INFLUENCE OF TREE DIAMETER ON CLIMBING ABILITY OF SMALL MAMMALS

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Climbing ability can be a major component of the capability of terrestrial mammals to use vertical habitats. Previous studies suggest that small mammals from central Chile have low climbing capabilities. However, those studies have not disentangled the influence of tree diameter in natural habitats from true climbing ability of different species. We carried out a laboratory experiment by studying the climbing ability of 4 central Chilean small mammals, 2 octodontid rodents (*Octodon bridgesi* and *O. degus*), 1 murid rodent (*Phyllotis darwini*), and 1 marsupial (*Thylamys elegans*), in situations with different stem diameters. Species showed distinctive climbing abilities. The marsupial *T. elegans* showed efficient climbing ability independent of stem diameter. *P. darwini* and *O. bridgesi* were both influenced by stem diameter, but the former species used smaller-diameter stems less frequently. *O. degus* showed the lowest climbing ability.

Key words: Chile, climbing ability, habitat use, marsupial, rodent, small mammal

Space use can influence survival and reproductive success. Predation risk, food distribution, vegetation structure, and microclimate vary in space, thus affecting habitat selection and use (Partridge 1978; Rosenzweig 1991). Such factors account for microhabitat use by small mammals of central Chile (Ebensperger and Simonetti 1996; Meserve 1981a, 1981b; Simonetti 1989; Vásquez 1996; Vásquez et al. 2002). Small mammals tend to concentrate their activities under shrub cover because it provides refuge from predators and more abundant food, whereas open ground between shrubs is more risky, and potentially covered by an herb layer that could hamper mobility (Meserve 1981a, 1981b; Simonetti 1989; Vásquez 1996; Vásquez et al. 2002).

A distinctive feature of small mammals of central Chile is the low climbing ability that they display (Meserve 1981a). Climbing ability should be expected in rodents such as Darwin's leaf-eared mouse (*Phyllotis darwini*) because of the similar morphology (e.g., long tail and big feet) it shares with North American peromyscine rodents, such as *Peromyscus leucopus* (and other species) that show significant climbing activity (Meserve 1977, 1981a). As in North American rodents, one factor that could account for the low climbing ability of Chilean small mammals is the diameter of stems on trees and shrubs available in their habitats (Meserve 1981a). In fact,

North American arboreal rodents most frequently used large-diameter branches (Meserve 1977). Tree stems of small diameter would make climbing more difficult, because they offer lesser surface for traction, everything else being equal (Layne 1970; Meserve 1977). Chilean shrublands and forests have suffered high rates of deforestation, which has modified their structure, as is reflected in a high proportion of small-diameter stems. Given that a smaller diameter offers less traction surface for climbing, we expected that small mammals would have reduced climbing activity on small-diameter stems compared to larger-diameter stems. We evaluated, through laboratory experiments, if variation in climbing activity of small mammals of central Chile results from variation in stem diameters.

Central Chile is a highly perturbed ecosystem, which shows a high rate of deforestation by forestry and agricultural activities. For that reason we assessed the climbing ability of 3 species of small mammals that occur in forested areas of central Chile, including Darwin's leaf-eared mouse (*P. darwini*), Bridge's degu (*Octodon bridgesi*), and the southern mouse opossum (*Thylamys elegans*). All of these species are reported to exhibit some climbing activity, either by using trees as refuge or food source, although reports are based on anecdotal evidence of climbing and morphologic characteristics of each species (Muñoz-Pedreros and Yáñez 2000). *P. darwini* is morphologically similar to species of *Peromyscus* (Glanz 1970; Meserve 1981a), and for that reason it is expected that both groups will have a similar climbing ability (Meserve 1977). *O. bridgesi* inhabits forests zones and there is anecdotal evidence of its climbing abilities (Rodríguez 1993). *T. elegans*

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has been described as an arboreal species (Meserve 1981a). Its prehensile tail and opposable thumb on its rear limbs support this statement (Muñoz-Pedreros and Yáñez 2000). Based on these features, we would expect *T. elegans* to be less affected by stem diameter than the rodents studied.

The selected species are affected by habitat modifications including the frequency distribution of stem diameters (Saavedra and Simonetti, in press), but it is not known if stem diameter influences their climbing ability. As a control, we included the degu (*O. degus*), a nonclimbing species (Muñoz-Pedreros and Yáñez 2000). For morphological features of species tested see Osgood (1943) and Mann (1978).

MATERIALS AND METHODS

All test individuals were wild-captured from coastal forests, near Tregualemu, Chile (Maule region, 35°55′S, 72°41′W). *O. degus* was captured in scrublands near Santiago, Chile (33°28′S, 70°53′W, 450 m above sea level). Animals were caged individually (in cages 35 × 30 × 15 cm), with a 14:10 light : dark regime. Experiments were carried out between October and December 2001. Animals were provided fresh vegetables, commercial rabbit pellets, and water ad libitum. Animal care and experimental procedures complied with the animal care and use guidelines of the American Society of Mammalogists (http://www.mammalogy.org/committees/index.asp). Animals were released in their capture sites after the experiments.

Climbing ability was observed in an experimental arena where animals were presented with stems of different diameters. Each animal was introduced alone into the experimental arena and climbing activity of each subject was recorded on videotape for 60 min, the time necessary for observing locomotion. After 60 min, the animals tended to decrease their activity or remain still. A single 1-m-high vertical stem (described below) was placed vertically at the center of a 1.6-m-diameter circular arena. The floor was covered with fine sand. Stems were made of cylindrical pieces of wood, coated with granular white paint (range of grain size, 1–4 mm) to maintain a constant surface texture.

We chose 4 diameters similar in size to stems available in areas with different levels of human disturbance, both in Río Clarillo (33°51′S, 70°29′W) and Los Queules (39°59′S, 72°41′W) Natural Reserves and adjacent areas. We evaluated the distribution of stem diameters by measuring stems (diameter at breast height in random plots of 10 × 10 m) in natural habitats. Diameters chosen were selected to include the range of diameters available in the field. Stems at the sites range in diameter from 3 to 600 mm, with highly disturbed habitats having only stems of the smallest diameters (<63 mm) and most stems (45 of 50) in habitats with little disturbance in the range between 120 and 300 mm. For the experiments, we used 4 artificial wooden stems, each 80 cm high and with diameters of 3, 10, 200, and 300 mm. Nine individuals of each species were tested singly with each 1 of the 4 stem diameters. Each subject was presented with stems of different diameters, with order determined by a Latin-square design to avoid any bias due to the experimental process (Zar 1996). Each animal was presented with 1 stem, with at least 3 days between trials. Fruit (apple slice of a fixed size, large enough to attract the animal) was placed on top of the stem.

Climbing activity was evaluated as number of subjects that climbed a stem out of total number of subjects tested, number of times an animal fell from an attempted climb (i.e., a measure of climbing ability), and climbing speed, measured as the time to reach the top of the 1-m stem, with pauses excluded. *T. elegans*, *P. darwini*, and *O.*

bridgesi differ in body mass (*T. elegans*, 56 ± 3 g [mean ± *SE*; *n* = 9]; *P. darwini*, 83 ± 2 g [*n* = 9]; and *O. bridgesi*, 175 ± 5 g [*n* = 9]; Kruskall–Wallis: $H = 23.2$, $P < 0.001$). Therefore, we standardized climbing speed by dividing by body mass (cm s^{-1} g^{-1}). Data on climbing speed for *O. degus* (body mass: 183 ± 4 g, *n* = 9) were insufficient for statistical analysis because few individuals climbed (see "Results").

We analyzed the proportion of individuals that climbed through a multiple comparison for proportions test (Zar 1996). We carried out a Pearson correlation with a subsequent randomization procedure (Manly 1997) for analyzing the proportion of climbing individuals among diameters. We evaluated the number of falls through the Scheirer–Ray–Hare nonparametric 2-way analysis of variance (ANOVA) for ranked data (Sokal and Rohlf 1995), followed by nonparametric comparisons based on Wilcoxon 2-sample tests (Sokal and Rohlf 1995). Finally, we analyzed climbing speed among species through 1-way ANOVA, climbing speed among species and diameters with repeated-measures 2-way ANOVA, and planned comparisons by following Sokal and Rohlf (1995).

RESULTS

All animals were active in the experimental arena, although not all reached the stem. Those animals that approached stems of different diameters climbed. *T. elegans* used its prehensile tail as a climbing aid, except at the largest 2 diameters (200 and 300 mm); the other species did not use their tails.

The proportion of subjects that climbed differed significantly among species ($\chi^2 = 14.64$, $d.f. = 3$, $P < 0.05$). More individuals of *T. elegans* climbed than did individuals of other species. *T. elegans* and *P. darwini* climbed significantly more frequently than did *O. degus* (multiple comparisons for proportions, $q > 3.63$, $P < 0.05$). The proportion of *O. bridgesi* that climbed was intermediate between that for *T. elegans*, *P. darwini*, and *O. degus* ($q < 3.630$, $P > 0.05$; Fig. 1a).

The proportion of individuals that climbed did not increase with larger stem diameters for *T. elegans* ($r = 0.81$, $P = 0.74$) or for *O. bridgesi* ($r = 0.02$, $P = 0.68$; Fig. 1b). In contrast, the proportion that climbed did increase with stem diameter for the other 2 species, *P. darwini* ($r = 0.88$, $P < 0.001$) and *O. degus* (although the proportion of *O. degus* that climbed was low; $r = 0.96$, $P < 0.001$; Fig. 1b).

The number of individuals that fell from a stem differed significantly among species and diameters (Scheirer–Ray–Hare nonparametric 2-way ANOVA, $H_{[species]} = 8.68$, $P < 0.05$; $H_{[diameter]} = 7.92$, $P < 0.05$; and $H_{[interaction]} = 5.98$, $P > 0.5$). Although the number of individual *O. degus* that fell tended to be higher than for the other species, particularly for small diameters (Table 1), the low number of times these animals climbed stems compared to the other 3 species precluded further analysis. Consequently, we compared the other 3 species for given stem diameters (Table 1). *T. elegans* fell significantly fewer times than any other species from stems of 3-mm diameter ($U_s \geq 30$, $P \leq 0.05$ in all cases). For stems of 3- and 10-mm diameter, no individual of *T. elegans* fell (Table 1). For 200-mm stems, *T. elegans* fell significantly less than *O. bridgesi* ($U_s = 25$, $P \leq 0.05$). *O. bridgesi* did not fall from stems of 10-mm diameter (Table 1). Comparisons of stem diameters within species revealed that *T. elegans* and *P.*
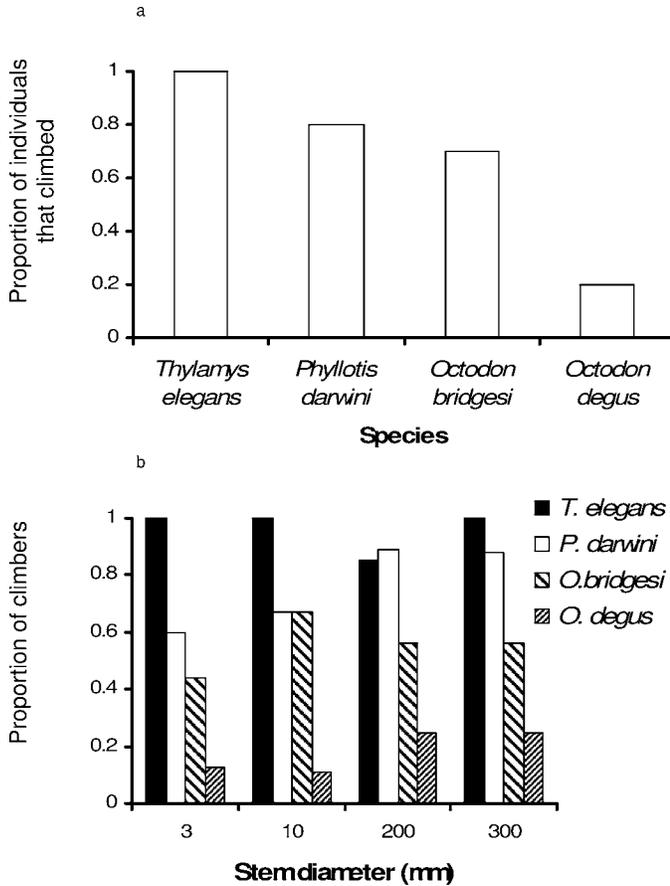
FIG. 1.—Stem climbing in 4 species of Chilean small mammals. a) Proportion of individuals that climbed the stem out of those that made contact with the stem. Sample sizes were: *Thylamys elegans* ($n = 8$), *Phyllotis darwini* ($n = 7$), *Octodon bridgesi* ($n = 7$), and *Octodon degus* ($n = 2$). b) Proportion of individuals of each species that climbed the stem for each stem diameter.

TABLE 1.—Number of falls of small mammals from central Chile. Number of falls taken by subjects of each species per 10 s (mean $\pm$ SE), at each stem diameter. Sample sizes are *Thylamys elegans*, $n = 8$; *Phyllotis darwini*, $n = 7$; *Octodon bridgesi*, $n = 7$; and *Octodon degus*, $n = 2$.

Species	Stem diameter (mm)			
	3	10	200	300
Thylamys elegans	0	0	0.21 ± 0.11	0.03 ± 0.03
Phyllotis darwini	0.23 ± 0.06	0.02 ± 0.01	0.61 ± 0.26	0.01 ± 0.01
Octodon bridgesi	0.30 ± 0.27	0	22.40 ± 19.50	0.72 ± 0.58
Octodon degus	15.20	1.00	1.95 ± 0.25	0.49 ± 0.31

mm and 10-mm stem diameter, as well as faster than *O. bridgesi* at 300-mm stem diameter (planned comparisons: $F > 6.10$, $d.f. = 1$, $P < 0.05$). *T. elegans* the fastest climber, was significantly slower at 200-mm than at 10-mm diameter (planned comparisons: $F = 7.31$, $d.f. = 1$, $P = 0.02$) and
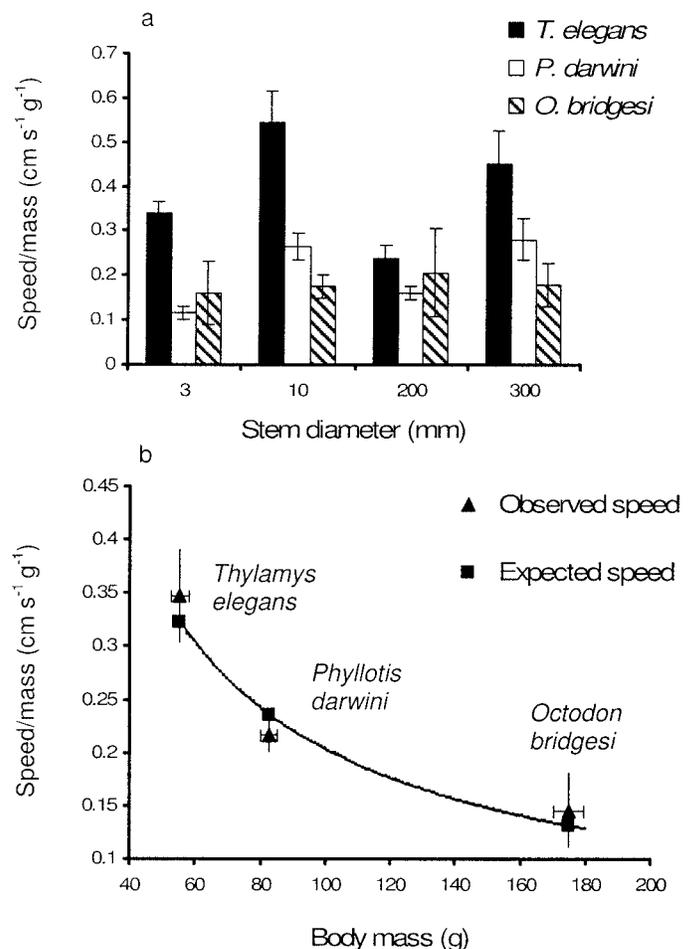
darwini fell more frequently from 200-mm stems than from 3- and 10-mm-diameter stems (Table 1). *P. darwini* fell significantly more often from 3-mm-diameter stems than from 10- and 300-mm-stems ($U_s \geq 29$, $P \leq 0.005$), and from stems of 200-mm diameter than from 10- and 300-mm stems ($U_s \geq 38$, $P \leq 0.01$).

Actual speeds (means for all climbs of each stem diameter) were 7.2–39.2 cm/s ($n = 8$) for *T. elegans*, 5.3–33.6 cm/s ($n = 7$) for *P. darwini*, and 7.9–52 cm/s ($n = 7$) for *O. bridgesi*. Mass-specific speeds take into account differences in body size. Mass-specific speeds were significantly different among species ($F = 8.75$, $d.f. = 2$, $P = 0.002$). *O. degus* was excluded from this analysis because few individuals climbed. *T. elegans* was significant faster than *P. darwini* (planned comparisons: $F = 7.01$, $d.f. = 1$, $P = 0.01$) and *O. bridgesi* (planned comparisons: $F = 16.8$, $d.f. = 1$, $P = 0.0006$), but the latter 2 species did not differ significantly (planned comparisons: $F = 1.97$, $d.f. = 1$, $P > 0.05$). Climbing speed also differed among stem diameters but there was no significant interaction between species and diameter (Fig. 2). *T. elegans* was significantly faster than *P. darwini* and *O. bridgesi* at 3-

FIG. 2.—Climbing speed of 3 species of Chilean small mammals. a) Mass-standardized speed (mean $\pm$ SE) for each species for each stem diameter. b) Mass-standardized climbing speed as a function of body mass for each species (mean $\pm$ SE in both axes). Expected speed is after Buddenbrock (1934; see text for details). Sample sizes as in legend of Fig. 1.

300-mm diameter (planned comparisons: $F = 8.98$, $d.f. = 1$, $P = 0.01$; Fig. 2a).

We calculated expected speed for each species by using $V_n = 0.33W^{0.21}$, where V_n is normal or optimal walking or running speed (m/s) and W is body mass (kg—Buddenbrock 1934), and compared expected and observed speeds (standardized by body mass; Fig. 2b). Observed speed per unit mass for each species was not significantly different from the expected speed (Student's *t*-test: *T. elegans*: $t = 0.19$, $P > 0.05$; *P. darwini*: $t = 0.29$, $P > 0.05$; *O. bridgesi*: $t = 0.23$, $P > 0.05$; Fig. 2b).

DISCUSSION

Climbing activity among small mammals of central Chile was affected by stem diameter, but the response differed by species. *T. elegans* was capable of climbing stems of all diameters tested (Fig. 1). This ability was related to morphology. *T. elegans* has feet with opposable thumbs and a prehensile tail, enabling a tight grip on thin, unstable branches (Mann 1978). Therefore, differences in availability of small-diameter trees and shrubs should not affect overall arboreal activity of *T. elegans*. On the other hand, climbing activity of *P. darwini* and *O. bridgesi* would be affected by such changes. Although *P. darwini* climbed the large-diameter stems more frequently than small-diameter stems, *O. bridgesi* tend to climb the smallest stem diameter less frequently (Fig. 1). These 2 species also showed good climbing performance, as evidenced by their low number of falls. Particularly for *P. darwini*, Meserve (1981a) suggested that this ability should be expected given its morphological similarities to well-known climbers such as species of *Peromyscus*, which have long tails and large feet (Dewsbury et al. 1980; Glanz 1970; Harney and Dueser 1987; Meserve 1977). However, climbing ability of *P. darwini* was affected by stem diameter.

Although *O. degus* showed the lowest climbing activity of the 4 species studied, the proportion of climbers increased significantly with larger-diameter stems (Fig. 1b). Interestingly, the 2 *Octodon* species, despite having very similar body sizes and morphologies, differ significantly in their climbing ability. *O. bridgesi* seems more specialized for woodland habitats than *O. degus* (e.g., Vásquez and Simonetti 1999); thus, there may be subtle adaptations for climbing in *O. bridgesi*.

Although our study did not focus on locomotion speed, we found a significant relationship between body size and mass-standardized speed of climbing. Climbing speeds of the 3 most active species (i.e., *T. elegans*, *P. darwini*, and *O. bridgesi*) did not differ from expected speeds from similar-sized mammals (Fig. 2b). Because previous estimates in terrestrial mammals have been generally assessed in horizontal locomotion, our results in vertical locomotion suggest that the force of gravity does not affect this feature in small mammals, at least in the range of speeds and body sizes studied.

The use of terrestrial microhabitats by small mammals in central Chile is affected by human disturbance, because anthropogenic activities increase the distance between shrubs (which are antipredatory refuges and food sources) and favor the presence of a dense layer of exotic herbs (which hamper

movement—Simonetti 1989). The low use of arboreal habitats by Chilean small mammals (Meserve 1981a) also could be explained by the high level of perturbation in central Chilean shrublands. A distinctive feature of the shrublands and forests of central Chile is the long-term human intervention (Aschman and Bahre 1977). Chilean forests and scrubs have been extensively exploited (CONAF et al. 1999). As a result of selective tree cutting and shrub removal, current vegetation is composed largely of stems of small diameter. An increase in the proportion of small-diameter trees could result in a reduction of suitable arboreal habitat, accounting for the low climbing activity depicted by small mammals. Because climbing ability appears affected by the diameter of vegetation stems, human-induced changes on landscape structure, as have occurred in central Chilean shrublands and forests, may have produced the currently observed low use of the arboreal stratum by small mammals.

RESUMEN

La habilidad trepadora es uno de los principales componentes que determinan el uso de hábitat vertical por parte de los mamíferos terrestres. Estudios previos sugieren que los pequeños mamíferos de Chile central exhiben bajas capacidades trepadoras. Sin embargo, estos estudios no han analizado la influencia del diámetro de los árboles sobre la capacidad trepadora de diferentes especies en hábitats naturales. A través de experimentos de laboratorio, estudiamos la habilidad trepadora de 4 especies de pequeños mamíferos de Chile central, incluyendo 2 roedores octodóntidos (*Octodon bridgesi* y *O. degus*), 1 roedor múrido (*Phyllotis darwini*), y 1 marsupial (*Thylamys elegans*), en situaciones con troncos de diámetros diferentes. Las especies exhibieron distintas capacidades trepadoras. El marsupial *T. elegans* mostró una eficiente habilidad trepadora independientemente del diámetro de los troncos. *P. darwini* y *O. bridgesi* fueron influenciados por el diámetro de los troncos, sin embargo, *P. darwini* trepó menos frecuentemente diámetros pequeños. *O. degus* mostró la menor habilidad trepadora entre las especies estudiadas.

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