

## The relation between maximal running speed and body mass in terrestrial mammals

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(With 3 figures in the text)

The available data on maximal running speeds of mammals are presented, and the relationship between speed and body mass is considered. For all mammals ( $n = 106$ ), maximal running speed scales as  $(\text{body mass})^{0.17}$ ; however, the largest mammals are not the fastest, and an optimal size with regards to running ability is suggested ( $\approx 119$  kg). Maximal running speeds are, on the average, somewhat more than twice maximal aerobic speeds.

Within the Artiodactyla, Carnivora or Rodentia, maximal running speed is mass independent, in agreement with theoretical expectations for geometrically similar animals (Thompson, 1917; Hill, 1950). McMahon's (1975*b*) model for elastic similarity is therefore not supported by the available data on maximal running speeds, and there appears to be no necessary correspondence between scaling of limb bone proportions and running ability.

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### Introduction

It would not be surprising if animals of different sizes could attain different maximal running speeds. Exactly how running ability should scale with body mass ( $M$ ) is not, however, obvious, and four competing theories offer different predictions. The reader is referred to Gunther (1975) and McMahon (1975*b*) for discussions of the assumptions involved in each theory. Thompson (1917) and Hill (1950) conclude that maximal running speed (MRS) should be mass independent among geometrically similar animals (cf. Gunther's, 1975 "kinematic similarity"). McMahon (1975*b*), however, argues that animals should be designed so as to meet the criteria of elastic similarity. Elastic similarity predicts that the speed at which animals will be running at their natural frequency will be proportional to

$M^{0.25}$ . If MRS is a constant multiple of this speed, then MRS should also scale as  $M^{0.25}$  among elastically similar animals. Alternatively, if animals were built for static stress similarity, MRS should scale as  $M^{0.40}$  (McMahon, 1975*b*). Finally, MRS is predicted to scale as  $M^{0.17}$  among dynamically similar animals (Gunther, 1975). (Dynamic similarity exists if homologous parts of differently sized animals experience similar net forces.)

There is thus no paucity of theory concerning how speed should vary with body mass. The purpose of this paper is to examine the available data on speeds of mammals, to determine the empirical relationship between maximal running speed and body mass, and to compare the running abilities of different groups of mammals. In addition, the empirically derived scaling relationships are compared with the above mentioned theoretical expectations.

### The data

Both original and secondary sources were consulted for estimates of maximal running speeds (MRS, in km/h); unfortunately, many secondary sources do not provide the original sources of their MRS data (e.g., Van Gelder, 1969; Walker, 1976). Recent papers by Coombs (1978 and pers. comm.) and Alexander, Langman *et al.* (1977) facilitated the literature search. The data may vary in accuracy for several reasons. Some estimates of MRS are more or less anecdotal or based on limited observations (e.g., estimates for *Ursus* spp., *Panthera tigris*, *P. pardus*, and lagomorphs). It is also difficult to measure the speed of a running animal accurately in the field. Speeds of some mammals (e.g., man, dog, horse) have been timed very accurately during races, but speeds of most large mammals have been estimated from the speedometer of a pursuing automobile. As pointed out by an anonymous reviewer, if an animal and a vehicle travel side by side around a curve, with the animal on the inside, the vehicle must travel faster to keep abreast of the animal. This could lead to (perhaps greatly) overestimating the animal's speed, but many workers seem to have been careful to avoid such a situation. Some large mammals have been filmed while running, and speed estimates from these films are lower than the highest reported speeds for the same species (Alexander, Langman *et al.*, 1977). Most small mammals have been timed with a hand-held stopwatch over a short distance (e.g., Layne & Benton, 1954; Kenagy, 1973). How the motivation to run varies under such different conditions is unknown, and as noted by Taylor (1977, and cf. comments in Heglund *et al.*, 1974; McMahon, 1975*b*; Alexander, Langman *et al.*, 1977), it may in any case be difficult to determine if an animal is actually running at top speed.

I have chosen to include all estimates of MRS of which I am aware. Therefore, the data set necessarily sacrifices some accuracy for completeness. The most critical assumption for the present analysis is that the accuracy of the data does not vary systematically with body mass. For many species, more than one reference could have been cited. The highest reported MRS have been chosen, and, where possible, the source closest to the original data. Three exceptions merit comment. The cheetah (*Acinonyx*) is generally considered to be the fastest mammal (Howell, 1944; Breland, 1963; Schaller, 1968; Van Gelder, 1969; Walker, 1976), but estimates of its MRS vary from 101 (Wood, 1972) to 121 km/h (Bourliere, 1964); I have used 110 km/h. Estimates of the MRS of *Antilocapra* generally range between 97 (Howell, 1944; Breland, 1963) and 113 km/h (Van Gelder, 1969), but Walker (1976: 1441) asserts that "*Antilocapra* is... able to run as fast as 65 km/h, not 95 km/h as is commonly

reported". Cottam & Williams (1943), however, cite several reports of *Antilocapra* running at least 72 km/h. I have used 100 km/h for the Pronghorn. The MRS of the African elephant (*Loxodonta*) is generally cited as 24 (Howell, 1944) or 40 km/h (Breland, 1963; Bourliere, 1964; Van Gelder, 1969; Wood, 1972). W. P. Coombs (pers. comm.) doubts the credibility of the higher figure, so I have used 35 km/h.

Body mass estimates are intended to represent typical adult sizes (mean of male and female masses for sexually dimorphic species). Within a species, it is assumed that there exists some optimal size (cf. Haldane, 1928) with regards to running ability; that is, neither the largest nor the smallest individuals are the fastest. Considering the size of the fastest human runners, this assumption seems justified. Schaller (1972) states that female lions, which are smaller than males, are also faster than males, so the cited body mass is for a typical female.

### Statistical analyses

Maximal running speed is here considered to represent a variable that has a functional dependence (see Kendall & Stuart, 1978) on body mass (the independent variable; cf. Maloiy *et al.*, 1979). Further, it is desirable to calculate predictive equations for  $\log_{10}$ MRS (e.g., Bakker, 1975) and to compare these equations among different groups of mammals. I have therefore employed least squares linear regression analysis of the  $\log_{10}$  transformed data to yield estimates of the parameters of allometric equations of the form:

$$\text{Maximal running speed (km/h)} = a(M)^b,$$

where  $M$  = body mass in kilogrammes. Analysis of covariance (ANCOVA; Kleinbaum & Kupper, 1978) is employed to compare various equations. Although body mass is here considered the independent variable, it can not be considered free of "error variance" (Joliceur & Heusner, 1971). To the extent that error variance is present in the body mass data of Table I, regression estimates of  $\log_{10}$ MRS on  $\log_{10}M$  are expected to underestimate the true slope,  $b$ . Unfortunately, the ratio of the error variances of the two variables is unknown, so no exact correction is possible (Kendall & Stuart, 1978). Some readers might have preferred major axis or reduced major axis analysis, but neither of these methods is free of assumptions concerning the error variance ratio (see Joliceur & Heusner, 1971; Brace, 1977; Kuhry & Marcus, 1977; Clarke, 1980). Inspection of scattergrams of the data in Table I, e.g., Figs 1–3, indicate that regressions provide satisfactory representations of the relationship between  $\log_{10}$ MRS and  $\log_{10}M$ .

### Results and discussion

#### *Scaling of maximal running speed*

Table I presents the available data on maximal running speeds of mammals; Fig. 1 is a scattergram of the  $\log_{10}$  transformed data. For all mammals ( $n = 106$ ), MRS scales as  $M^{0.165 \pm 0.036}$  ( $b \pm 95\%$  confidence interval,  $r^2 = 0.439$ ; see Table II). However, it is apparent from Fig. 1 that there is a curvilinear relationship between  $\log_{10}$ MRS and  $\log_{10}M$ , and a polynomial regression equation of the form

$$\log_{10}\text{MRS} = 1.47832 + 0.25892(\log_{10}M) - 0.06237(\log_{10}M)^2, \quad (1)$$

yields a significantly better fit to the data ( $r^2 = 0.574$ ; Fig. 1). As has been noted by many previous workers (e.g., Currey, 1977), the largest living mammals are not the fastest. Instead,

TABLE I

*Maximal running speeds (MRS) of mammals. Body mass estimates are intended to represent average adult size, not the maximum attained by a species*

Species	Body mass† (kg)	Maximal running speed (km/h)	Reference, method*
Proboscidae			
<i>Loxodonta africana</i>	6000	35	see text, T, E
<i>Elephas maximus</i>	4000	26	Wood, 1972, U
Perissodactyla			
<i>Ceratotherium simum</i>	3000	25	Guggisberg, 1966, U
<i>Diceros bicornis</i>	1400	45	Bourliere, 1964, U
<i>Equus caballus</i>	400	70	McWhirter & McWhirter, 1980, T
<i>Equus burchelli</i>	350	70	Demmer, 1966‡; Gambaryan, 1974, U
<i>Equus zebra</i>	300	64	Bourliere, 1964, U
<i>Equus hemionus</i>	260	70	Andrews, 1933, S; Gambaryan, 1974, F
<i>Tapirus americanus</i>	250	40	Gambaryan, 1974, U
Artiodactyla			
<i>Hippopotamus amphibius</i>	3800	25	cited in Bakker, 1975, U
<i>Giraffa camelopardalis</i>	1000	60	Demmer, 1966‡; Gambaryan, 1974, U
<i>Taurotragus oryx</i>	900	70	Schaller, 1972, U
<i>Bison</i>	900	56	Fuller, 1960§, U
<i>Bos sauveli</i>	800	29	Bourliere, 1964, U
<i>Syncerus caffer</i>	750	57	Bourliere, 1964, U
<i>Camelus dromedarius</i>	500	32	Wood, 1972, U
<i>Alces alces</i>	450	56	Cottam & Williams, 1943, S
<i>Cervus elaphus</i>	300	72	Cottam & Williams, 1943, S
<i>Connochaetes gnu</i>	300	90	Gambaryan, 1974, U
<i>Connochaetes taurinus</i>	250	80	Howell, 1944, U
<i>Hippotragus equinus</i>	250	56	Howell, 1944, S, E
<i>Alcelaphus buselaphus</i>	170	80	Demmer, 1966‡, U
<i>Ovis canadensis</i>	150	48	Cottam & Williams, 1943, S
<i>Damaliscus korrigum</i>	130	70	Schaller, 1972, U
<i>Rangifer tarandus</i>	120	80	Gambaryan, 1974, U
<i>Odocoileus hemionus</i>	120	61	Rue, 1978, E
<i>Oreamnos americanus</i>	110	33	Howell, 1944, U
<i>Odocoileus virginianus</i>	100	64	Rue, 1978, E
<i>Phacochoerus aethiopicus</i>	85	55	Schaller, 1972, S
<i>Cervus (Dama) dama</i>	80	65	Chapman & Chapman, 1975, U
<i>Lama guanacoe</i>	72	56	Walker, 1976, U
<i>Capra caucasica</i>	70	45	Gambaryan, 1974, U
<i>Ovis ammon</i>	65	60	Gambaryan, 1974, U
<i>Gazella granti</i>	62	81	Howell, 1944, U
<i>Antilocapra americana</i>	50	100	see text, S, E
<i>Capreolus capreolus</i>	50	60	Gambaryan, 1974, U
<i>Rupicapra rupicapra</i>	50	40	Gambaryan, 1974, U
<i>Aepyceros melampus</i>	50	47	Alexander, Langman <i>et al.</i> , 1977, F
<i>Antelope cervicapra</i>	37	105	Breland, 1963, U
<i>Saiga tatarica</i>	35	80	Gambaryan, 1974, U
<i>Antidorcas marsupialis</i>	34	97	Bourliere, 1964, U
<i>Gazella subgutturosa</i>	30	97	Howell, 1944, S

TABLE I  
(Continued)

Species	Body mass† (kg)	Maximal running speed (km/h)	Reference, method*
<i>Procapra gutturosa</i>	30	80	Gambaryan, 1974, U
<i>Capra aegagrus</i>	30	45	Gambaryan, 1974, U
<i>Gazella thomsonii</i>	20	81	Howell, 1944; Schaller, 1968, S, E
Carnivora			
<i>Thalarcos maritimus</i>	400	40	Perry, 1966, E
<i>Ursus horribilis</i>	300	48	Breland, 1963, S
<i>Panthera tigris</i>	230	56	Schaller, 1967, E
<i>Panthera leo</i>	150 <sup>¶</sup>	59	Schaller, 1972, E
<i>Ursus americanus</i>	135	48	Burt & Grossenheider, 1976, U
<i>Crocota crocuta</i>	65	65	Bourliere, 1964, U
<i>Panthera pardus</i>	60	60	Turnbull-Kemp, 1967; Schaller, 1972, E
<i>Acinonyx jubatus</i>	55	110	Walker, 1976, T
<i>Hyaena vulgaris</i>	45	50	Walker, 1976, U
<i>Canis lupus</i>	40	64	Mech, 1970, S, E
<i>Canis familiaris</i>	25	67	McWhirter & McWhirter, 1980, T
<i>Lycaon pictus</i>	20	70	Schaller, 1972, U
<i>Canis latrans</i>	16	65	Walker, 1976, U
<i>Procyon lotor</i>	12	24	MacClintock, 1981, U
<i>Meles meles</i>	11	30	Neal, 1977, U
<i>Canis aureus</i>	10	56	Wood, 1972, U
<i>Canis mesomelas</i> or <i>adustus</i>	7	60	Schaller, 1972, U
<i>Vulpes fulva</i>	6	72	Howell, 1944, S
<i>Urocyon cinereoargenteus</i>	5	64	Howell, 1944, S
<i>Nasua narica</i>	5	27	Kaufmann, 1962, S
<i>Mephitis mephitis</i>	3	16	Verts, 1967, S, T
Primates			
<i>Gorilla gorilla</i>	127	32	Van Gelder, 1969, E
<i>Homo sapiens</i>	70	40	Hill, 1950; McWhirter & McWhirter, 1980, T
<i>Presbytis</i> (?) (lemur)	13	37	Van Gelder, 1969, U
Rodentia			
<i>Erithizon dorsatum</i>	9	3.2	Cottam & Williams, 1943, S
<i>Marmota monax</i>	4	16	Van Gelder, 1969, U
<i>Spermophilopsis leptodactylus</i>	0.6	36	Gambaryan, 1974, T
<i>Citellus undulatus</i>	0.6	20	Gambaryan, 1974, T
<i>Sciurus carolinensis</i>	0.55	27	Layne & Benton, 1954, T
<i>Citellus citellus</i>	0.5	18	Gambaryan, 1974, T
<i>Sciurus vulgaris</i> and <i>persicus</i>	0.4	20	Gambaryan, 1974, T
<i>Citellus beldingi</i>	0.3	13	Cottam & Williams, 1943, S
<i>Rattus</i>	0.25	9.7	Wood, 1972, U
<i>Tamiasciurus hudsonicus</i>	0.22	15	Layne & Benton, 1954, T
<i>Mesocricetus brandti</i>	0.11	9	Gambaryan, 1974, T
<i>Tamias striatus</i>	0.1	17	Layne & Benton, 1954, T
<i>Dipodomys microps</i>	0.056	21	Kenagy, 1973, T
<i>Microtus pennsylvanicus</i>	0.05	11	Layne & Benton, 1954, T
<i>Eutamias minimus</i>	0.045	16	Cottam & Williams, 1943, S
<i>Dipodomys merriami</i>	0.035	32	Kenagy, 1973, T

TABLE I  
(Continued)

Species	Body mass† (kg)	Maximal running speed (km/h)	Reference, method*
<i>Notomys cervinus</i>	0.035	14	Marlow, 1969, T
<i>Pitymys pinetorum</i>	0.03	6.8	Layne & Benton, 1954, T
<i>Peromyscus maniculatus</i>	0.03	9.1	Layne & Benton, 1954, T
<i>Peromyscus leucopus</i>	0.025	11	Layne & Benton, 1954, T
<i>Napeozapus insignis</i>	0.025	8.6	Layne & Benton, 1954, T
<i>Zapus hudsonicus</i>	0.018	8.9	Layne & Benton, 1954, T
<i>Mus musculus</i>	0.016	13	Layne & Benton, 1954, T
Insectivora			
<i>Talpa europaea</i>	0.1	4.0	Wood, 1972, U
<i>Scalopus aquaticus</i>	0.1	2.4	Van Gelder, 1969, U
<i>Blarina brevicauda</i>	0.016	3.6	Layne & Benton, 1954, T
Lagomorpha			
<i>Lepus arcticus</i>	4.6	64	Van Gelder, 1969, U
<i>Lepus alleni</i>	4.4	72	Andrews, 1937, S
<i>Lepus europeus</i>	4.0	72	Bourliere, 1964, U
<i>Lepus townsendii</i>	3.5	56	Howell, 1944, S
<i>Lepus californicus</i>	2.0	64	Wood, 1972, U
<i>Oryctolagus cuniculus</i>	1.9	56	Wood, 1972, U
<i>Lepus americanus</i>	1.5	50	Terres, 1941, S
<i>Sylvilagus</i>	1.5	40	Walker, 1976, U
Marsupialia			
<i>Macropus</i>	50	65	Windsor & Dagg, 1971, S
<i>Didelphis marsupialis</i>	5	7.4	McManus, 1970, T
<i>Antechinomys spenceri</i>	0.024	13	Marlow, 1969, F
Edentata			
<i>Bradypus tridactylus</i>	4	1.6	Wood, 1972, T

\*S, Speedometer reading; T, timed over measured distance; F, film; E, subjective estimate; U, unknown; many large mammals probably from speedometer reading.

†Body mass estimates from source of speed data or Sachs (1967), Burt & Grossenheider (1976), or Walker (1976).

‡Cited in Schaller (1972).

§Cited in Meagher (1973).

¶Female body mass; see text and Schaller (1972).

there appears to be an "optimal" body size with regards to running ability (Coombs, 1978). Setting the first derivative of eq. (1) equal to zero, the body mass at which predicted MRS is a maximum (56 km/h) is 119 kg. Similar observations led Taylor (1973: 40) to conclude: "that very large animals do not run as fast as intermediate sized animals cannot be explained on energetic terms (but) . . . suggests . . . structural limitations." The largest known land mammal was *Baluchitherium*, with an estimated body mass of 20,000 kg (see Economos, 1981). Equation (1) predicts a MRS of 27 km/h for a mammal of this size.

From the Tables and Figures, it is apparent that maximal running speed is highly variable, even among mammals of similar size. For example, the three species of Insectivora are considerably slower than similarly sized rodents. The porcupine (*Erithizon*) is very slow. This

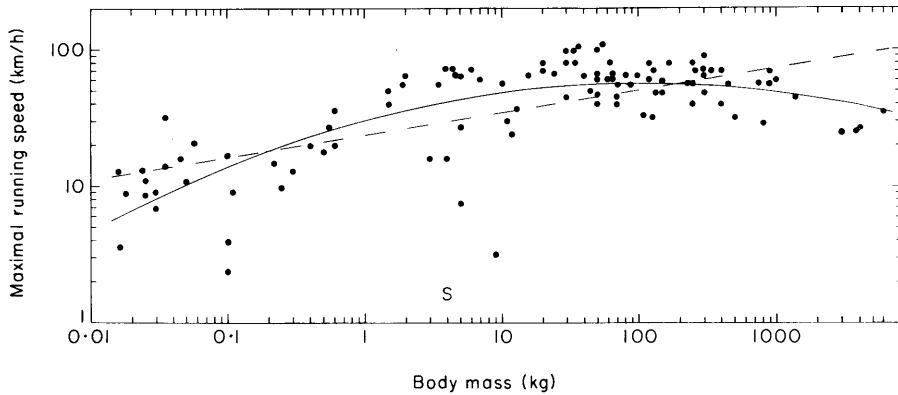


FIG. 1. Maximal running speeds (MRS) of 107 species of mammals (data from Table I). Dashed line represents allometric equation for all mammals (except sloth, represented by "S"), with a slope of 0.17 (see Table II). Solid curve represents a polynomial regression equation that fits the data significantly better (see text eq. (1)). An optimal body mass for running ability is suggested; approximately 119 kg.

species may have lost the (presumably) greater running ability of its ancestors as it evolved an alternative mechanism of defence, although adaptation for tree climbing ability may also have been important. The skunk (*Mephitis*) is also slow, and, like the porcupine, possesses an alternative to flight for avoiding predators. The relatively low MRS of *Mephitis* is reflected in its muscle fibre composition (Frederick & Goslow, 1976; Van de Graff *et al.*, 1977; see also Marechal *et al.*, 1976; Maxwell *et al.*, 1977). The badger (*Meles*) is relatively slow, and it might be argued that adaptations for a fossorial existence have compromised its MRS (cf. the moles *Talpa* and *Scalopus*). *Hippopotamus* is the largest and slowest member of the Artiodactyla, and the only one that is neither cursorial nor subcursorial (Coombs, 1978 and pers. comm.).

For four of the orders represented in Table I, MRS has been estimated for enough species to justify separate statistical consideration (Table II). In addition, ANCOVA allows the comparison of maximal running speeds among various groups of mammals. A variety of comparisons are possible; I present a few which seem of interest based on phylogenetic, morphological or behavioral considerations (Table II).

Within the Artiodactyla, maximal running speed is either a decreasing function of body mass or mass independent, depending on whether *Hippopotamus* is included in the regression analysis (see Fig. 2). If it is excluded, the exponent (b) for scaling of MRS is  $-0.094 \pm 0.095$ , which is virtually identical to the exponent obtained by Alexander, Langman *et al.* (1977) for ten species of Artiodactyla ( $-0.08 \pm 0.12$ ), neither value being significantly different from zero. Alexander *et al.* (1977) filmed artiodactyls running in the field and their data set is presumably quite accurate. The similarity of the two exponents suggests that the accuracy of MRS estimates included in the present analysis does not vary systematically with body mass, although the values presented by Alexander, Langman *et al.* (1977) are generally lower than the maximal reported values for the same species (see their discussion, p. 298). Within the Carnivora, MRS is also mass independent. It is interesting to note that the skunk, coati, badger, and raccoon are all rather slow for their size (see Fig. 2, Table II). Unlike canids, felids, and ursids, none of these four Carnivora regularly rely on speed for capturing prey.

TABLE II

Least squares linear regression analyses of  $\log_{10}$  transformed maximal running speed versus body mass data (from Table I). Analysis of covariance (ANCOVA) was used to compare various groups of mammals

Data set	n	Body mass range (kg)	Speed range (km/h)	Linear regression estimate of speed = $a(\text{Mass})^b$		
				a	b $\pm$ 95% C.I.	r <sup>2</sup>
All mammals	106*	0.016–6000	3.2–110	23.6	0.165 $\pm$ 0.036†	0.439
Artiodactyla	36	20–3800	25–105	114.4	–0.130 $\pm$ 0.087†	0.214
Artiodactyla minus <i>Hippopotamus</i>	35	20–1000	29–105	97.8	–0.094 $\pm$ 0.095	0.110
Carnivora	21	3–400	16–110	37.5	0.089 $\pm$ 0.138	0.087
Carnivora minus <i>Mephitis</i> , <i>Nasua</i> , <i>Meles</i> , <i>Procyon</i>	17	5–400	40–110	79.3	–0.072 $\pm$ 0.077	0.209
Rodentia	23	0.016–9	3.2–36	13.7	0.004 $\pm$ 0.138	0.000
Rodentia minus <i>Erithizon</i>	22	0.016–4	6.8–36	19.9	0.142 $\pm$ 0.122†	0.228
Rodentia minus <i>Erithizon</i> , <i>Notomys</i> , and <i>Dipodomys</i>	19	0.016–4	6.8–36	20.0	0.183 $\pm$ 0.106†	0.438
Lagomorpha	8	1.5–4.6	40–72	42.8	0.318 $\pm$ 0.257†	0.604
Lagomorpha vs. Rodentia	31	0.016–9	3.2–72	58.3	Lagomorpha	0.656
				13.6	Rodentia	
“Hoppers” vs. “Quadrupeds” (Fig. 3)	30	0.016–4.6	6.8–72	45.7	“Hoppers”	
					0.213 $\pm$ 0.067†	0.847
				21.2	“Quadrupeds”	
Artiodactyla minus <i>Hippo.</i> vs. Selected Carnivora (Fig. 2)	52	5–1000	29–110	83.9	–0.069 $\pm$ 0.060†	0.096

\*Sloth not included in regression analysis.

†Slope (b) significant at  $P < 0.05$ .

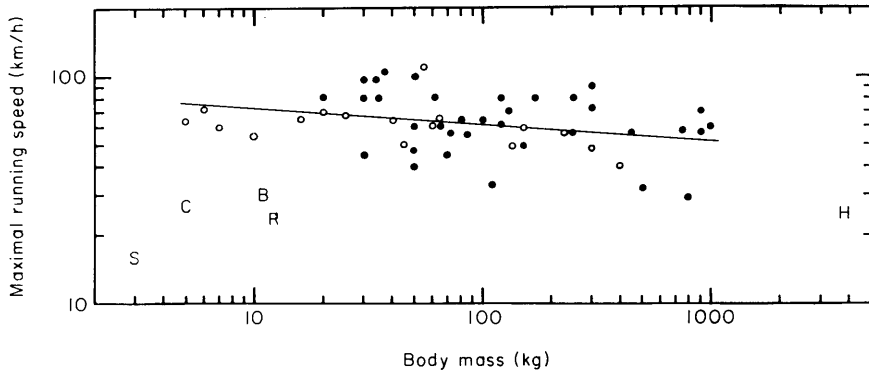


FIG. 2. Maximal running speeds (MRS) of Artiodactyla (closed circles) and Carnivora (open circles) (data from Table I). Analysis of covariance (see Table II) indicates that the regression lines for the two orders are coincident, with a common slope of  $-0.07$ , if the skunk (“S”), coati (“C”), badger (“B”), raccoon (“R”), and *Hippopotamus* (“H”) are excluded.

Within the Rodentia, MRS is mass independent (Table II, Fig. 3). Deleting the porcupine, or the porcupine and the three bipedal rodents, yields a significantly positive slope for the other rodents. Within the Lagomorpha, MRS is an increasing function of body mass (Fig. 3, Table II), but with the only eight species and a body mass range of only 1.5 – 4.6 kg, little confidence can be placed in the exponent ( $0.318 \pm 0.257$ ). In addition, estimates of lagomorph speeds are generally anecdotal, but it does seem likely that some of the larger *Lepus* are actually faster than the smaller *Sylvilagus*.

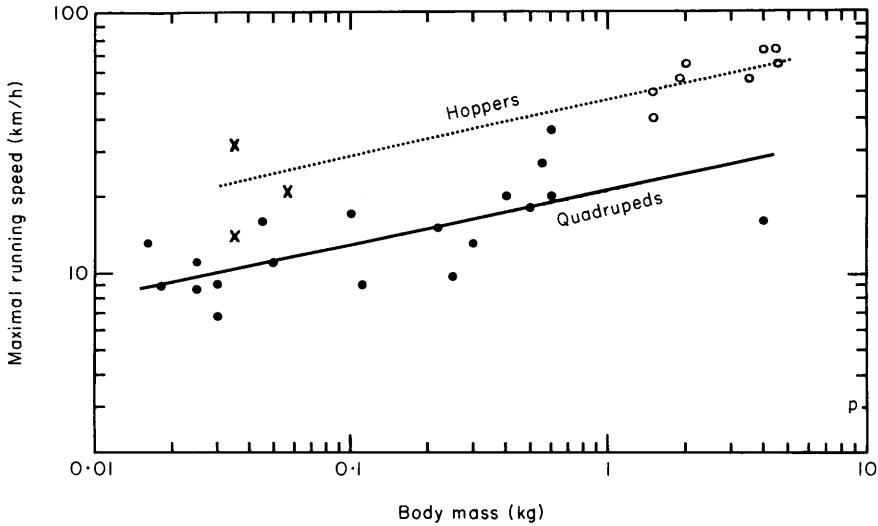


FIG. 3. Maximal running speeds (MRS) of Rodentia (closed circles) and Lagomorpha (open circles) (data from Table I). Analysis of covariance (see Table II) indicates that “Hoppers” (upper dotted line = lagomorphs plus two *Dipodomys* and *Notomys*, with the three bipedal rodents represented by “X”) are, on the average, more than twice as fast as other quadrupedal rodents (“Quadrupeds”, excluding the porcupine (“P”)).

#### Comparisons of running ability among groups

The Carnivora and Artiodactyla regressions are significantly different, but intersect within the body mass range common to both (20–400 kg). From Fig. 2 it is apparent that these predators and prey attain similar maximal speeds, and an ANCOVA comparison between the Carnivora (minus skunk, coati, badger, and raccoon = canids, felids, and ursids) with the Artiodactyla (minus *Hippopotamus*) yields coincident regression lines for the two groups, with a common slope of  $-0.069 \pm 0.060$  (Table II, Fig. 2). It is also noteworthy that lagomorphs attain maximal speeds (40–72 km/h) that are similar to those attained by some of their potential predators, the canids and felids (see Table I).

ANCOVA of Rodentia vs. Lagomorpha indicates that MRS may be represented as mass independent within either group, but that lagomorphs are, on the average, more than four times as fast as similarly sized rodents (Table II). Within the combined Lagomorpha and Rodentia (excluding the porcupine), “Hoppers” (lagomorphs plus *Dipodomys* and *Notomys*) are more than twice as fast as quadrupedal rodents (“Quadrupeds” in Fig. 3 and Table II).

(It is not implied that lagomorphs and the bipedal rodents have identical gaits. The two zopodid rodents possess somewhat enlarged hind limbs, but are not nearly as specialized as *Dipodomys*, *Notomys* or lagomorphs (Marlow, 1969; Burt & Grossenheider, 1976; Walker, 1976.) It is tempting to conclude that bipedality may confer an advantage in terms of MRS for small mammals (e.g., rodents and lagomorphs) but not for large mammals—kangaroos do not seem to be especially fast for their size (see Table I and Windsor & Dagg, 1971). On the other hand, bipedal hopping does lower the energetic cost of locomotion in kangaroos (Dawson & Taylor, 1973), but does not do so for small mammals (Thompson *et al.*, 1980; and see Alexander, Jayes *et al.*, 1981; Biewener *et al.*, 1981). Selective factors favouring bipedality are hence likely to differ between large and small animals.

#### *Maximal running speed versus maximal aerobic speed*

It is of interest to compare maximal running speeds with maximal aerobic speeds, defined as the running speed at which  $\dot{V}O_2$ max is attained (John-Alder & Bennett, 1981; and see Seeherman *et al.*, 1981). The available data are too few to allow a species-by-species comparison, but a general comparison may be derived as follows. Taylor *et al.* (1981) provide the following equation for  $\dot{V}O_2$ max for 22 species of wild and domestic mammals:

$$\dot{V}O_2\text{max (ml O}_2\text{/h)} = 6912 M^{0.809 \pm 0.061}, \quad (2)$$

where  $r^2 = 0.974$  and the body mass range is 0.007—263 kg. Taylor (1980) provides the following equation for the total cost of transport in mammals:

$$\text{Cost of transport (ml O}_2\text{/h)} = 531 M^{0.70} (\text{speed}) + 926 M^{0.61}, \quad (3)$$

(confidence intervals for exponents not provided; body mass range not specified but presumed similar to that for  $\dot{V}O_2$  max equation). Setting eq. (2) equal to eq. (3), we may solve for the speed at which  $\dot{V}O_2$ max is attained:

$$\text{Maximal aerobic speed (km/h)} = 13.0 M^{0.11} - 1.74 M^{-0.09}. \quad (4)$$

Equation (4) cannot be simplified directly; however, by using it to calculate maximal aerobic speeds at several body masses between 0.007 and 263 kg, an approximate allometric equation can be derived by regressing these calculated values on body mass:

$$\text{Maximal aerobic speed (km/h)} = 11 M^{0.15}. \quad (5)$$

(It is not possible to calculate meaningful confidence intervals for this equation.) For all mammals ( $n = 106$ ; from Table II):

$$\text{Maximal running speed (km/h)} = 23.6 M^{0.165 \pm 0.036}. \quad (6)$$

Considering only mammals weighing less than 300 kg ( $n = 87$ ):

$$\text{Maximal running speed (km/h)} = 23.3 M^{0.225 \pm 0.042}, \quad (7)$$

( $r^2 = 0.570$ ). Comparing eq. (5) (and Taylor *et al.*, 's 1981 eq. 3) with eqs (6) and (7) suggests that maximal running speeds are, on the average, somewhat more than twice maximal aerobic speeds. This general comparison is in agreement with records of human performance; marathons are won at speeds ( $\approx 20$  km/h) that are about one-half as fast as maximal running speeds ( $\approx 40$  km/h) (see Hill, 1950; McWhirter & McWhirter, 1980). However, comparing

the few species for which estimates of both MRS (this study) and maximal aerobic speed (see Seeherman *et al.*, 1981; Taylor *et al.*, 1981) are available, it is apparent that there is considerable interspecific variability in the ratio of the two performance measures.

### *Comparisons with theoretical expectations*

How do theoretical expectations concerning the scaling of maximal running speed compare with the available data? The four competing models (see Introduction) predict that speed should scale as:  $M^0$ , geometric similarity;  $M^{0.17}$ , dynamic similarity;  $M^{0.25}$ , elastic similarity;  $M^{0.40}$ , static stress similarity. For all mammals, MRS scales as  $M^{0.17 \pm 0.04}$ , in agreement with the predictions for dynamically similar animals. It is therefore interesting to note Gunther's (1975; 672) statement: "dynamic similarity is the main factor when we are analysing mechanical problems, where gravitational forces predominate—movements of the head, legs, and of the body in general, related to skeleton, joints, and tendons and caused by the contraction of striated musculature." However, the relationship for all mammals is obviously non-linear (Fig. 1), and the data in Table I are not a representative sample of Mammalia, but a taxonomically biased sample of species, many of which possess very different morphologies. Therefore, agreement with the predictions of dynamic similarity may be fortuitous, and the usefulness of comparing such an overall slope with theoretical expectations seems limited, even without the above-mentioned statistical questions.

Within the Artiodactyla, MRS is mass independent (present study and Alexander, Langman *et al.*, 1977), which is consistent with predictions for geometrically similar animals. McMahon (1975a), however, has demonstrated that within artiodactyl limbs, bone lengths scale approximately as  $M^{0.25}$ , bone diameters as  $M^{0.375}$ , and hence bone lengths scale as (bone diameter) $^{0.67}$ , in agreement with the morphological predictions of elastic similarity. Therefore, within the Artiodactyla, the skeleton may be scaled for elastic similarity, but maximal running speed scales consistent with the expectations for geometrically similar animals! A similar "paradox" is found when considering mammals in general: limb bone proportions scale consistent with geometric similarity (Alexander, Jayes *et al.*, 1979 for shrews to elephants), but maximal running speed scales in closest agreement with dynamic similarity (this study). This lack of correspondence between morphological and physiological (performance) scaling suggests that it may be impossible to formulate any general theory of biological similarity that will accurately predict the scaling relationships of various parameters (cf. Emmerson, 1978).

Within the Carnivora or Rodentia, MRS is also mass independent (Table II). Within the Lagomorpha MRS scales to an exponent ( $0.32 \pm 0.26$ ) that includes the exponents predicted by elastic (0.25) and static stress similarity (0.40), but, as mentioned above, little confidence should be placed in the lagomorph data set.

Heglund *et al.* (1974) found that running speed at the trot-gallop transition scaled as  $M^{0.24}$  among domestic mice, rats, dogs, and horses. They went on to "propose that the speed at the trot-gallop transition point is a 'physiologically similar' speed for animals of different size." McMahon (1975b) then cited the exponent obtained by Heglund *et al.* (1974) as evidence for the occurrence of elastic similarity among quadrupedal mammals. There are, however, objections to McMahon's conclusion. First, as noted by Alexander, Langman *et al.* (1977), mice and rats are non-cursorial whereas dogs and horses are cursorial. This difference may well have biased Heglund *et al.*'s slope upwards. Inspection of McMahon's (1975b) fig. 4 indicates no mass dependence of speed among mice and rats, which agrees with the findings

of the present study for rodents in general. The second objection to McMahon's (1975*b*) conclusion is that Heglund *et al.* (1974) never defined what is meant by a "physiologically similar speed", and it is not clear that speed at the trot-gallop transition is such a speed. Maximal aerobic speed might be a better choice if one wishes to compare "physiologically similar" speeds. For comparisons with theoretical predictions, however, it is probably best to compare maximal running speeds, assuming one can obtain accurate and unbiased estimates of MRS. To quote Taylor (1977: 134): "top speed as an equivalent speed for animals of different size . . . is a theoretically sound choice . . .".

### Summary

The available data on maximal running speeds (MRS) of mammals have been compiled. For all mammals, MRS scales as  $M^{0.17}$ , in closest agreement with predictions for dynamically similar animals (see Gunther, 1975). The usefulness of this overall comparison seems limited, however, because for all mammals a curvilinear relationship exists between  $\log_{10}MRS$  and  $\log_{10}M$ . A polynomial regression equation predicts an optimal body mass for running ability of about 119 kg. For mammals in general, maximal running speeds are generally somewhat more than twice maximal aerobic speeds.

Within the Artiodactyla, Carnivora or Rodentia, MRS is mass independent, in agreement with theoretical expectations for geometrically similar animals (Thompson, 1917; Hill, 1950). McMahon's (1975*b*) model for elastic similarity is therefore not supported by the available data, and, contrary to theoretical expectations, there appears to be no necessary correspondence between the type of scaling evidenced by limb proportions and the scaling relationships for running ability. Gunther's (1975: 672) conclusion thus seems appropriate: "no single similarity criterion can provide a satisfactory quantitative explanation for every single function of an organism that can be submitted to dimensional analysis".

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