

Population abundance, natural history, and habitat use by the arboreal marsupial *Dromiciops gliroides* in rural Chiloé Island, Chile

JUAN L. CELIS-DIEZ,* JENNIFER HETZ, PAULA A. MARÍN-VIAL, GONZALO FUSTER, PABLO NECOCHEA, RODRIGO A. VÁSQUEZ, FABIÁN M. JAKSIC, AND JUAN J. ARMESTO

Fundación Senda Darwin, Casilla 114-D, Santiago, Chile (JLC-D, JH, GF, PN, JJA)

Instituto de Ecología y Biodiversidad, Casilla 653, Santiago, Chile (JLC-D, PAM-V, RAV, JJA)

Center for Advanced Studies in Ecology & Biodiversity (CASEB), Departamento de Ecología, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile (JLC-D, FMJ, JJA)

Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile (RAV)

* Correspondent: jlcelis@gmail.com

Populations of the endemic and threatened marsupial *Dromiciops gliroides* were studied in logged and unlogged forest patches and shrublands in a rural area of northern Chiloé Island (42°S), Chile. We expected to find differences in abundance, with higher densities in unlogged, old-growth remnant forests. Individuals were livetrapped over 4 years (2005–2009) at the peak of their breeding (November) and nonbreeding (February) seasons. We estimated population densities using capture–mark–recapture procedures. Home range, diet (through fecal content), and health status (ectoparasite loads) were assessed for captured individuals. We estimated the length of the breeding season by the levels of reproductive hormones, whereas winter torpor was documented using artificial nest boxes. Population densities varied seasonally in accordance with breeding, with higher densities recorded during summer, and were similar in old-growth and in logged forests, but were considerable higher in forests than in shrublands. *D. gliroides* reproduced well in both unlogged and logged forests. Social torpor was documented for the 1st time and was fairly frequent (64%), especially among juveniles. Home ranges were 2 times larger for males than for females. We confirmed the omnivorous diet of *D. gliroides*, with predominant consumption of arthropods, and a higher consumption of fleshy fruits during summer. Habitat and animal age had significant effects on ectoparasite prevalence, with higher incidences among juveniles in logged forests. We conclude that *D. gliroides* is not a rare species in remnant forests in the rural landscape of Chiloé Island. This result is crucial for the assessment of its conservation status and offers clues for designing better conservation strategies for this living fossil in anthropogenic landscapes.

Key words: capture–recapture, communal nesting, countryside, old-growth forest, population density, selectively logged forest, temperate rain forest

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Dromiciops gliroides (Microbiotheriidae) is the only extant member of the order Microbiotheria (Reig 1955), showing stronger phylogenetic affinity with Australasian marsupials than with other South American marsupials (Palma and Spotorno 1999; Phillips et al. 2006; Springer et al. 1998). This relict species is endemic to temperate rain forests of southern South America (Hershkovitz 1999; Marshall 1978) with a distribution that extends along the Chilean Pacific Rim from Talca (approximately 35°50'S—Lobos et al. 2005) to Chiloé Island (43°21'S) and adjacent forested habitats of Neuquén, Río Negro, and Chubut provinces (42°32'S) in southwestern Argentina (Martin 2003, 2010).

From the late 1800s forest clearing has become intensive in southern South America (Armesto et al. 1998; Echeverría et al.

2007), including Chiloé Island (Echeverría et al. 2007; Jaña-Prado et al. 2006; Willson and Armesto 1996). In addition, degradation of remnant forests through logging, grazing by cattle, fire, and by altering forest structure and tree species composition affects populations of forest vertebrates (Cornelius 2007; Díaz et al. 2005; Jaña-Prado et al. 2006; Sieving et al. 1996). The rural landscape of Chiloé Island currently comprises a mosaic of remnant forest fragments (including old-growth and secondary-growth forests), wet shrublands, pastures, and agricultural fields (Aravena et al. 2002; Willson and Armesto 1996).



The massive loss of forested habitat, together with the limited geographical range of *D. gliroides*, may be leading to population decline over recent decades, as shown by inclusion of the species in the *IUCN Red List* 1st as “Vulnerable,” and recently modified to “Near Threatened” (Díaz and Teta 2008). In addition, according to the Chilean legislation, *D. gliroides* is classified as “inadequately known,” which means that its threatened status remains to be assessed (Ministerio Secretaría General de la Presidencia, 2007).

Despite the near-threatened condition of the species in the temperate forest region, the natural history, behavior, and population sizes of this arboreal marsupial remain poorly documented (Jiménez and Rageot 1979; Kelt and Martínez 1989; Marshall 1978; Meserve et al. 1988; Muñoz-Pedreros and Palma 2000; Patterson et al. 1989). There is a need for data on population sizes and habitat use in rural landscape mosaics, which presently prevail throughout its geographic range (Fontúrbel and Jiménez 2009; Fontúrbel et al. 2010; Rodríguez-Cabal et al. 2008; Smith-Ramírez et al. 2010). *D. gliroides* has been described as scansorial and nocturnal, most commonly found in relatively undisturbed evergreen, broad-leaved, temperate rain forests (Hershkovitz 1999), often dominated by southern beeches (*Nothofagus*: Nothofagaceae), with dense understory of native bamboos of the genus *Chusquea* (Patterson et al. 1990). *D. gliroides* nests and reproduces in cavities of snags, or inside dense bamboo understory, and undergoes hibernation during the cold-temperate winter or during food shortages, or both (Bozinovic et al. 2004; Mann 1978). According to Mann (1978), individuals reach sexual maturity in their 2nd year of life and are monestrous, seasonal breeders, producing 1 litter per year, with most births occurring in early spring (Muñoz-Pedreros et al. 2005). Based on summer analyses of stomach contents of an Andean population, the species was classified as primarily insectivorous (Meserve et al. 1988); however, recent studies highlight the role of this marsupial as a seed disperser of several fleshy-fruited trees and vines (Amico and Aizen 2000; Amico et al. 2009; Armesto et al. 1987; García et al. 2009; Rodríguez-Cabal et al. 2007), and have reported it as nest predator of eggs and juveniles of *Aphrastura spinicauda*, among other birds (Cornelius 2007; Jiménez and Rageot 1979).

Current knowledge of this endemic marsupial is greatly limited to populations inhabiting Andean forests; however, *D. gliroides* is widespread in lowland and coastal Chilean forests. Because of this fact coupled with the rapid change occurring in lowland areas due to human land use (Echeverría et al. 2007, 2008), we believe that a more in-depth knowledge of the ecology of *D. gliroides* is crucial. This knowledge can be gained by surveying populations of *D. gliroides* in remnant wild habitats within a rural landscape, and thus assessing its propensity to become threatened by the loss of forested habitat. We concentrated our study in the major remnant habitats within the lowland rural landscape where this species dwells, including patches of both old-growth forest (OGF) and selectively logged forest (SLF) and adjacent shrublands

developed after clearing of forests. We did not sample other rural habitats, such as pastures and agricultural fields, because previous intensive trapping efforts in Chiloé Island (E. Palma and M. Bustamante, Universidad Católica de Chile, pers. comm.), and surveys in mainland sites (Fontúrbel et al. 2010) yielded no evidence of the presence of *D. gliroides* in such habitats.

Our specific goals were to assess population sizes of *D. gliroides* in OGF and SLF patches and shrublands; to assess lifetime home range and diet of these animals in such habitats; to establish the periods of breeding and hibernation of *D. gliroides*; and to describe its ectoparasite loads. We use this information to discuss the conservation status of this marsupial in a rural habitat mosaic of Chiloé Island, which resembles the cover types over extensive areas of south-central Chile. Such knowledge is critical to develop science-based conservation guidelines, especially in lowland areas where OGFs are becoming more scarce (Armesto et al. 2009; Gutiérrez et al. 2009) and where limited land can be allocated to reserves.

MATERIALS AND METHODS

Study site.—Our study was conducted in a rural area of northeastern Chiloé Island, Chile (Fig. 1). The prevailing climate is wet-temperate with a strong oceanic influence (Di Castri and Hajek 1976). We studied 2 types of forest habitat: 2 patches of OGFs at Senda Darwin Biological Station and Caulín and 2 patches of SLFs at Llanquihue and Quilar. On the SLF site valuable timber trees had been removed by the landowner, with no defined silvicultural treatment (Cornelius 2007). We also looked for *D. gliroides* by setting traps in 2 dense secondary shrublands (ESSs) adjacent to forested areas within Senda Darwin (ESS1 and ESS2). Remnant OGF habitats had an age of at least 300 years based on tree-ring counts of dominant canopy trees, and had no visible signs of recent logging or fire (Aravena et al. 2002; Gutiérrez et al. 2004). OGF patches were characterized by a multilayered canopy (25 m high), with large emergent trees of *Nothofagus nitida* (Nothofagaceae), *Drimys winteri* (Winteraceae), and *Podocarpus nubigena* and *Saxegothaea conspicua* (both Podocarpaceae), plus a few individuals of *Eucryphia cordifolia* (Eucryphiaceae) and *Caldcluvia paniculata* (Cunoniaceae) in the lower canopy. Trees often were covered with vines and epiphytes such as ferns, mosses, and bromeliads (Muñoz et al. 2003). Significant amounts of dead biomass (snags and logs) were frequent within OGF stands (Carmona et al. 2002). The understory had a high density of shade-tolerant tree saplings, and dense thickets of 2- to 3-m-tall native bamboo (*Chusquea* spp.), which were especially dense within tree-fall gaps (Gutiérrez et al. 2004). SLF patches are frequent in the rural landscape due to the widespread practice of removing selected timber trees, and had a heterogeneous canopy, with areas of closed canopy and dense patches of juvenile trees (10–20 m tall) under felled tree gaps, predominantly shade-intolerant *D. winteri* and *N. nitida*. There were also few large trees, legacies from the predisturbance forest. In

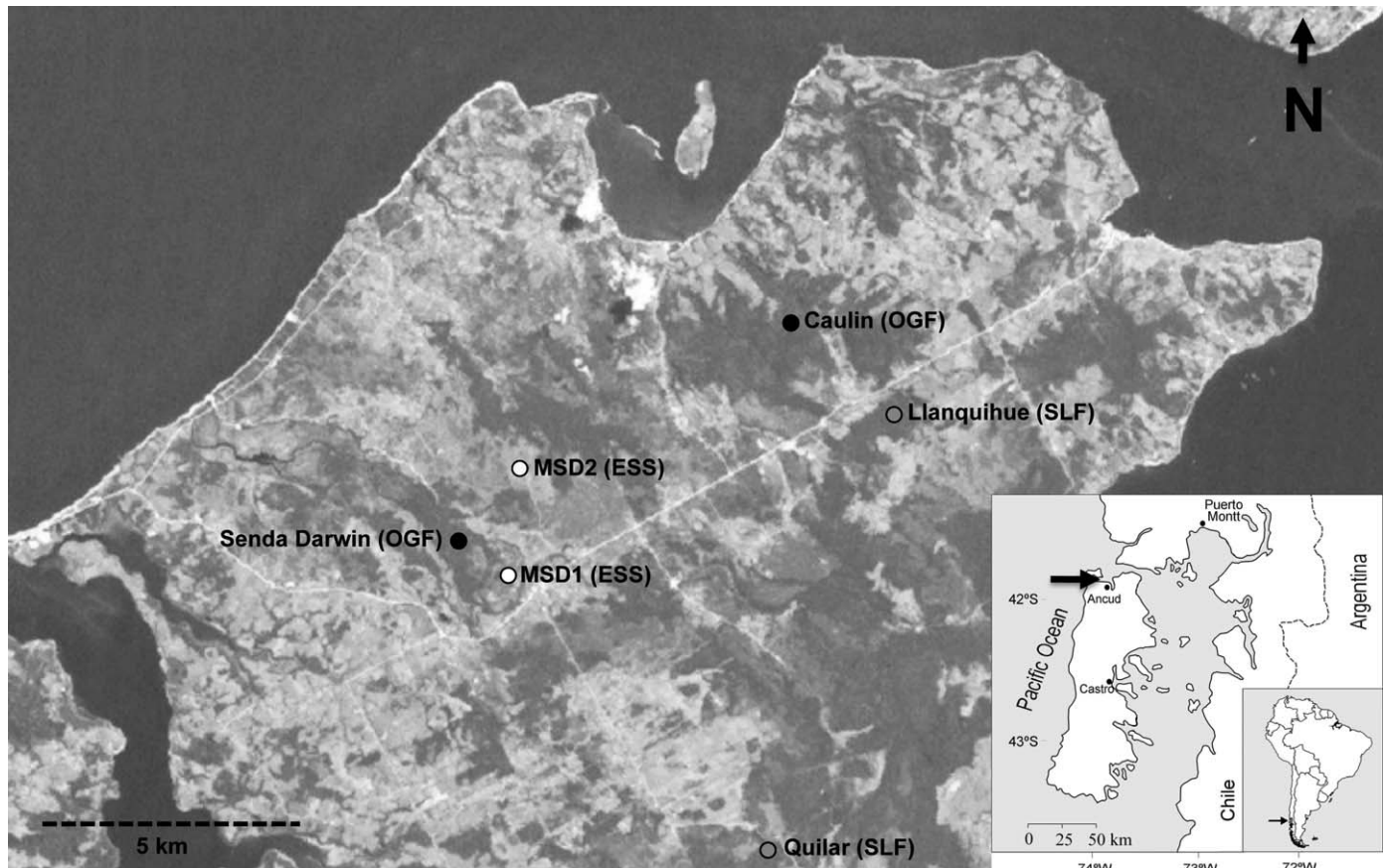


FIG. 1.—Landsat image of the rural landscape of northern Chiloé Island taken in 2001. Darker areas indicate wooded habitats; lighter areas indicate shrublands or pastures or both. Circles show sites where unlogged old-growth forests (OGFs), selectively logged forests (SLFs), and secondary shrublands (ESSs) were sampled.

the SLF areas dense bamboo cover was frequent, due to the extent of canopy opening, with a sparse presence of tree seedlings and saplings due to shading (Pérez et al. 2009). Following human-set fires to clear forest for farming and pastures, ESSs developed over abandoned land. The plant community was dominated by a 1- to 2-m-tall layer of *Baccharis magellanica* (Asteraceae) and a <1-m-tall fern layer of *Blechnum chilense* (Dicksoniaceae), with sparse cover of *Berberis darwinii* and *B. microphylla* (Berberidaceae—Díaz et al. 2005). Shrublands had sparse regeneration of shade-intolerant trees such as *D. winteri* and *N. nitida* (1–3 m tall).

Animal trapping and field data.—Live captures of *D. gliroides* were carried out in forest habitats from 2005 to 2009 (during both spring and summer) and in shrubland sites only until the summer of 2007. Trapping was conducted over 10 consecutive nights in midspring (November–December), after torpor and before the onset of the breeding season, and in late summer (February–March), after breeding ended. Trapping was not conducted in autumn or winter because animals are largely inactive and mortality risk of trapped animals increases due to harsh environmental conditions. We used small, custom-made, wire-mesh traps, similar to Tomahawk traps (26 × 13 × 13 cm—Fontúrbel and Jiménez 2009), because Sherman traps were ineffective for capturing this species

(Fontúrbel and Jiménez 2009; Kelt and Martínez 1989; Patterson et al. 1989). Traps baited with banana were placed on tree branches 1–2 m high, well above the dense understory of forest and shrublands, and arranged spatially in a web design, consisting of 12 radial lines, 100 m each, starting from a central point. Each trapping line had 12 stations; the first 4 were at 5-m intervals from the center (5, 10, 15, and 20 m), and the following 8 were at 10-m intervals (from 30 m up to 100 m). Thus, 144 traps were set in each habitat sampled per trapping night (see Parmenter et al. [2003] for trapping protocol). The area covered by each web was 3.46 ha. Each trap was checked daily between 0600 and 0800 h.

Following capture we classified animals according to sex, age, breeding status (based on scrotum size, pouch morphology, and mammary gland development), and body mass, using a Pesola spring balance (0.1 g precision; Pesola, Baar, Switzerland). Each animal was marked with a numbered 2-mm-long aluminum tag (tag 1005-1; National Band and Tag Co., Newport, Kentucky) and released at the capture site. Capture procedures followed guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) and complied with current Chilean laws (Servicio Agrícola y Ganadero, Chile, permit 1776, 15 April 2005, and permit 2605, 15 May 2009). The effect of habitat type (OGF, SLF,

and ESS), season, and sex on adult body mass were analyzed using a 3-way analysis of variance (ANOVA; STATISTICA—StatSoft, Inc. 2001), with log-transformed mass as the dependent variable, and habitat type, season, and sex as grouping factors. Shrublands were excluded from the analysis because of low sample sizes. To avoid pseudoreplication, only new, unmarked individuals were considered in this statistical analysis.

Population density.—We estimated population density using capture-mark-recapture procedures (Lebreton et al. 1992), using the software DENSITY (version 4.1, 2007—Efford et al. 2004). Data consisted of capture–recapture history obtained on 9 primary occasions. We used a full-likelihood closed population model (Otis et al. 1978), with a logit link function, and the Burnham and Overton (1979) jackknife estimator, which does not assume homogeneity of capture probabilities. This method was adopted because heterogeneity was likely to be present in the population, because many individuals were only caught once ($n = 269$ from a total of 504) and few were trapped 10 times or more ($n = 6$ of 504). In some trapping sessions, data were unsuitable for using the jackknife estimator. In those cases, we followed the procedure of Quental et al. (2001), which corrects data using the ratio jackknife estimate/minimum number known alive estimate as a correction factor to multiply the minimum number known alive estimates when only the latter are available (Quental et al. 2001). Relative population densities were estimated as the ratio between population abundance and the effective area sampled, calculated as the grid area plus a buffer area, with a width of one-half of the largest recapture distance for each site and season (Parmenter et al. 2003).

Home range.—We estimated lifetime home ranges (over 4 years) in both forest habitats for marked–recaptured individuals during the entire study period (2005–2009), using capture positions (x–y coordinates from trap data) and analyzed using Animal Movement SA ArcView GIS 3.2 version 2.04 beta (Hooge et al. 1999). Despite some limitations of mark–recapture data, this method is still widely used to estimate home range of small mammals (Ribble et al. 2002). For adult males and females trapped more than 3 times, the 95% minimum convex polygon was used as an estimate of home-range size (Agüero and Simonetti 1988). The minimum convex polygon method is more robust than other home-range estimators (e.g., radiotracking) when the number of fixes is low (Agüero and Simonetti 1988). The effect of habitat type and sex on home range was analyzed using 2-way ANOVA (STATISTICA—StatSoft, Inc. 2001), with log-transformed minimum convex polygon areas as the dependent variable, and habitat type and sex as grouping factors. In addition, we assessed the relationship between home range and adult body mass (for both sexes) using nonparametric Spearman rank correlation (STATISTICA—StatSoft, Inc. 2001).

Diet analysis.—We studied the diet of *D. gliroides* by examining animal and plant remains in fecal samples during the first 3 years of trapping. Feces were collected from inside or under traps in both forest fragments. Feces were placed in

labeled 1.5-ml Eppendorf vials with 70% alcohol (Pinheiro et al. 2002) and dried in the laboratory. Feces were later teased apart under a 40× binocular dissecting scope and remains of arthropods were determined to at least ordinal level with keys for exoskeleton fragments (Pinheiro et al. 2002). Seeds were identified to species using reference samples for plants in the forest and surrounding areas. Frequencies of occurrence were estimated by counting the number of each prey or seed type in feces and then dividing by the total number of prey or seeds identified, without correction for differential digestibility (Jiménez 2007). We compared variation in the proportions of items in the diet between forest habitats (OGF versus SLF) and seasons (spring versus summer) using the log-likelihood ratio (G -test—Zar 1999). For this comparison, we pooled data for juveniles and adults because of insufficient sample size ($n < 30$) in each category for a simultaneous analysis. In addition, we explored differences in prey content between juvenile and adult individuals only for summer, when a larger number of juveniles was available. Finally, we described the overall composition of the diet of *D. gliroides* in terms of items in feces using all samples regardless of season and habitat type. For graphical comparisons, dietary results by habitat type and season were simplified further by combining categories into 3 broad classes (Meserve et al. 1988): arthropods and vertebrates, vegetative plant material and fungi, and fruits and seeds. For illustration purposes, we used De Finetti diagrams (Meserve et al. 1988), where the trophic position of a group is represented as a single point whose distance to each endpoint of an equilateral triangle is proportional to the dietary composition.

Ectoparasites.—Ectoparasites were collected from unmarked individuals captured by livetrapping from spring 2005 to summer 2007. Ectoparasites were collected following visual examination (Marín-Vial et al. 2007). Samples were placed in labeled 1.5-ml Eppendorf vials with 70% alcohol and identified to taxon in the laboratory by using descriptive keys. We assessed prevalence and abundance according to definitions by Bush et al. (1997). To analyze the effect of habitat type, season, sex, and age of *D. gliroides* in ectoparasite prevalence, a generalized linear model selection with binomial distribution was conducted in R project software (version 2.7.1—R Development Core Team 2008). Mass of parasitized adults versus nonparasitized individuals was analyzed using 1-way ANOVA (STATISTICA—StatSoft, Inc. 2001). Proportions of individuals recaptured at least once, as a proxy of survival, were compared between infected and noninfected animals using the proportion test in R project software (version 2.7.1—R Development Core Team 2008).

Nest-box occupancy and torpor.—In winter 2002 and 2004, we installed artificial nest boxes in 2 OGFs (Senda Darwin and Caulín), as part of a parallel survey of cavity-nesting birds (see Moreno et al. 2005). All nest boxes ($n = 194$) were placed more than 500 m away from the trapping area and were fastened to tree trunks or branches about 150 cm above the ground. Nest-box dimensions were described in Moreno et al. (2005). To determine torpor behavior of *D. gliroides* we

TABLE 1.—Mean body mass ($g \pm 1 SE$) of *Dromiciops gliroides* captured during spring and summer from 2005 to 2009, and differences between sex and age classes in forest and shrubland habitats of Chiloé Island. OGF = old-growth forest; SLF = selectively logged forest; ESS = secondary shrubland; ND = no data.

Habitat type	Site	Season	Sex											
			Male						Female					
			Adult	SE	n	Juvenile	SE	n	Adult	SE	n	Juvenile	SE	n
OGF	Senda Darwin	Spring	26.5	0.70	35	ND	ND	ND	25.8	1.15	13	ND	ND	ND
		Summer	29.1	1.20	12	18.0	0.71	34	31.1	1.38	9	18.9	1.04	16
	Caulín	Spring	26.3	0.61	46	17.5	4.14	1	24.9	1.25	11	20.3	2.39	3
		Summer	29.6	1.57	7	17.0	0.93	20	31.2	1.38	9	17.3	1.15	13
SLF	Llanquihue	Spring	27.0	0.64	42	27.0	4.14	1	28.4	0.95	19	20.3	2.07	4
		Summer	29.0	1.31	10	18.8	0.57	53	31.4	1.00	17	19.5	0.74	31
	Quilar	Spring	28.1	0.90	21	ND	ND	ND	28.3	1.31	10	20.3	2.39	3
		Summer	28.1	1.46	8	19.9	0.80	27	37.4	1.57	7	18.4	1.69	6
ESS	ESS1	Spring	28.0	ND	1	ND	ND	ND	27.8	2.93	2	ND	ND	ND
		Summer	ND	ND	ND	22.5	ND	1	ND	ND	ND	ND	ND	ND
	ESS2	Spring	28.8	2.39	3	ND	ND	ND	26.3	2.39	3	ND	ND	ND
		Summer	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND

monitored nest boxes in the austral winter period (July–August) during 2005 and 2006, when birds did not use them (see Moreno et al. 2005). At the end of summer, nest boxes were cleaned, removing all nest material from the previous season's nest users. Individuals of *D. gliroides* found in boxes were measured and marked as those captured with the livetrapping method. To assess the effect of age and sex on the probability of communal compared to solitary nesting in the occupied boxes, data were analyzed using a generalized linear model selection with binomial distribution in R software (version 2.7.1, 2008).

Reproduction.—We assessed sexual maturity and breeding activity by measuring the blood levels of testosterone in males; progesterone levels in females were measured as indicators of follicular and corpora lutea development. Blood samples (100 μ l) were obtained from anesthetized (isoflurane inhalation in 0.5- to 10-ml volume) adults or juveniles placed in a closed chamber for 20–30 s. Blood was extracted from the infraorbital sinus with heparinized hematocrit capillary tubes (van Herck et al. 2001). Samples were centrifuged and the plasma analyzed. Following recovery from anesthesia, individuals were released at the site of capture. Because of the small amount of plasma, individuals of similar age captured at different sites were pooled. Plasma testosterone and progesterone concentrations were analyzed with solid-phase I^{125} radioimmunoassay, using a total testosterone or progesterone Siemens kit (Siemens Medical Solutions Diagnostics, Los Angeles, California). Spearman rank correlation was used to test the relationship between reproductive hormones and secondary sexual traits, such as testicular size. Testicular volume was calculated with the following formula: $V = 0.524 \times L \times W^2$, where V = volume (cm^3), L = length (cm), and W = width (cm) (Wildt 1996). Because males have a shallow, nonpendulous scrotum, measurement of scrotal circumference is not possible. We quantified the proportion of reproductive females at all sites and counted in-pouch young throughout the study period. To confirm that *D. gliroides* only becomes

sexually active during the 2nd year of life (Mann 1978), we recorded the age at maturity of juvenile individuals based on morphological changes (i.e., testicular size and pouch development), with previously recorded body mass information.

RESULTS

Population size of *Dromiciops*.—From spring 2005 to summer 2009, we livetrapped 504 different individuals for a total of 1,065 captures in all habitats and sites. A total of 119 and 111 animals were trapped at Senda Darwin and Caulín OGFs, respectively, 181 and 83 at Llanquihue and Quilar SLFs, respectively, and 4 and 6 in shrublands ESS1 and ESS2, respectively (Appendix I). Only 2 juveniles captured in shrubland ESS2 were trapped again as adults in the forest at Senda Darwin. On average, each animal was recaptured 2.1 times ($SE = 0.08$, $n = 504$; 3.4 times, $SE = 0.14$, $n = 235$, for recaptured individuals). Accidental death due to trapping was 1.8% (19 of 1,065 captures), and was slightly higher during spring ($\chi^2_1 = 3.31$, $P = 0.06$; Table 1).

Population densities varied seasonally each year in all habitats (Fig. 2). In both forested habitat types (logged and unlogged), we observed higher densities in the austral summer (February), which is the period of juvenile recruitment. Even though densities were much lower in shrublands, we observed an inverse trend with higher densities in spring, when mating took place (Fig. 2). Population densities in forests were as high as 20 individuals/ha, but in spring were occasionally lower than 2 individuals/ha. In shrublands, densities were always lower than 3 individuals/ha. For all seasons, years, and sites, OGFs had a mean of 5.91 individuals/ha ($SE = 0.8$); SLFs a mean of 8.21 individuals/ha ($SE = 1.5$), and shrublands a mean of 0.53 individuals/ha ($SE = 0.3$).

We found no significant differences in adult body mass among habitat types ($F_{1,268} = 3.75$, $P > 0.06$; Table 1). However, adult mass differed significantly between seasons

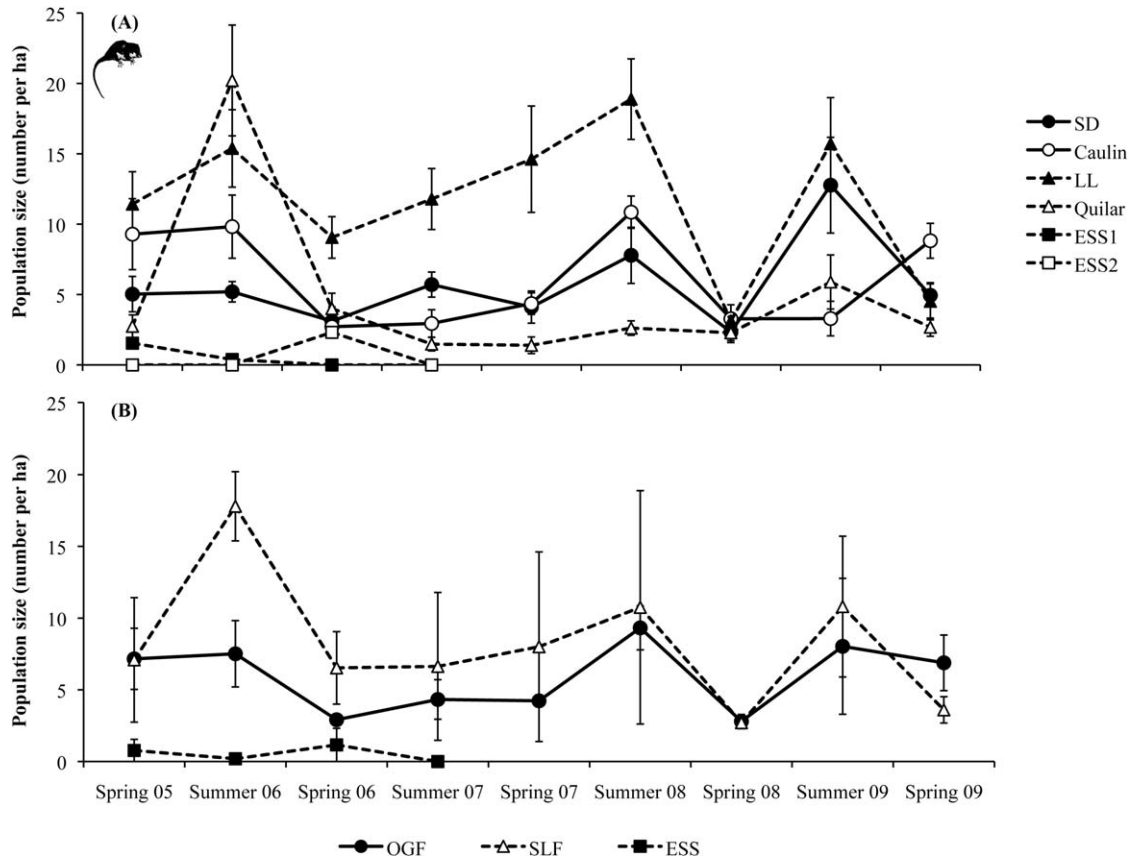


FIG. 2.—Population density of *Dromiciops gliroides* (mean ± 1 SE) in the study sites of Chiloé Island. A) Densities in different habitat types and sites: SD = Senda Darwin old-growth (OG) forest; Caulín = Caulín OG forest; LL = Llanquihue selectively logged (SL) forest; Quilar = Quilar SL forest; ESS1 = Senda Darwin shrubland 1; ESS2 = Senda Darwin shrubland 2. B) Densities in different habitat types: OGF = old-growth forest; SLF = selectively logged forest; and ESS = shrubland.

within a year ($F_{1,268} = 28.71$, $P < 0.01$; Table 2) and between sexes ($F_{1,268} = 5.43$, $P = 0.02$; Table 1), with lower body mass during spring, when individuals were recovering from torpor ($\bar{X} \pm SE = 26.9 \pm 0.4$ g, $n = 197$), and higher body mass at the end of summer (30.5 ± 0.6 g, $n = 79$). On the other hand, females (29.5 ± 0.5 g, $n = 95$) were heavier than males (27.9 ± 0.46 g, $n = 181$). In addition, the interaction between seasons and sex of the animals was statistically significant ($F_{1,268} = 5.52$, $P < 0.02$), because body mass of females was higher in summer than in spring and higher than that of males in both seasons.

Home range.—Of a total of 287 adult individuals trapped overall, 80 adults were captured 3 or more times during the study period (Table 2); this enabled reliable estimation of lifetime home ranges. Because no individuals were captured more than 3 times in shrublands, we did not estimate home range in this habitat. Home-range size of the 80 individuals from forest habitats ranged from 0.12 to 0.35 ha (Table 2) and was not statistically different between OGFs and SLFs, although it was significantly larger for males than for females (Table 2). Body mass and home range were uncorrelated ($r_s = 0.12$, $P = 0.29$, $n = 80$).

Diet.—We obtained a total of 146 fecal samples from animals captured in forested habitats (OGF and SLF) in 2

seasons of the year (spring and summer), from 2005 to 2008. Only 1 fecal sample was obtained from a shrubland animal, and hence we excluded this habitat from further analysis. Arthropods were the most frequent item in feces, representing more than 40% in both forest habitats and seasons. Significant differences were found, however, in the relative proportions of all food items between forest habitats and seasons ($G_6 = 13.95$, $P < 0.03$; Fig. 3). The proportion of arthropods was higher in SLFs than in OGFs in both spring and summer, whereas the proportion of seeds in feces was the reverse between forests, a difference that increased in summer (Fig. 3). No differences were found between juveniles and adults in the proportion of food items in summer samples ($G_2 = 4.74$, $P < 0.09$). In OGF, adults showed a higher proportion of seeds in summer than in spring, and higher than adults from SLFs.

Among arthropods, Coleoptera and Orthoptera were the most frequent items, with 43% and 25% of occurrence, respectively (Table 3). Lepidoptera (mostly larvae and pupae), Hymenoptera, and Hemiptera also were found at lower frequencies (Table 3). Two spring fecal samples contained bird bones and feathers. Seeds of 12 plant species were identified in the feces, including forest epiphytes, vines, and shrubs. *Tristerix corymbosus*, *Gaultheria insana*, and

TABLE 2.—Mean home-range size ($\text{ha} \pm 1 \text{ SE}$) for adult males and females of the marsupial *Dromiciops gliroides* in forested habitats of Chiloé Island. OGF = old-growth forest ($n = 2$); SLF = selectively logged forest ($n = 2$).

Habitat type	Home range					
	Males	SE	<i>n</i>	Females	SE	<i>n</i>
OGF	0.26	0.04	26	0.14	0.05	18
SLF	0.23	0.05	20	0.15	0.05	16

Luzuriaga polyphylla were represented in 45%, 19%, and 8% of the feces (Table 3). Considering the total number of seeds in feces, *T. corymbosus*, *Myrteola nummularia*, and *Gaultheria* were the most frequently consumed fruits (Table 3).

Ectoparasites.—Four different taxa of ectoparasites were identified infesting *D. gliroides*: ticks, fleas, mites, and leeches. Among ticks, we detected *Ixodes neuquenensis*, and among fleas, *Chiliopsylla allophyla* and *Plocopsylla diana*. A total of 102 (55%) of 185 individuals sampled over all sites were infested with some or all of these ectoparasites (Table 4). Excluding shrublands, a generalized linear model that included forest type (OGFs versus SLFs), season (spring versus summer), and animal age best explained the prevalence of ectoparasites (Akaike information criterion = 236.91, residual deviation = 220.91). Prevalence of ectoparasites, particularly fleas, was statistically different between forest habitats (generalized linear model $W = 5.33$, $P < 0.039$), with higher values in SLFs (62.73%) than in OGFs (44.78%), and higher among juveniles (62.1%) than adults (50.9%). In addition, tick prevalence was higher in spring (33.3%) than summer (15.7%). No significant differences were found between sexes (generalized linear model $W = 5.33$, $P > 0.05$). Body mass of infested adults was not significantly different from that of noninfested individuals ($F_{1,115} = 2.24$, $P = 0.14$). Further, the recapture rate of infested adults did not

differ from that of noninfested individuals ($\chi^2_1 = 0.04$, $P = 0.8$).

Nest-box occupancy and torpor.—Of 194 nest boxes, 28 were used by *D. gliroides* as denning sites during 2005 in the 2 OGFs: 23 nest boxes were occupied in Senda Darwin and 5 in Caulín. Similar levels of occupancy were observed in the winter of 2006, with 26 and 6 boxes used in Senda Darwin and Caulín, respectively. Nests inside boxes were spherical, with a single entrance, built with plant materials from epiphytes, vines, and understory vegetation (*Chusquea* leaves and *Hymenophyllum* ferns), and lined with ferns or mosses.

During the winters of 2005 and 2006, 77 and 62 torpid animals, respectively, were found nesting inside boxes. Overall nest occupancy was 17% ($n = 388$ boxes). Mean number of animals per nest was 2.3 ± 0.2 (1 SE; range, 1–9) and 64% of the boxes occupied were communal nests, a proportion significantly greater than that expected by random ($\chi^2_1 = 9.03$, $P = 0.002$). Age had significant effects on communal nesting (Fisher's exact test, $d.f. = 1$, $P = 0.05$; Table 5): juveniles were found solitary in 17% and communally in 38% of the nests, whereas adults were solitary in 83% of nests. Contrary to expectations, neither sex (Fisher's exact test, $d.f. = 1$, $P = 0.34$) nor body mass (3-way ANOVA, $F_{1,139} = 0.0049$, $P = 0.94$) influenced communal nesting.

Reproduction.—A total of 44 blood samples were obtained from adult males captured throughout the study period. Plasma testosterone levels had a single annual peak during spring (November), followed by a steady decline toward winter (July), when males entered torpor (Fig. 4). Levels of plasma testosterone were significantly correlated with testicular volume ($r_s = 0.12$, $n = 36$, $P < 0.001$), and associated with mating period.

A total of 21 blood samples were obtained from females (19 adults and 2 subadults). Plasma progesterone concentration showed an increase during spring (November) lasting until summer (February), followed by a reduction toward winter (August), when females entered torpor (Fig. 4). During spring, subadult females had lower progesterone concentrations than mature individuals (22.3 ng/ml versus 73.0 ng/ml). Overall, we recorded 27 adult females with their young still attached to the teats within the marsupium, with a mean litter size of 2.3 ± 0.17 (1 SE). Two pregnant females also were trapped in the previous reproductive season (November). Moreover, in summer (post-reproduction) of 2009, 6 females were trapped with young still attached to the teats within the marsupium ($\bar{X} \pm \text{SE}$: 2.2 ± 0.17). Three of these females were found breeding in the previous (reproductive) trapping session, suggesting the occurrence of a 2nd reproductive event. In spring of 2005, we observed parturition and migration of 2 immature embryos into the pouch of a captured animal. This female was retrapped 3 days later with the young inside the pouch.

Based on hormonal profiles or primary sexual characters, or both, we propose that subadult individuals become sexually mature when they reach a body mass of 25.2 ± 0.47 g ($\bar{X} \pm 1 \text{ SE}$; $n = 21$) for males and 27.0 ± 0.98 g ($n = 8$) for females, at an approximate age of 10 months.

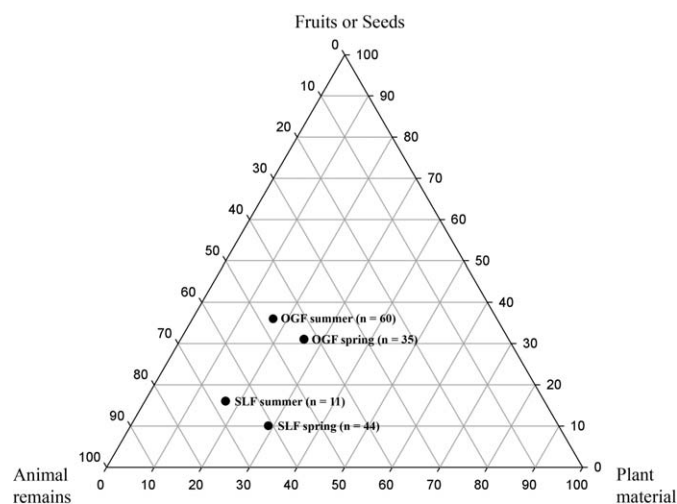


FIG. 3.—Trophic niche of *Dromiciops gliroides* in forest habitats of Chiloé Island during spring and summer. OGF = old-growth forest; SLF = selectively logged forest.

TABLE 3.—Frequency of occurrence (FO%) of arthropods in feces of *Dromiciops gliroides* and relative abundance (%) of seeds, and total number of seeds of 12 fleshy-fruited forest species found in feces ($n = 146$) of *D. gliroides* captured in Chiloé Island forests and shrublands. Known dispersal agent is from Armesto and Rozzi (1989).

	Growth form	FO%	Abundance (%)	No. seeds	Known dispersal agent
Plant species ($n = 359$)					
<i>Tristerix corymbosus</i>	Hemiparasite	43.08	25.07	90	<i>D. gliroides</i> , birds
<i>Gaultheria insana</i>	Shrub	18.46	13.93	50	Unknown
<i>Gaultheria mucronata</i>	Shrub	10.77	15.32	55	Birds
<i>Luzuriaga polyphylla</i>	Vine	7.69	4.46	16	Unknown
<i>Sarmienta repens</i>	Epiphyte	6.15	5.85	21	Unknown
<i>Mitraria coccinea</i>	Epiphyte	3.08	3.34	12	Unknown
<i>Griselinia racemosa</i>	Vine	3.08	5.29	19	Unknown
<i>Asteranthera ovata</i>	Epiphyte	1.54	2.23	8	Unknown
<i>Raukaua laetevirens</i>	Hemiepiphyte	1.54	1.67	6	Unknown
<i>Myrteola numularia</i>	Shrub	1.54	22.28	80	Birds
<i>Philesia magellanica</i>	Shrub, vine	1.54	0.28	1	Birds
<i>Amomyrtus luma</i>	Tree	1.54	0.28	1	Birds
Arthropod order ($n = 126$)					
Coleoptera		42.9			
Orthoptera		24.6			
Lepidoptera		11.9			
Hymenoptera		2.4			
Hemiptera		1.6			
Aranea		0.8			
Acari		1.6			
Unidentified		14.3			

DISCUSSION

The presence of the arboreal marsupial *D. gliroides* was recorded in all 3 wild habitat types remaining in the rural landscape of Chiloé Island, but population densities were considerably higher in both forested habitats (logged and unlogged) than in ESS.

We found high and similar population densities in unlogged OGFs and forests subjected to logging, despite previous reports that considered *D. gliroides* a rare species of forest-dwelling mammal (Kelt 2006) that was largely restricted to OGF habitats or large forest fragments (Fontúrbel et al. 2010; Hershkovitz 1999; Kelt and Martínez 1989; Mann 1978;

TABLE 4.—Number of adult and juvenile *Dromiciops gliroides* with and without ectoparasites in different habitat types of rural Chiloé Island. OGF = old-growth forest; SLF = selectively logged forest; ESS = secondary shrubland.

Habitat type	Sites	With ectoparasites		Without ectoparasites		Total
		Adults	Juveniles	Adults	Juveniles	
OGF	Senda Darwin	10	6	10	7	67
	Caulín	10	4	15	5	
	Total OGF	20	10	25	12	
SLF	Quilar	11	11	7	4	110
	Llanquihue	27	20	21	9	
	Total SLF	38	31	28	13	
ESS	ESS1	0	1	2	0	8
	ESS2	2	0	3	0	
	Total ESS	2	1	5	0	
	Total all sites	60	42	58	25	

Patterson et al. 1989; Rodríguez-Cabal et al. 2007; Saavedra and Simonetti 2005). This finding is in line with recent reports for Andean OGFs (at Las Cascadas in Osorno, Chile), where densities of *D. gliroides* were similar to those on Chiloé Island (Fontúrbel et al. 2010), and considerably higher than densities of other Neotropical marsupials, which seldom exceed 1 individual/ha (Quental et al. 2001; Robinson and Redford 1986), especially for threatened species inhabiting habitats supporting biodiversity hot spots (see Fonseca et al. 2003).

Densities and home ranges of the marsupial in OGFs and SLFs of Chiloé were similar, indicating that changes in habitat structure and resources due to selective logging did not translate into population consequences for this species. In addition, adult male home ranges in both types of forests were larger in spring, when mating occurs, which could indicate a polygynous reproductive behavior (Belcher and Darrant 2004; Kraaijeveld-Smit et al. 2002).

In both forest types in Chiloé, higher densities were recorded in summer, associated with offspring weaning period and more favorable weather. Nevertheless, in spring 2008 we recorded a drastic reduction in population size of *D. gliroides* (Fig. 2), probably related to a severe summer drought in 2007 that lowered resource availability (150 mm of rainfall versus a mean summer precipitation of 290 mm in the last 10 years).

As with many other marsupials, *D. gliroides* is omnivorous. Arthropods and fruits were common items in its diet, pointing out that it might be more frugivorous, and less strictly insectivorous, than previously thought (Meserve et al. 1988). In line with other Neotropical marsupials, where food specialization is not the rule (Astúa de Moraes et al. 2003),

TABLE 5.—Mean body mass ($g \pm 1 SE$) and number of individuals of *Dromiciops gliroides* found inside artificial nest boxes in Chiloé Island. ND = data not available.

Mass	Solitary				Communal			
	Males		Females		Males		Females	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
$\bar{X}$	34.7	28.0	32.2	27.7	32.4	26.9	34.6	27.0
SE	1.82	ND	1.55	0.44	0.85	0.75	1.04	0.54
n	12	1	5	3	51	16	24	27

a higher proportion of insects in spring could be associated with a need for protein-rich diets for mating, whereas a more frugivorous diet at the end of summer could be related to higher sugar and fat accumulation in preparation for the winter season (Astúa de Moraes et al. 2003).

Dromiciops gliroides consumed a diverse array of fleshy fruits, particularly in OGFs, where it disperses seeds of several epiphytes and vines (Amico et al. 2009; Armesto et al. 1987; García et al. 2009; Rodríguez-Cabal et al. 2007). Among mammals, *D. gliroides* was responsible for the dispersal of up to 24% of all fleshy-fruited species in Chiloé forests (J. L. Celis-Diez, pers. obs.). Because in rain forests of Chiloé Island about 70% of the woody flora bears fleshy fruits (Armesto and Rozzi 1989), animal frugivores such as *D. gliroides* should facilitate the processes of seed dispersal and forest regeneration. In this context, it was interesting to find seeds of the 3 species of epiphytic Gesneriaceae in feces of *D. gliroides*. Because of its arboreal behavior, this marsupial could facilitate regeneration of fleshy-fruited epiphytes in the tree canopy of south-temperate rain forests (Salinas 2008). Frugivory by *D. gliroides* increases in summer, when many fleshy-fruited species produce ripe fruit (Smith-Ramírez and Armesto 1994). Arthropods are a particularly important resource during spring–summer (Díaz 2008), especially in the months following hibernation. It is possible that, after

logging opens the forest canopy (Pérez et al. 2009), followed by an increased cover of bamboo that sustains a greater abundance of arthropods (Reid et al. 2004), this may account for the higher proportion of arthropods found in the diet of *D. gliroides* in logged forests.

Reproduction in marsupials is usually cued to seasonal temperature and resource abundance (Quental et al. 2001; Tyndale-Biscoe and Renfree 1987), because the end of lactation and weaning are critical periods for offspring survival (Lee and Cockburn 1985). Accordingly, higher temperatures on Chiloé Island during spring–summer and food availability, when arthropods and fruits are in peak abundance (Díaz 2008; Smith-Ramírez and Armesto 1994), favor synchronous reproduction with maximum sex hormone levels associated with the development of secondary sexual traits. Nevertheless, there was a delay of 1 month in the female reproductive cycle in comparison to mainland populations (Muñoz-Pedreros et al. 2005).

A 2nd reproductive event—or a delayed one—could sustain high hormone levels during summer in Chiloé forests. This event is contrary to previous reports stating that *D. gliroides* breeds only in spring (Mann 1978; Muñoz-Pedreros et al. 2005). In contrast to those reports, examination of our data on sex hormone levels and secondary sexual traits (testicular size in males and pouch development in females) suggests that

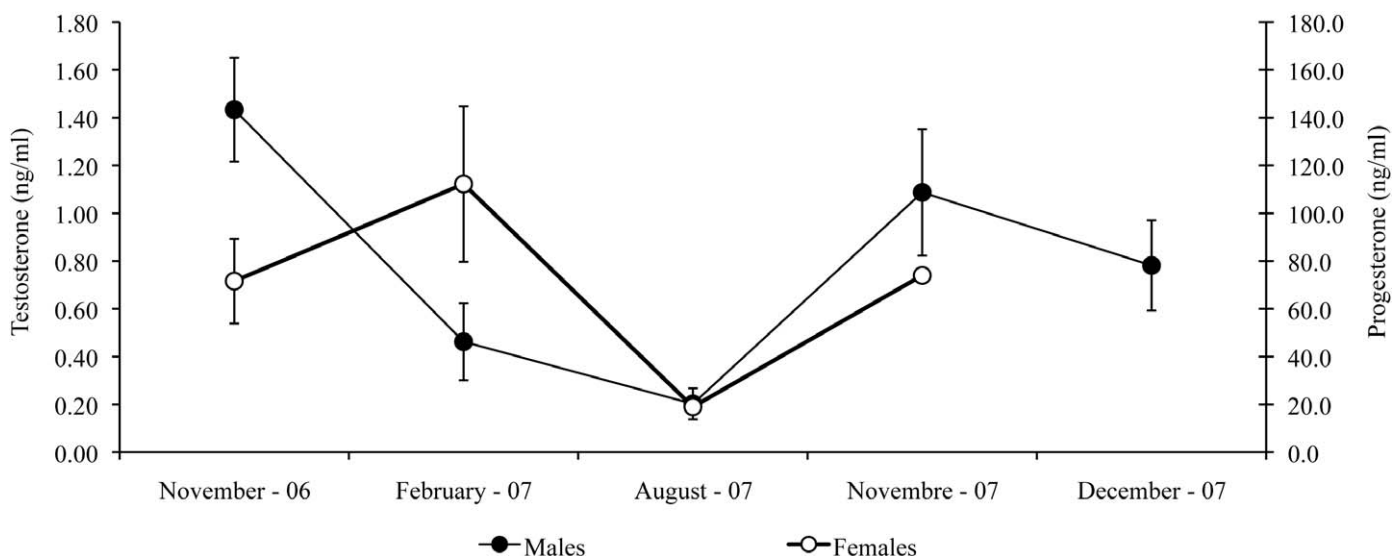


FIG. 4.—Mean ($\pm 1 SE$) plasma testosterone and progesterone concentration (ng/ml) in blood samples from 44 males (black) and 19 females (white) of *Dromiciops gliroides* from pooled data for all forest sites in Chiloé Island.

individuals born in midspring (November) could reach sexual maturity in the next breeding season, if they reach a minimum body mass (25 g in males and 27 g in females).

Mann (1978) reported torpor of solitary individuals in *D. gliroides*, and a physiological study by Bozinovic et al. (2004) and Cortés et al. (2009) reported the 1st incidence of hibernation in *D. gliroides*. Nesting and torpor are common in Australasian marsupials that use tree hollows, and appear to be a way to enhance winter survival (Bozinovic et al. 2004; Canals et al. 1998; Geiser 1994). The number of animals nesting in the same place shows wide variation among marsupials (Lee and Cockburn 1985; Lindenmayer 1997). We report here, for the 1st time, the occurrence of communal nesting for a South American arboreal marsupial.

Communal nesting or huddling (i.e., social grouping for thermoregulatory benefits) appears as an efficient response to low temperature with important consequences in energy saving and allocation of energy, which in turn affect survival and individual fitness (Bozinovic et al. 1988; Cortés et al. 2009; Lee and Cockburn 1985; Rhind 2003). In our case, it is unknown whether huddling is composed of genetically related animals. Although we have no data to assess this possibility, we infer that groups might be genetically unrelated, because we found groups with 5 or more juveniles, and a single litter never exceeds 4 animals. Effectiveness of huddling is influenced by ontogeny and group size, because a larger number of animals induces metabolic depression without hypothermia and is mainly attributed to the reduced surface-to-volume of the huddling group (Canals and Bozinovic 2011; Canals et al. 1998). Accordingly, communal nests in rural populations of *D. gliroides* often were composed of juveniles with lower body mass, as opposed to solitary nests, which were mostly occupied by adults. Communal nesting also reduces time needed for nest construction, because 1 individual can use more than 1 nest already present within its home range (Lee and Cockburn 1985). We observed winter movement of animals among nests between torpor events; however, further analysis is needed to determine the relevance of communal nesting to sociality.

We are certain that *D. gliroides* builds nests inside artificial nest boxes. Based on 6 years of monitoring, only 2 species of birds nested in these nest boxes during spring on Chiloé Island (Moreno et al. 2005; S. Ippi, Pontificia Universidad Católica de Chile, pers. comm.): *A. spinicauda* (Furnariidae) and *Troglodytes musculus* (Troglodytidae). Both constructed open-cup nests made of twigs inside the boxes (see Moreno et al. [2005] for a complete nest description), unlike the nesting material used by *D. gliroides*, which contained *Chusquea* leaves, mosses, and *Hymenophyllum* ferns. In addition, nests of *D. gliroides* were occasionally built on top of old nests of *A. spinicauda*. Thus, rather than using abandoned bird's nests, *Dromiciops* seems to prefer to build a new one.

Although higher parasitism has generally been attributed to greater stress and lower habitat quality (Daszak and Cunningham 1999), greater prevalence (55%) of ectoparasites in populations of *D. gliroides* in SLFs as compared to OGFs did

not have noticeable effects on the animals' health. This conclusion is inferred from our information on body mass, recapture rate, and population density. *Ixodes neuquenensis* is the only tick reported from *D. gliroides* in Chiloé (Marín-Vial et al. 2007). Unlike the findings of Guglielmone et al. (2004) in Argentina, no difference was found in prevalence of *I. neuquenensis* between sexes for Chiloé forests. This result could explain the equal incidence in both sexes of a newly described and species-specific hemoparasite carried by *I. neuquenensis* (see Merino et al. 2009). In addition, the 2 species of fleas recorded on *D. gliroides* were shared with other temperate rain-forest rodents (Alarcón 2003).

Conservation implications.—New World ecosystems, considered as global biodiversity hot spots, hold 17 (73.9%) of the threatened species of world marsupials identified in the *IUCN Red List* (Fonseca et al. 2003); including 2 Chilean rain-forest species, *D. gliroides* and *Rhyncholestes raphanurus* (Paucituberculata). Taking into account that the estimated rate of forest loss per year on Chiloé Island is about 1.1% (Echeverría et al. 2007), and assuming that the proportion of SLFs will tend to increase in the next decades (Armesto et al. 2010; Echeverría et al. 2007, 2008; Jaña-Prado et al. 2006), our estimates of population density of *D. gliroides* constitute an important baseline of information. Because this arboreal marsupial is negatively affected by forest fragmentation (Rodríguez-Cabal et al. 2007), and open pastures are severe barriers preventing the movement of animals between forest fragments (Fontúrbel et al. 2010; Rodríguez-Cabal et al. 2007), ESSs and managed remnant forests are key habitats that could facilitate the movement of this species across rural landscapes. SLF patches provide suitable habitat for *D. gliroides* in areas where OGF cover is declining. In addition, shrublands that are continuous with remnant forest habitat could facilitate animal dispersal, even though shrublands do not seem to provide conditions for residency. Recent studies of forest-dwelling mammals have shown that matrix "permeability" plays a critical role in maintaining biodiversity in fragmented landscapes (Umetsu and Pardini 2007). Identification of matrix quality parameters to enhance habitat connectivity and conservation of biodiversity are critical issues for managing rural landscapes (Castellón and Sieving 2006, 2007), especially where limited land can be allocated to new reserves (Daily et al. 2003), or where reserves are insufficient (Tognelli et al. 2008). We show here that populations of *Dromiciops* can persist in managed landscapes using habitats such as shrublands and logged forests.

Some authors suggest that the decline of large, old-canopy trees as a result of logging may affect population abundance and winter survival of arboreal mammals (Laurance and Laurance 1996; Lindenmayer et al. 1997) and of specialist, cavity-nesting forest birds (Cornelius 2007; Díaz et al. 2005). This is also the case of the arboreal marsupial *Hemibelideus lemuroides* in the Australian tropical forest (Laurance and Laurance 1996) and of the bird *A. spinicauda* in Chilean temperate rain forest (Cornelius 2007). However, we found no evidence of a reduction in population density of *Dromiciops* in

forests where large canopy trees have been selectively removed. Hence, small-scale logging, commonly practiced in rural forest patches, has no effect on population sizes and nesting of *D. gliroides*; this occurrence is in part probably attributable to the increase in native bamboo cover in this ecosystem.

According to our results in rural areas and recent data derived from fragmented landscapes in the Chilean mainland (Fontúrbel et al. 2010; Smith-Ramírez et al. 2010), we propose that *D. gliroides* is not a rare species in this anthropogenic landscape. *Dromiciops* is indeed a unique representative of an ancient phylogenetic lineage, and the species should be included in national legislation as an example of biological patrimony. We believe the recent international reclassification of the conservation status to “Near Threatened” (Díaz and Teta 2008) seems appropriate. However, in both Chile and Argentina, the species continues to be classified by the conservation agencies as “insufficiently known” and “vulnerable” in each country, respectively. In sum, knowledge of the population density, reproductive behavior, and food habits of *D. gliroides* and other forest-dwelling species that use remnant forest patches in human-dominated rural environments (Castellón and Sieving 2006, 2007; Fontúrbel et al. 2010; Smith-Ramírez et al. 2010) offers important clues for designing effective conservation measures in changing landscapes where humans also live.

RESUMEN

Poblaciones del marsupial *Dromiciops gliroides* fueron monitoreadas durante 4 años (2005–2009) en hábitat de bosque antiguo, bosques con tala selectiva y matorrales en la zona rural del norte de la Isla de Chiloé (42°S), Chile. Las capturas se realizaron en el período reproductivo (noviembre) y no-reproductivo (febrero). En base a los individuos capturados se estimó el ámbito de hogar, la dieta (por medio de análisis de fecas), el estado sanitario (carga parasitaria) y la densidad poblacional utilizando el método captura-marcaje-recaptura. El período reproductivo se estimó cuantificando la concentración de hormonas reproductivas en la sangre y se caracterizó el sopor invernal mediante el uso de cajas nidos artificiales. En todos los sitios, la densidad poblacional varió estacionalmente, con mayores densidades en verano y sin diferencias significativas entre bosques antiguos y con tala selectiva. Sin embargo estos valores fueron significativamente mayores que la densidad estimada en los matorrales. La nidificación comunal fue muy frecuente durante el sopor invernal (64% de los casos), especialmente entre individuos juveniles. Los machos registraron un ámbito de hogar dos veces mayor que el de las hembras. Se documentó una dieta omnívora con una alta proporción de artrópodos y frutos en verano. Tanto el tipo de hábitat como la edad influyeron en la carga parasitaria, con una mayor incidencia en juveniles y en bosques con tala selectiva. Futuros estudios sobre la dinámica poblacional de esta especie son cruciales para entender su viabilidad en los remanentes de bosques nativos en ambientes

rurales. En la zona rural del norte de Chiloé, tanto los bosques antiguos como aquellos con tala selectiva constituyen hábitat adecuado para *Dromiciops gliroides*.

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APPENDIX I

Estimated population parameters of the arboreal marsupial *Dromiciops gliroides* in different habitat types of rural Chiloé Island. OGF = old-growth forest; SLF = selectively logged forest; ESS = secondary shrubland; MNKA = minimum number of animals known alive; MMDM = mean maximum distance of movement in meters; ND = data not available. Population size was estimated with the Burnham and Overton (1979) jackknife estimator except for the season denoted by an asterisk (*), when the MNKA method was used (see "Materials and Methods").

Date	OGF					SLF					ESS						
	Senda Darwin			Caulín		Llanquihue		Quilár		ESS1		ESS2					
	MNKA	Population size ($\pm$ SE)	MMDM	MNKA	Population size ($\pm$ SE)	MMDM	MNKA	Population size ($\pm$ SE)	MMDM	MNKA	Population size ($\pm$ SE)	MMDM	MNKA	Population size ($\pm$ SE)	MMDM		
November 2005	16	29.1 (7.29)	71.4	16	46.7 (12.75)	53.7	25	50.7 (10.22)	37.77	10	17.6 (5.27)	87.72	4	7.7 (ND)*	51.8	0	ND
February 2006	22	27.7 (3.86)	60.4	22	43.7 (9.97)	38.1	32	66.1 (11.82)	33.85	28	101.3 (19.71)	52.6	1	1.9 (ND)*	51.8	0	ND
November 2006	8	12.8 (4.15)	28.5	10	14.2 (3.05)	58.5	30	47.5 (7.74)	58.38	11	22.6 (6.17)	68.1	0	ND	ND	6	11.5 (ND)*
February 2007	19	24.8 (3.86)	35.3	8	12.8 (4.23)	35.0	36	63.5 (11.68)	61.98	6	7.6 (2.46)	55.7	0	ND	ND	0	ND
November 2007	14	24.1 (6.71)	73.5	17	22.0 (3.87)	53.5	21	67.7 (17.48)	42.76	5	5.6 (2.37)	26.6					
February 2008	25	40.2 (10.29)	56.4	37	47.2 (4.97)	35.3	48	82.1 (12.43)	35.21	13	14.2 (2.76)	62.5					
November 2008	10	13.8 (3.55)	74.8	8	15.4 (ND)*	44.4	7	15.4 (5.63)	50.15	8	11.1 (3.36)	48.0					
February 2009	19	63.1 (16.83)	50.9	7	15.4 (5.77)	44.4	26	97.5 (20.34)	81.09	10	30.1 (9.82)	55.2					
November 2009	21	27.5 (4.53)	66.31	27	38.8 (5.46)	36.6	8	22.2 (6.49)	50.15	10	12.2 (2.93)	40.4					

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