MAXIMAL RUNNING SPEEDS OF BIPEDAL AND QUADRUPEDAL RODENTS

MINOU DJAWDAN AND THEODORE GARLAND, JR.

Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92717
Present address of TG: Department of Zoology, University of Wisconsin, Madison, WI 53706

ABSTRACT.—Maximal running speeds of both bipedal (*Dipodomys, Microdipodops*) and quadrupedal (*Chaetodipus, Perognathus*) heteromyid rodents, and some sympatric nocturnal cricetids and diurnal sciurids, were measured in the laboratory (17 species, 131 individuals) and in the field (eight species, 138 individuals). We found significant, repeatable differences among individuals within species. Significant differences also were found among species: *Perognathus longimembris* (8.9 g, 9.9 km/h) and *Onychomys torridus* (19.3 g, 10.3 km/h) were relatively slow; *Microdipodops megacephalus* (12.3 g, 10.9 km/h) and *Peromyscus crinitus* (13.7 g, 11.4 km/h) were somewhat faster; *Chaetodipus baileyi* (39.1 g, 12.4 km/h), *Perognathus parvus* (24.4 g, 12.5 km/h), *Chaetodipus fallax* (18.0 g, 12.8 km/h), *Peromyscus eremicus* (19.8 g, 13.1 km/h), and *Peromyscus maniculatus* (18.2 g, 13.4 km/h) attained similar speeds; *Peromyscus truei* (19.3 g, 14.3 km/h) was faster still; *Neotoma lepida* (110.6 g, 17.1 km/h) and three squirrel species were the fastest tested in the laboratory. Kangaroo rats (*Dipodomys*) did not exert themselves maximally in the laboratory, but attained speeds significantly higher than pocket mice (*Chaetodipus, Perognathus*) or other sympatric rodents in the field. In addition, *Dipodomys* displayed erratic escape behavior (zig-zagging) when pursued in the field significantly more frequently than *Chaetodipus* or *Perognathus*. Higher sprint speeds and erratic escape behavior may allow kangaroo rats to escape from some predators (e.g., raptors, canids), and hence exploit open microhabitats (of presumed higher predation risk) to a greater extent than slower sympatric rodents.

Direct measures of organismal performance perhaps are the most appropriate starting point for attempting to integrate physiological and ecological approaches to the study of adaptation (Arnold, 1983; Huey and Stevenson, 1979). Motivated by this perspective, a number of workers have studied locomotion, because various aspects of locomotor performance (e.g., speed and stamina) are thought to be important determinants of the success of animals in such natural activities as foraging and escaping from predators (Garland, in press; Huey and Hertz, 1984). Although reptilian locomotion has been the subject of several studies (Bennett, 1980; Garland, 1984, 1985, in press, 1988; John-Alder et al., 1986; van Berkum et al., 1986), direct measures of mammalian locomotor performance are rare (Garland, 1983*a*; Layne and Benton, 1954). Most recent physiological studies of mammalian locomotion focused on energetic costs (MacMillen, 1983; Taylor et al., 1982; Thompson, 1985).

One notable feature of mammalian locomotion is bipedality, which evolved independently several times (e.g., primates, macropod marsupials, members of five families of rodents). Neither the selective regimes prevailing during the origin of bipedality nor the ecological conditions favoring the maintenance of bipedality are well understood (Bartholomew and Cary, 1954; Bartholomew and Caswell, 1951; Eisenberg, 1975; Howell, 1944; Mares, 1980, 1983; Nikolai and Bramble, 1983). Bipeds and quadrupeds do not show differences in energetic costs of locomotion (Garland, 1983*b*; MacMillen, 1983; Taylor et al., 1982; Thompson, 1985). However, several authors suggested that bipedal and quadrupedal small mammals may differ in other aspects of locomotor performance, such as acceleration, speed, and stamina (Bartholomew and Caswell, 1951; Eisenberg, 1975; Garland, 1983*a*; MacMillen, 1983). These putative differences have been suggested to play a role in determining the relative abilities of different species to forage or to escape from predators (Rosenzweig, 1973; Rosenzweig and Winakur, 1969; Thompson, 1982*a*, 1982*b*).

Limited observations suggest that bipedal kangaroo rats (Heteromyidae) may be faster than quadrupedal mammals of similar size (Garland, 1983*a*; Kenagy, 1973). However, there are no data available for maximal running speeds of quadrupedal heteromyids, or for any other small

rodents that occur sympatrically with kangaroo rats. We, therefore, measured maximal running speeds of both bipedal and quadrupedal heteromyids and several other rodent species that co-occur with them.

Materials and Methods

Rodents were trapped January–August 1985, in Sherman live traps at four locations in California:1) mixed Joshua tree (*Yucca brevifolia*) woodland and creosote bush (*Larrea tridentata*) scrub, 3.3 km S Joshua Tree, San Bernardino Co.; 2) Quail Springs Wash, a boulder-strewn hillside 4 km S Joshua Tree, San Bernardino Co.; 3) Dale Dry Lake, a creosote bush and sand-dune habitat 38 km E 29 Palms, San Bernardino Co.; 4) Benton Valley, a Great Basin sage brush (*Artemisia tridentata*) community 6.4 km N Benton, Mono Co. These sites were chosen because they provided syntopic bipedal and quadrupedal species of different size, and because previous ecological studies had been conducted at each site (Thompson, 1980, 1982*a*, 1982*b*, 1985 for sites 1 and 3; Eidemiller, 1982 for site 2; Day, 1981 for site 3; Lawhon, 1984 for site 4). *Chaetodipus baileyi* was collected for us by Scott Osborne at sites 10–30 km N Tucson, Pima Co., Arizona (site 5).

Laboratory and field timing.—Maximal running speeds were obtained by timing animals as they were chased along a microprocessor-controlled, photocell-timed racetrack (Garland, 1985; Huey and Hertz, 1984). Timing of all species began within 3 days of capture, with exception of *C. baileyi*, for which testing began within 4–21 days of capture. The track was 8 m long by 25 cm wide, with plywood walls 60 cm high. Twelve sets of six vertically-aligned photocells were placed at 10–50 cm intervals over the first 4 m of the track. Artificial grass carpet was used as floor covering to provide good traction for the animals. A darkened cardboard refuge was placed at the end of the runway, toward which the rodents ran.

To familiarize animals with the track, each individual was chased slowly back and forth along the track a few times before timing. During timed runs, rodents were chased down the track with a padded meterstick, then walked slowly back to the beginning. For each individual, five to 15 timed trials were recorded until no increase in speed occurred with subsequent trials. Various methods of making noise, including rattling pieces of cardboard and plastic bags against the track walls, clapping of the hands, and yelling also were used to prompt animals to run. Each animal was tested for 2 or 3 consecutive days. For each timed run, the fastest 1.0-m interval ($\geq$3 consecutive photocells) was recorded. Preliminary tests indicated that animals tested at night were not significantly faster than those tested during the day; subsequently, all trials were conducted during the day.

For field trials, clearings were selected at collecting sites 1, 3, and 4. Distances of 3, 7, and 11 m were measured from a center point in the clearing and marked with half-circles of spray paint. Animals were livetrapped at night and taken to the clearing early the next morning. Individuals were shaken out of traps, allowed to sit for a few seconds, then startled by dropping the trap immediately behind them. Rodents then were chased by one of us, and they usually ran toward the largest bush at the edge of the clearing. They were timed with hand-held, digital stopwatches to the nearest 0.01 s as they crossed the marked distances. Distances other than between the marked half-circles were measured to the nearest 0.1 m immediately following each trial. For each trial we also noted whether rodents ran in a zig-zag pattern, in a straight line, or in a gentle arc. When animals did not run in a straight line, paths run were estimated from memory and measured with a tape measure; these distances were used for calculations of speed. Three or four people timed each run, and average speeds were used in the analyses. Laboratory simulations (using a tennis ball rolled at various speeds over marked distances of $\geq$4 m) indicated that our field times are reliable within about 10% (Belkin, 1961).

Statistical analyses.—To compare maximal running speeds among species in the laboratory, we conducted one-way analysis of variance using SPSS^X (SPSS Inc., 1985). For these comparisons, we used only the single fastest speed recorded for each individual (Garland, 1985). Data were $\log_{10}$ transformed before analysis to achieve homogeneity of variances among species. We employed Scheffe's procedure because this is the most conservative multiple-range comparison for unequal sample sizes (Neter and Wasserman, 1974; Nie et al., 1975). Statistical significance was judged at $P < 0.05$ in all cases.

For laboratory data, we also sought to determine if maximal running speeds of individuals within species differ significantly and if maximal running speeds change following extended periods of captivity. We conducted two-way analysis of variance for each species, using each individual's single fastest speed on each trial day (Sokal and Rohlf, 1981). We report intraclass correlation coefficients (r_i = proportion of variance among individuals) as a measure of repeatability (Lessells and Boag, 1987; Sokal and Rohlf, 1981). For species that showed significant differences in speed between trial days, the mean square between trial days was excluded before computation of among-individual components of variance (r_i).

TABLE 1.—*Maximal running speeds of rodents measured in the laboratory.*

Family and species	*n* ♂	*n* ♀	Body mass (g) $\bar{X} \pm SD$	Body mass (g) Range	Body mass (g) Fastest individual	Speed (km/h) $\bar{X} \pm SD$	Speed (km/h) Range
Cricetidae							
Neotoma lepida	4	6	110.6 ± 24.4	81.3–160.1	105.2	17.1 ± 1.3	14.9–19.2
Onychomys torridus	3	2	19.3 ± 3.2	16.0–24.5	16.0	10.3 ± 0.7	9.3–11.0
Peromyscus crinitus	8	6	13.7 ± 1.6	11.1–16.3	16.3	11.4 ± 0.8	9.9–12.5
Peromyscus eremicus	4	3	19.8 ± 3.1	15.4–24.6	18.6	13.1 ± 1.1	11.2–14.2
Peromyscus maniculatus	6	6	18.2 ± 3.2	12.0–23.0	22.7	13.4 ± 1.2	11.1–15.9
Peromyscus truei	1	1	19.3 ± 2.1	17.8–20.8	17.8	14.3 ± 0.2	14.2–14.4
Heteromyidae							
Chaetodipus baileyi	9[a]		39.1 ± 5.9	27.7–46.4	39.7	12.4 ± 1.4	10.8–14.9
Chaetodipus fallax	9	3	18.0 ± 2.2	15.0–21.6	16.0	12.8 ± 0.9	11.4–14.2
Dipodomys deserti	4	1	97.6 ± 24.0	73.3–133.3	73.3	15.0 ± 2.5	12.0–18.3
Dipodomys merriami	4	5	35.7 ± 4.7	28.0–44.0	32.0	11.4 ± 1.2	10.1–14.0
Dipodomys ordii	4	3	47.8 ± 7.1	34.0–55.5	50.0	14.1 ± 0.9	12.7–15.3
Microdipodops megacephalus	5	3	12.3 ± 1.6	10.0–15.0	11.0	10.9 ± 1.6	9.4–14.2
Microdipodops megacephalus (pregnant)		3	13.5 ± 0.5	13.0–14.0	13.5	9.9 ± 0.9	9.0–10.9
Perognathus longimembris	7	6	8.9 ± 0.6	8.0–10.0	8.6	9.9 ± 0.7	8.7–11.7
Perognathus parvus	5	4	24.4 ± 2.3	21.0–29.0	26.0	12.5 ± 1.6	10.4–14.6
Sciuridae							
Ammospermophilus leucurus	2[a]		75.9 ± 0.4	75.7–76.2	76.2	17.2 ± 2.1	15.7–18.7
Eutamias minimus	2	1	29.3 ± 1.2	28.0–30.0	28.0	16.8 ± 0.8	15.9–17.4
Spermophilus tereticaudus		1	112.6			15.2	

[a] Sex unknown.

RESULTS

Laboratory speeds: interspecific and individual differences.—A total of 17 species and 131 individual rodents was timed in the laboratory (Table 1). All species appeared to run at maximal speeds, with exception of kangaroo rats, which consistently refused to run at top speed in the racetrack (compared to previous studies and our field trials). Even a mild electric shock failed to elicit maximal performance from *Dipodomys* in the laboratory. Prior familiarization with the racetrack, for several hours or over night, also failed to improve their performance.

Species differed significantly in $\log_{10}$ maximal running speeds ($F = 29.0$; $d.f. = 9, 89$; $P < 0.0001$). Scheffe's procedure indicates homogeneous subsets, in order of increasing speed, as follows: (*Perognathus longimembris* = *Onychomys torridus* = *Microdipodops megacephalus* = *Peromyscus crinitus*) ≤ (*M. megacephalus* = *P. crinitus* = *Chaetodipus baileyi* = *Perognathus parvus* = *C. fallax*) ≤ (*P. crinitus* = *C. baileyi* = *P. parvus* = *C. fallax* = *Peromyscus eremicus* = *Peromyscus maniculatus*) < *Neotoma lepida*. Kangaroo rats were omitted from the analysis of variance because their laboratory speeds were not considered maximal. We also omitted *Peromyscus truei* and the sciurids from the analysis of variance because of small sample sizes. At least two of the three sciurids are approximately as fast as *Neotoma* (Table 1).

Considering only the heteromyids, there also was significant heterogeneity in $\log_{10}$ maximal speeds ($F = 13.8$; $d.f. = 4, 46$; $P < 0.0001$). Homogeneous subsets were: (*P. longimembris* = *M. megacephalus*) ≤ (*M. megacephalus* = *C. baileyi* = *P. parvus*) ≤ (*C. baileyi* = *P. parvus* = *C. fallax*). Considering only cricetids, heterogeneity also was significant ($F = 49.7$; $d.f. = 4,$

TABLE 2.—*Maximal running speeds of rodents timed in the field.*

Species	Tested (*n*)	Zig-zagged (*n*)	Actually timed (*n*)	Speed (km/h) $\bar{X} \pm SD$	Speed (km/h) Range
Dipodomys deserti	39	22	35	18.3 ± 3.0	13.9–29.9
Dipodomys merriami	76	15	67	14.8 ± 3.1	9.5–25.8
Dipodomys panamintinus	4	1	4	13.4 ± 0.9	11.7–14.2
Chaetodipus fallax	11		9	11.4 ± 2.3	6.9–15.0
Perognathus longimembris	19	2	15	9.9 ± 1.5	7.7–13.7
Perognathus parvus	1		1	12.2	
Microdipodops megacephalus	4		2	9.9 ± 0.8	9.3–10.4

43; $P < 0.0001$), with the following homogeneous subsets: (*O. torridus* = *P. crinitus*) < (*P. eremicus* = *P. maniculatus*) < *N. lepida*.

Within most species, individuals showed consistent and statistically significant differences in speed. Two-way analyses of variance demonstrated significant among-individual components of variance for *C. baileyi* (run 3 days, $n = 9$, $F = 7.00$, $P = 0.001$, $r_i = 0.67$), *C. fallax* (run 2 days, $n = 12$, $F = 5.96$, $P < 0.005$, $r_i = 0.73$), *M. megacephalus* (run 2 days, $n = 11$, $F = 8.19$, $P < 0.0001$, $r_i = 0.79$), *P. parvus* (run 2 days, $n = 9$, $F = 3.65$, $P < 0.05$, $r_i = 0.60$), *P. eremicus* (run 3 days, $n = 7$, $F = 4.92$, $P = 0.009$, $r_i = 0.57$), and *P. maniculatus* (run 3 days, $n = 12$, $F = 11.63$, $P < 0.0001$, $r_i = 0.77$). For *N. lepida* (run 3 days), *P. longimembris* (run 2 days), and *P. crinitus* (run 2 days), among-individual components of variance in speed were not significant.

Speed and body mass were not correlated significantly within any species.

Four species showed significant increases in speed from day 1 to day 2 (*C. baileyi*, +12.0%; *N. lepida*, +15.8%; *P. crinitus*, +14.7%; *P. eremicus*, +17.0%). These differences in speed were adjusted for in the calculations of r_i. No species showed a significant increase in speed from day 2 to day 3.

Nine individuals of *C. fallax* were maintained in captivity in plastic cages (27.5 by 20 by 15 cm) with wire tops and tested on days of captivity 1–6, 15, 16, 29, 30, 71, 72, 180, and 181. Among-individual components of variance were significant ($F = 8.38$; $d.f. = 8, 104$; $P < 0.0001$; $r_i = 0.35$) across all 14 trial days; however, mean running speed was not consistent across all 14 trial days ($F = 6.94$; $d.f. = 13, 104$; $P < 0.0001$). Two-way analyses of variance of various combinations of trial days indicated that speed did not vary significantly over days 1–6, dropped 13.4% between days 6 ($\bar{X} \pm SD$ of speed = 11.8 ± 1.28 km/h) and 15 (10.2 ± 1.97 km/h), then showed no further change. Four *P. maniculatus* individuals maintained in captivity and tested on days 1–6, 15, 16, 29, 30, 71, and 72 showed significant among-individual components of variance across all 12 trial days ($F = 5.04$; $d.f. = 3, 33$; $P < 0.01$; $r_i = 0.28$), but no significant change in speed ($F = 0.59$; $d.f. = 11, 33$; $P = 0.827$).

Field trials.—We tested eight species and 160 individuals in the field; of these, speeds were obtained for 138 individuals (Table 2). *Dipodomys* species attained higher speeds than *Chaetodipus* or *Perognathus* in the field. Considering the two *Dipodomys*, one *Chaetodipus*, and one *Perognathus* species with adequate sample sizes, there was significant heterogeneity in maximal running speeds ($F = 44.2$; $d.f. = 3, 122$; $P < 0.0001$). Homogeneous subsets were: (*P. longimembris* = *C. fallax*) < *D. merriami* < *D. deserti*.

We also compared laboratory and field speeds for these four species using *t*-tests for independent samples. We used $\log_{10}$-transformed data and separate variance estimates because field data were significantly more variable than laboratory data (except for *D. deserti*). Laboratory (Table 1) and field speeds (Table 2) did not differ significantly for either *P. longimembris* or *C. fallax*, however, field speeds of *D. merriami* ($t = 5.74$; $d.f. = 18.43$; $P < 0.001$) and *D. deserti* ($t = 2.69$; $d.f. = 38$; $P = 0.010$) were significantly higher than laboratory speeds. These results agree with our subjective impressions that *Dipodomys* did not run at maximal speed in our laboratory racetrack.

Kangaroo rats zig-zagged during field runs significantly more frequently than pocket mice.