Comparative locomotor performance of marsupial and placental mammals

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(With 6 figures in the text)

Marsupials are often considered inferior to placental mammals in a number of physiological characters. Because locomotor performance is presumed to be an important component of fitness, we compared marsupials and placentals with regard to both maximal running speeds and maximal aerobic speeds (= speed at which the maximal rate of oxygen consumption, $\dot{V}O_2max$, is attained). Maximal aerobic speed is related to an animal's maximal sustainable speed, and hence is a useful comparative index of stamina.

Maximal running speeds of 11 species of Australian marsupials, eight species of Australian murid rodents, two species of American didelphid marsupials, and two species of American rodents were measured in the laboratory and compared with data compiled from the literature. Our values are greater than, or equivalent to, those reported previously. Marsupials and placentals do not differ in maximal running speeds (nor do Australian rodents differ from non-Australian rodents). Within these groups, however, species and families may differ considerably. Some of the interspecific variation in maximal running speeds is related to differences in habitat: species inhabiting open habitats (e.g. deserts) tend to be faster than are species from habitats with more cover, or arboreal species.

Maximal aerobic speeds (compiled from the literature) were higher in large species than in small species. However, marsupials and placentals show no general difference with regard to maximal aerobic speeds.

Maximal running speeds and maximal aerobic speeds for 18 species of mammals were not correlated, after correcting for correlations with body size. Thus, the fastest sprinters do not necessarily have high maximal aerobic speeds.

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Introduction

Maximal running speed is of obvious importance to many animals for escaping from predators and/or for capturing prey. In an earlier study, the available data on maximal running speeds of terrestrial mammals were compiled from the literature and analysed primarily in relation to body mass (Garland, 1983a). Another ecologically relevant measure of locomotor performance is the maximal aerobic speed (MAS = running speed at which the maximal rate of organismal oxygen consumption, $\dot{V}O_2max$, is attained). The maximal aerobic speed is often a good predictor of the maximal sustainable running speed (Seeherman, Taylor, Maloiy & Armstrong, 1981). In nature, most mammals and lizards appear to move routinely at speeds below the maximal aerobic speed (Dawson & Taylor, 1973; John-Alder, Garland & Bennett, 1986; Hoyt & Kenagy, 1988; Garland, In press; Hertz, Huey & Garland, In press; but see Thompson, 1985), presumably to avoid fatigue. Previous studies have noted a positive relationship between maximal aerobic speed and body mass in mammals (Taylor et al., 1981; Garland, 1983a), but have not compared groups of mammals.

The first purpose of the present study was to measure maximal running speeds of some Australian small mammals, and to compare these with existing data. Of particular interest was a comparison of marsupial versus placental mammals; previously, data were available for only three marsupial species, so a general comparison with placentals was impossible.

Such a comparison is of interest for several reasons. First, fossil evidence indicates that marsupial and placental mammals have been separated evolutionarily for at least 75 million years (Eisenberg, 1981; Dawson, 1983; Archer & Clayton, 1984). Extant members of the two clades differ qualitatively in several features of reproduction, exchange of maternal and foetal materials, early embryology and anatomy. For example, marsupials possess an external pouch, in which the young develop from a very early stage, and an epipubic bone. Placentals, on the other hand, have neither a pouch nor an epipubic bone.

Marsupials and placentals may differ also in a number of quantitative physiological traits; traditionally, marsupials have often been depicted as exhibiting lower or more primitive values. As noted by Dawson (1983: iii): '. . . . marsupials have tended to have a 'bad press'. Generally they have been considered to be primitive and conservative, and not really proper mammals like the placental mammals.' Perhaps the best-known example of a supposed marsupial 'inferiority' is basal metabolic rate (BMR). MacMillen & Nelson (1969) and Dawson & Hulbert (1970) found that marsupial BMRs averaged about 30% lower than the Kleiber-Brody 'mouse-elephant' curve relating BMR to body mass. Hayssen & Lacy's (1985) recent analysis of a much larger data set supports this conclusion: BMRs of marsupials average about 75% that of placentals of similar size. However, orders (and families) of placentals differ significantly in BMR, and marsupial BMRs are greater than those of Edentata, and are not significantly different from those of

Chiroptera and Primates. Comparisons of field metabolic rates of marsupials and placentals indicate similar values, at least for medium-sized animals (Nagy, 1987).

Although BMR may on average be lower in marsupials than in placentals, metabolic rates below thermoneutrality are equivalent in the two groups (Hinds & MacMillen, 1984; see also Hinds & MacMillen, 1986). Limited data suggest that maximal rates of oxygen consumption in response to cold exposure (summit metabolism; Dawson & Dawson, 1982) may also be similar. Maximal rates of oxygen consumption in response to exercise ($\dot{V}O_2$max) are an important determinant of the maximal aerobic speed; unfortunately, data for marsupials are almost nonexistent (Baudinette, 1982). [Maximal heart rates of the two groups are similar (Baudinette, 1978), although marsupials may exhibit generally lower resting heart rates and larger stroke volumes (Dawson & Needham, 1981; Dawson, 1983).] Finally, marsupials and placentals do not differ in the energetic cost of locomotion (Taylor, 1980; Baudinette, 1982; Taylor, Heglund & Maloiy, 1982).

The ecological and evolutionary significance of the foregoing differences and similarities is unclear, because marsupials and placentals have rarely been compared with regard to whole-animals performance (*sensu* Huey & Stevenson, 1979; Arnold, 1983; Bartholomew, 1986). We therefore sought to compare the two groups with regard to both maximal running speeds and maximal aerobic speeds, the latter being compiled from the literature.

The ecological correlates of interspecific differences in speed have been little studied (but see Howell, 1944; Huey, Bennett, John-Alder & Nagy, 1984; Djawdan & Garland, 1988). The second purpose of this study was, therefore, to analyse one possible correlate of maximal running speed in small mammals, namely, habitat openness. We categorized species by habitat openness (see **Methods**), then asked whether maximal running speeds varied in relation to habitat type (after correcting for differences related to body size and phylogeny). We hypothesized that species inhabiting relatively open habitats would be faster than those inhabiting habitats with more cover, and that both would be faster than arboreal species. [We presume that morphological adaptations for arboreal locomotion may compromise an animal's maximal running speed on level ground (cf. Hildebrand, 1982; Garland, 1983a; Hildebrand, Bramble, Liem & Wake, 1985).] In addition, we compare locomotor performance of some potential predators and their prey.

Finally, we wished to know if fast mammals also had high maximal aerobic speeds, or whether there exists a 'tradeoff' between capacities for sprint versus sustained locomotion. The available data now allow comparison of maximal running speeds and maximal aerobic speeds for 18 species of mammals.

Methods

Study animals

Australian animals were obtained from several sources. Most were field-captured individuals that had been held in captivity at either Flinders University or the University of Adelaide (provided courtesy of W. Breed) for several months. Some were laboratory raised animals from either Flinders University or the Evolutionary Biology Unit of the South Australian Museum (provided courtesy of H. Aslin, P. Baverstock, M. Smith and C. Watts). These animals were tested during the austral autumn, 1–13 May 1984. Sample sizes were limited by the availability of animals, most of which are rare or difficult to obtain.

We also tested 2 American marsupials at the University of California, Irvine: adult *Monodelphis brevicaudata* from a captive colony at U. C., Irvine; 1 juvenile *Didelphis virginiana*, wild-caught on the U. C.,

Irvine campus. Finally, we tested 2 American rodents (2 *Zapus trinotatus* and a single *Eutamias amoenus*) at the University of Washington.

Ideally, we would have tested animals fresh from the field, since it might be expected that prolonged captivity could result in significant detraining and hence lower maximal running speeds. This was not possible, however, due to logistical constraints. Djawdan & Garland (1988) report that *Peromyscus maniculatus* maintained in captivity in small cages for 2·5 months showed no significant decrease in maximal running speed. *Chaetodipus fallax*, on the other hand, exhibited a 13·4% decrease in speed (possibly related to weight gain) between days 6 and 15 of captivity, but no further decrease over the next 5·5 months (Djawdan & Garland, 1988). Given these small changes in maximal running speed following captivity (see also Garland, 1985, regarding lizards), and the observation that all animals appeared in good health, we doubt such considerations are of much concern for the broad scale comparisons made herein.

Measurement of maximal running speed

Animals were timed as they were chased along a microprocessor-controlled, photocell-timed racetrack, as described previously (Garland, 1985; Djawdan & Garland, 1988). The track was 8 m in total length by approximately 25 cm wide, with plywood walls 60 cm high. Twelve sets of photocells were placed at 10–50 cm intervals covering a total of 2·0 m. For the largest animals (*Bettongia, Uromys*) we doubled photocell spacing (and track width), so a total of 4·0 m was timed. Short-pile carpeting served as substratum and provided good traction.

To familiarize animals with the track, each was chased slowly back and forth along its length a few times. Animals were then timed as they were chased down the track with a padded meterstick. On some runs, we tapped the animal's tail with the padded meterstick as it was chased. Following each timed run, animals were walked slowly back to the starting end. We timed each individual 5–15 times, until no increase in speed occurred on subsequent runs. Various methods of making noise were also used in an attempt to motivate animals to run at top speed. In addition, we alternated lighting versus darkening the end of the track towards which aninals were chased. We attempted to ensure that all possible combinations of these various chasing techniques were tried on each individual.

Each individual was tested on each of 2 or 3 consecutive days. Djawdan & Garland (1988) demonstrated that 2 or 3 consecutive trial days are sufficient to elicit maximal speeds (i.e. animals do not exhibit significantly higher speeds on further trial days) and that individual differences in speed are consistent across trial days (cf. Bennett, 1980; Garland, 1985, regarding lizards). For each timed run, we calculated the single fastest 0·5 m interval (1·0 m interval for *Bettongia* and *Uromys*; in either case this was ≥ 2 consecutive photocells). We report the single fastest such interval ever recorded for each individual as a measure of its maximal running speed (Garland, 1985; Djawdan & Garland, 1988). All trials were conducted during the day, since Djawdan & Garland (1988) found that testing nocturnal rodents at night yields speeds no higher than obtained during the day. Because *Macropus eugenii* would not run at maximal speed on our racetrack, these animals were timed as they were chased along a fence in a large outdoor enclosure (see Table I).

Literature values

Single fastest speeds reported for a species were compiled from the literature and used for statistical comparisons among taxa (cf. Garland, 1983a). We use single fastest reported values in an attempt to reduce the effects of differences in procedure and/or motivation among studies. (This is analogous to human exercise physiologists analysing personal best times). Using single fastest reported speeds also allows use of the greatest amount of data, because this is usually the only value reported in field studies or natural history observations.

Data for Artiodactyla ($n=36$), Carnivora ($n=21$), Edentata ($n=1$), Insectivora ($n=3$), Lagomorpha ($n=8$), Perissodactyla ($n=7$), Primates ($n=3$) and Proboscidae ($n=2$) are listed in Table I of Garland (1983a)

and are not repeated here; we know of no other data for these taxa. We have omitted data for 2 zapodid rodents (from Layne & Benton, 1954), because we believe the published values do not represent true maximal speeds (cf. our speed for *Zapus trinotatus* in Table I). Speeds obtained for *Antechinomys laniger* (= *spenceri*), *Didelphis virginiana* (= marsupials) and *Notomys cervinus* in the present study (Table I), as well as speeds for *Eutamias minimus* and *Peromyscus maniculatus* reported by Djawdan & Garland (1988), and for *Sciurus carolinensis* by Garland (unpubl.) are higher than, and hence replace, speeds listed previously in Garland's (1983a) Table I.

Ecological correlates of maximal running speed

We categorized each species as to 'Habitat type' (3 = open country, e.g. deserts; 2 = terrestrial, but habitat less open than in 3; 1 = intermediate between terrestrial and arboreal, including rock-dwelling forms, and species frequenting relatively dense cover; 0 = arboreal) based on our knowledge of their natural history and a variety of primary and secondary sources (e.g. Strahan, 1983). Although these categories represent only crude approximations of habitat differences among species, we feel they are justified in a preliminary, exploratory analysis. As more sophisticated information regarding possible ecological correlates becomes available, other workers may enhance our analysis, because we present in the Tables all raw speed data, as well as our categorizations as to Habitat type.

Statistical analyses

Least squares linear regressions of $\log_{10}$ speed on $\log_{10}$ body mass (M) were computed to describe relations between speed and size (see Garland, 1983a, 1985, for justifications of regression slopes in this context). Analysis of covariance (ANCOVA) was used to compare slopes and elevations among taxa. Computations were done primarily via multiple regression, with taxa coded by dummy variables (see Kleinbaum & Kupper, 1978).

After analysing the relation between speed on the one hand and size and phylogeny on the other, we tested whether maximal running speeds varied also in relation to Habitat type. Thus, we entered Habitat type (which ranged from 0 to 3; see Tables I and II) into multiple regression equations which already contained $\log_{10}$ body mass and/or dummy variables adjusting for differences among taxa. All computations were done on an IBM-PC or AT compatible microcomputer using routines in SPSS/PC+ (Norusis, 1986).

Results

Including our measurements (Table I), maximal running speeds are now available for a total of 144 species of mammals. Literature values for Marsupialia (*n* = 15) and Rodentia (*n* = 48) are listed in Table II. Within taxa, maximal running speed is not generally correlated with mass (Table III; see also Garland, 1983a).

Comparisons of maximal running speed among taxa and habitat types

Australian marsupials and Australian murid rodents attain similar maximal running speeds (Fig. 1). The two groups do not differ significantly in the allometric relation between speed and body mass (ANCOVA: pooled within groups slope = $M^{0.196 \pm 0.057}$; $\pm 95\%$ C.I.; partial r^2 for body mass = 73.1%). Adding Habitat type to this equation explains an additional 11.9% of the variance

TABLE I

Laboratory maximal running speeds of Australian and American small mammals measured in the present study

Species	n	Body mass (g) $\bar{x} \pm$ S.D., fastest	Speed (km/h) $\bar{x} \pm$ S.D., fastest	Habitat type*
PLACENTALS				
Muridae				
Leggadina forresti	3	19·2 ± 3·51, 15·5	11·9 ± 0·70, 12·6	3
Notomys alexis	5	24·5	13·1 ± 1·08, 14·9	3
N. cervinus	1	52·5	15·7	3
Pseudomys australis	4	51·4 ± 3·33, 50·0	15·9 ± 0·64, 16·4	3
P. hermannsbergensis	4	14·0 ± 3·58, 18·0	12·4 ± 0·22, 12·6	3
P. nanus	5	70·9 ± 12·4, 61·0	12·8 ± 1·71, 14·4	2
Uromys caudimaculatus	2	1035 ± 205·1, 1180	15·6 ± 1·42, 16·6	0
Zyzomys argurus	1	60·5	12·4	1
Sciuridae				
Eutamias amoenus[1]	1	51	19·4	1·5
Zapodidae				
Zapus trinotatus[1]	2	24·8 ± 5·30, 28·5	14·1 ± 0·16, 14·3	2
MARSUPIALS				
Burramyidae				
Cercartetus concinnus	2	17·5 ± 3·54, 15·0	5·5 ± 0·12, 5·6	0
Dasyuridae				
Antechinomys laniger	1	25·0	13·8	3
Antechinus flavipes	7	33·4 ± 8·77, 52·0	12·3 ± 0·66, 13·2	1
A. stuartii	5	26·2 ± 5·16, 31·5	12·9 ± 1·28, 15·1	1
Dasyuroides byrnei	3	115·3 ± 4·51, 120·0	17·6 ± 0·95, 18·6	3
Sminthopsis crassicaudata	6	15·3 ± 2·14, 17·0	9·7 ± 0·96, 10·9	3
S. macroura	6	23·1 ± 2·01, 20·0	11·4 ± 1·33, 13·4	3
Didelphidae				
Didelphis virginiana[1]	1	850 (juvenile)	10·2	1
Monodelphis brevicaudata[1]	6	88·1 ± 17·75, 74·5	10·3 ± 0·90, 11·4	1
Macropodidae				
Macropus eugenii[2]	5	4000	40	2
Peramelidae				
Isoodon obesulus	2	718 ± 60·1	14·3 ± 0·08, 14·4	2
Potoroidae				
Bettongia penicillata[3]	2	1105 ± 35·4, 1130	20·9 ± 4·61, 24·2	2
Potorus tridactylus	4	910 ± 194·6, 998	19·5 ± 2·51, 21·4	2

* 3 = open country, e.g. deserts; 2 = terrestrial, but habitat less open than in 3; 1 = intermediate between terrestrial and arboreal, rock-dwelling forms and species frequenting relatively dense cover; 0 = arboreal: see text for discussion.

[1] Denotes American species; others are Australian.

[2] Highest speed ever recorded over a 5·5 m interval as animals were chased along a fence in a large outdoor enclosure at Flinders University and timed with hand-held stopwatch.

[3] Seeherman *et al.* (1981) report a maximal treadmill speed of 24·8 km/h for 1100 g *Bettongia penicillata*: we use their values in figures and statistical analyses.

in maximal running speed, which is statistically significant ($P = 0.0014$). Thus, faster species (for their body size) tend to occur in more open habitats.

Restricting our analysis to two families, we compared Australian marsupials of the family Dasyuridae ($n = 6$) with Australian rodents of the family Muridae ($n = 8$). Maximal running speeds

TABLE II

Maximal running speeds of marsupials and rodents compiled from other sources

Species	Body mass (g)	Speed (km/h)	Habitat type*	Reference, method[1]
MARSUPIALIA[2]				
Dasyuridae				
Dasyurus viverrinus	1120	> 16[3]	2	R. V. Baudinette, unpubl.
Macropodidae				
Macropus spp.	50000	65	3	Windsor & Dagg, 1971; Bennett, 1987, FF, S
Myrmecobiidae				
Myrmecobius fasciatus	480	33	2	Calaby, 1960, S
RODENTIA				
Cricetidae				
Neotoma lepida	105·2	19·2	1	Djawdan & Garland, 1988, P
Onychomys torridus	16·0	11·0	2	Djawdan & Garland, 1988, P
Peromyscus crinitus	16·3	12·5	1	Djawdan & Garland, 1988, P
P. eremicus	18·6	14·2	2	Djawdan & Garland, 1988, P
P. leucopus	25	11	1	in Garland, 1983a, TF
P. maniculatus	22·7	15·9	1	Djawdan & Garland, 1988, P
P. truei	17·8	14·4	1	Djawdan & Garland, 1988, P
Erithizontidae				
Erithizon dorsatum	9000	3·2	1	in Garland, 1983a, S
Heteromyidae				
Chaetodipus baileyi	39·7	14·9	2	Djawdan & Garland, 1988, P
C. fallax	16·0	14·2	1·5	Djawdan & Garland, 1988, P
Dipodomys deserti	112	29·9	3	Djawdan & Garland, 1988, TF
D. merriami	35	32	3	Kenagy, 1973, TF
D. microps	56	21	2	Kenagy, 1973, TF
Heteromys desmarestianus	50	12·5	1	M. Djawdan, pers. comm., P
Liomys pictus	42	17·2	1	M. Djawdan, pers. comm., P
Microdipodops megacephalus	11·0	14·2	2	Djawdan & Garland, 1988, P
Perognathus longimembris	8·6	11·7	2	Djawdan & Garland, 1988, P
P. parvus	26·0	14·6	2	Djawdan & Garland, 1988, P
Microtinae				
Mesocricetus brandti	110	9	1	in Garland, 1983a, T?
Microtus pennsylvanicus	50	11	1	in Garland, 1983a, TF
Pitymys pinetorum	30	6·8	1	in Garland, 1983a, TF
Muridae				
Mus musculus	16	13·1	1	in Garland, 1983a, TF
Rattus norvegicus (?)	250	9·7	1	in Garland, 1983a, U
Sciuridae				
Ammospermophilus leucurus	76·2	18·7	3	Djawdan & Garland, 1988, P
Eutamias minimus	28·0	17·4	1·5	Djawdan & Garland, 1988, P
Marmota monax	4000	16	1·5	in Garland, 1983a, U
Sciurus carolinensis	500	30	1	Garland, unpubl., S
S. niger	1078	24	1	Moore, 1957, S
S. persicus and *vulgaris*	400	20	1	in Garland, 1983a, T?
Spermophilopsis leptodactylus	600	36	3	in Garland, 1983a, T?
Spermophilus beldingi	300	13	2	in Garland, 1983a, S
S. citellus	500	18	2?	in Garland, 1983a, T?
S. saturatus	222	22·2	2	G. J. Kenagy and D. F. Hoyt, pers. comm., TF over 10 m
S. tereticaudus	112·6	15·2	3	Djawdan & Garland, 1988, P
S. tridecemlineatus	125	12·2	2	Biewener, 1983, FL
S. undulatus	600	20	2?	in Garland, 1983a, T?
Tamias striatus	100	17·1	1·5	in Garland, 1983a, TF
Tamiasciurus hudsonicus	220	14·6	1	in Garland, 1983a, TF

* 3 = open country, e.g. deserts; 2 = terrestrial, but habitat less open than in 3; 1 = intermediate between terrestrial and arboreal, rock-dwelling, or frequenting relatively dense cover; 0 = arboreal: see text for discussion.

[1] Reference is for speed. Methods are: FF, filmed in field; FL, filmed in laboratory; P, photocell-timed racetrack in laboratory, same method as present study; S, speedometer reading; TF, timed over measured distance in field; T?, timed over measured distance in laboratory; U, unknown.

[2] Bennett's (1987) speeds of 12 km/h for *Bettongia gaimardi* and 28 km/h for *Thylogale billardieri* seemed too low in comparison with our speeds of 24·2 km/h for *B. penicillata* (see also Seeherman *et al.*, 1981) and 40 km/h for *Macropus eugenii*, respectively (Table I); hence they were not included in our analyses.

[3] Highest speed attained on a motorized treadmill; probably not maximal and hence not used in statistical analyses or plotted on figures.
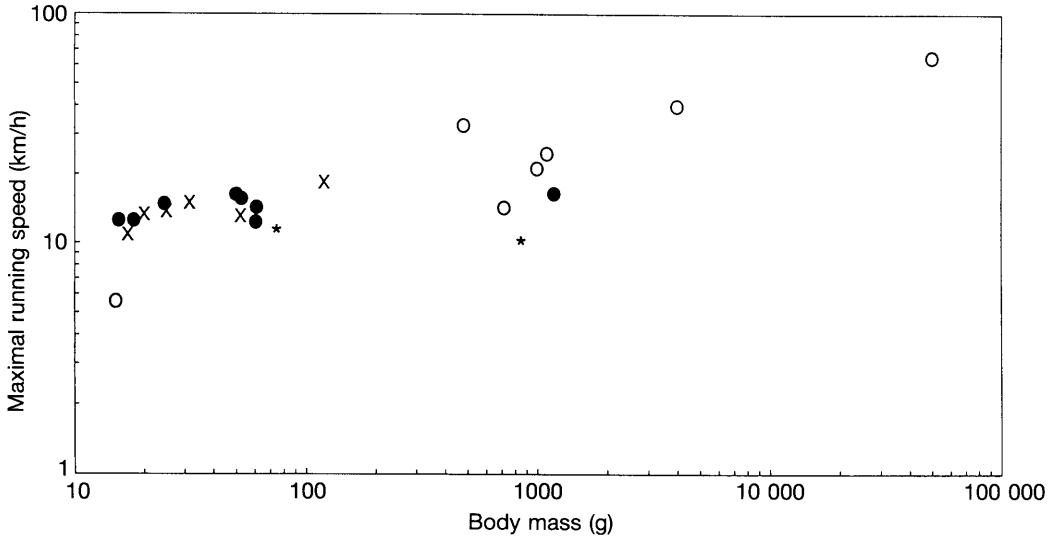
FIG. 1. Log-log plot of maximal running speed vs. body mass for Australian murid rodents versus Australian marsupials (six species of the carnivorous Dasyuridae plus seven species in other families) and two American didelphid marsupials. Speeds of murids and Australian marsupials are statistically indistinguishable (see text). ● Australian Muridae $n = 8$; X Dasyuridae $n = 6$; ○ Australian marsupials $n = 7$; ⋆ Didelphidae $n = 2$.

of the two families are statistically indistinguishable by ANCOVA, but body mass explains 37·7% ($P = 0.0040$) and Habitat type 17·2% ($P = 0.0653$) of the variance in speed. Considering only the eight Australian Muridae, the log-log regression of speed on mass is insignificant (Table III). In a multiple regression, however, $\log_{10}$ body mass accounts for 36·1% ($P = 0.0014$) and Habitat type accounts for 53·1% ($P = 0.0043$) of the variance in $\log_{10}$ speed. Finally, considering only the six Dasyuridae, speed scales positively with body mass (Table III), but Habitat type explains only 1·0% of the additional variance in speed, which is insignificant. In summary, after allowing for possible correlations with body mass, Australian mammals occurring in more open habitats tend to exhibit higher maximal running speeds than do species occurring in less open habitats.

Maximal running speeds of Australian murid rodents fall within the range of variation exhibited by other rodents (Fig. 2). We compared six rodent taxa statistically: Australian Muridae ($n = 8$), Cricetidae ($n = 7$), Sciuridae ($n = 16$), Microtinae ($n = 3$), *Dipodomys* (kangaroo rats, $n = 3$), non-*Dipodomys* Heteromyidae ($n = 7$). [We separated the Heteromyidae because Djawdan & Garland (1988) showed that bipedal kangaroo rats are significantly faster than other heteromyids for which data are available.] Multiple regression indicates that: (1) speed increases with mass as $M^{0.102 \pm 0.045}$ (pooled within groups slope $\pm 95\%$ confidence interval; partial $r^2 = 18.1\%$); (2) Australian Muridae, Sciuridae, Cricetidae and non-*Dipodomys* Heteromyidae from a homogeneous subset; (3) *Dipodomys* are significantly faster (partial $r^2 = 19.0\%$); and (4) Microtinae are significantly slower (partial $r^2 = 24.7\%$) than this homogeneous subset (see Fig. 1; $n = 44$, multiple $r^2 = 61.7\%$). Slopes did not vary significantly among these taxa.

After attempting to account for the effects of size and phylogeny with the foregoing equation, do rodent species occurring in more open habitats display higher maximal running speeds? Although

TABLE III

Least-squares linear regression analyses of $\log_{10}$ transformed maximal running speeds and maximal aerobic speeds versus body mass; data from Tables I, II and III

Group	n	Linear regression estimates of speed $= a$ (Mass)^b			
		$a \div / \times 95\%$ C.I.	$b \pm 95\%$ C.I.	r^2, %	S.E.E.*
Maximal running speeds					
Marsupials	15	$5 \cdot 51 \div / \times 1 \cdot 693$	$0 \cdot 211 \pm 0 \cdot 090^1$	$66 \cdot 3$	$0 \cdot 16001$
Australian marsupials	13	$5 \cdot 57 \div / \times 1 \cdot 568$	$0 \cdot 223 \pm 0 \cdot 076^1$	$78 \cdot 9$	$0 \cdot 13088$
Dasyuridae	6	$6 \cdot 87 \div / \times 1 \cdot 970$	$0 \cdot 201 \pm 0 \cdot 188^1$	$68 \cdot 7$	$0 \cdot 04779$
Rodentia	48	$14 \cdot 3 \div / \times 1 \cdot 415$	$0 \cdot 012 \pm 0 \cdot 075$	$0 \cdot 2$	$0 \cdot 17304$
Rodentia minus *Erithizon*	47	$10 \cdot 3 \div / \times 1 \cdot 326$	$0 \cdot 096 \pm 0 \cdot 063^1$	$17 \cdot 4$	$0 \cdot 12974$
Cricetidae	7	$6 \cdot 85 \div / \times 2 \cdot 194$	$0 \cdot 219 \pm 0 \cdot 241$	$52 \cdot 1$	$0 \cdot 06647$
Heteromyidae	10	$6 \cdot 58 \div / \times 2 \cdot 678$	$0 \cdot 280 \pm 0 \cdot 281$	$39 \cdot 7$	$0 \cdot 12514$
Heteromyidae minus *Dipodomys*	7	$10 \cdot 9 \div / \times 1 \cdot 795$	$0 \cdot 081 \pm 0 \cdot 183$	$20 \cdot 5$	$0 \cdot 05286$
Muridae	10	$13 \cdot 0 \div / \times 1 \cdot 511$	$0 \cdot 013 \pm 0 \cdot 098$	$1 \cdot 3$	$0 \cdot 07513$
Australian Muridae	8	$11 \cdot 6 \div / \times 1 \cdot 350$	$0 \cdot 054 \pm 0 \cdot 072$	$36 \cdot 1$	$0 \cdot 04565$
Sciuridae	16	$13 \cdot 3 \div / \times 1 \cdot 989$	$0 \cdot 062 \pm 0 \cdot 121$	$8 \cdot 0$	$0 \cdot 11860$
Maximal aerobic speeds					
All mammals	39	$2 \cdot 23 \div / \times 1 \cdot 475$	$0 \cdot 186 \pm 0 \cdot 049^1$	$61 \cdot 9$	$0 \cdot 19418$
Excluding two *Bos*	37	$1 \cdot 99 \div / \times 1 \cdot 471$	$0 \cdot 206 \pm 0 \cdot 050^1$	$66 \cdot 6$	$0 \cdot 18531$

* Standard error of estimate
[1] Slope differs significantly ($P < 0 \cdot 05$) from zero
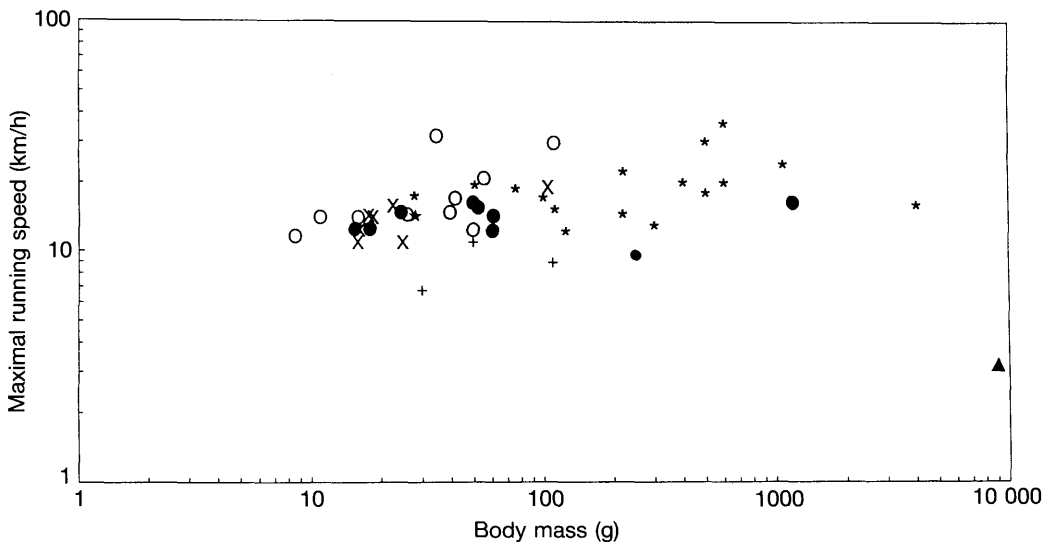

FIG. 2. Log-log plot of maximal running speed vs. body mass for Rodentia ($n = 48$). Speeds of Australian murid rodents are statistically indistinguishable from those of Cricetidae, Sciuridae and non-*Dipodomys* Heteromyidae (see text). In comparison with this homogeneous subset, the three kangaroo rats (*Dipodomys*) are significantly faster, whereas the three microtines are significantly slower (see text). ● Australian Muridae $n = 8$; ○ Heteromyidae $n = 10$; ★ Sciuridae $n = 16$; X Cricetidae $n = 7$; + Microtinae $n = 3$; ★ Zapodidae $n = 1$; ▲ Erithizontidae $n = 1$; ● non-Australian Muridae $n = 2$.

the trend was in the expected direction, adding Habitat type to the above multiple regression equation ($n=44$) increased r^2 by only 1·3%, which is insignificant ($P=0·2442$). Habitat type was also insignificant when the two non-Australian Muridae and the single Zapodidae were included in the analysis ($n=47$; partial $r^2=2·2$%, $P=0·1471$), and even when the single Erithizontidae was added ($n=48$; partial $r^2=1·8$%, $P=0·2962$).

Finally, we included the Dasyuridae ($n=6$) in a multiple regression analysis with the 47 rodents (excluding *Erithizon*). Speeds of this family of carnivorous marsupials are statistically indistinguishable from the homogeneous subset of Australian Muridae, Sciuridae, Cricetidae and non-*Dipodomys* Heteromyidae, noted above. Again, Habitat type explained an insignificant fraction of the variance (partial $r^2=1·5$%, $P=0·1894$).

Maximal aerobic speeds

Maximal aerobic speed (39 species, Table IV) scales with body mass as $M^{0·186 \pm 0·049}$ (Table III). Maximal aerobic speeds of marsupials appear to be at least as high as those of placentals (Fig. 3). (Note that the datum for *Macropus* is an underestimate and for young animals.) Analysis of covariance of Artiodactyla, Carnivora, Marsupialia and Rodentia confirms that maximal aerobic speeds of the four marsupials are not significantly different from these 32 placentals ($F=1·358$, $P=0·2522$).

Our equation for the scaling of maximal aerobic speed is similar to those presented by Taylor *et al.* (1981) and Garland (1983*a*). Surprisingly, however, ANCOVA indicates that the 10 Artiodactyla have significantly lower maximal aerobic speeds than do Carnivora, Marsupialia and Rodentia ($F=5·185$, $P=0·0294$). Taylor *et al.* (1981) note that aerobic capacities of domestic animals (e.g. *Bos*, *Capra hircus*, *Ovis aries*) may be lower than related wild species. Thus, their inclusion in the above analysis may bias the Artiodactyla data set towards lower values. Indeed, omitting the two *Bos*—the two largest species in the data set—from the calculations reduces the difference to insignificance ($F=3·995$, $P=0·0545$). Moreover, several of the Artiodactyla represent young animals (see Seeherman *et al.*, 1981; Taylor *et al.*, 1981), and maximal aerobic speeds probably increase during ontogeny (cf. Garland & Else, 1987). Thus, we doubt that (wild) Artiodactyla actually have lower maximal aerobic speeds than do other mammals of similar size.

Discussion

Comparison of present speeds with values from the literature

Comparisons of the laboratory speeds observed in the present study with values reported previously in the literature suggest that ours represent maximal or near maximal speeds for the individuals tested. Marlow (1969) filmed one individual each of *Antechinomys laniger* (*spencer*) and *Notomys cervinus* running over 0·5–1·0 m; for both species his top speeds are lower than ours (13·0 vs. 13·8 km/h and 14·4 vs. 15·7 km/h, respectively). Baudinette, Nagle & Scott (1976*b*) timed *Notomys alexis* running briefly at speeds up to 11 km/h on a motorized treadmill, which is lower than our observation of 13·1 km/h. Our speed for *Didelphis virginiana* (10·2 km/h) is also higher than reported previously (7·4 km/h, see Garland, 1983*a*). Our speed for *Zapus trinotatus* (14·3 km/h) is higher than reported by Layne & Benton (1954) for *Zapus hudsonicus* (8·9 km/h) and

TABLE IV

Maximal aerobic speeds of mammals

Species	Body mass (g)	Maximal aerobic speed (km/h)	References
ARTIODACTYLA			
Bos indicus	207000	15·2	Taylor *et al.*, 1981
Bos taurus	180000	9	estimated from Kuhlmann, Hodgson & Fedde, 1985
Capra hircus	21150	11·2	Taylor *et al.*, 1981
Connochaetes taurinus*	98000	21·4	Taylor *et al.*, 1981
Gazella granti*	11200	7·2	Taylor *et al.*, 1981
Kobus defassa	114000	19·8	Taylor *et al.*, 1981
Madoqua kirkii	4400	6·1	Taylor *et al.*, 1981
Nesotragus moschatus	3500	10·1	Taylor *et al.*, 1981
Ovis aries	22650	11·2	Taylor *et al.*, 1981
Sus scrofa	19500	17	Seeherman *et al.*, 1981; R. B. Armstrong, pers. comm.
CARNIVORA			
Acinonyx jubatus*	39000	20	Taylor *et al.*, 1981
Canis familiaris*	21000	40	Seeherman *et al.*, 1981
Dingo	11500	22	R. V. Baudinette, unpubl.
Genetta tigrina	1458	6·1	Taylor *et al.*, 1981
Helogale pervula	583	6·1	Taylor *et al.*, 1981
Mungos mungo	1151	9·6	Taylor *et al.*, 1981
Mustela vison	898	9·7	estimated from Williams, 1983
Panthera leo*	30000	10·8	Seeherman *et al.*, 1981
MARSUPIALIA			
Antechinomys laniger	30	$\geq 2^2$	Baudinette, Nagle & Scott, 1976*a*
Antechinus flavipes	41	$\geq 3·3^2$	Baudinette *et al.*, 1976*b*
Bettongia penicillata*	1100	20·1	Seeherman *et al.*, 1981
Dasyuroides byrnei*	115	7·8	Baudinette *et al.*, 1976*b*
Dasyurus viverrinus	1120	$> 7·8^2$	Baudinette *et al.*, 1976*b*
Macropus rufus	25000	$> 22^2$	Dawson & Taylor, 1973
Sarcophilus harrisii	5200	10	estimated from Nicol & Maskrey, 1986
Setonix brachyurus	3000	7·5	Baudinette, 1977, unpubl.
Sminthopsis crassicaudata	15	$\geq 3·2^2$	Baudinette *et al.*, 1976*b*
PERISSODACTYLA			
Equus caballus*	105000	40	Fedak & Seeherman, 1979; Seeherman *et al.*, 1981
PRIMATES			
Cebus capucinus	3340	9	Taylor & Rountree, 1973
Homo sapiens*	70000	20	Margaria, Cerretelli, Aghemo & Sass, 1963
RODENTIA			
Baiomys taylori	7	5	Seeherman *et al.*, 1981
Chaetodipus fallax	20	$\geq 4^2$	R. E. MacMillen, pers. comm.
Dipodomys deserti*	104	7	Thompson *et al.*, 1980; Thompson, 1985
D. merriami*	32	6	Thompson, 1985
D. ordii	57	3·5	MacMillen, 1983, pers. comm.
D. panamintinus	67	3	R. E. MacMillen, pers. comm.
Heteromys desmarestianus	84	$\geq 4^2$	R. E. MacMillen, pers. comm.
Liomys salvini	50	3	R. E. MacMillen, pers. comm.
Microdipodops megacephalus*	14	3·5	R. E. MacMillen, pers. comm.
Neotoma lepida*	100	5	estimated from Thompson, 1985; J. A. Lubina, pers. comm.
Notomys alexis*	27	3	Baudinette *et al.*, 1976*a*
Pedetes capensis	3000	10·1	Seeherman *et al.*, 1981
Peromyscus maniculatus*	21	1·8	Chappell, 1984
Rattus norvegicus*	205	4·4	Seeherman *et al.*, 1981; but see Gleeson & Baldwin, 1981
Spermophilus saturatus*	230	10·8	Hoyt & Kenagy, 1988
Tamias striatus*	90	9·4	Seeherman *et al.*, 1981

* 18 species for which estimates of maximal running speeds are also available, from Table I or II or Garland (1983*a*). These 18 species were analysed for Fig. 6 (see text).

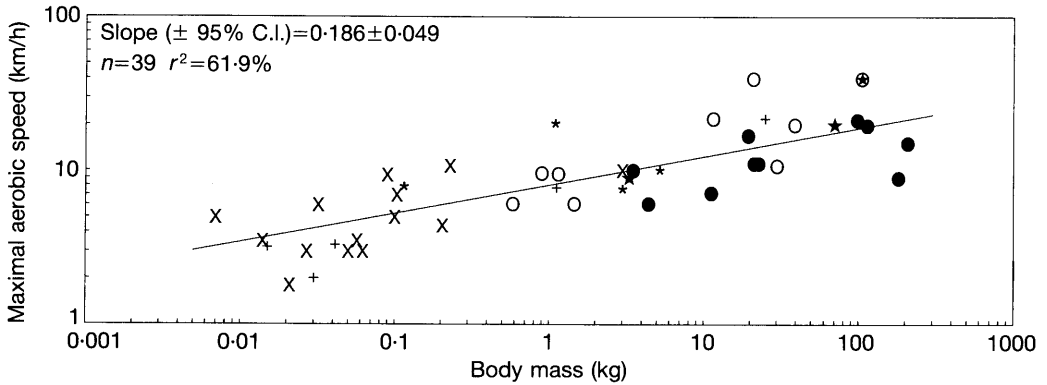[2] Not used in regression analysis; rodents also not plotted in figures.

FIG. 3. Log-log plot of maximal aerobic speed vs. body mass. Marsupials for which the value is or may be an underestimate ($+$; $n=5$; see Table IV) were excluded from the regression equation. ● Artiodactyla $n=10$; ○ Carnivora $n=8$; ⋆ Marsupialia $n=4$; ⊕ Perissodactyla $n=1$, ★ Primates $n=2$; X Rodentia $n=14$.
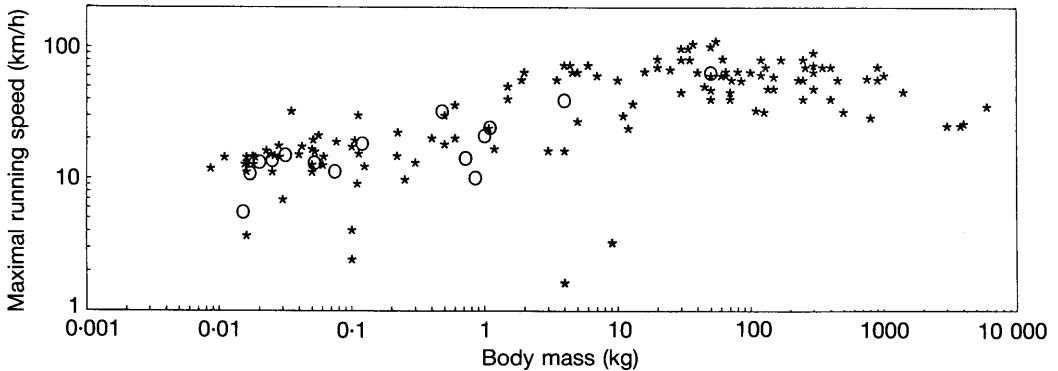

FIG. 4. Log-plot of maximal running speed vs. body mass for marsupials (○; $n=15$) vs. placentals (⋆; $n=128$).

Napeozapus insignis (8·6 km/h). (We did not include Layne and Benton's values for these two species in our analyses). Djawdan & Garland (1988) also obtained racetrack speeds for two species of rodents that were higher than reported previously.

Bennett (1987) reports a speed of 21·2 km/h for *Potorous apicilis* (= *tridactylus*; Strahan, 1983) chased in a large outdoor enclosure, which is virtually identical to our value of 21·4 km/h obtained in the racetrack (Table I). However, Bennett's (1987) speed of 12 km/h for *Bettongia gaimardi* is much lower than both the 24·2 km/h we obtained for *B. penicillata* (Table I) in the racetrack and the maximal treadmill speed of 24·8 km/h obtained for *B. penicillata* by Seeherman *et al.* (1981).

Maximal running speeds of marsupials versus placentals

Considering all available data, marsupials and placentals show no general difference in maximal running speed (Fig. 4). Similarly, marsupials and placentals do not differ with regard to energetic costs of locomotion (Taylor, 1980; Baudinette, 1982; Taylor *et al.*, 1982). However, within either infraclass, some taxa appear to be either relatively fast or relatively slow for their size (see also Garland (1983*a*). Within the Rodentia, for example, *Dipodomys* are fast, whereas microtines are slow.

Correlation between maximal running speed and habitat type

We hypothesized that animals living in more open habitats (e.g. deserts) would be faster, because they would have faced generally stronger natural selection for maximal running speed (and perhaps stamina). We also hypothesized that arboreal species might be slower than their terrestrial relatives, assuming that adaptations for arboreality compromise abilities for speed on level ground (cf. Hildebrand, 1982; Cartmill, 1985). Consistent with these hypotheses, speed tended to correlate positively with Habitat type (see **Methods** and Tables I and II for scoring). In agreement with this trend, an arboreal New Guinean tree kangaroo (*Dendrolagus matchii*), maintained at Flinders University, was much slower than the terrestrial *Macropus eugenii* (40 km/h). Although we did not actually time sprints of the tree kangaroo, we estimate it might attain a top speed of no more than about 20 km/h (16 km/h was attained on a motorized treadmill). These preliminary analyses suggest that further searches for correlations between locomotor performance and habitat characteristics or movement patterns (e.g. home range size, daily movement distance, Garland, 1983*b*) are jusitifed.

Other ecological considerations

As noted by Pellis & Nelson (1984), carnivorous marsupials are sometimes considered to have a more primitive predatory capability than do carnivorous placentals. However, with regard to locomotor performance, which may be a major component of predatory abilities, dasyurids appear similar to placentals in both maximal running speeds and maximal aerobic speeds (e.g. Fig. 2). Moreover, Keast (1982), inferring locomotor abilities from comparisons of skeletal proportions, suggests that the (extinct) marsupial Thylacine compares favourably with canids.

Several Australian marsupials have declined in numbers since the introduction of European placental carnivores (cats, foxes; Strahan, 1983, references therein). At the same time, some introduced herbivorous placentals have done remarkably well (e.g. rabbits). Whether these patterns reflect causal relationships is somewhat controversial. In any case, macropods often do fall prey to cats or foxes (e.g. Hornsby, 1982). It is therefore interesting to note that the large macropods attain maximal speeds (about 65 km/h, although speeds up to 88 km/h have been reported; Bennett, 1987) that are somewhat lower than many of the fastest ungulates (see Garland, 1983*a*). Moreover, the highest speeds that we observed for *Macropus eugenii* (40 km/h) and that Bennett (1987) recorded for *Thylogale billardieri* (28 km/h) are lower than those reported for some similarly-sized lagomorphs (50–72 km/h; see Garland, 1983*a*). On the other hand, Dawson & Taylor (1973) speculate that kangaroos have relatively high maximal aerobic (sustainable) speeds, which might 'explain how they survived the introduction of man and . . . the dingo, while the large
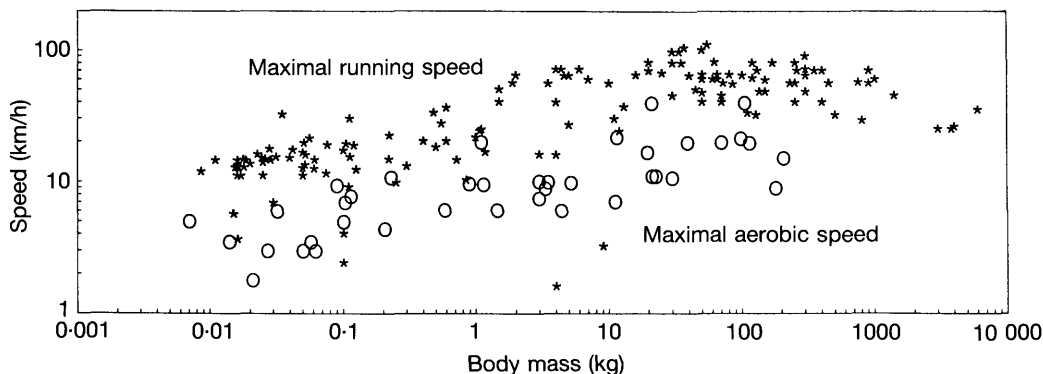
FIG. 5. Comparison of maximal running speeds ($n = 144$) with maximal aerobic speeds ($n = 39$) for all mammals.

quadrupedal marsupials became extinct.' [Possible energetic advantages of the bipedal hopping of kangaroos are discussed by Dawson & Taylor (1973), Taylor (1980) and Garland (1983b)]. A direct comparison of the stamina of a series of macropods and both carnivorous and herbivorous placentals would be of considerable interest.

Speeds of carnivorous marsupials (Dasyuridae) and the Australian Muridae are similar (Fig. 2). Consistent with this comparison of potential predators and their prey, Garland (1983a) noted the general similarity of maximal speeds of Artiodactyla versus Carnivora (but see Bakker, 1983) and lagomorphs versus some canids and felids.

Maximal aerobic speeds

Maximal aerobic speeds of marsupials and placentals are similar (Fig. 3). This similarity is not surprising, given that neither $\dot{V}O_2$max (Baudinette, 1982; D. S. Hinds and R. V. Baudinette, unpubl. obs.) nor the energetic cost of locomotion (Baudinette, 1982; Taylor et al., 1982) appear to differ between the two groups. Thus, maximal sustainable speeds, and, by inference, endurance capacities (cf. John-Alder et al., 1986; Garland, In press), of marsupials and placentals are probably similar.

Maximal aerobic speeds versus maximal running speeds

Do mammals that can attain high maximal running speeds also have high maximal aerobic (sustainable) speeds? As noted previously (Garland, 1983a), maximal running speeds of mammals are, on average, 2–3-fold higher than maximal aerobic speeds (Fig. 5). For 18 species (Table IV), measurements of both maximal running speeds and maximal aerobic speeds are available. The correlation (log-log) between maximal running speed and maximal aerobic speed is 0·719 ($P = 0·0008$). However, this positive correlation may be attributable simply to the positive correlation of both with body mass (see Fig. 5). We therefore regressed both maximal aerobic and maximal running speed on body mass (log-log), and computed residuals from the respective allometric equations. A plot of these residuals (Fig. 6) shows no significant correlation ($r = 0·135$, $P = 0·5925$). Thus, once the confounding effects of body size are removed, it appears that good
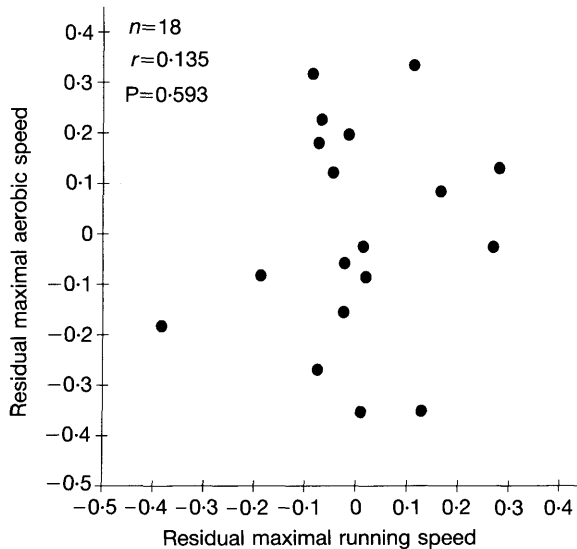
FIG. 6. Lack of correlation for residual (from log-log regressions on body mass) variation in maximal aerobic speeds versus residual maximal running speeds for 18 species of mammals (from Table IV).

sprinters do not necessarily have high maximal aerobic speeds, nor is there any evidence for a necessary tradeoff between capacities for speed versus stamina.

Summary

We have measured maximal running speeds of several species of Australian small mammals, and compared our results with data compiled from the literature. Depending on which species are compared, body size, phylogenetic position, and habitat may all account for significant fractions of the variation in maximal running speed. Thus, our analyses demonstrate that both adaptations to particular ecological conditions and past phylogenetic history may be important determinants of locomotor performance. However, marsupials and placentals in general do not differ in either maximal running speed or maximal aerobic speed (the treadmill speed at which the maximal rate of oxygen consumption is attained; data compiled from the literature). These results are consistent with those of several recent comparisons of quantitative physiological traits of marsupials versus placentals (references in **Introduction**). Thus, for several aspects of locomotor performance and metabolism (e.g. maximal running speeds, maximal aerobic speeds, maximal rates of oxygen consumption, maintenance of body temperature in response to environmental challenge), little evidence suggests that physiological constraints have limited the evolutionary adaptability of marsupials, as compared with placentals.

REFERENCES

Archer, M. & Clayton, G. (Eds) (1984). *Vertebrate zoogeography and evolution in Australasia*. Carlisle, Western Australia, Australia: Hesparin Press.

Arnold, S. J. (1983). Morphology, performance and fitness. *Am. Zool.* **23:** 347–361.

Bakker, R. T. (1983). The deer flees, the wolf pursues: incongruencies in predator-prey coevolution. In *Coevolution:* 350–382. Futuyma, D. J. & Slatkin, M. (Eds). Sunderland, Mass.: Sinauer Assoc. Inc.

Bartholomew, G. A. (1986). The role of natural history in contemporary biology. *Bioscience* **36:** 324–329.

Baudinette, R. V. (1977). Locomotory energetics in a marsupial, *Setonix brachyurus. Aust. J. Zool.* **25:** 423–428.

Baudinette, R. V. (1978). Scaling of heart rate during locomotion in mammals. *J comp. Physiol.* **127:** 337–342.

Baudinette, R. V. (1982). The energetics of locomotion in dasyurid marsupials. In *Carnivorous marsupials:* 261–265. Archer, M. (Ed.). Mosman, N.S.W., Australia: Royal Zool. Soc. N.S.W.

Baudinette, R. V., Nagle, K. A. & Scott, R. A. D. (1976a). Locomotory energetics in a marsupial (*Antechinomys spenceri*) and a rodent (*Notomys alexis*). *Experientia* **32:** 583–585.

Baudinette, R. V., Nagle, K. A. & Scott, R. A. D. (1976b). Locomotory energetics in dasyurid marsupials. *J. comp. Physiol.* **109:** 159–168.

Bennett, A. F. (1980). The thermal dependence of lizard behaviour. *Anim. Behav.* **28:** 752–762.

Bennett, M. B. (1987). Fast locomotion of some kangaroos. *J. Zool., Lond.* **212:** 457–464.

Biewener, A. A. (1983). Locomotory stresses in the limb bones of two small mammals: the ground squirrel and chipmunk. *J. exp. Biol.* **103:** 131–154.

Calaby, J. H. (1960). Observations on the Banded Ant-eater *Myrmecobius f. fasciatus* Waterhouse (Marsupialia), with particular reference to its food habits. *Proc. zool. Soc. Lond.* **135:** 183–207.

Cartmill, M. (1985). Climbing. In *Functional vertebrate morphology:* 73–88. Hildebrand, M., Bramble, D. M., Liem, K. F. & Wake, D. B. (Eds). Cambridge, Mass.: Belknap, Harvard.

Chappell, M. A. (1984). Maximum oxygen comsumption during exercise and cold exposure in deer mice, *Peromyscus maniculatus. Respir. Physiol.* **55:** 367–377.

Dawson, T. J. (1983). Monotremes and marsupials: the other mammals. London: Edward Arnold.

Dawson, T. J. & Dawson, W. R. (1982). Metabolic scope and conductance in response to cold of some dasyurid marsupials and Australian rodents. *Comp. Biochem. Physiol. (A)* **71:** 59–64.

Dawson, T. J. & Hulbert, A. J. (1970). Standard metabolism, body temperature and surface areas of Australian marsupials. *Am. J. Physiol.* **218:** 1233–1238.

Dawson, T. J. & Needham, A. D. (1981). Cardiovascular characteristics of two resting marsupials: an insight into the cardio-respiratory allometry of marsupials. *J. comp. Physiol. (B)* **145:** 95–100.

Dawson, T. J. & Taylor, C. R. (1973). Energetic cost of locomotion in kangaroos. *Nature, Lond.* **246:** 313–314.

Djawdan, M. & Garland, T., Jr (1988). Maximal running speeds of bipedal and quadrupedal rodents . *J. Mammal.* (In press).

Eisenberg, J. F. (1981). *The mammalian radiations*. Chicago: University of Chicago Press.

Fedak, M. A. & Seeherman, H. J. (1979). Re-appraisal of energetics of locomotion shows identical cost in bipeds and quadrupeds including ostrich and horse. *Nature, Lond.* **282:** 713–716.

Garland, T., Jr. (1983a). The relation between maximal running speed and body mass in terrestrial mammals. *J. Zool., Lond.* **199:** 157–170.

Garland, T., Jr. (1983b). Scaling the ecological cost of transport to body mass in terrestrial mammals. *Am. Nat.* **121:** 571–587.

Garland, T., Jr. (1985). Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis. J. Zool., Lond. (A)* **207:** 425–439.

Garland, T., Jr. (In press). Locomotor performance and activity metabolism of *Cnemidophorus tigris* in relation to natural behaviors. In *The biology of whiptail lizards (**Cnemidophorus**)*. Wright, J. (Ed.). Seattle: Nat. Hist. Museum of Los Angeles County and University of Washington Press.

Garland, T., Jr. & Else, P. L. (1987). Seasonal, sexual, and individual variation in endurance and activity metabolism in a lizard. *Am. J. Physiol.* **252** (*Regulatory Integrative Comp. Physiol.* **21**): R439–R449.

Gleeson, T. T. & Baldwin, K. M. (1981). Cardiovascular response to treadmill exercise in untrained rats. *J. appl. Physiol.* **50**: 1206–1221.

Hayssen, V. & Lacy, R. C. (1985). Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comp. Biochem. Physiol. (A)* **81**: 741–754.

Hertz, P. E., Huey, R. B. & Garland, T., Jr. (In press). Time budgets, thermoregulation, and maximal locomotor performance: are ectotherms Olympians or Boy Scouts? *Am. Zool.*

Hildebrand, M. (1982). *Analysis of vertebrate structure.* 2nd edn. New York: John Wiley & Sons.

Hildebrand, M., Bramble, D. M., Liem, K. F. & Wake, D. B. (Eds) (1985). *Functional vertebrate morphology.* Cambridge, Mass.: Belknap, Harvard.

Hinds, D. S. & MacMillen, R. E. (1984). Energy scaling in marsupials and eutherians. *Science, Wash.* **225**: 335–337.

Hinds, D. S. & MacMillen, R. E. (1986). Scaling of evaporate water loss in marsupials. *Physiol. Zool.* **59**: 1–9.

Hornsby, P. E. (1982). Predation of the euro *Macropus robustus* (Marsupialia: Macropodidae) by the European fox *Vulpes vulpes* (Placentalia: Canidae). *Aust. Mamm.* **5**: 225–227.

Howell, B. A. (1944). *Speed in animals.* New York: Hafner Publ. Co.

Hoyt, D. F. & Kenagy, G. J. (1988). Energy costs of walking and running gaits and their aerobic limits in Golden-mantled ground squirrels. *Physiol. Zool.* **61** (In press).

Huey, R. B., Bennett, A. F., John-Alder, H. B. & Nagy, K. A. (1984). Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. *Anim. Behav.* **32**: 41–50.

Huey, R. B. & Stevenson, R. D. (1979). Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* **19**: 357–366.

John-Alder, H. B., Garland, T., Jr. & Bennett, A. F. (1986). Locomotory capacities, oxygen consumption, and the cost of locomotion of the shingle-back lizard (*Trachydosaurus rugosus*). *Physiol. Zool.* **59**: 523–531.

Keast, A. (1982). The thylacine (Thylacinidae, Marsupialia): how good a pursuit carnivore? In *Carnivorous marsupials*: 675–683. Archer, M. (Ed.). Mosman, N.S.W., Australia: Royal Zool. Soc. N.S.W.

Kenagy, G. J. (1973). Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. *Ecology* **54**: 1201–1219.

Kleinbaum, D. G. & Kupper, L. L. (1978). *Applied regression analysis and other multivariable methods.* North Scituate, Mass.: Duxbury Press.

Kuhlmann, W. D., Hodgson, D. S. & Fedde, M. R. (1985). Respiratory, cardiovascular, and metabolic adjustments to exercise in the Hereford calf. *J. appl. Physiol.* **58**: 1273–1280.

Layne, J. N. & Benton, A. H. (1954). Some speeds of small mammals. *J. Mammal.* **35**: 103–104.

MacMillen, R. E. (1983). Adaptive physiology of heteromyid rodents. *Great Basin Nat. Mem.* No. 7: 65–76.

MacMillen, R. E. & Nelson, J. E. (1969). Bioenergetics and body size in dasyurid marsupials. *Am. J. Physiol.* **217**: 1246–1251.

Margaria, R., Cerretelli, P., Aghemo, P. & Sassi, G. (1963). Energy cost of running. *J. appl. Physiol.* **18**: 367–370.

Marlow, B. J. (1969). A comparison of the locomotion of two desert-living Australian mammals, *Antechinomys spenceri* (Marsupialia: Dasyuridae) and *Notomys cervinus* (Rodentia: Muridae). *J. Zool., Lond.* **157**: 159–167.

Moore, J. C. (1957). The natural history of the fox squirrel, *Sciurus niger shermani*. *Bull. Am. Mus. Nat. Hist.* **113**: 1–71.

Nagy, K. A. (1987). Field metabolic rate and food requirements scaling in mammals and birds. *Ecol. Monogr.* **57**: 111–128.

Nicol, S. & Maskrey, M. (1986). Arterial blood acid-base regulation in the Tasmanian devil, *Sarcophilus harrisii*, during exercise. *Physiol. Zool.* **59**: 212–219.

Norusis, M. J. (1986). *SPSS/PC+ for the IBM PC/XT/AT.* Chicago: SPSS Inc.

Pellis, S. M. & Nelson, J. E. (1984). Some aspects of predatory behaviour of the quoll, *Dasyurus viverrinus* (Marsupialia: Dasyuridae). *Aust. Mamm.* **7**: 5–15.

Seeherman, H. J., Taylor, C. R., Maloiy, G. M. O. & Armstrong, R. B. (1981). Design of the mammalian respiratory system. II. Measuring maximum aerobic capacity. *Respir. Physiol.* **44**: 11–23.

Strahan, R. (Ed.) (1983). *The complete book of Australian mammals.* Sydney: Angus & Robertson.

Taylor, C. R. (1980). Energetics of locomotion: primitive and advanced mammals. In *Comparative physiology: primitive mammals*: 192–198. Schmidt-Nielsen, K., Bolis, L. & Taylor, C. R. (Eds). Cambridge: Cambridge University Press.

Taylor, C. R. & Rountree, V. J. (1973). Running on two legs or four: which consumes more energy? *Science, Wash.* **179**: 186–187.

Taylor, C. R., Maloiy, G. M. O., Weibel, E. R., Langman, V. A., Kamau, J. M. Z., Seeherman, H. J. & Heglund, N. C. (1981). Design of the mammalian respiratory system. III. Scaling maximum aerobic capacity to body mass: wild and

domestic mammals. *Respir. Physiol.* **44:** 25–37.

Taylor, C. R., Heglund, N. & Maloiy, G. M. O. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. exp. Biol.* **97:** 1–21.

Thompson, S. D. (1985). Bipedal hopping and seed-dispersion selection by heteromyid rodents: the role of locomotion energetics. *Ecology* **66:** 220–229.

Thompson, S. D., MacMillen, R. E., Burke, E. M. & Taylor, C. R. (1980). The energetic cost of bipedal hopping in small mammals. *Nature, Lond.* **287:** 223–224.

Williams, T. M. (1983). Locomotion of the North American mink, a semi-aquatic mammal. 2. The effect of an elongate body on running energetics and gait patterns. *J. exp. Biol.* **105:** 283–295.

Windsor, D. E. & Dagg, A. I. (1971). The gaits of the Macropodinae (Marsupialia). *J. Zool., Lond.* **163:** 165–175.