

SCALING THE ECOLOGICAL COST OF TRANSPORT TO
BODY MASS IN TERRESTRIAL MAMMALS

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The energetic cost of transport has been scaled to body mass in a variety of vertebrates (Taylor et al. 1970; Tucker 1970, 1975*a*, 1975*b*; Schmidt-Nielsen 1972; Pedley 1977; Gleeson 1979; Taylor 1980*a*). Large animals have a lower mass-specific cost of transport than do small animals, but the ecological significance of this relationship is unclear (Taylor 1977*a*). Bourlière (1975, p. 7) has stated that "the fact that a horse can move one gram of its body weight over one kilometre more cheaply than a mouse is another evolutionary advantage of a large body size." Such a view seems illogical at best. Animals do not live on a per-gram basis but rather as intact individuals (cf. McNab 1971), and whole-animal transport costs are, of course, greater for large animals than for small ones.

In order to consider the ecological relevance of transport cost allometry, I define the Ecological Cost of Transport (ECT) as the percentage of an animal's Daily Energy Expenditure (DEE) that is devoted to transport costs. Two questions must then be answered: (1) How does the ECT vary as a function of body mass? (2) What is the magnitude of the ECT?

In nature, many animals travel at speeds which elicit their maximal rate of oxygen consumption ($\dot{V}O_2$ max; e.g., see Layne and Benton 1954; King 1955; Bradley 1967; Kruuk 1972; Schaller 1972; Pennycuick 1979; Thompson 1980; Taylor et al. 1981). Because $\dot{V}O_2$ max is generally about 10-fold greater than resting metabolic rate in mammals (Taylor et al. 1981), locomotion can be a costly activity. Many workers have therefore implicitly assumed that the ECT is high and hence of considerable energetic and selective importance. For instance, Fedak et al. (1974, p. 1042) concluded that energetic "economy might be one important factor in determining the effects of natural selection on the mechanical characteristics of running animals." Man's bipedal form of locomotion has been claimed as both energetically efficient and inefficient (review in Taylor and Rowntree 1973), and Taylor et al. (1971, p. 600) remarked that "man may have paid a high (energetic) price in freeing his hands for purposes other than locomotion." From the perspective of optimization theory, Pyke (1978, 1981) has considered "optimal body size" and "optimal travel speeds" based on energetic considerations. Bertram (1979, p. 225) concluded that scavenging favors particular

adaptations; "one of these adaptations is the ability to travel long distances with low expenditure of energy" (vultures and hyenas were cited as examples). Finally, Reichmann and Atkinson (1981) have argued that mammals adjust their movement paths so as to increase locomotory efficiency, as dictated by body mass and slope angle (Taylor et al. 1972).

The validity of such arguments depends on the magnitude of the ECT. If the ECT is low, arguments concerning the energetic and selective consequences of locomotory efficiency would seem less important. If the ECT is high, then it would be easier to imagine rather intense natural selection for decreasing the ECT, either through morphological or physiological specializations which increase locomotory efficiency, or through behavioral adaptations that reduce daily movements. If the ECT varies with body mass, then so should the selective importance of transport costs.

The ECT may be estimated as follows. The distance an animal moves per day is multiplied by the cost of transport to yield daily transport costs. This latter quantity is then divided by DEE to yield ECT. In order to develop a general model for the scaling of ECT, allometric equations for Daily Movement Distance (DMD, in km/day), Incremental Cost of Locomotion (ICL, in J/km), and Daily Energy Expenditure (DEE, in J/day) are required. An allometric equation for DEE of small rodents has been calculated by King (1974), and may be cautiously extended for mammals in general. All allometric equation for ICL is available in Taylor (1980*b*) for mammals of approximately 0.01 to 260 kg. I have calculated an allometric equation for DMD based on data for 76 species of mammals (0.056–6,000 kg).

From these allometric equations it is concluded that the ECT must be an increasing function of body mass, and that the most variable component of the model is DMD. Hence it becomes of interest to consider factors which scale with body mass and may affect DMD. A model is therefore developed which relates home range size, daily food consumption, and stomach capacity to yield an estimate of Daily Foraging Distance (DFD). This estimate of DFD is then compared with the calculated allometric equation for DMD in an attempt to elucidate factors affecting DMD. Finally, the ecological and evolutionary significance of the ECT are considered. A list of acronyms used here is in the Appendix.

DAILY MOVEMENT DISTANCE

Although considerable information is available concerning home range areas of mammals (reviews in McNab 1963; Stickel 1968; Leuthold 1977; Harestad and Bunnell 1979), far less information exists on DMD, i.e., how far animals actually move per day. Such data are best obtained by direct observation of marked individuals for at least one 24-h period. Many of the data presented in table 1 are of this type. Less reliable estimates (generally underestimates) of DMD may sometimes be obtained from periodic sightings or radiotelemetric fixes, if locations are obtained frequently enough to allow estimation of an animal's actual path of movement. I have chosen to analyze all movement data of which I am aware that provide what seems to be adequate information for estimation of DMD. Most

of the data on primate movements have been taken from Mitani and Rodman (1979) and/or Harvey and Clutton-Brock (1981). According to the latter authors, some of these data may underestimate actual distances moved by primates. Considering all of the data presented in table 1, however, I doubt that the accuracy varies systematically with body mass, so conclusions regarding the scaling exponents for DMD and ECT should be reliable.

For all 76 species of mammals, DMD scales as (exponent \pm 95% confidence interval):

$$\text{DMD (km/day)} = 1.038 M^{0.25 \pm 0.10} \quad (1)$$

in which M = body mass in kg, $r^2 = 0.264$, $P < .001$. Figure 1 presents (1) and the data, and demonstrates that DMD can vary by almost two orders of magnitude at a given body mass. Some of this variability is attributable to phylogenetic and/or ecological differences among mammals. Analysis of covariance indicates that members of the order Carnivora move an average of 4.4 times as far as other mammals, but that the exponents for the scaling relationships within the two groups are not significantly different, such that:

$$\text{DMD Carnivora (km/day)} = 3.877 M^{0.22 \pm 0.08} \quad (2)$$

$$\text{DMD other mammals (km/day)} = 0.875 M^{0.22 \pm 0.08} \quad (3)$$

in which $N = 13$ Carnivora, $N = 63$ other mammals, multiple $r^2 = 0.490$, $P < .001$.

INCREMENTAL COST OF LOCOMOTION

The Incremental Cost of Locomotion (ICL; also referred to as minimum or net cost of locomotion; see Taylor et al. 1970; Taylor 1977a; John-Alder and Bennett 1981) is defined as "the slope of the relationship between metabolic power input (usually measured as the rate of oxygen consumption) and speed" and "is a constant for each animal" (Taylor 1980a, p. 193). This ICL is expressed in units of energy used per unit distance traveled, and is independent of the speed at which the distance is traveled. The ICL may therefore be multiplied by DMD to estimate the minimum amount of energy an animal expends on daily transport costs. Taylor (1980b) provides the following equation for ICL of mammals (\approx 0.01–260 kg; converted to joules by assuming 1 ml $O_2 = 20.1$ J):

$$\text{ICL (J/km)} = 10,678 M^{0.70} \quad (4)$$

No confidence interval is provided, but there is "remarkably little variability in the relationship" (Taylor 1980b, p. 239) between ICL and body mass.

DAILY ENERGY EXPENDITURE

Basal Metabolic Rate (BMR) of mammals is generally considered to scale as

$$\text{BMR (kJ/day)} = 293 M^{0.75} \quad (5)$$

(Kleiber 1961). The scaling relationship for DEE of free-living mammals is much

TABLE 1
ESTIMATED DAILY MOVEMENT DISTANCES OF SEVENTY-SIX SPECIES OF MAMMALS

Species	Body* Mass (kg)	DMD (km)	Source
Proboscidea			
<i>Loxodonta africana</i>	6,000	12	Carrington 1959; Wyatt and Eltringham 1974; Guy 1976
<i>Elaphus maximus</i>	4,000	1.7	McKay 1973
Artiodactyla			
<i>Hippopotamus amphibius</i>	3,800	10	Olivier and Laurie 1974
<i>Giraffa camelopardalis</i>	1,000	1.4	MacClintock 1973; Dagg and Foster 1976
<i>Syncerus caffer</i>	750	7.5	Grimsdell and Field 1976; Sinclair 1977
<i>Bos gaurinus</i>	680	4	Schaller 1967
<i>Alces alces</i>	450	1.5	Phillips et al. 1973
<i>Cervus elaphus</i>	275	2.5	Darling 1963; Craighead et al. 1973; Bowyer 1981
<i>Connochaetes taurinus</i>	180	10	Pennuquick 1979
<i>Cervus duvauceli</i>	160	1†	Schaller 1967
<i>Tragelaphus scriptus</i>	100	1.7	Okiria 1980
<i>Phacochoerus aethiopicus</i>	85	6.8	Clough and Hassam 1970
<i>Axis axis</i>	65	4	Schaller 1967
<i>Pseudois nayaur</i>	60	2	Schaller 1967
<i>Aepyceros melampus</i>	50	3	Jarman and Jarman 1979
<i>Ovis aries</i> (domestic sheep)	50	10	Osuji 1974; Squires 1975
<i>Capra aegagrus</i>	34	4.5	Schaller 1977
<i>Nemorhaedus goral</i>	32	2	Schaller 1977
Rodentia			
<i>Cynomys ludovicianus</i>82	1.7	King 1955
<i>Dipodomys spectabilis</i>12	.35	Schroder 1979
<i>Dipodomys deserti</i>11	.7‡	Thompson 1980
<i>Ammospermophilus leucurus</i>085	1	Karasov 1981
<i>Dipodomys microps</i>056	.58§	Kenagy 1973
Marsupialia			
<i>Thylogale thetis</i>	7.5	2	Johnson 1980
Insectivora			
<i>Erinaceus</i> or <i>Hemiechinus</i>8	2.5	Haymob 1960
Carnivora			
<i>Ursus horribilis</i>	350	15†	Craighead 1979
<i>Panthera tigris</i>	230	24	Schaller 1967
<i>Panthera leo</i>	160	6	Schaller 1972
<i>Felis concolor</i>	60	20†	Young and Goldman 1964; Seidensticker et al. 1973
<i>Acinonyx jubatus</i>	55	2	Schaller 1968
<i>Crocutta crocutta</i>	50	10	Kruuk 1972
<i>Hyaena vulgaris</i>	45	20	Kruuk 1976
<i>Canis lupus</i>	40	15	Mech 1970; Peterson 1977
<i>Canis familiaris</i> (feral)	17	6†	Scott and Causey 1973
<i>Canis latrans</i>	16	16	Burt and Grossenheider 1976
<i>Nasua narica</i>	5	3†	Kaufmann 1962; Lanning 1976
<i>Mephitis mephitis</i>	3	4†	Verts 1967
<i>Mungos mungo</i>	1.5	3	Rood 1975

(Continued)

TABLE 1 (Continued)

Species	Body* Mass (kg)	DMD (km)	Source
Primates			
<i>Gorilla gorilla</i>	127	.5	D. Watts, personal communication
<i>Pongo pygmaeus</i>	53	.5	Harvey and Clutton-Brock 1981
<i>Pan troglodytes</i>	45	3.9	Mitani and Rodman 1979
<i>Homo sapiens</i> (Kalahari bushmen)	44	10	Lee and DeVore 1976
<i>Papio hamadryas</i>	20	9.5	Siggs and Stolba 1981
<i>Papio ursinus</i>	19	6.4	Mitani and Rodman 1979
<i>Papio cynocephalus</i>	18	5.5	Mitani and Rodman 1979
<i>Papio anubis</i>	17	3.6	Harvey and Clutton-Brock 1981
<i>Theropithecus gelada</i>	14	.63	Mitani and Rodman 1979
<i>Presbytis entellus</i>	13	1.6	Mitani and Rodman 1979
<i>Indiri indiri</i>	13	.35	Mitani and Rodman 1979
<i>Symphalangus syndactylus</i>	11	1	Mitani and Rodman 1979
<i>Colobus satanas</i>	11	.45	Harvey and Clutton-Brock 1981
<i>Colobus guereza</i>	11	.53	Harvey and Clutton-Brock 1981
<i>Colobus badius</i>	8.2	.65	Mitani and Rodman 1979
<i>Cercocebus albigena</i>	8.0	1.3	Waser 1975
<i>Cercocebus galertus</i>	7.9	1.3	Harvey and Clutton-Brock 1981
<i>Macaca mulatta</i>	7.9	1.4	Mitani and Rodman 1979
<i>Erythrocebus patas</i>	7.8	2.3	Mitani and Rodman 1979
<i>Alouatta seniculus</i>	7.3	.58	Mitani and Rodman 1979
<i>Presbytis obscura</i>	7.1	.95	Harvey and Clutton-Brock 1981
<i>Presbytis melalophos</i>	6.7	1.2	Harvey and Clutton-Brock 1981
<i>Alouatta palliata</i> = <i>villosa</i>	6.6	.44	Nagy and Milton 1979
<i>Hylobates lar</i>	5.5	1.7	Harvey and Clutton-Brock 1981
<i>Macaca radiata</i>	5.5	.79	Mitani and Rodman 1979
<i>Macaca fascicularis</i>	5.0	.70	Harvey and Clutton-Brock 1981
<i>Cercopithecus mitis</i>	4.5	1.3	Mitani and Rodman 1979
<i>Cercopithecus aethiops</i>	4.1	1.4	Mitani and Rodman 1979
<i>Propithecus verreauxi</i>	3.6	.75	Mitani and Rodman 1979
<i>Cercopithecus ascianus</i>	3.6	1.4	Mitani and Rodman 1979
<i>Lemur catta</i>	2.7	.95	Mitani and Rodman 1979
<i>Lemur mongoz</i>	2.1	.61	Mitani and Rodman 1979
<i>Lemur fulvus</i>	2.1	.14	Mitani and Rodman 1979
<i>Miopithecus talapoin</i>	1.3	2.3	Mitani and Rodman 1979
<i>Callicebus torquatus</i>	1.1	.82	Harvey and Clutton-Brock 1981
<i>Callicebus moloch</i>68	.64	Mitani and Rodman 1979
<i>Saimiri oerstedii</i>67	3.4	Mitani and Rodman 1979
<i>Lepilemur mustelinus</i>6	.27	Mitani and Rodman 1979

* Body mass estimates are from source of DMD, Burt and Brossenheider 1976; Clutton-Brock and Harvey 1977a, 1977b; Napier and Napier 1967; Walker 1976, and are intended to represent typical adult weights; for sexually dimorphic species, they represent the mean of male and female weights.

† DMD considered a rough estimate.

‡ Calculated assuming 5.5 min of movement at 6.33 km/h.

§ Calculated assuming 10 min of movement at 4.23 km/h.

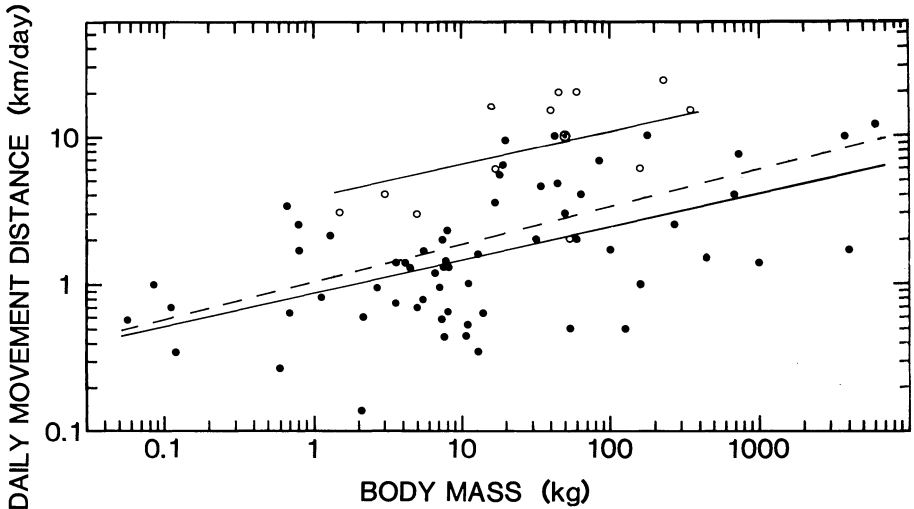


FIG. 1.—Daily Movement Distances of 76 species of mammals, data from table 1. Dashed line is least squares linear regression line for all mammals; slope = 0.25; see text equation (1). Upper solid line and open circles are Carnivora ($N = 13$), which move an average of 4.4 times as far as other mammals ($N = 63$), the latter represented by lower solid line; common slope = 0.22; see text equations (2) and (3).

less well documented. King (1974) has calculated an equation for small rodents (8.7–600 g):

$$\text{DEE (kJ/day)} = 753 M^{0.67 \pm 0.12} \quad (6)$$

King's data set ($N = 19$) included estimates from doubly-labeled water studies, time-energy budgets, and extrapolations from laboratory data. Considering only data from doubly-labeled water studies ($N = 11$, body mass range = 0.014–9 kg; from Nagy et al. [1978, table 3] for seven species and 10 estimates, plus data from Nagy and Milton [1979], 3,080 kJ/day was predicted for a 9-kg howler monkey from their fig. 1):

$$\text{DEE (kJ/day)} = 802 M^{0.66 \pm 0.08} \quad (7)$$

in which $r^2 = 0.913$, $P < .001$. Recently completed doubly-labeled water studies of Australian marsupials (K. A. Nagy, personal communication) also indicates that DEE scales to an exponent lower than 0.75. In other words, the percentage increase in energy expenditure of mammals living under natural conditions, as compared with the same animals under basal conditions, may be less for large animals than for small ones (see also equations in Grodzinski and Wunder 1975; Farlow 1976). But the exponents of (6) and (7) may be too low to yield accurate predictions of DEE for very large mammals. McKay (1973), for example, estimated that *Elephas maximus* exists in the wild on about 401,664 kJ/day, which is 2.7-fold greater than the predicted BMR of a 4,000-kg mammal using (5). However, (6) predicts a DEE of only 195,063 kJ/day for a 4,000-kg mammal, which is only 1.3-fold greater than predicted BMR. Therefore, the true value of the expo-

ment for scaling of DEE in mammals in general probably falls somewhere between 0.67 and 0.75. I arbitrarily use the following approximate equation in subsequent calculations

$$\text{DEE (kJ/day)} = 800 M^{0.71}. \quad (8)$$

Equation (8) predicts a DEE of 288,770 for a 4,000-kg mammal, which is 2.0X BMR, and much closer to McKay's (1973) estimate for *Elephas* than the value predicted by (6) or (7).

ECOLOGICAL COST OF TRANSPORT

The ECT is defined as

$$\text{ECT (\% DEE)} = 100 \times \frac{\text{DMD (km/day)} \times \text{ICL (J/km)}}{\text{DEE (J/day)}}. \quad (9)$$

Substituting (1) for DMD, (4) for ICL, and (8) for DEE into (9), we obtain

$$\text{ECT mammals (\% DEE)} = 1.39 M^{0.24}. \quad (10)$$

Substituting (2) for (1) in (9) we obtain

$$\text{ECT Carnivora (\% DEE)} = 5.17 M^{0.21}. \quad (11)$$

Substituting (3) for (1) in (9), we obtain

$$\text{ECT other mammals (\% DEE)} = 1.17 M^{0.21}. \quad (12)$$

From equations (10), (11), and (12), large mammals are predicted to spend a greater fraction of their DEE on transport costs than do small mammals. In addition, Carnivora should have a greater ECT than other mammals regardless of body size. Table 2 presents ECT's calculated for mammals of a variety of body masses.

The sensitivity of (10), (11), and (12) to errors of estimation of their component parameters can be considered qualitatively as follows. First, how reliable are the component allometric equations? Equation (8) for DEE is necessarily an approximation, since few data are available concerning the energy expenditure of free-living large mammals. It seems doubtful, however, that the exponent of (8) errs by more than ± 0.04 (see *Daily Energy Expenditure*). In any case, the accuracy of the exponent of (8) makes little difference to the conclusion that ECT must be an increasing function of body mass. Because the exponents of (4) for ICL and (8) for DEE are quite similar (0.70 and ≈ 0.71 , respectively), these two exponents essentially cancel in (9) for ECT. Therefore, so long as large mammals move farther than do small mammals on a daily basis (i.e., exponents of [1], [2], and [3] are significantly positive), ECT must increase with body mass. It should be noted that animals with a high DMD and/or ICT might also have a slightly higher than typical DEE; this would tend to obscure differences in ECT, since ECT is calculated as a percentage of DEE. However, major differences in ECT (e.g., differences between Carnivora and most other mammals) should not be obscured.

There are too few data available to state with any certainty how much DEE can

TABLE 2
 PREDICTED ECOLOGICAL COST OF TRANSPORT (% of Daily Energy Expenditure)
 FOR MAMMALS OF VARIOUS BODY MASSES

	Text Equation	Body Mass (kg)*							
		.001	.01	.1	1	10	100	1,000	10,000
All mammals	10	.26	.46	.80	1.4	2.4	4.2	7.3	13
Carnivora	11	1.2	2.0	3.2	5.2	8.4	14	22	36
Other mammals	12	.27	.44	.72	1.2	1.9	3.1	5.0	8.1

* Estimates at extreme body masses are included for comparison, but represent extrapolations and hence are less reliable than estimates for mammals of intermediate size.

vary among mammals of similar size. Mammalian BMR's show considerable interspecific variability (review in McNab 1980), but it is as yet impossible to say whether such variation in BMR generally translates into proportional variation in DEE. Three-toed sloths (*Bradypus tridactylus*) may represent an extreme example of deviation from the norm: DEE (as measured with doubly-labeled water) is about 1.75 times BMR, but BMR is only 41% of that predicted by (5), and DEE is only 28% of that predicted by (8) (see Nagy and Montgomery 1980).

The ICL seems less variable than DEE. For 66 species of lizards, birds, and mammals, Fedak and Seeherman (1979) found that "for any given size animal, . . . (ICL) . . . may vary by a factor of nearly two" (see also Taylor and Rowntree 1973; Taylor et al. 1974; Thompson et al. 1980; Taylor 1980a, 1980b). Among mammals, only young lions have been found to deviate significantly from predicted values (Chassin et al. 1976).

DMD are by far the most variable component of the ECT. Inspection of figure 1 indicates that DMD may vary by almost two orders of magnitude among mammals of similar size. Many studies have shown that, even within a species, movement distances are affected by numerous factors, e.g., age, sex, resource density and distribution, habitat, weather, and season (e.g., Ballenberghe and Peek 1971; Montgomery and Lubin 1977; Rood 1975; Squires 1975; Waser 1975; Peterson 1977; Bowyer 1981). That the Carnivora generally move greater distances each day than do other mammals is apparent (fig. 1) and not surprising. Other phylogenetic and/or trophic effects are presumably important, but their elucidation must await the collection of further data on DMD's. Clutton-Brock and Harvey (1977a, 1977b) and Harvey and Clutton-Brock (1981) discuss factors which may influence energy requirements, home range size, and ranging behavior among primates.

DAILY FORAGING DISTANCE

Given the tremendous variability in DMD (fig. 1), it is of interest to consider factors that may affect DMD. In addition, it is surprising that DMD scales to such a low exponent ($\approx 0.21-0.25$), considering that home range area scales approxi-

mately as $M^{1.0}$ (Harestad and Bunnell 1979). This difference in exponents suggests that small mammals must travel over their home ranges much more frequently than do large mammals. For example, moose (*Alces alces*, 450 kg) move only about 1.5 times as far as do antelope ground squirrels (*Ammospermophilus leucurus*, 85 g; see table 1), yet moose have home ranges (1,160 ha; Harestad and Bunnell 1979) that are 268 times as large as those of *Ammospermophilus* (6 ha; Bradley 1967). Here I attempt to explain the discrepancy between home range and DMD scaling.

Although animals travel for a variety of reasons, foraging is one of the most basic activities undertaken by any mammal. Furthermore, for mammals in general, it may be that "ranging patterns are primarily a function of feeding patterns," as suggested by Mitani and Rodman (1979, p. 248) for primates. If so, then assuming that most movements within a home range are connected with foraging activities, and that estimates of home range area thus largely reflect the extent of an animal's foraging movements, it is possible to derive a relationship between home range area and the length of a typical foraging bout. If one also knows how often animals forage, i.e., how many foraging bouts are undertaken per day, then the total distance moved during daily foraging activities may be estimated. I have derived an estimate of DFD as follows.

The best available allometric analysis of mammalian home ranges is provided by Harestad and Bunnell (1979) for North American species. Home Range area scales as

$$\text{HR (ha)} = 14.9 M^{1.083 \pm 0.245} \quad (13)$$

in which $r^2 = 0.601$, $N = 55$, and the body mass range is 4.5 g (shrew) to 411 kg (moose). Assuming that home ranges are, on the average, circular, and that a typical foraging bout may be modeled as extending from the center of the HR to the periphery and back, then Foraging Bout Distance would vary as

$$\text{FBD} = 2 \left(\frac{\text{HR}}{\pi} \right)^{0.5}, \quad (14)$$

or, by substitution of (13) into (14),

$$\text{FBD (m)} = 436 M^{0.541}. \quad (15)$$

If Foraging Frequency is assumed to be proportional to Daily Food Consumption divided by the amount of Food Gained per Foraging Bout, then

$$\text{FF (bouts/day)} = \frac{\text{DFC (g/day)}}{\text{FG/FB (g/bout)}}. \quad (16)$$

Using data from Davis and Golley (1963, table 4-4, $N = 27$) and Bourlière (1964, table 9, $N = 19$ additional species), I have calculated the following equation for DFC (in grams fresh weight):

$$\text{DFC (g/day)} = 152 M^{0.738 \pm 0.066} \quad (17)$$

in which $r^2 = 0.921$, and the data include a variety of placental mammals ($N = 46$), ranging in size from a 2.5-g shrew to a 3,672-kg elephant. These data are for

captive animals, and so might be expected to underestimate the DFC of free-living mammals (e.g., see Schaller 1968). On the other hand, Bourlière (1964, p. 334) states that "most mammals eat much more in captivity than in the wild, and therefore tend to fatten considerably." I assume that such considerations have little effect on the exponent of (17).

Assuming that stomach capacity scales as $M^{1.0}$ (see Calder 1974), that stomach capacity is 5% of body mass (e.g., Tileston and Lechleitner 1966; Fitzgerald and Lechleitner 1974; Andersen 1970; but see Parra 1978), and that animals fill their stomachs during each foraging bout (cf. Pennycuick 1979; Vleck et al. 1981), then the amount of FG per FB is

$$\text{FG/FB (g/bout)} = 0.05 M^{1.00}. \quad (18)$$

Substituting (17) and (18) into (16), we obtain Foraging Frequency:

$$\text{FF (bouts/day)} = 3.03 M^{-0.262}. \quad (19)$$

DFD is now obtained by multiplication of (15) and (19):

$$\text{DFD (km/day)} = 1.32 M^{0.28}. \quad (20)$$

Large mammals are thus predicted to move greater distances during daily foraging activities than do small mammals, and predicted DFD's are quite similar to predicted DMD's (1) of mammals in general. In fact, the 95% confidence interval for the exponent of (1) includes the exponent for DFD (20). Therefore, the discrepancy between home range (13) and DMD scaling has been at least partially explained by considering some factors that also scale with body mass and affect foraging behavior.

To the extent that agreement between DFD and DMD is more than coincidental, then variation in the components of DFD may be examined to gain insight into factors affecting DMD. Much of the variability in home range data may be explained by variations in home range size among trophic groups. Harestad and Bunnell (1979) have demonstrated (using analysis of covariance) that the regressions of home range area on body mass are statistically different among carnivores, herbivores, and omnivores. Daily Food Consumption will also vary among trophic groups because of differing caloric values of food and differing assimilation efficiencies (Davis and Golley 1963). Stomach capacity also differs between carnivores and herbivores (Parra 1978; Pennycuick 1979; see also Voronstov 1960; Pianka and Pianka 1970, fig. 6). Furthermore, movement patterns and degree of stomach filling must certainly differ among groups. All of these sources of variation will result in interspecific variability in DFD, DMD, and hence ECT. In the absence of better data concerning phylogenetic or ecological differences among mammals, with regard to the component parameters of DFD, DMD, and ECT, further speculation is not useful. Interspecific comparisons of the component parameters should, however, prove useful for understanding factors affecting movement parameters in general, home range size, and the ECT.

DISCUSSION

The ECT is predicted to be an increasing function of body mass (table 2). Small mammals (less than about 500 g), and especially non-Carnivora, may spend only about 1% or less of their DEE on transport costs. Very large mammals (more than about 1,000 kg), and especially Carnivora, may, however, exhibit an ECT of 5%–15% or more. Only a few studies have actually estimated the ECT. Pennycuik (1979) calculated that a 180-kg wildebeest moving an average of 10 km/day would spend about 8% of its yearly energy budget on transport costs (predicted from [12] = 3.5%). Nagy and Milton (1979) estimated that a 6.5-kg howler monkey would move about 443 m/day (through the trees) and spend 2.3% of its DEE on transport costs (predicted = 1.7%). Thompson (1980) estimated ECT's of 0.1%–4.0% for three species of heteromyid rodents (10–110 g; predicted = 0.4–0.7%). Karasov (1981) estimated that an 85-g antelope ground squirrel moving 1.5 km/day would have an ECT of 4.4% in August; however, the same animal, moving 1 km/day in April (when DEE was 35% higher than in August) would have an ECT of only 2.2% (predicted = 0.7%). These data are consistent with my prediction that ECT should be greater in larger mammals, and give some hint of the variation in ECT that may occur among similarly sized mammals. They may also suggest that values predicted by (12) are uniformly low.

At any body mass, the ECT is lower than many workers have apparently assumed (references in introduction). If any locomotory specializations do exist that have evolved primarily to increase locomotory efficiency (i.e., decrease the ICL), they would be expected to occur among large animals. It is of interest to note that Alexander et al. (1981) and Biewener et al. (1981) have shown that energy savings during running by elastic storage in tendons cannot be as important in small mammals as it can be in large ones. In any case, it might be expected that cursorial adaptations among large mammals have resulted in a reduction in the ICL. Currently, however, there is no evidence that cursorial adaptations have resulted in any reduction in the energetic cost of transport (see Taylor et al. 1974; Bakker 1975; Coombs 1978; Taylor 1980a; Thompson et al. 1980).

Locomotory specializations, such as cursorial adaptations in general or bipedalism in particular, may, of course, have important effects on other performance parameters, e.g., speed or endurance (see Howell 1944). It is therefore of interest to reconsider arguments that have been presented concerning the selective advantages of some locomotory specializations. Kangaroos are unusual in that they exhibit an actual decrease in the cost of locomotion at high speeds (>18 km/h) as compared with typical quadrupedal mammals (Dawson and Taylor 1973). Taylor (1980a, p. 197) states that "kangaroos do normally move long distances in nature at high speeds (25 to 30 km/h) . . . and their hopping mechanism does appear to save them large amounts of energy." Unfortunately no data are available for DMD's of large kangaroos. The largest kangaroos may reach 90 kg, and a 90-kg mammal moving 10 km/day would be predicted (using [4] and [8]) to spend 13% of its DEE on transport costs. If large kangaroos do normally move such long or longer distances on a daily basis, then they could save a few percent of their DEE in transport costs. But the kangaroo's hopping mechanism may be of selective

advantage in other ways. Although kangaroos are not absolutely faster than quadrupedal mammals of similar size (see Windsor and Dagg 1971; Garland 1983), they may be able "to sustain higher speeds when being pursued (as compared with) other large terrestrial marsupials . . . (and) this could explain how they survived the introduction of man and . . . the dingo, while the large quadrupedal marsupials became extinct" (Dawson and Taylor 1973, p. 314).

Similar arguments have concerned the ecological and evolutionary significance of bipedality in small rodents. Several workers have concluded that the chief benefit of bipedal hopping is related to enhancement of abilities to escape predators (references in Thompson et al. 1980). Recently, however, Reichman (1981 and references cited therein) and others have argued that bipedality, assumed to be an efficient way to locomote at high speeds (Dawson and Taylor 1973; Dawson 1976), allows some heteromyid rodents (*Dipodomys*) to move long distances inexpensively while foraging on dispersed resources (seeds), hence facilitating coexistence of bipedal hopping and quadrupedal small rodents (the latter assumed to move shorter distances and feed on more clumped seeds). *Dipodomys* do not appear to move exceptionally long distances for their size (see table 1, fig. 1), however, and the predicted ECT for a 100-g non-Carnivora (from [12]) is only 0.7% of DEE (see also Thompson 1980). It seems rather unlikely that reducing such a small component of DEE could be of as much selective value as the possible benefits of bipedality for avoiding predation, and *Dipodomys* do appear to be rather fast for their size (see Garland 1983). In addition, recent studies have demonstrated that there is actually no difference in the cost of locomotion for bipedal hopping and quadrupedal small mammals (Thompson et al. 1980; R. E. MacMillen, personal communication).

In summary, I agree with Parsons and Taylor (1977, p. 188) who concluded: "When interpreting the relative advantages of different types of locomotion, we must be careful not to place undue emphasis on the cost of locomotion simply because it can be easily quantified." It would also seem important to consider at what body size a particular locomotory specialization first evolved. For example, bipedal hopping might confer a selective advantage in terms of maximal running speed for small mammals, but be of little energetic significance. On the other hand, for large mammals, or those that typically move long distances, benefits in terms of energetic economy and/or endurance capacity might favor the evolution of kangarootype bipedality, even if it conferred no advantage in terms of maximal running speed. It is also possible that a locomotory specialization that evolved because it was of selective advantage at one body size in an evolving lineage could later be favored for different reasons in differently sized descendants (cf. Garland, 1983).

SUMMARY

The Ecological Cost of Transport (ECT) is defined as the percentage of a free-living animal's Daily Energy Expenditure (DEE) that is attributable to transport costs. It is concluded that the ECT must be an increasing function of body mass, with the result that some small mammals may have a very low ECT (<1% DEE)

whereas large mammals may have an ECT of 5%–15% or more. For small mammals, or those that move little, daily transport costs would seem to be of little energetic significance.

Daily Movement Distance (DMD) scales approximately as $M^{0.25}$, in contrast to home range area, which scales approximately as $M^{1.0}$. This discrepancy in scaling exponents is partially explained by a model which relates home range size, stomach capacity, and daily food consumption to yield an estimate of Daily Foraging Distance, the latter being quite similar to the empirically derived equation for DMD. Members of the order Carnivora move an average of 4.4 times as far as other mammals on a daily basis; therefore, Carnivora should spend considerably more on transport costs than do most other mammals.

The ECT is discussed in the context of arguments concerning the energetic significance of the cost of locomotion and its relevance to the origin of locomotory specializations.

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APPENDIX

LIST OF ACRONYMS

Acronym	Quantity Represented	Text Equation(s)
BMR	Basal Metabolic Rate	5
DEE	Daily Energy Expenditure	6,7,8
DFC	Daily Food Consumption	17
DFD	Daily Foraging Distance	20
DMD	Daily Movement Distance	1,2,3
ECT	Ecological Cost of Transport	9,10,11,12
FBD	Foraging Bout Distance	14,15
FG/FB	Food Gained per Foraging Bout	18
FF	Foraging Frequency	16,19
HR	Home Range	13
ICL	Incremental Cost of Locomotion	4

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