In the eastern United States, apparent lean body mass (ALBM) of raccoons (*Procyon lotor*) increased from south to north, and appeared to follow Bergmann's rule: subtropical Key Vaca, females = 2.0 kg, males = 2.4 kg; mild temperate southeastern United States, females = 3.2 kg, males = 3.5 kg; harsh to severe temperate Michigan and Minnesota, females = 4.5 kg, males = 5.0 kg. We postulated that selection has favored large lean mass in the cold parts of the raccoon's range because it provides greater fasting endurance. In mammals, as lean body mass (LBM) increases, the potential to store energy as fat (F_s = $LBM^{1.0}$) increases out of proportion to the cost of basal metabolism (H_b = $mass^{0.75}$). Thus, big fat raccoons should be able to fast for a longer period of time than small fat ones. We modeled these relationships for raccoons. We found that each increase in ALBM substantially increased the length of time they could fast. Since the increased fasting times were necessary for their winter survival, the model supported our hypothesis. We also concluded that the northern edge of their range is determined by the limits of their genetic potential to increase ALBM. The amount of fat deposited in the fall also varied geographically: subtropical raccoons achieved 14 to 17% apparent body fat (ABF), those from Florida to Virginia 19 to 42% ABF, and those around the Great Lakes 31 to 50% ABF. Geographic variation in ABF suggests that seasonal lipogenesis is coupled, via neuroendocrine mechanisms, to environmental cues that stimulate the appropriate degree of fat deposition in each local area. The data also suggest that there may be geographic differences in the capacity to fatten.

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RESUMEN

El peso magro aparente (ALBM) de los mapaches (*Procyon lotor*) en el este de los Estados Unidos aumenta de sur a norte y parece seguir la regla de Bergmann: en la zona subtropical de Key Vaca, las hembras pesan 2.0 kg y los machos 2.4 kg; en el sudeste templado de los Estados Unidos, las hembras pesan 4.5 kg, los machos 5.0 kg. Postulamos que la selección ha favorecido los pesos magros aparentes grandes en las zonas frías del área de distribución del mapache, en razón que esta provee mayor resistencia al ayuno. Los incrementos en el peso magro (LBM) en mamíferos, son acompañados por incrementos en la capacidad para almacenar energía en forma de grasa ($Fs=LBM^{1.0}$) fuera de proporción con respecto al costo del metabolismo basal ($H_b=peso^{0.75}$). Por tanto, los mapaches grandes y gordos deberían ser capaces de ayunar por más tiempo que aquellos gordos y pequeños. Nosotros modelamos esas relaciones para mapaches. Encontramos que cada incremento en ALBM resulta en un incremento sustancial en el tiempos que ellos pueden ayunar. Dado que el alargue en el tiempo de ayuno es necesario para la sobrevivencia durante el invierno, el modelo apoya nuestra hipótesis. También concluimos que, el límite norte de su distribución es determinado por sus límites en el potencial genético para aumentar el ALBM. La cantidad de grasa depositada durante el otoño también varió geograficamente: los mapaches subtropicales alcanzaron 14% or 17% de gordura aparente (ABF), aquellos desde Florida a Virginia 19-42% ABF), y aquellos alrededor de los Grandes Lagos 31-50% ABF. La variabilidad geográfica en ABF sugiere que la lipogénesis estacional está ligada, mediante mecanismos neuro endocrinos, a señales medioambientales que estimulan el grado de deposición de grasa apropiado para cada área. Los datos sugieren asímismo que, pueden existir diferencias geográficas en la capacidad para engordar.

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INTRODUCTION

The North American raccoon, *Procyon lotor* (Fig. 1), has a distribution that extends from 8°N in tropical Panama to 60°N in Alberta, Canada (Lotze and Anderson 1979; Kaufmann 1982). Geographic variation in the size of this widely distributed species has been examined by several investigators. Johnson (1970) reports that, east of the Mississippi River in the United States, adult male raccoons from northern states are larger (6.1 to 8.0 kg) than those from southern states (2.4 to 5.2 kg). He speculates that their body mass follows Bergmann's rule. Raccoons also display similar size-latitude correlations for head-body length (McNab 1971), and, in the eastern United States, skull characteristics (Kennedy and Lindsay 1984; Ritke and Kennedy 1988). In the western United States, skull characteristics show a size-longitude, rather than a size-latitude relationship (Ritke and Kennedy 1988).

Bergmann's rule states that "...races from cooler climates, in species of warm-blooded vertebrates, tend to be larger than races of the same species living in warmer climates..." (Mayr 1963:319). Many authors relate geographic variation in size to adaptive differences in heat-exchange characteristics (surface to volume ratio, insulative value of fur or feathers, etc.), and the assumption is that selection favors size variation for thermoregulatory reasons (Mayr 1956, 1963; Rensch 1959; Hamilton 1961; Bartholomew 1968; Brown and Lee 1969; Kendeigh 1969; James 1970, 1991; Kleiber 1972; Calder 1974, 1984; Searcy 1980). Calder (1974) summarizes the size-related variation in heat-exchange characteristics that influence thermoregulation: (1) the magnitude of the thermoneutral zone varies directly with size, and (2) mass specific thermal conductance varies inversely with size. In this scheme, the wider thermoneutral zone and lower thermal conductivity of large size are a benefit in cold climates because they slow down heat loss, while, for the opposite reasons, small size is a benefit in warm climates. Some investigators contend that since there are selection pressures other than temperature that also act on body size, it is difficult, or even impossible, in some cases, to demonstrate that size variation functions primarily as a thermoregulatory adaptation (Scholander 1955; Rosenzweig 1968; McNab 1971; Searcy 1980; Kennedy and Lindsay 1984).

Another advantage to geographic variation in size, and one that may be fundamentally more important than thermoregulatory superiority, is fasting endurance, which varies directly with mass (Lindsey 1966; Rosenzweig 1968; Calder 1974, 1984; Downhower 1976; Ketterson and Nolan 1976; Young 1976; Adler 1984; Lindstedt and Boyce 1985; French 1986, 1988). Variation in size is accompanied by variation in lean body mass (LBM). As LBM increases, the ability to store energy as fat ($F_s = LBM^{1.0}$, where F_s is fat storage; Calder 1984) increases out of proportion to the rate of basal metabolism ($H_b = m^{0.75}$, where H_b is basal metabolism and m is total body mass). Consequently, large fat

Figure 1.--North American raccoon, *Procyon lotor*.

individuals can withstand a longer fast than small fat ones.   This suggests the following hypothesis. In the northern part of the raccoons'range, where they are forced to retreat to a den and live without eating for several months each winter (Stuewer 1943; Mech et al. 1968; Schneider et al. 1971), large lean body mass has been selected for because it increases the length of time these individuals can fast. The selection force in this case would be the length and severity of the winter period.

　　　　To test this hypothesis we examined published and unpublished body-mass data for raccoons from eight different latitudes in the eastern United States. We were able to estimate apparent lean body mass (ALBM), and apparent amount of fat deposited each fall (ABF) at each location. From the latitudinal differences in these variables, and the differences in maximum fasting times associated with variations in ALBM, we concluded that survival of raccoons in the northern part of their range is dependent on selection for large LBM. Our data suggest there is

a genetic basis for geographic variation in LBM, and that the northern edge of the raccoon's distribution may be determined by the limits of its genetic potential to increase LBM.

ACKNOWLEDGMENTS

MATERIALS AND METHODS

Body masses of adult raccoons from 25° to 45° north latitude were taken from literature (Table 1): Minnesota (Mech et al. 1968), southern Michigan (Stuewer 1943), southwestern Tennessee (Moore and Kennedy 1985), east central and southwestern Alabama (Johnson 1970), central Florida (Goldman 1950), and Key Vaca, Florida (Goldman 1950). Data for adult raccoons from north central Virginia (38°N) were obtained from a five-year investigation of the Posey Hollow raccoon population at the National Zoological Park's Conservation and Research Center (CRC, Front Royal, Virginia). Raccoons at CRC were live-trapped during the first 10 days of each month (May 1980 through December 1984) on a fixed trapping grid of 30 to 35 stations (one or two live-traps per station). Within a few hours after capture all trapped animals were weighed, sexed, aged, and categorized with respect to reproductive status, physical condition, and parasite load before being released (Seidensticker et al. 1988; Hallett et al. 1991). Mass data of juvenile raccoons were obtained for Minnesota (Mech et al. 1968) and for north central Virginia (Posey Hollow study, CRC).

At CRC, body mass was at its maximum (MBM) in late fall or early winter when raccoons were fattest. During the winter months raccoons gradually depleted their fat stores, and, by spring, their body masses were at their annual minimum. These animals were in poor condition and very skinny in the spring, and this annual minimum was used to approximate their apparent lean body mass (ALBM). ALBM was constant from year to year, which indicated that body fat was depleted to about the same extent each winter, and that ALBM was a stable feature of the population. Because of the constancy in ALBM, we could estimate the approximate mass of body fat (ABF) deposited each fall, and the resultant percent body fat, from the difference between MBM and ALBM. This same logic was used to estimate MBM, ALBM, and ABF from mass data for raccoons from other geographic areas (Table 1). Except for adult raccoons from Minnesota, where data are for individual animals, all body mass values in Table 1 are averages for each geographic area.

Based on climate data from Kincer (1941), we classified the severity of winter for each of these locations as either warm, mild, moderate, harsh, or severe (Table 2). Isotherm maps of average January, and average annual temperatures for the eastern United States (Fig. 2) place these climate categories, and the locations from which data were obtained, into perspective.

Table 1.—Annual Change in *Procyon lotor* body mass.

Location (°N)	Annual Body Mass (kg)		Body Fat[b]		Ref[h]
	Maximum[a]	Minimum[a]	Maximum (kg)	%MBM	
ADULTS					
Key Vaca (25°N)					1
Male	2.8[c]	2.4[c] 1.8-2.7(5)	0.4	14	
Female	2.4[c]	2.0[c] 1.8-2.3(2)	0.4	17	
Florida (28°N)					1
Male	5.0[d] 4.5-5.4(5)	3.8[d]	1.2	24	
Female	4.1[d] 3.5-4.5(3)	3.3[d]	0.8	19	
Alabama, southwestern (32°N)					2
Male	4.3 ±0.2 (56)	3.6 ±0.2 (32)	0.7	16	
Female	3.8 ±0.2 (30)	3.2 ±0.3 (15)	0.6	16	
Alabama, east central (34°N)					2
Male	5.3 ±0.9 (12)	3.5 ±0.4 (10)	1.8	34	
Female	4.3 ±0.4 (17)	3.2 ±0.2 (8)	1.1	26	
Tennessee (36°N)					4
Male	6.8[e]	4.2[e]	2.6	38	
Female	5.5[e]	3.2[e]	2.3	42	
Virginia (38°N)					7
Male	6.7 ±0.9 (7)	4.0 ±0.5 (53)	2.7	40	
Female	5.6 ±0.8 (17)	3.6 ±0.6 (50)	2.0	36	

Table 1 Continued.

Location (°N)	Annual Body Mass (kg)		Body Fat[b]		Ref[h]
	Maximum[a]	Minimum[a]	Maximum (kg)	%MBM	
Michigan (42°N)					5
Male	7.4[e]	5.1[e]	2.3	31	
	(7)	(15)			
Female	6.9[e]	4.7[e]	2.2	32	
	(4)	(11)			
Minnesota[f] (45°N)					3
608, Female	9.5	5.0	4.5	47	
170, Male	10.4	5.2	5.2	50	
634, Female	9.0	4.5	4.5	50	
JUVENILES					
Virginia (38°N)					7
Male	3.3	3.1	0.2	6	
	±0.9 (19)	±0.5 (12)			
Female	3.0	2.4	0.6	20	
	±0.7 (22)	±0.6 (22)			
Minnesota[g] (45°N)					3
Sex?	4.3	2.1	2.2	51	
	±0.9 (18)	±0.3 (6)			

[a] Annual maximum body mass = MBM; annual minimum body mass = apparent lean body mass = ALBM; in kg, with $\pm$SD, or range of values, and (n) = number of individuals if known.

[b] Annual maximum body fat in kg = apparent body fat = ABF; ABF = MBM - ALBM; %MBM = (ABF·100/MBM).

[c] Data obtained in late winter and considered representative of ALBM. MBM = (0.18·ALBM) + ALBM; based on fall mass gain of raccoons in southwestern Alabama (Johnson 1970).

[d] Data obtained in winter and considered representative of MBM. ALBM estimated assuming 25% ABF for males and 30% ABF for females (Johnson 1970; Zeveloff and Doerr 1985).

[e] Tennessee raccoons from Fig. 1 in Moore and Kennedy (1985). Michigan raccoons from Table 3 in Stuewer (1943).

[f] Each number is for an individual animal from the original study of Mech et al. 1968.

[g] Calculated from Fig. 1 of Mech et al. (1968).

[h] 1. Goldman (1950); 2. Johnson (1970); 3. Mech et al. (1968); 4. Moore and Kennedy (1985); 5. Stuewer (1943); Zeveloff and Doerr (1985); 7. This study.
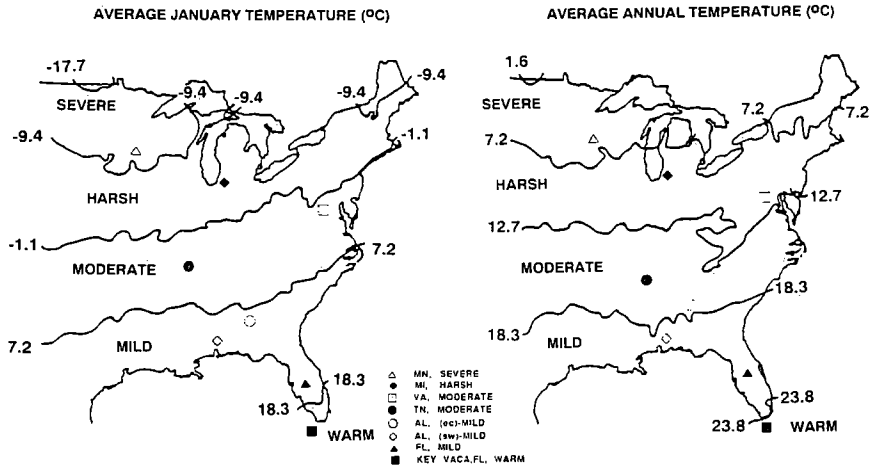
AVERAGE JANUARY TEMPERATURE (°C)   AVERAGE ANNUAL TEMPERATURE (°C)

Figure 2.—Locations from which body mass data for *Procyon lotor* were selected, and isotherms for the eastern United States.

Table 2.—Climate data.[a]

Geographic Area and Climate	Days With Snow Cover[b]	Frost- Free Days	Depth of Frost (inches)	Temperatures (°C)		
				Average Annual Minimum	Average January	Average Annual
Key Vaca (25°N)						
Warm	0[c]	365[c]	0[c]	4.4	21.0	23.9
Florida/Alabama (28° to 34°N)						
Mild	<10	240-320	0-3	-9.4/-1.1	7.2/15.6	18.3/21.1
Tennessee/Virginia (36° to 38°N)						
Moderate	10-40	180-200	3-10	-17.7/-9.4	-1.1/4.4	12.7/15.6
Southern Michigan (42°N)						
Harsh	80-100	160	25-42	-26.1/-23.3	-6.7/-3.8	7.2/10.0
Minnesota (45°N)						
Severe	100-120	140	60-72	-37.2/-31.7	-12.2/-9.4	4.4/7.2

[a]Except where indicated all data are taken from climate maps for the United States (Kincer 1941). Where two values are given for a variable they represent the range of values from lowest to highest.
[b]One inch or more of snow cover.
[c]From climate maps for Florida (Norton 1941).

GEOGRAPHIC VARIATION IN APPARENT LEAN BODY MASS

Results

Adults

At all latitudes males were heavier than females in both fall and spring (Table 1). The difference in mass between sexes was greater in fall than in spring (0.8 $\pm$ 0.3 vs 0.5 $\pm$ 0.24 kg; p < 0.025). This indicates that ALBM of males is, on average, 0.5 kg greater than that of females, and that, in fall, males fatten proportionately more than females.

In general, ALBM increases with increasing latitude (Y = 0.12·X - 0.36; r^2 = 0.77, where Y is ALBM and X is latitude; Fig. 3), but it is obvious that the relationship is not a smooth continuum. ALBM is stable across some latitudes but changes across others. There are two regions of change in ALBM: one between Key Vaca and the mainland, and the other somewhere between 35 and 40°N (Fig. 3). In each case, the transition zone separates a latitudinal change in ALBM of more than 1 kg. This gives ALBM a steplike distribution from Key Vaca to Minnesota, and produces three distinct, stable, size classes: Key Vaca, 25°N, females = 2.0 kg, males = 2.4 kg; southeastern United States, 28 to
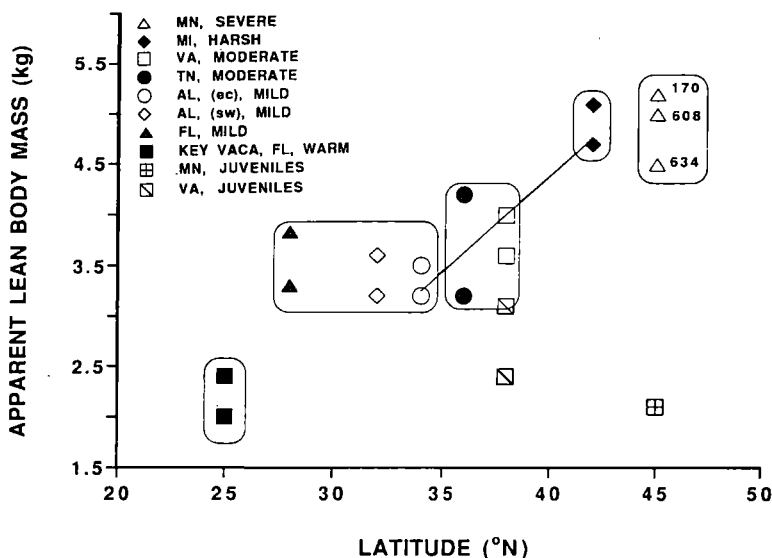

Figure 3.--Relationship between apparent lean body mass and latitude for *Procyon lotor*. The lowest mass value for each pair of symbols represents females, and the highest value males. Symbols for Minnesota are for individual animals. Symbols for adults from each climate type are surrounded by a line.

34°N, females = 3.2 kg, males = 3.5 to 3.8 kg; and southern Great Lakes region, 40 to 45°N, males = 5.1 to 5.2 kg, females = 4.5 to 5.0 kg (Fig. 3). As a species, therefore, raccoons display a wide range of variation in ALBM.

The amount of fat deposited in the fall appears to depend on the severity of the climate to which they are exposed (Table 1, Fig. 4). Thus, ABF is variable both within each climate zone and between climate zones; compare body fat of raccoons from the mild (16 to 34% body fat) and moderate (36 to 42% body fat) climates, and body fat of raccoons from the harsh (31 to 32% body fat) and severe (47 to 50% body fat) climates. This indicates that fall fattening is not an all-or-none phenomenon, but, rather, that it is a graded response, whose degree of expression is determined by the physiological response to local climate. Within any given geographic area, therefore, several environmental cues (changing daylength, changing temperature, changing food abundance, changing food type, to name a few), and the animal's metabolic response to them, as orchestrated by its neuroendocrine system, determine how much body fat is actually deposited during each fall period.

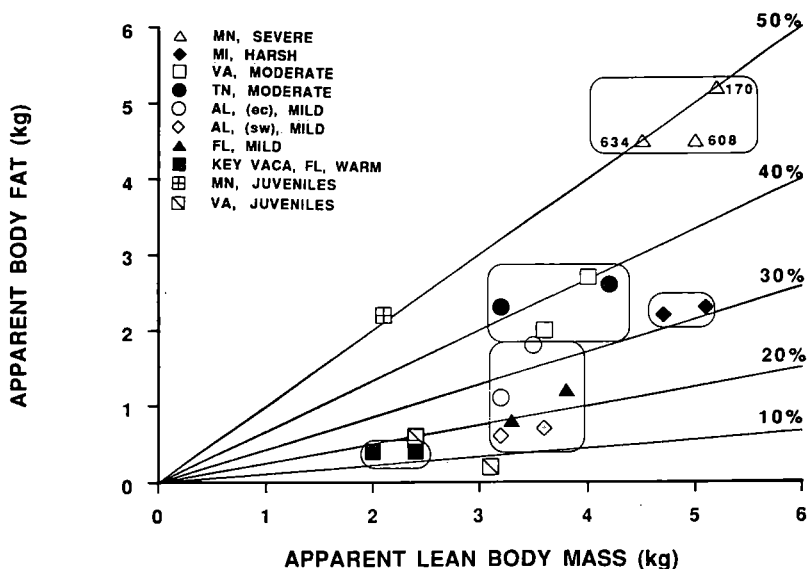Figure 4.—Relationship between apparent body fat and apparent lean body mass for *Procyon lotor*. The lowest apparent lean body mass value for each pair of symbols represents females, and the highest value males. Symbols for adults from each climate type are surrounded by a line. Symbols for Minnesota are for individual animals. The diagonal isolipid lines represent 10, 20, 30, 40, and 50% body fat.

All raccoons may be able to fatten to 50% body fat, but only those in the heaviest size class, living in the most severe climate (Minnesota), apparently achieved this level of obesity (Fig. 4). This could simply mean that in areas south of Minnesota conditions were not severe enough to stimulate maximum fattening. Alternatively, different size classes may have different capacities to fatten. If the latter is true, then there may be geographic differences between populations with respect to their capabilities to fatten.

Juveniles

Young of the year from Minnesota and north central Virginia also fattened in the fall, and reached MBM by early December. Between December and early spring they depleted this fat reserve. The minimum mass achieved at the end of their first winter was less than that of adult animals, and was considered to be their ALBM. ABF was taken as the difference between this value and the MBM attained during their first fall. During the spring and early summer, following their first winter, these young animals increased their ALBM up to the adult level, and maintained it there until they started to fatten during their second fall. This pattern was evident in data from CRC as well as in Figure 2 of Mech et al. (1968). Raccoons in Michigan (Stuewer 1943) and Alabama (Johnson 1970) also do not attain adult mass until fall of their second year. Young of the year from Minnesota had a lower ALBM (2.1 kg) than those from Virginia (females = 2.4 kg, males = 3.1 kg), but young of the year from Minnesota accumulated more fat (2.2 kg = 51% body fat) than those from Virginia (females = 0.6 kg or 20% body fat; males = 0.2 kg or 6% body fat; Table 1, Fig. 4). For young of the year, therefore, the gain in ALBM and the degree of fattening both appear to be linked to length and severity of local winter climate.

Discussion

Adults

Throughout the United States, raccoons fatten during fall, and they attain their annual MBM in the interval from November to early January (Stuewer 1943; Mech et al. 1968; Johnson 1970; Moore and Kennedy 1985; Zeveloff and Doerr 1985).

In climates with severe winter weather (Minnesota, for example; Mech et al. 1968; Schneider et al. 1971), raccoons may remain in their dens for three months or more in the interval from mid-November to mid-March. Since they

keep their body temperature (T_b) above 35°C during this confinement (Thorkelson 1972), their thermogenic requirement is, at the very least, equivalent to their basal metabolic rate (Mugaas et al. 1993). All through this period of forced fasting, their body fat serves as the primary energy source to maintain endothermy. By end of winter, their body fat is depleted, and their mass is at its minimum.

In milder climates, winter weather may confine raccoons to their dens for short periods of time, only occasionally, or not at all (Sharp and Sharp 1956; Johnson 1970; Zeveloff and Doerr 1985; Seidensticker et al. 1988). During winter in these areas, food may be in short supply, difficult to find, and of poor quality. Consequently, even though raccoons may be active nearly every night, they may not find enough food to meet their energy requirements. In this case, their body fat serves as an important energy supplement to their diet, and, as in colder climates, it is depleted during the course of the winter (Johnson 1970; Zeveloff and Doerr 1985). Fall fattening, therefore, appears to be an important adaptation for the winter survival of this species in the United States.

Adult raccoon response to warm climate

Raccoons on Key Vaca (25°N) live in the warmest climate (Fig. 2), and have the smallest ALBM (2.0 to 2.4 kg; Table 1, Fig. 3). These are values for individuals taken on the island in late winter (Goldman 1950), which is near the time that raccoons on the adjacent mainland reach their annual minimum mass (Johnson 1970; Zeveloff and Doerr 1985). Raccoons from the adjacent mild continental climate zone have ALBMs that are 1.2 to 1.4 kg larger than those of the Key Vaca raccoons (Fig. 3).

Unfortunately, little is known of the natural history of these diminutive island raccoons, and the factors that have selected for their small size have not been identified. However, small ALBM would reduce their muscle mass, and total energy requirement (McNab 1978, 1986, 1989). This would provide these animals with a thermoregulatory advantage in this hot humid climate (Calder 1974), and, compared to the heavier mainland raccoons, this would also reduce their total food requirement. This latter point could be important if Key Vaca has a lower level of productivity than the mainland. If food availability on this island does undergo a small seasonal increase, there could be a period of fattening in Key Vaca raccoons. If Key Vaca animals fattened to the same extent as those from coastal southwestern Alabama, they would gain about 0.4 kg of fat each fall (Table 1, Fig. 4). Even though these values are only approximations, we plotted them on Fig. 4 to illustrate that this would provide these animals with a fairly large caloric supplement to help them through lean times.

Adult raccoon response to mild climate

Data for raccoons from Florida and Alabama span the mild climate zone (Figs. 2 and 3), and these are the smallest of the continental forms (Fig. 3). Raccoons in this climate zone fatten less in fall than those from other continental areas (Fig. 4). They also display a wide range of variability in their fattening response, 16 to 34% body fat (Fig. 4), with raccoons from colder areas (east central Alabama) fattening more than those from milder areas (southwestern Alabama). Raccoons in this climate zone are active year-round (Johnson 1970; Zeveloff and Doerr 1985), and the fat they store in fall must function primarily as a caloric supplement to their normal winter diet. Within these latitudes, variations in the requirement for winter energy supplementation are met simply with differences in the amount of body fat stored during the fall.

Adult raccoon response to harsh and severe climates

Raccoons from harsh (southwestern Michigan), and severe (Minnesota) climates are confined to their dens for several months each winter (Stuewer 1943; Schneider et al. 1971), and fat stored in the fall is their only source of calories during this period of fasting. Raccoons from these areas have ALBMs that are, on average, 1.5 kg greater than those from Florida and Alabama (Table 1, Fig. 3).

In Minnesota, raccoons enter the winter with 47 to 50% body fat, while on Stuewer's (1943) study area in Michigan they acquire only 31 to 32% body fat. Winters on Stuewer's study area are milder than those in Minnesota, and raccoons in that part of Michigan are only confined to their dens for about 60 days each winter. Those at Cedar Creek, Minnesota, however, are usually obliged to den continuously for 90 days or more (Mech et al. 1968; Schneider et al. 1971). In other parts of Michigan, where winters are more severe, raccoons den for longer periods of time (Stuewer 1943). We assume those animals meet that challenge by fattening to a greater extent than raccoons on Stuewer's study area. Thus, even in these colder climates, where selection favors an increase in ALBM, the degree of fall fattening is still dependent on local climate conditions.

Adult raccoon response to moderate climate

Between 35 and 40°N, ALBM increases with increasing latitude (Fig. 3). These latitudes appear to form a transition zone between the large raccoons of the southern Great Lakes region and the smaller forms in the southeast, making this a region of phenotypic variability for ALBM. Within these latitudes, ALBM changes by 0.19 kg/°latitude ($Y = 0.19 \cdot X - 3.214$; $r^2 = 0.75$, where Y is ALBM

and X is latitude; solid line in Fig. 3). Separate regression equations for males and females from these latitudes were not different from each other, or from the equation for combined data ($p > 0.1$). Within this transition zone, therefore, gene flow and selection for ALBM appear to have the same effect on both sexes.

This climate zone, situated at the mid-latitudes of the eastern United States, has winter conditions that are intermediate to those north and south of it. In some areas within this zone, winter weather may be so mild that raccoons are active all during that season, in which case their fat stores would simply supplement their diet. In other areas, such as southwestern Tennessee (Moore and Kennedy 1985) and north central Virginia (Seidensticker et al. 1988), periodic intervals of harsh winter weather confine raccoons to their dens for a few days or weeks at a time. In these areas, fat stores serve as both a primary and a supplementary source of calories.

Response of juvenile raccoons to seasonal and geographic variation in climate

In the eastern United States, most raccoon births occur in the interval from March to mid-June (Lotze and Anderson 1979), but, in Florida, some may be born as late as October (Kaufmann 1982). Weaning occurs between week 7 and month 4 (Lotze and Anderson 1979), and survival of the young during their first winter, in any of the climate zones, depends on their ability to acquire enough fat during fall to meet the energy requirements imposed on them by their local climate. Because of the relationship between F_S and H_b, it is important that young of the year first produce enough lean body mass during summer to support the fat required to meet their winter energy requirement. Thus, these constraints should exert a strong selective influence on the timing of births, particularly in areas north of Florida (Table 2, Fig 2).

Young of the year from Virginia and Minnesota do not complete growth of their lean body mass until after their first winter (Table 1, Fig. 3). As young raccoons enter their first fall, growth of lean mass must be slowed, or even suspended, in order to allow fattening to take place. In Minnesota, young of the year (ALBM = 2.1 kg) entered their first winter with 51% body fat (Table 1, Fig. 4), which suggests that, in the severe Minnesota climate, growth of lean body mass was actually suspended in the fall in favor of fat deposition. In Virginia, where winter climate is considerably milder than in Minnesota, ALBM was larger, but ABF amounted to only 6 to 20% body fat (Table 1, Fig. 4). This appears to be a contradiction to our hypothesis, but, in Virginia, young of the year do not need as much fat for winter survival, and growth of lean body mass in the fall must have simply been slowed, rather than suspended. This would give Virginia juveniles a larger ALBM at the end of their first winter.
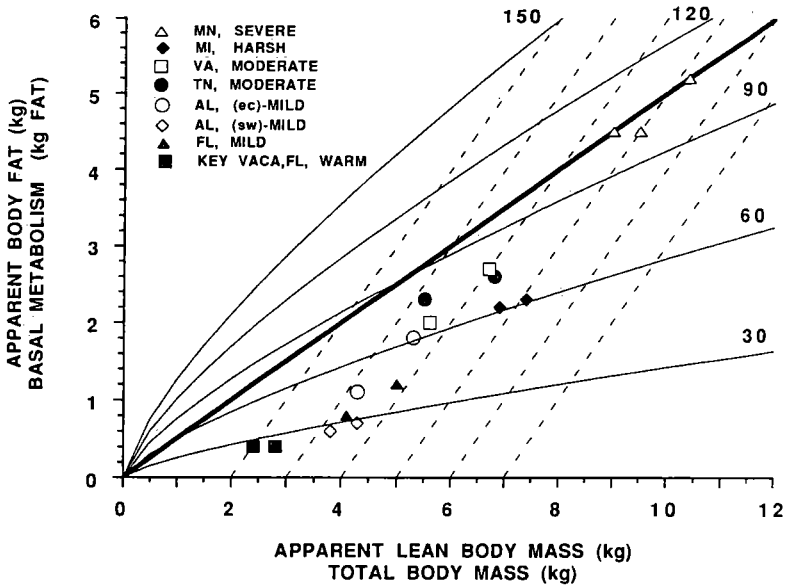
Figure 5.--Model of fattening and fasting ability of *Procyon lotor*. Apparent body fat (ABF = kg), and basal metabolism (H_{bf} = kg fat) are represented by the Y-axis. Apparent lean body mass (ALBM = kg) and total body mass (TBM = kg) are represented by the X-axis. The heavy diagonal line portrays 50% body fat. Each diagonal dashed line represents the relationship between ABF and TBM. When ABF = 0, the diagonal dashed line intersects the X-axis, and TBM = ALBM. Diagonal dashed lines, therefore, represent fattening trajectories for raccoons of various ALBM, and they intersect the heavy solid diagonal line at 50% body fat. The relationship between H_{bf} and TBM, as calculated from Eq. 1, is shown by the thin curved solid lines, which describe the mass of fat required to fuel H_{bf} for 30, 60, 90, 120, or 150 days. Intersection of a fattening trajectory with a thin curved line describes the mass of fat required for a raccoon of that ALBM to fast for that number of days. Symbols represent fall fattening, and its related fasting potential for adult raccoons from eastern United States.

MODEL OF THE CAPACITY FOR FATTENING AND FASTING

Total Body Mass, Apparent Lean Body Mass, and Apparent Body Fat Relationships

In developing the model shown in Figure 5, the following assumptions were made for adult raccoons. (1) TBM = ALBM + ABF, where TBM is total

body mass. (2) Changes in ALBM during the year are small compared to those for ABF, so that ALBM is considered constant, and annual changes in TBM are due to variations in ABF. (3) Body fat content is a function of $LBM^{1.0}$ (Calder 1984); therefore, ABF will always be less than, or, at most, equal to ALBM. Thus, in the spring, when ABF = 0, TBM = ALBM, but as the animal fattens ABF and TBM both increase.

Temporal changes in ABF and TBM, for various ALBMs, are plotted on Figure 5 as thin dashed diagonal lines, and we refer to these as fattening trajectories. For example, one of the Minnesota raccoons (608) has an ALBM of 5.0 kg. In the spring when ABF = 0, and TBM = ALBM, we plot (TBM, ABF) as (5.0, 0). In late summer and fall as the animal fattens, ABF and TBM both increase. If the increases are plotted at various times, the points follow the thin dashed line that runs diagonally upward from (5.0, 0) to (9.5, 4.5). The smallest Minnesota raccoon (634) has an ALBM of 4.5 kg. Its fattening trajectory begins at (4.5, 0), and follows a path that runs parallel to the other thin dashed lines. At the end of fall fattening, ABF = 4.5 kg, and the final point on its trajectory is (9.0, 4.5).

Physiological Limits of Fattening

Raccoons may be able to achieve 50% body fat, and this is shown in the model by the heavy solid diagonal line (Fig. 5). For each ALBM, this degree of obesity occurs at the point where its fattening trajectory intersects the heavy solid diagonal line. In the above examples, the smallest raccoon from Minnesota (ALBM = 4.5 kg) achieved maximal fattening (50% body fat), whereas the other animal (ALBM = 5.0 kg) realized a little less than maximal fattening (47% body fat; Fig. 5).

Days of Fasting

In winter, the lower critical temperature (T_{lc}) of raccoons from Virginia is 11°C, but when they are in their tree den it is reduced to -5°C (Mugaas et al. 1993). The average January temperature for Front Royal, Virginia, is 1°C (Crockett 1972), therefore, even during this coldest month, thermal conditions in their dens are, on average, within their thermoneutral zone, and their thermoregulatory requirement is equivalent to their H_b. We do not have metabolic data for raccoons from other areas, but it is reasonable to assume that geographic variation in thermal conductance is such that the thermogenic demands

associated with winter denning are, in general, not much greater than H_b. Consequently, we modeled fasting ability in terms of the mass of fat required to fuel H_b. Equation 1 describes raccoon basal metabolism as kg of fat:

$$H_{bf} = (H_b \cdot TBM^{0.75} \cdot t \cdot J_{O2})/J_f \qquad\qquad \text{Eq. 1}$$

where H_{bf} is basal metabolic rate (kg fat); H_b is measured basal metabolic rate (16.44 $LO_2 \cdot kg^{-0.75} \cdot day^{-1}$, average for raccoons in winter; Mugaas et al. 1993); $TBM^{0.75}$ is metabolic body mass (kg); t is time (number of days); J_{O2} is heat equivalent for oxygen (0.020087 MJ/L); and J_f is heat equivalent for fat (39.329 MJ/kg). Equation 1 was used to estimate the mass of fat (kg) required to fuel basal metabolism of raccoons ranging in TBM from 1 to 25 kg for 30, 60, 90, 120, and 150 days (thin curved lines, Fig. 5).

The fattening trajectory of each ALBM crosses the thin curved metabolism lines, and their points of intersection describe ABF required to fuel H_b for 30, 60, 90, 120, or 150 days. The smallest raccoon from Minnesota (ALBM = 4.5 kg) requires 0.9, 2.1, and 3.7 kg ABF to fuel basal metabolism for 30, 60, and 90 days, respectively (Fig. 5). If this animal gained 5.8 kg of fat, it could fuel H_b for 120 days (Fig. 5). However, since this represents 1.3 kg more fat than it is capable of depositing (5.8 - 4.5 = 1.3), the model predicts that this raccoon would not be able to fast for 120 days, and would not be able to survive in areas that required it to do so.

Lessons From the Model

Sexual dimorphism

Male raccoons have a 0.5 kg larger ALBM than female raccoons. Males also have a more massive skull (Kennedy and Lindsay 1984), and larger canines (Grau et al. 1970). Kennedy and Lindsay (1984) argue that selection favors larger size in male raccoons because it benefits them in competition for mates. Our model predicts that the 0.5 kg difference in ALBM between sexes changes fasting time within each size class by only 2.5 to 3.0 days. Selection for larger males, for whatever reason, has not produced sexes with vastly different fasting potentials. Because they are larger, however, males have a higher daily energy requirement than females. In the fall, therefore, males would need more food than females to achieve an equivalent degree of obesity, and potential for fasting. This suggests that the increased food requirement associated with their larger size may be a constraint that keeps male raccoons from becoming grossly bigger than females.

Apparent lean body mass

Each solid line on Figure 6 describes the relationship between days of fasting, and ABF for a particular ALBM. Coordinates (ABF, days of fasting) used to construct these lines were determined from an expanded version of Figure 5, and are the intersections of the fattening trajectories with the thin curved metabolism lines for days of fasting. The large dots describe days of fasting possible when starting with 50% body fat. The coordinates for each dot, therefore, could be written as (ALBM, days of fasting), and the X-axis could represent ALBM. Thus, the maximum days of fasting associated with any ALBM can be estimated from Eq. 2, which describes a line drawn through the large dots:

$$Y = 69.2 \cdot X^{0.258} \qquad \text{Eq. 2}$$

where Y is days of fasting, and X is ALBM. As ALBM increases, the *incremental* increase in days of fasting decreases (Fig. 6). Thus, while a 3-kg increase in ALBM from 2 to 5 kg can yield a 24-day gain in fasting time, a similar change in ALBM from 8 to 11 kg will produce only an 8.5-day increase. This
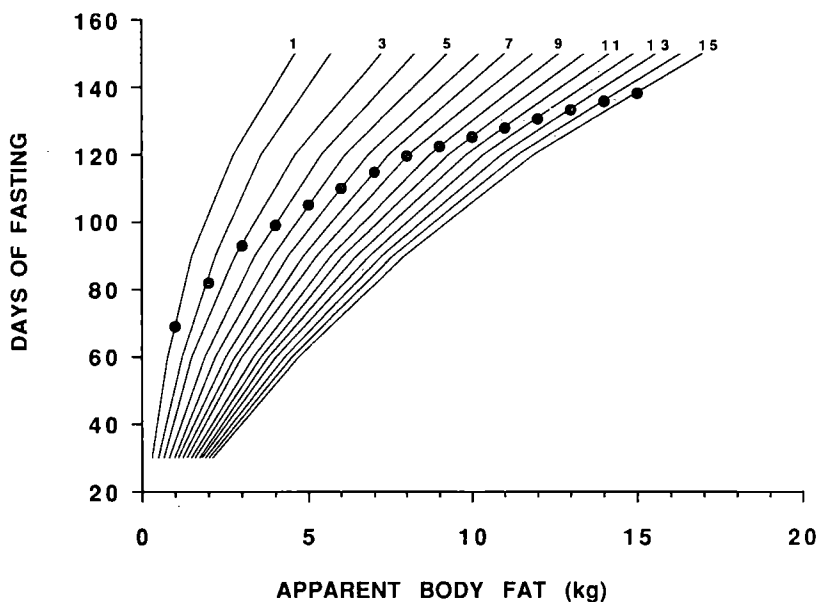

Figure 6.--Relationship between days of fasting and apparent body fat for apparent lean body masses from 1 to 15 kg (curved lines). Dots represent days of fasting at 50% body fat for each apparent lean body mass.

indicates that, for raccoons, the strategy of increasing ALBM to increase fasting time reaches a critical point of diminishing returns at about 8 kg.

Data from Key Vaca suggest that the smallest ALBM for raccoons is about 2 kg. What is the largest ALBM? For the following reasons we think it is around 8 kg. Lotze and Anderson (1979:2) state that the largest raccoons are "from Idaho and vicinity," and Ritke and Kennedy (1988) report that, based on an analysis of 22 skull characteristics from 128 sampling quadrants in the United States, Mexico, and Central America, the largest raccoons are found in eastern Washington, eastern Oregon, western Idaho, and California. However, neither reference provides any body mass data for those areas. The largest raccoon body masses reported in the literature are for animals taken by hunters and trappers in northern Minnesota, Maine, and west central Illinois, and these animals had TBM's between 12 and 14 kg (Goldman 1950; Whitney and Underwood 1952; Sanderson 1983). These animals were taken in late fall; therefore, 40 to 50% of their mass would have been fat. ALBM of a 12-kg raccoon would have varied from 6.0 to 7.2 kg, and that of a 14-kg animal from 7.0 to 8.4 kg. Since raccoons at the northern edge of their range may not need to fast for more than 120 days, and since it would take a very large increase in ALBM to boost fasting time much beyond 120 days (Fig. 6), 8 kg may closely approximate maximum ALBM for this species. This implies that, for *Procyon lotor*, ALBM ranges from about 2 to 8 kg.

This model supports our hypothesis that geographic variation of ALBM in raccoons is selected for by latitudinal differences in length and severity of winter climate. In the parlance of adaptational biology (Prosser 1986), the wide range of variation in ALBM has acclimatized this *species* to a wide range of climates and habitats. In climates with short mild winters, selection favors raccoons with small ALBM because it lowers their absolute energy requirement, and improves their ability to dissipate heat. In the northern part of their range, where winters are long, and fasting endurance is of critical importance, selection favors raccoons with large ALBM. Even though large ALBM carries with it a greater absolute energy cost (McNab 1971), this is obviously less of a disadvantage in cold climates than the advantage it provides via its attendant increase in fasting endurance. While we do not know what limits the southern spread of the raccoon, this analysis suggests that the northern limit of their range is physiologically determined by the size of their ALBM.

Fall fattening

In warm and mild climates, where the fattening response is minimal, raccoons still deposit enough fat in fall to support a fast of nearly 30 days (Fig. 5). For raccoons in the continental United States, this may represent the minimum

response that occurs whenever environmental cues stimulate the fattening process. If all raccoons have the physiological potential to attain 50% body fat, then the difference between the degree of fattening actually achieved, and their potential for fattening, may represent a physiological reserve that goes unutilized unless it is activated by the appropriate environmental stimuli. This physiological reserve for fat deposition may be an adaptation that would acclimatize *each raccoon* to winter conditions over a wide geographic area (Prosser 1986).

But, not all raccoons may have the physiological potential to attain 50% body fat, particularly those that live in areas where that degree of obesity is never required for survival. If this is the case then we would expect to find small raccoons from warm climates having less potential to fatten than larger raccoons from mild and moderate climates, and those, in turn, to have less potential than raccoons from harsh and severe climates. In this case the physiological reserve for fat deposition would also vary geographically, and raccoons with small ALBM would have a narrower range of acclimatization than those with large ALBM.

POSSIBLE GENETIC BASIS OF GEOGRAPHIC VARIATION IN RACCOON BODY SIZE

In the eastern United States, raccoons can be divided into at least four geographic populations that display distinctly different ALBMs and potentials for maximum fasting (Figs. 3, 5, 6): (1) Florida Keys, (2) southeastern United States, (3) transition zone, and (4) southern Great Lakes region. If ALBM is an adaptation, selected for by winter climate on the basis of its survival value, then each region of stable ALBM could represent an area of genetic homogeneity maintained by ease of gene flow and a common selective pressure (Beck and Kennedy 1980), while the transition zone could be a hybrid zone where populations on either side of it meet, mate, and produce hybrids of intermediate ALBM (Mayr 1963; Barton and Hewitt 1989). Variation in ALBM between populations could be the result of (1) true genetic adaptation to local conditions, or (2) environmental induction or modification during development, ie., phenotypic plasticity (Berven et al. 1979; Berven and Gill 1983; Stearns 1989).

These genetic speculations need to be tested by a wide variety of studies done both within and between the populations identified. These should include data on breeding and pedigree, survival rates and reproductive success, electrophoretic variability of gene products as well as nuclear and mitochondrial DNA sequences, and chromosomal variation. This would provide information on how ALBM, and the capacity to fatten are inherited, how they are genetically coupled between populations, and how natural selection, gene flow, and genetic drift function to maintain the observed patterns of variation (James 1991). One

could then determine the relative contribution of genetic differences, and phenotypic plasticity to the observed geographic variation, and interpret correctly the adaptive significance of the phenotypic variation (Berven et al. 1979; Barton and Hewitt 1989; James 1991).

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