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HOME RANGE AND BODY WEIGHT—A REEVALUATION[1]

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Abstract. Area of home range (H) can be related empirically to body weight (W) by the formulation $H = aW^k$. The computed values of exponent k have generated controversy concerning potential differences between trophic groups and whether they differ from 0.75 (the value expected if area of home range is a function of basal metabolic rate). When large mammals are considered, the empirical relationship assumes the form $H = .002W^{1.02}$ for herbivores, $H = .059W^{.92}$ for omnivores, and $H = .11W^{1.36}$ for carnivores. By treating the animal's energetic requirements and the productivity of its habitat explicitly, empirical values of $k > 0.75$ are shown to result from declining rates of production of utilizable energy per unit area of habitat with increasing body weight. While trophic status and weight modify the utilizable proportion of energy in the habitat, broad correlations also exist between size of home range and surrogate variables for productivity (precipitation and latitude).

Differences in weight alone account for a large portion of the differences between male and female or subadult and adult home ranges. Behavioral phenomena need not be invoked. Differences between herbivores and carnivores are in the direction suggested for birds and mammals. Criticisms regarding inter-class and inter-trophic comparisons appear resolved.

Key words: *body weight; energetic requirements; habitat productivity; home range; mammals.*

INTRODUCTION

Relationships between size of home range and body weight are patterns which natural historians and ecologists have been discussing for at least 60 yr. Seton (1909) stated that "the size of home region corresponds somewhat with the size of the animal. Flesh eaters as a class have a larger home region than herb eaters." Seton's statement was elaborated by Mohr (1940) for mammalian species. McNab (1963) demonstrated that among mammals size of the home range varied as a power of the body weight which did not differ statistically from the relationship between body weight and basal metabolic rate reported by Kleiber (1961). Yet Armstrong (1965) concluded that avian territory sizes were adjusted to exceed metabolic requirements. Schoener (1968) distinguished birds of different trophic status and noted differences between herbivores and carnivores which he ascribed to mammals as well (using data of McNab 1963). However, Turner et al. (1969) were not convinced of the distinctions between birds and mammals.

Since McNab's (1963) paper, far more information on mammalian home ranges has become available. It is now possible not only to offer a more integrative framework relating factors influencing size of home ranges, but also to address the criticism of Turner et al. (1969) that too few species were included in previous analyses.

Our objectives in treating the concept of home range as it relates to body weight are threefold:

(1) to present a simple extension of present models of home range and body weight which incorporates explicitly both productivity of habitat and trophic status;
(2) to collate and summarize recent information on sizes of home ranges of North American mammals; and
(3) to evaluate the general model of size of home range utilizing the collated information.

We do not treat in detail why an animal might have a home range but, given that it does, we consider the nature of relationships between size of home range and body weight.

METHODS

Home range is the area normally traversed by an individual animal or group of animals during activities associated with feeding, resting, reproduction, and shelter-seeking (Burt 1943). We do not consider infrequent movements outside this area as part of the home range but have found it difficult to apply unambiguous criteria to published studies.

Data obtained from primary sources whenever possible were summarized and the following attributes recorded: species, sex and age class of the subject animals, sample size, mean area of home range, extremes of the home range estimates, methods used to collect the information, location of the study area, dates during which the data were collected, and comments by the author or ourselves that we felt might be important during comparison of the data.

Most authors used the method of "minimum home range" (Dalke and Sime 1938, Hayne 1949) to estimate the size of home ranges. However, some authors provided no estimates of area for reported home ranges. In these instances, and where maps were provided, we used the method of "minimum home range" to

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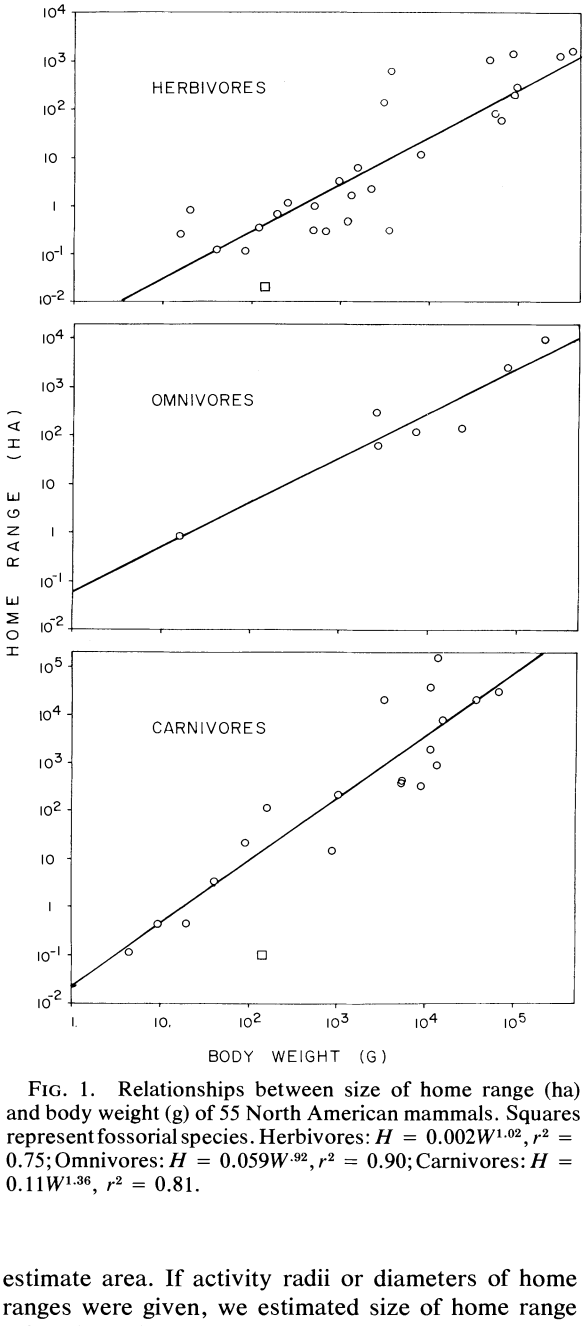

FIG. 1. Relationships between size of home range (ha) and body weight (g) of 55 North American mammals. Squares represent fossorial species. Herbivores: $H = 0.002W^{1.02}$, $r^2 = 0.75$; Omnivores: $H = 0.059W^{.92}$, $r^2 = 0.90$; Carnivores: $H = 0.11W^{1.36}$, $r^2 = 0.81$.

estimate area. If activity radii or diameters of home ranges were given, we estimated size of home range using the "circular home range" method (Burt 1940, Hayne 1949).

Home range can be defined over any time interval. Where seasonal home ranges were given, we treated these separately; otherwise, estimates of annual home ranges were used.

We calculated grand means of the size of home range for each species by weighting each study by its sample size. Studies not reporting sample size were assigned a sample size of 1.

Most studies do not provide information on body weight, so these have been obtained from the literature. Both male and female weights are used and the average of these 2 estimates is employed as the body weight for the species. Although the value for home range assigned a particular species may be the weighted mean of means from several studies, often only 1 estimate for weight is employed. The degrees of freedom in the regression analyses are therefore those of the number of estimates of weight equivalent to the number of species. We have applied the same approach in our recalculation of other data. Log_{10} transformations of body weights and home ranges were made in all cases.

We employed 3 groups: herbivores, omnivores, and carnivores (including insectivores) which we define following Schoener (1968). Herbivores ingest <10% animal matter; carnivores ingest >90% animal matter on an annual basis. All groups ingesting 10 to 90% animal matter are omnivores.

Models of home range.—Among vertebrates there is a well-documented relationship between size of home range, H, and body weight W, of the form $H = aW^k$ (McNab 1963, Armstrong 1965, Schoener 1968, Turner et al. 1969). Disagreement exists concerning the meaning of exponent k and whether it truly differs between trophic groups. Let us assume that size of home range is largely determined by an animal's energetic requirements. If so, we expect a fundamental relationship with weight of the form $H = aW^k$, but modified in a predictable fashion by the trophic status of the animal and the density and productivity of its resource base.

Assume that an animal utilizes the minimum area that can sustain its energetic requirements. Consider that an animal of weight W has energetic requirements R ($\text{kcal}\cdot\text{day}^{-1}$). The environment provides utilizable energy at a rate P ($\text{kcals}\cdot\text{day}^{-1}\cdot\text{unit area}^{-1}$). The simplest expression of home range (H) is thus

$$H = R/P \tag{1}$$

The effects of body weight, trophic status, productivity of the habitat, and season can be synthesized by considering how these factors affect either R or P.

Energetic requirements, R.—R should increase with weight. If R is proportional to basal metabolic rate then (from Kleiber 1961)

$$R = aW^{.75} \tag{2}$$

For deer and elk (Moen 1973) and domestic ruminants (Osuji 1974) estimated daily requirements are between 1.25 and 2.0 times the fasting metabolic requirements. One could refine Eq. 2 further by considering terrain, climate, activities pursued, and physiological status of the animal, but R should remain proportional to $W^{.75}$. Only the proportionality factor, a, would change.

Production of utilizable energy, P.—The production of utilizable energy is affected by animal weight, trophic status, productivity of the habitat, and season.

1) *Body weight.*—We expect P, the density of uti-

TABLE 1. Mean area of home range and body weight of mammal species treated in this study

Species	Body weight (g)[1]	Mean area of home range (ha)	Total sample size	Source[2]	Feeding category[3]
Didelphis marsupialis	2724.0	59.88	76	Fitch and Sandidge 1953 (T, C) Holmes and Sanderson 1965 (RT, C) Verts 1963 (T, C)	*O*
Sorex vagrans and *S. obscurus*	4.5	0.11	80	M. Hawes 1976, *personal communication* (T, C)	*C*
Blarina brevicauda	20.0	0.43	7	Blair 1941 (T, Q)	*C*
Neurotrichus gibbsii	9.5	0.41	12	M. Hawes 1976, *personal communication* (T, C)	*C*
Scapanus townsendi	142.0	0.10	1	Giger 1973 (T, C)	*C*
Ochotona princeps	122.0	0.35	6	Barash 1973 (O, E)	*H*
Sylvilagus bachmani	695.0	0.28	122	Connell 1954 (T, C) Shields 1960 (T, C)	*H*
Sylvilagus floridanus	1322.0	1.62	137	Allen 1939 (T, M) Brown 1961 (T, M) Dalke and Sime 1938 (T, M) Haugen 1942 (T, Q) Janes (TO, M) Schwartz 1941 (T, M)	*H*
Sylvilagus transitionalis	1191.0	0.46	1	Dalke 1937 (T, M)	*H*
Sylvilagus auduboni	963.0	3.18	2	Fitch 1947 (T, C) Madsen 1973 (R, C)	*H*
Sylvilagus aquaticus	2198.0	2.12	14	Toll et al. 1960 (TO, M)	*H*
Lepus americanus	1543.0	5.93	27	O'Farrell 1965 (T, Q) Rongstad 1971 (R, R)	*H*
Lepus californicus	3039.0	145.55	1	Madsen 1973 (R, C)	*H*
Lepus alleni	3632.0	642.82	1	Madsen 1973 (R, C)	*H*
Tamias striatus	85.0	0.11	40	Yerger 1953 (T, M)	*H*
Marmota flaviventris	3628.0	0.31	1	Armitage 1962 (T, R)	*H*
Spermophilus tridecemlineatus	193.0	0.66	1	Evans 1951 (T, C)	*H*
Sciurus carolinensis	500.0	0.95	99	Flyger 1960 (T, M) Layne 1954 (T, M)	*H*
Sciurus griseus	500.0	0.30	8	Ingles 1947 (O, M)	*H*
Tamiasciurus hudsonicus and *T. douglasi*	254.0	1.10	40	Mohr 1965 (T, M) Smith 1968 (T, R) Zirul and Fuller 1970 (T, Q)	*H*
Thomomys talpoides	140.0	0.02	1	Turner et al. 1973 (TO, N)	*H*
Peromyscus maniculatus gracilus	16.0	0.81	41	Blair 1942 (T, Q)	*O*
Clethrionomys gapperi	16.0	0.25	7	Blair 1941 (T, Q)	*H*
Microtus pennsylvanicus	40.0	0.12	96	Blair 1940 (T, Q)	*H*
Microtus oregoni	20.0	0.81	18	D. Hawes 1976, *personal communication* (T, C)	*H*
Erethizon dorsatum	7882.0	11.29	2	Marshall et al. 1962 (R, N)	*H*
Canis latrans	15890.0	7597.57	3	Ozoga and Harger 1966 (O, E)	*C*
Canis lupus	37422.0	20276.88	30	Banfield 1954 (U, E) Cowan 1947 (O, E) Kolenosky and Johnston 1967 (R, C) Mech 1966 (O, R) Mech 1973 (RO, R) Pimlott et al. 1969 (TO, N) Thompson 1952 (O, E) Stebler 1944 (O, M) Stenlund 1955 (U, E)	*C*
Vulpes fulva and *V. vulpes*	5448.0	387.34	17	Ables 1969 (R, M) Arnold and Schofield 1956 (O, C) Murie 1936 (O, E) Sargeant 1972 (R, R) Schofield 1960 (O, C) Sheldon 1950 (T, C) Storm 1965 (R, M)	*C*
Vulpes fulva regalis	5448.0	409.76	2	Scott 1943 (O, M*)	*C*
Ursus americanus	76204.0	2413.09	3	Erickson and Petrides 1964 (T, C) Hardy 1973 (R, N) Jonkel and Cowan 1971 (T, R)	*O*
Ursus arctos	204120.0	9283.13	12	Craighead and Craighead 1965 (R, N) Craighead and Craighead 1973 (R, M) Pearson 1972 (R, M)	*O*

TABLE 1. Continued

Species	Body weight (g)[1]	Mean area of home range (ha)	Total sample size	Source[2]	Feeding category[3]
Procyon lotor	7264.0	113.73	107	Ellis 1964 (R, N) Schneider et al. 1971 (R, R) Stuewer 1943 (TO, M) Urban 1970 (R, M)	*O*
Martes americana	1043.0	209.31	20	Francis and Stephenson 1972 (T, M) Hawley and Newby 1957 (T, M) Miller et al. 1955 (T, C)	*C*
Martes pennanti	3459.0	20342.49	1	DeVos 1951 (O, C)	*C*
Mustela erminea	93.0	20.64	3	Lockie 1966 (T, R) Nyholm 1959 (O, E)	*C*
Mustela rixosa	42.0	3.28	17	Lockie 1966 (T, R)	*C*
Mustela frenata	165.0	111.29	2	Quick 1944 (O, C) Quick 1951 (O, E)	*C*
Mustela vison	908.0	14.10	2	Mitchell 1961 (T, M)	*C*
Gulo gulo	13835.0	150000.00	1	Myrberget et al. 1969 (O, N)	*C*
Taxidea taxus	13620.0	849.87	1	Sargeant and Warner 1972 (R, R)	*C*
Mephitis mephitis	2586.0	294.67	26	Storm 1972 (R, M)	*O*
Felis concolor	67000.0	29733.33	6	Bruce 1925 (O, E) Seidensticker et al. 1973 (R, M)	*C*
Lynx lynx	11567.0	35546.15	6	Haglund 1967 (O, R)	*C*
Lynx canadensis	11567.0	1852.40	8	Berrie 1973 (R, R) Saunders 1963 (O, R)	*C*
Lynx rufus	9072.0	320.82	10	Hall 1973 (R, N) Provost et al. 1973 (R, M)	*C*
Pecari tajacu	23814.0	135.21	11	Ellisor and Harwell 1969 (T, M) Schweinburg 1971 (R, M)	*O*
Cervus canadensis	300510.0	1292.54	73	Craighead et al. 1973 (RT, R) Martinka 1969 (T, M) Shoesmith 1973 (RTO, N)	*H*
Odocoileus hemionus californicus	54432.0	79.44	1	Leopold et al. 1951 (TO, C)	*H*
Odocoileus hemionus columbianus	64638.0	58.85	81	Dasmann and Taber 1956 (TO, C) Miller 1970 (T, M)	*H*
Odocoileus hemionus hemionus	97524.0	285.27	110	Hanson and McCulloch 1955 (O, C) Mackie 1970 (TO, N) Robinette 1966 (T, C*) Zalunardo 1965 (T, C*)	*H*
Odocoileus virginianus	90720.0	196.06	64	Byford 1970 (R, R) Jeter and Marchington 1964 (R, M) Marchington and Jeter 1966 (R, R) Michael 1965 (T, R) Montgomery 1963 (T, M) Progulske and Baskett 1958 (TO, M) Sparrowe and Springer 1970 (RT, M) Wohlgemuth 1968 (R, N)	*H*
Alces alces	411075.0	1609.53	39	Phillips et al. 1973 (RT, R) Van Ballenberghe and Peek 1971 (R, M)	*H*
Antilocapra americana	48000.0	1060.47	16	Bayliss 1969 (RT, M)	*H*
Ovis canadensis	87000.0	1433.40	4	Davis 1938 (O, E) Geist 1971 (O, E) Seton 1929 (O, E) Woolf et al. 1970 (O, E*)	*H*

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[1] Weight is the mean of average male and average female adult weights. Sources are Cowan 1956, Cowan and Guiget 1965, Geist 1971, Hall and Kelson 1959, Holter and Toll 1960, Jackson 1961, Jonkel and Cowan 1971, Mohr 1947, Palmer 1954, and Walker et al. 1964. Some weights from sources of home range listed in the Table.

[2] Letters in parentheses indicate methodologies. The letter(s) preceding the comma code the technique for acquiring data (O = direct observation, R = radiotelemetry, T = tagging, U = unknown). Letters following the comma indicate the method of computing size of home range (C = circular home range method including elliptical methods, E = estimation, M = minimum area method, N = not stated, Q = quadrant methods, trap grid and trap squares methods, R = minimum area method with various degrees of removal of low use areas or exclusion of nonutilized habitats, * = home range calculated on basis of data provided by author).

[3] *H* ingest <10% animal matter, *O* ingest 10 to 90% animal matter, *C* ingest >90% animal matter.

TABLE 2. Relative sizes of female and male home ranges among North American mammals

Species	Mean home range size (ha)				Ratio of ♀♀:♂♂ home range size	Source	Comments
	♂♂	*n*	♀♀	*n*			
Didelphus marsupialis	257.00	8	249.00	5	0.969	Fitch and Shirer 1970	
Sylvilagus floridanus	3.36	11	1.17	17	0.348	Dalke and Sime 1938	
Sylvilagus floridanus	3.61	9	3.14	9	0.870	Janes 1959	
Sylvilagus floridanus	1.46	17	0.90	19	0.616	Allen 1939	
Sylvilagus floridanus	2.39	7	1.86	7	0.778	Toll et al. 1960	
Tamias striatus	0.15	13	0.10	19	0.667	Yerger 1953	
Microtus pennsylvanicus	0.12	34	0.08	27	0.667	Blair 1940	Moist grassland
Vulpes fulva	155.40	1	103.74	3	0.668	Ables 1969	Small samples
Ursus americanus	3082.19	...	518.00	...	0.168	Jonkel and Cowan 1971	No samples sizes given
Ursus arctos	29526.90	1	6993.21	8	0.237	Pearson 1972	Small sample size for males
Procyon lotor	203.56	19	108.46	17	0.533	Stuewer 1943	
Martes americana	238.77	6	70.01	5	0.293	Hawley and Newby 1957	
Martes americana	357.43	4	113.96	4	0.319	Francis and Stephenson 1972	Summer home ranges
Mustela rixosa	1.70	...	1.21	...	0.714	Nyholm 1959	No samples sizes given
Mustela frenata	34.40	...	7.28	...	0.212	Nyholm 1959	No sample sizes given
Mephitis mephitis	511.54	2	377.98	5	0.739	Storm 1972	
Felis concolor	29300.00	1	14750.00	4	0.503	Seidensticker et al. 1973	Small samples, summer–fall home ranges
Felis concolor	12550.00	4	10655.00	8	0.849	Seidensticker et al. 1973	Winter home ranges
Lynx canadensis	1942.56	2	1554.00	1	0.800	Saunders 1963	Small sample sizes
Lynx canadensis	1950.00	2	1280.00	1	0.656	Berrie 1973	Small sample sizes
Lynx rufus	494.14	3	97.13	3	0.196	Hall 1973	
Cervus canadensis	1243.23	1	1243.23	21	1.000	Martinka 1969	Small male sample sizes
Odocoileus hemionus columbianus	100.36	2	69.61	8	0.694	Miller 1970	
Odocoileus hemionus hemionus	393.37	29	248.48	75	0.632	Robinette 1966	
Odocoileus virginianus	175.63	1	59.49	1	0.339	Marchington and Jeter 1966	Small sample sizes
Odocoileus virginianus	184.54	1	82.15	3	0.445	Zagata and Haugen 1972	Small sample sizes
Alces alces	1450.80	21	1788.77	15	1.233	Phillips et al. 1973	

lizable production of energy, to decrease with increasing energetic requirements R which increase with body weight. The relationship results from "patchiness" of resources in the environment. An animal with small requirements can exploit a single, high density patch while an animal with large requirements commonly must incorporate a number of patches with resulting lower average density of utilizable production.

2) *Trophic status*.—Utilizable energy per unit area, P, is greater for herbivores than for carnivores (Englemann 1966, Golley 1968). From Eq. 1, H will be smaller for herbivores.

3) *Productivity of habitat*.—Within a specific trophic group and weight-class, habitats of greater productivity (P) will generate smaller home ranges, for the energetic requirements (R) will not change.

4) *Season*.—Among herbivores, both R and P are affected, R by the quality of forage. As their food dies, becomes dormant, or is covered with snow, P should decrease below summer values. The direction of change in size of home range will depend on the relative rates of change of P and R. Among carnivores, R should not change dramatically. Carnivorous species dependent upon prey that show a seasonal decline in density through hibernation, migration, or other phenomena should experience a decrease in P during the winter.

Home ranges of mammals.—Calculated means of home range and body weights for 55 North American mammals are presented in Table 1. The relationship between area of home range and body weight is illustrated in Fig. 1. *Scapanus townsendi* and *Thomomys talpoides* are depicted by squares; they are fossorial and their home ranges may not be comparable with species which are largely or entirely surface-dwelling.

For all 55 species, home range, H, is related to body weight, W, as $H = .008W^{1.08}$, $r^2 = 0.60$. The fit is closer when trophic groups are treated separately (Fig. 1). Mammalian carnivores have a larger home range than do omnivores or herbivores of similar size. Analysis of covariance indicates that the intercepts of the 3 regressions are statistically different ($P \leq .01$). The areas of home range of herbivores and omnivores increase at a nearly constant rate as body weight increases ($k = 1.02 \pm .11$ and $0.92 \pm .13$ respectively). Slopes of the regressions for herbivores and omnivores do not differ significantly ($P \leq .38$). In contrast, the size of home ranges of carnivores increases at an increasing rate as their body weight increases ($k = 1.36 \pm 0.16$) and the slope of the carnivore regression differs significantly from that for herbivores. The probability that k is the same for carnivores and omnivores is $\leq .07$.

For most mammals, the area of home range differs between sexes and with age. The female:male and subadult:adult ratios of area of home range were calculated when possible. In only 1 of 27 studies were mean home ranges of females > those of males (Table 2). The sign test (Siegel 1956:68) was used to test the null hypotheses that female home ranges were > male home ranges. For carnivores the probability of the null hypothesis being correct is $\leq .003$ and for herbivores $\leq .006$. When all trophic groups are considered, the probability is $\leq .00005$.

We used the same statistical procedure to evaluate ratios of home ranges of subadults:adults (Table 3). The null hypothesis was that subadult home ranges are larger. The probability of home ranges being equal in size or larger for subadults is $\leq .001$ when all trophic groups are considered. Treating the trophic groups separately, however, yields values of $P \leq .004$ for herbivores and $P \leq .227$ for carnivores. In the 2 instances where nonadult home ranges of carnivores were > adult ranges, we suspect post-juvenile dispersal was operating. Ables (1969) did not note whether the subadult foxes were attempting to establish new territories but the yearling lynx had just made movements that Berrie (1973) considered post-juvenile dispersal.

Female carnivores commonly weigh only 33 to 50% as much as male carnivores. Given such differences in body weight, the expected sizes of home ranges of female carnivores should be ≈24 to 39% the size of home ranges for male carnivores (utilizing $W^{1.36}$). Among herbivores and omnivores, adult females are usually between 50% and 75% as heavy as the adult males. Hence the size of home range of female herbivores and omnivores is expected to be 49 to 75% that of males. In fact, ratios of female:male sizes of home ranges are $0.52 \pm .08$ for carnivores and $0.69 \pm .07$ for herbivores (Table 2). These differences are in the direction predicted by sexual differences in weight but, among carnivores, sex-related differences in size of home range are < those predicted from differences in weight.

Interspecific differences between sizes of subadult and adult home ranges are less clear. Subadult mammals usually weigh 35 to 75% of the adult weight. Such differences in body weight suggest ratios of size for subadult:adult home ranges ranging from 0.22 to 0.75, depending upon trophic status. The calculated, average ratio among herbivores is $0.49 \pm .06$, slightly < that expected if subadults were half the weight of adults. However, for the only 2 carnivorous species for which appropriate data are available, the ratio is $1.13 \pm .27$, $n = 7$. In 1 of these (Berrie 1973), the subadults were establishing new territories which would overestimate their home range size. If subadults were being forced into suboptimal habitat, the resulting lower value of P also would generate larger home ranges.

EVALUATION OF THE MODEL AND DISCUSSION

Home range and body weight.—Our findings agree with those of McNab (1963); among mammals, the area of home range, H, is related to body weight, W,

TABLE 3. Relative sizes of subadult and adult home ranges among North American mammals

Species	Adult	*n*	Subadult	*n*	Ratio of subadult to adult home range size	Source	Comments
Sylvilagus floridanus	3.36	11	1.02	5	0.304	Dalke and Sime 1938	Males
Sylvilagus floridanus	1.17	17	0.26	5	0.222	Dalke and Sime 1938	Females
Tamias striatus	0.12	32	0.07	8	0.583	Yerger 1953	Author compares adults and juveniles, data are not separated by sex
Vulpes vulpes	155.40	1	95.51	1	0.615	Ables 1969	Males, small samples
Vulpes vulpes	103.73	3	193.04	2	1.860	Ables 1969	Females, small samples
Procyon lotor	203.56	19	108.46	27	0.533	Stuewer 1943	Males
Procyon lotor	108.46	17	44.92	24	0.414	Stuewer 1943	Females
Procyon lotor	89.04	. . .	16.99	. . .	0.191	Urban 1970	Male and female data not given separately, total sample size of 9
Mephitis mephitis	511.54	2	283.69	6	0.554	Storm 1972	Males
Mephitis mephitis	377.99	5	234.32	13	0.620	Storm 1972	Females
Lynx canadensis	1280.00	1	2100.00	2	1.641	Berrie 1973	Females, small samples
Lynx rufus	358.56	1	352.24	1	0.982	Provost et al. 1973	Males, small samples
Lynx rufus	462.57	1	246.87	1	0.534	Provost et al. 1973	Females, small samples
Cervus canadensis	1243.23	21	983.23	11	0.791	Martinka 1969	Females
Odocoileus hemionus columbianus	63.94	27	25.09	7	0.392	Dasmann and Taber 1956	Males
Odocoileus hemionus columbianus	100.36	2	59.89	2	0.597	Miller 1970	Males, small samples
Odocoileus hemionus columbianus	69.61	8	38.85	2	0.558	Miller 1970	Females
Odocoileus virginianus	59.49	9	30.35	4	0.510	Michael 1965	Females, adults and fawns are compared

by the function $H = aW^k$. Our extensions of McNab's work primarily concern the exponent, k. McNab (1963) found no statistical difference between the computed exponent relating home range and body weight and 0.75. We find that the computed exponent differs significantly from 0.75, at least among herbivores and carnivores. The 95% confidence limits about the exponents are: 0.80 to 1.24 for herbivores, 0.57 to 1.26 for omnivores, and 1.04 to 1.68 for carnivores. Among herbivores the relationship between size of home range and body weight closely approximates linearity. The exponent for omnivores also does not depart significantly from linearity but shows a large standard error.

Increases in metabolic rate with activity of free-ranging animals should appear in the proportionality factor and not the exponent. Exponents > 0.75 imply that with increasing size a mammal must (or at least does) increase its home range beyond that expected from the fundamental metabolic relationship. When $k = 1$ a plot of apparent energy requirements per unit weight (aW^k/W) against W has zero slope. As they become larger, free-ranging herbivores and perhaps omnivores apparently enjoy no economies of scale in terms of their energy requirements. Such a relationship would constrain the evolution of larger body size more severely than would a relationship with size of home range proportional to $W^{.75}$.

Sex-related differences in size of home range appear largely attributable to sex-related differences in weight. Benefits derived from resource partitioning could encourage sexual dimorphism in carnivores. The weight-related differences in size of home range then would be consistent with predation upon prey of different sizes. Sexual dimorphism in weight, and resultant resource partitioning, would provide fewer benefits to herbivores and omnivores which are much less likely to exploit "prey" of different sizes. While there are no apparent benefits through economies of scale, in terms of energy requirements per unit of body weight, the costs of becoming larger may not be severe. Actual costs of traversing the home range are generally unknown but appear small. Osuji (1974) calculated that such costs increase the energy requirements of a 50-kg sheep only 15%. We suggest that among noncarnivorous forms, the value of larger size of the male is more likely to be associated with increased success in intraspecific contests and the frequency of encountering mates associated with increased facility in visiting larger areas (increased fitness *sensu* Orians 1969) than with resource partitioning.

Among herbivorous mammals, many of the observed differences between sizes of subadult and adult home ranges also can be attributed to differences in weight. Behavioral phenomena need not be invoked, although close association of subadults with adult females (who have smaller home ranges than adult males) would help to constrain their mean size of home range below that of the mean of adults of both sexes.

Home range and trophic status.—The criticisms of Turner et al. (1969) appear to be resolved. Distinctions between carnivores and herbivores exist and are found in both birds and mammals. Among carnivorous birds and mammals, the relationships between body weight and size of home range are similar ($.034W^{1.31}$ for birds as recomputed from Schoener (1968); $0.11W^{1.36}$ for mammals). Among both birds and mammals, a unit increase in body weight is associated with a greater increase in size of home range or territory for carnivores than for noncarnivores. Similarly, as Schoener (1968) noted for birds, carnivorous mammals have larger home ranges than do herbivorous mammals of the same weight. The differences between trophic groups can be explained if the density and productivity of their food base is considered. More energy/unit area is present in primary production than in secondary production. A herbivore is therefore able to satisfy its energy requirements by exploiting a smaller area than can a carnivore of similar size.

Using the adjusted data of Turner et al. (1969) for carnivorous lizards, we compute 95% confidence limits about k as 0.63 to 1.26. Lizard carnivores thus do not exhibit a significantly lower exponent than homeothermic carnivores. We suggest that the apparent tendency towards a lower value for the exponent among lizard carnivores ($H = 0.017W^{.95}$) is a function of hunting style. Many lizards are ambush predators exploiting patches of their environment which have high densities of forage. As a result, P would decline less rapidly with increasing weight for lizards than for mammals or birds which have a higher proportion of stalking predators among the data treated.

Omnivores exhibit home ranges of intermediate size (Fig. 1), but an increase in body weight of omnivorous birds or mammals is not associated with as large an increase in home range or territory as is evident in either carnivorous or herbivorous forms (Fig. 1 and Schoener 1968). An omnivore does not need as large an area as a carnivore, as some of its intake of energy is obtained from plant sources already available within the area used to obtain animal food. However, omnivores may need a larger area than herbivores of the same weight even if they do not require an animal component in their diet, for they appear less efficient at extracting energy from the plant component of their diet than are herbivores (F. L. Bunnell, *personal observation*). The less rapid increase of home range with body size should hold across broad taxa, as it reflects the omnivore's greater probability of encountering a food source, plant, or animal.

We can extend our analyses beyond the relationships of Fig. 1 by relating the empirically derived function $H = aW^k$ to our model $H = R/P$. We suggested that R should be a function of $W^{.75}$, or basal metabolic rate. An alternative approach is to consider directly the average food consumption per day as a function of weight. Among mammals, the greatest departure from 0.75 of empirical exponents is that for carnivores. We have collated data on g food consumed/g body weight for carnivorous mammals from Springer 1937, Llewellyn 1942, Hamilton 1944, Golley 1960, Short 1961, Buckner 1964, Golley et al. 1965, Barrett 1969, Hornocker 1970, Kuyt 1972, Vogstberger and Barrett 1973, Barrett and Stueck 1976, and Hatler 1976. The relationship is remarkably similar to that obtained for birds ($FC = 0.51W^{.63 = .11}$) by Nice 1938.

$$FC = 1.7W^{.68 \pm .02} \tag{3}$$

where FC is g food consumed per day and W is the body weight (g) of the carnivore. In both cases the exponents are significantly <1.0. These relationships justify equivalence of the daily energy requirements, R, with $W^{.75}$. Changes in R are not solely responsible for changing size of home range with increased body size, nor are they responsible for the greater increase in size of home range per increase in body weight that is observed among carnivorous birds and mammals as compared with herbivorous or omnivorous forms. Changes in P with body weight are implicated.

Reconciliation of Eq. 1 with empirical relationships requires that P be a decreasing power function of body weight. The nature of this relationship is clarified by expressing the empirical relationship between size of home range and body weight for herbivores as:

$$H = a(W^{.25}\ W^{.75}) \tag{4}$$

Combining Equations 1 and 4 for herbivores we obtain:

$$H = W^{.75}/a'W^{-.25} \tag{5}$$

where a' is kcals·area^{-1}·day^{-1} rather than ha·W^{-1} as in Eq. 4. For herbivores and omnivores P of Eq. 1 must be proportional to $W^{-.25}$ and for carnivores proportional to $\approx W^{-.5}$. Equation 5 indicates a declining ability of habitat to meet the energy requirements of larger animals.

Observed relationships suggest that accessible and acceptable food of mammals decreases with increasing body weight just as it does in carnivorous birds (Schoener 1968). We suggest that this reduction is associated with patchiness in the environment. The probability of unproductive patches being encompassed by the home range of a mouse-sized herbivore is far $<$ is the same probability for a large cervid. Further, the large cervid often requires distinctly different areas for shelter and foraging. Because the larger herbivore either encounters or utilizes unproductive areas the productivity of its habitat declines with size (Fig. 2).

The decline is steeper for carnivores primarily because of the greater energy expenditure of the act of predation as compared to grazing. Small prey items occur infrequently among foods of larger carnivores such as *Felis concolor, Canis lupus,* and *Ursus maritimus* (Hornocker 1970, van Ballenberghe et al. 1975, Stirling and McEwan 1975, see also Rosenzweig 1966 and Schoener 1969). Because the larger predator must ignore smaller prey items the productivity of its habitat declines rather steeply with increasing size, more steeply than that of its prey (Fig. 2). Expressed as the empirical relationship $H = aW^k$, these differences must appear in exponent k. As the size of home range of prey items increases linearly with body weight, the size of home range of the carnivore must increase at a rate $>$ linear unless productivity of the prey or spatially overlapping prey species can compensate.

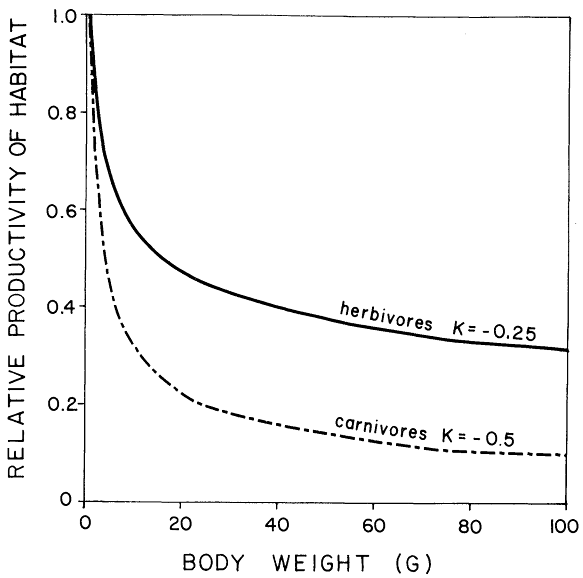

FIG. 2. Apparent relationships between density of energy production in the habitat and body weight of herbivores and carnivores.

The decline in apparent productivity of the habitat with increasing body weight is least steep among omnivores. We expect less patchiness or a more homogeneous distribution of utilizable resources for omnivores than for either herbivores or carnivores. With greater homogeneity of utilizable resources, P should not decrease as rapidly with increasing body weight. Our expectations are thus congruent with observations for all trophic groups.

Productivity of habitat and season.—From Eq. 1 we note that, within a trophic class, animals in habitats of high productivity will have a smaller home range than animals in habitats of lower productivity. Thus, an animal living in a habitat of low productivity will have a larger home range than that predicted by the generalized relationship between home range and body weight and vice versa. Broad patterns can be evaluated by relating size of home range to surrogate variables for productivity such as latitude and precipitation. The work of Rosenzweig (1968) and recent

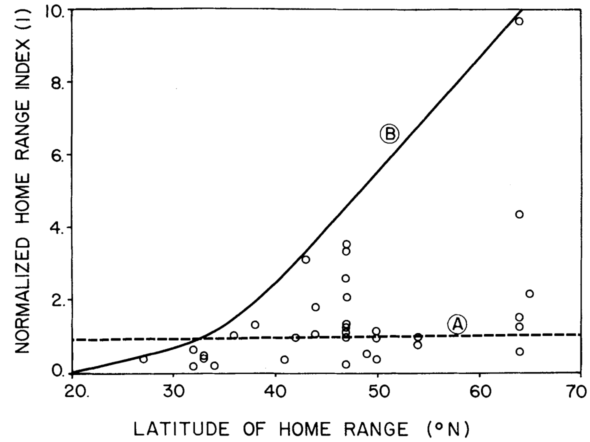

FIG. 3. Index of area utilized per g body weight (normalized for trophic status and total weight) as a function of latitude. See Eq. 6 for derivation of index I. A = Expected size of home range; B = Observed limit of home range expansion.

overview of primary productivity of the biosphere (Lieth and Whittaker 1975) suggest that these variables are appropriate surrogates.

If increasing latitude is broadly associated with decreasing primary productivity, we would expect the size of home range of a given species to increase with latitude. Utilizable productivity of the habitat is a function of both trophic status and weight. The area of home range used (ha) per g of animal can be expressed in a manner which incorporates differences in trophic status and normalizes for the weight of the species. The index, I, is obtained by algebraic manipulation of $H = aW^k$.

$$I = (H/a)^{1/k}/W \qquad (6)$$

In computing I for a given species the values of a and k are those of the appropriate regression equation. I equals 1.0 when the relationship between H and W is identical to that of the regression equation for that trophic group.

Using the Spearman rank formulation (Siegel 1956:202), the correlation between I and latitude for 36 studies is $r_s = 0.86$ with a probability of zero slope $<.0005$. Regardless of trophic status or weight of the species there is a clear tendency for larger home ranges at higher latitudes (Fig. 3).

If primary production is assumed directly proportional to precipitation, we would expect the sizes of home ranges for a given species to be inversely related to precipitation. Most studies do not record precipitation so we have estimated values from the North American Precipitation Map (Gerlach 1970). Size of home range generally increases with increasing aridity. When index I is related to precipitation the Spearman rank correlation is $r_s = 0.37$ with a probability of zero slope $<.10$. The broad patterns observed are consistent with Eq. 1 and extend the findings of specific studies which have manipulated food resources (Martinsen 1968, Mares et al. 1976).

Seasonal differences in the size of home range are more clearly defined than are relationships with the surrogate variables of productivity. Among herbivores the winter home range is < nonwinter home ranges; on average 26 ± 7% of the size of nonwinter ranges (9 studies). Sizes of winter home ranges of carnivores are 130 ± 30% of the nonwinter home ranges (4 studies). There appears to be little change in size of home range of the larger carnivores (*Lynx* and *Felis*), while smaller carnivores (*Martes* and *Mustela*) may increase their home range during winter.

These observations are consistent with Eq. 1. For example, among ruminant herbivores, both R and P vary with season. Ruminants usually can find sufficient food to fill themselves during the winter but food intake is limited by the rate of processing of food (Moen 1973). As R declines more rapidly than P, home ranges of ruminants should shrink during winter. For *Cervus canadensis* and *Alces alces* the shrinkage of home range is dramatic, 6 to 21% of the size of summer home ranges. The decrease in size of home range of *Tamiasciurus* (to 23%) is predicted for different reasons. It is primarily spermivorous, does not hibernate, and the value of R is unlikely to change dramatically with season. However, *Tamiasciurus* gathers and stores food, thus modifying its environment to effectively increase P.

The energy and nutrient content of carnivore food remains similar throughout the year so consumption rates should not change substantially. Decreasing temperatures are largely accommodated by increased insulation. Seasonal changes in size of home range thus should be associated with P. Carnivores experiencing a decrease in P during winter will show larger home ranges. Smaller mammals experience more dramatic seasonal declines in abundance than do larger mammals, thus altering P more markedly for smaller predators than for larger predators. We expect and observe smaller predators to respond to the decrease in prey during winter by expanding their home ranges while larger carnivores whose prey does not decrease remain unaffected.

CONCLUSIONS

Among mammals, birds, and lizards, the exponent of the equation relating size of home range to body weight, $H = aW^k$, differs significantly from that relating metabolic rate and body weight. Indeed, there is no compelling reason to believe that metabolic rate should govern size of home range or feeding territory independent of the distribution of the food resource. Explicit consideration of the rates at which utilizable energy is produced in the habitat suggests that these decline with increasing body size. The decline is steeper for carnivores. While size of home range among herbivorous birds and mammals may increase linearly or more slowly with body weight, among carnivorous birds and mammals the relationship must be > linearity. The broad influences of habitat productivity can be predicted by considering the effects of food quality and quantity. Thus, ruminant herbivores show predicted and observed reductions in home range during the winter as do spermivorous mammals which hoard food. Similarly, smaller carnivores show predicted and observed expansions of home range during winter while large carnivores show little change. Despite the changes in productivity of habitat associated with trophic status and weight, broad correlations exist between size of home range and latitude and size of home range and precipitation.

Although density of food resource is an important modifier, the influences of body weight on size of home range are significant and account for 75–90% of the interspecific variation in size of mammalian home ranges. Moreover, weight alone may account for a large portion of the differences between male and female or subadult and adult home ranges.

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