

Geographic distribution and historical occurrence of *Dromiciops gliroides* Thomas (Metatheria: Microbiotheria)

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Occurrence records represent the key to understanding species distribution patterns. I analyzed the historical and geographical occurrence of *Dromiciops gliroides*, a marsupial endemic to the temperate rain forests of southern Chile and Argentina and the sole living representative of the order Microbiotheria. Eighty-eight localities spanning 7°31' latitude (~850 km) and 3°13' longitude (~350 km) are known for the species and were taken from previous works and museum specimens and integrated in a geographic information system. Species distribution was analyzed in a historical, geographic, and biogeographic context, with the use of maps at different scales (region, subregion, province, ecoregion, and forest type). The software MaxEnt was used to generate 2 potential distribution models with environmental data. Generated models show a northern contraction and southern expansion in the species' potential distribution, with variation in habitat suitability throughout the current species range. Precipitation and some temperature-related variables influenced both generated models. The species' occurrence lies within the Andean region; Subantarctic and Patagonia subregions; and Maule, Valdivian, and Subandean Patagonia provinces. At a smaller scale, most of the localities occur within the Valdivian Temperate Forests ecoregion, and in the majority of the forest types described for it, implying broader ecological requirements than expected. Identification of critical areas through potential distribution modeling may have implications on species conservation and biogeographic patterns. DOI: 10.1644/09-MAMM-A-347.1.

Key words: biogeography, distribution records, forest types, MaxEnt, monito de monte, Valdivian Temperate Forests ecoregion

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The monito de monte (*Dromiciops gliroides*) is the only living representative of the marsupial order Microbiotheria, considered more closely related to the Australian marsupial radiation (cohort Australidelphia) than to any other American groups (cohort Ameridelphia—Martin 2008). Restricted to the southwestern portion of South America, *D. gliroides* mainly inhabits the cold and moist temperate rain forests known as the Valdivian Temperate Forests ecoregion (Olson et al. 2001), a biogeographic island with a highly endemic biota that can be considered partially relictual (Hinojosa 2005; Murúa 1997; Villagrán 1994).

The objectives of this work were to summarize the recorded localities and habitats for the species; to identify areas, through potential distribution models, where the species has not been recorded but might occur; to describe which environmental variables have more influence on the distribution models; and to analyze the distribution of the species and its relationship to biogeographic schemes at different levels.

MATERIALS AND METHODS

Recorded localities of *D. gliroides* were taken from previous works and collection specimens (Martin 2008). Latitude and longitude for each record were verified with maps (Instituto Geográfico Militar 1998) or gazetteers (*GEOnet* [<http://earth-info.nga.mil/gns/html/index.html>] and *Global Gazetteer* [<http://www.fallingrain.com/world/index.html>]), or both. If records lacked precise coordinates, these were assigned by plotting them into a geographic information system with different shapefiles of Argentina and Chile (e.g., roads, lakes, political divisions, and cities and towns) through the software DIVA-GIS version 5.2 (Hijmans et al. 2005b). Integration of localities into a geographic information system was done by converting them into decimal degrees using the formula (degrees + min/60 + s/3,600) × -1 and later



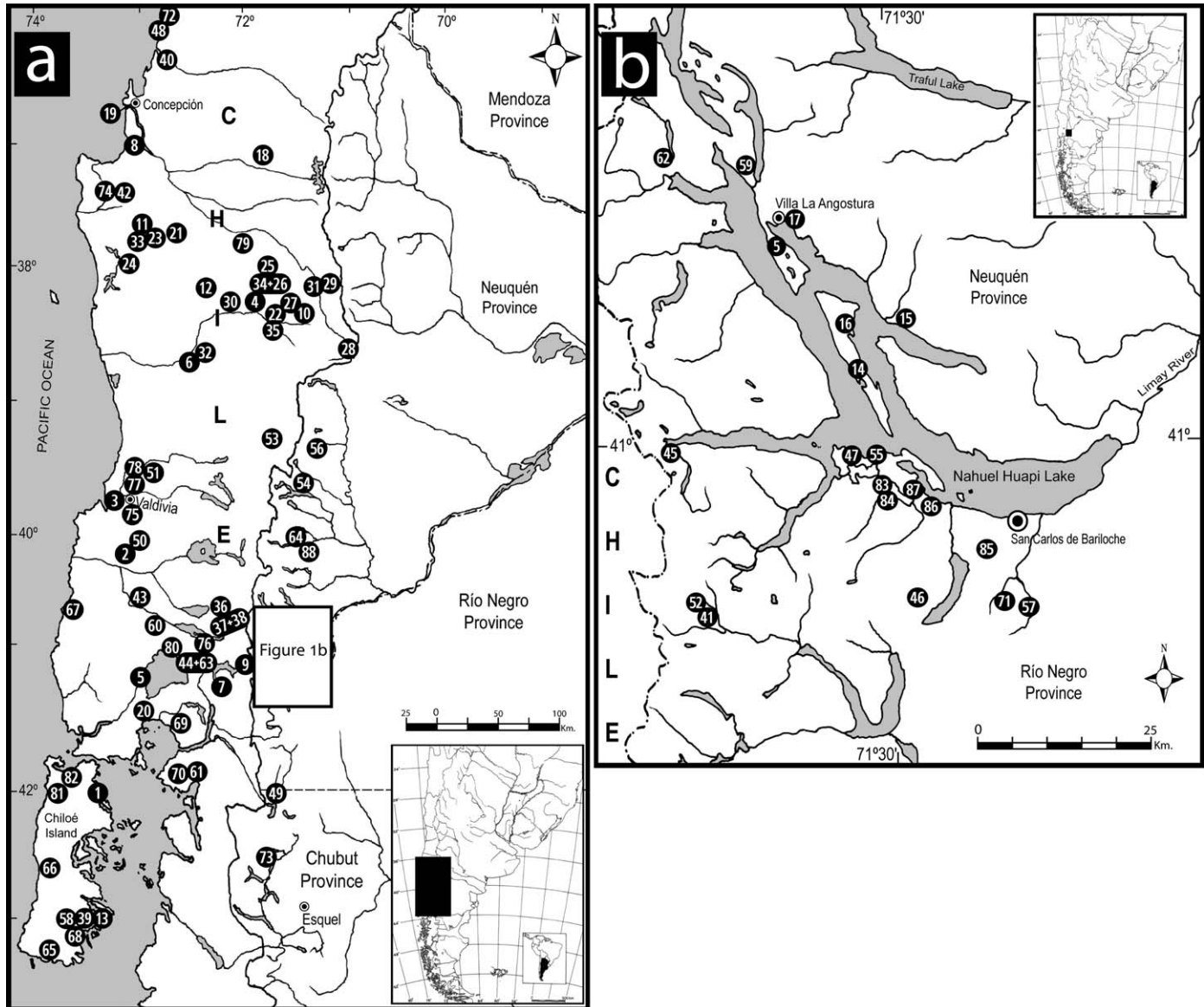


FIG. 1.—a) Recording localities for *Dromiciops gliroides* throughout the species' range and organized by date (see Table 1 for place names and geographic coordinates). b) Recording localities for *D. gliroides* in the area of Nahuel Huapi National Park (Argentina) organized by date (see Table 1 for place names and geographic coordinates).

exporting the file in .txt or .csv formats. Subsequently, localities were used to analyze the distribution in a historical perspective, generate maps at a regional and local scale (Fig. 1), and generate potential distribution models. Information about the habitat and microhabitat was based on published (Kelt and Martínez 1989; Mann 1955; Patterson et al. 1989, 1990; Pearson and Pearson 1982) and unpublished (G. Martin, pers. obs.) information.

Potential distribution maps were generated with the software MaxEnt version 3.2.19 (Phillips et al. 2006), using species localities (Table 1) and WorldClim environmental variables with a spatial resolution of 30 arc-seconds, from the period 1950–2000 (Hijmans et al. 2005a). The variables used in the analyses included altitude; monthly precipitation; mean, maximum, and minimum monthly temperatures; and 19 other variables (Hijmans et al. 2005a).

The potential distribution of *D. gliroides* was modeled using 2 different approaches, 1 with all localities known for the species (All model, $n = 86$), and the other using only the records after 1950 (1950 model, $n = 69$). This was done to test for differences in total area and general potential distribution patterns with the 2 different data sets, the 2nd one having temporal correspondence (Phillips et al. 2006) with the climatic data set. The following selections to the MaxEnt software were made: 25% test data, 1,000 replications, random seed, and 10,000 background points (Phillips and Dudik 2008). Models were generated with a continuous output, which was used to generate maps in which prediction values range from 0 to 100. Three intervals were distinguished (Fig. 2): higher prediction values (100–51), medium prediction values (50–11), and low prediction values (10–1). Areas having 0 probabilities of species presence also were

recognized. The intervals were selected to maximize lower prediction levels and therefore reflect critical areas where the species has yet to be recorded (Phillips et al. 2006; R. P. Anderson, American Museum of Natural History and City University of New York, pers. comm.). The main environmental variables and their heuristic estimate of relative contribution to the models, and a jackknife test for variable importance are presented. Information from the models also is presented in quantitative way, as threshold dependent and independent tests (Phillips et al. 2006). This is done to test for better predictions in the models than those randomly generated through the binomial omission test (Phillips et al. 2006); to determine within which limits omission values fluctuate (preferentially, they should be low or closer to 0); to estimate the potential area of each model in relation to the total analyzed area; and to assess if area under curve values indicate better predictions than random and can be considered useful (Phillips and Dudik 2008).

The distribution of the species was analyzed in a biogeographic context using shapefiles of regions, subregions, and provinces (Morrone 2001, 2006); ecoregions (Olson et al. 2001); and forest type (FT—Lara et al. 1999; Appendix I), providing the 1st biogeographic scheme for the species. This allowed for a characterization from a broader to a finer scale in the progression of biogeographic region → subregion → province → ecoregion → forest type (Lara et al. 1999; Morrone 2001, 2006; Olson et al. 2001).

RESULTS

Chronology and occurrence.—A total of 88 localities has been recorded for the species since its discovery in 1871 to 2008 (Table 1; Fig. 1). This includes 16 new localities, most of them from museum specimens, which were not included in Brown (2004), the latest work on the distribution of New World marsupials (see also Martin 2007, 2008). Most of the records are from Chile ($n = 62$, 70.5%), with a high percentage of them located in Los Lagos Region (53.2%), some in Araucanía Region (30.6%), and a few (16.1%) in Bio-Bio Region. Only 26 (29.5%) of the records come from Argentina, most of them from Río Negro Province ($n = 15$, 57.7%), 9 from Neuquén (34.6%), and only 2 are from northwestern Chubut Province (7.7%; Table 1).

The latitudinal and longitudinal range for the species are 7°31' (~850 km) and 3°13' (~350 km), respectively. The marginal occurrence records are all located in Chile: to the north, Reserva Nacional Los Ruiles (35°50'S, 72°30'W); to the south and west, the mouth of Río Inio (43°20'03"S, 74°08'08.5"W), Chiloé Island; and to the east, Pino Hachado pass (38°40'S, 70°54'W; Table 1).

Taking 4 equal periods of 35 years between 1870 and 2009, the marginal records have increased the distribution extension of the species in latitude and longitude as follows: 2.30° N–S, 0.39° E–W in 1870–1905; 3.67° N–S, 1.83° E–W in 1906–1940; 6.29° N–S, 2.78° E–W in 1941–1975; and 7.52° N–S, 3.22° E–W in 1976–2009. This implies a linear increase in

area for every period under study, both in latitude and longitude.

Habitat.—*Dromiciops gliroides* mainly inhabits the central and parts of the northern Valdivian Temperate Forests ecoregion (Olson et al. 2001), where differences in vegetation at local scales can be found (Martin 2008). The most common subregions (Tecklin et al. 2001) of the Valdivian Temperate Forests ecoregion with which *D. gliroides* has been associated are Andean forests with *Nothofagus–Fitzroya* and *Araucaria–Nothofagus* associations and coastal Maulino and Valdivian forests (with 33, 14, 12, and 11 records, respectively), which account for ~80% of all known records.

The species lives in dense to moderately dense cold and humid forests, with a dense herbaceous and bamboo (*Chusquea* spp.) understory, on well-drained soils (Greer 1965; Muñoz Pedreros and Palma 2000; Osgood 1943). The altitudinal range is from sea level at Chiloé Island and coastal zones of the Llanquihue Province (Region X, Chile) to the timberline of the temperate subantarctic forest near Bariloche (Refugio Neumeyer, Río Negro, Argentina), 1,500–1,600 m elevation (Marshall 1978; Trejo and Ojeda 2004). The only quantitative analysis of habitat association in which this species was included showed a preferred association of *D. gliroides* with open, short-statured forests with low density of shrubs, high herbaceous ground cover, and at medium–high elevations (Patterson et al. 1990).

Potential distribution.—The 2 models generated for *D. gliroides* (All and 1950) show an area of higher (>50) prediction in the eastern portion of the Valdivian Temperate Forests ecoregion between 38° and 42°S (black shading in Fig. 2), with the smaller area predicted from the model that uses only post-1950 records (black shading in Fig. 2b). The most striking differences between models are the reduction in high prediction areas (black shading in Fig. 2), especially in Chiloé Island and the area around the city of Valdivia (arrows 1 and 2 in, Fig. 2a), which are more evident in the 1950 model; and the apparent reduction in potential distribution to the north (arrow 4 in Fig. 2b) and an increased (corresponding?) southern extension (arrow 5 in Fig. 2b) in the 1950 model. Also, changes in medium prediction values (dark gray shading) from All to 1950 are evident in areas A and B (Fig. 2b).

Ten environmental variables (Table 2) contributed the most to the 2 models. Taken together, 3 of them (i.e., July precipitation, mean temperature of wettest quarter, and precipitation seasonality) contribute >80% to each of the models (86% in All and 81.8% in 1950). The remaining variables, with smaller (but >10%) contributions, are directly related to precipitation and minimum temperature of some months (Table 2). Results of the jackknife test for variable importance show the same variable as the most important for both models, and 2 different variables that contain information not present in the remainder (Table 2). The information presented above shows a strong relationship between the potential distribution of *D. gliroides* with precipitation.

Both models showed better predictions than those randomly generated at cumulative threshold values of 1, 5, and 10, with

TABLE 1.—Occurrence localities for *Dromiciops gliroides* ordered by publication date. Geographic coordinates are south and west for latitude and longitude. All localities are shown in Figure 1a except where noted. NP = National Park; ecoregion (Olson et al. 2001) is given in square brackets; forest type (Lara et al. 1999) is given in parentheses. See Appendix I for complementary information.

Locality no.	Locality	Latitude	Longitude	Reference ^a
1	Huite, NE Chiloé Island [Valdivian] (FT16)	42°05'25"	73°26'46"	1 (see also 3, 27)
2	Fundo San Juan, near La Unión [Valdivian] (FT16)	40°17'	73°05'	2
3	Valdivia [Valdivian] (FT19)	39°48'	73°14'	2 (see also 6, 7, 13, 18, 27)
4	Curacautín [Valdivian] (FT19)	38°26'	71°53'	4
5 (see Fig. 1b)	Beatriz (currently known as Península Quetrihué, Arrayanes NP) [Valdivian] (FT8)	40°48'54"	71°38'29"	5
6	Temuco [Matorral] (FT19)	38°44'	72°36'	5
7	Cayutué (cited as Cayetué), Lago Todos Los Santos [Valdivian] (FT7)	41°14'	72°17'	8
8	Lota [Valdivian] (FT19)	37°05'	73°10'	8 (see also 27)
9	Peulla, Todos los Santos [Valdivian] (FT7)	41°06'	72°02'	8 (see also 27)
10	Río Colorado, Malleco [Valdivian] (FT19)	38°27'	71°22'	8
11	Sierra Nahuelbuta [Valdivian] (FT19)	37°43'	73°04'	8
12	Victoria [Matorral] (FT18)	38°13'	72°20'	8
13	Quellón [Valdivian] (FT7)	43°05'26"	73°43'43"	8
14 (see Fig. 1b)	Estación Forestal Puerto Anchorena, Isla Victoria [Valdivian] (FT5)	No precise locality		9 (see also 23)
15 (see Fig. 1b)	Huemul (locality not peninsula) [Valdivian] (FT9)	40°53'10"	71°29'27"	9
16 (see Fig. 1b)	Puerto Madera (near zoological station at Puerto Radal), Isla Victoria [Valdivian] (FT5)	No precise locality		9 (see also 23)
17 (see Fig. 1b)	Villa (La) Angostura [Valdivian] (FT19)	40°46'55"	71°38'38"	9
18	Huépil, north of Laja River [Matorral] (FT18)	37°14'	71°56'	10
19	Parque Pedro del Río [Valdivian] (FT17)	36°50'	73°03'	10
20	Puerto Montt [Valdivian] (FT19)	41°28'18"	72°56'13"	11
21	Angol [Valdivian] (FT16)	37°48'	72°43'	12
22	Baños Río Blanco (cited as Termas Río Blanco) [Valdivian] (FT20)	38°34'	71°34'	12
23	Cerro Nahuelbuta [Valdivian] (FT5)	37°48'	73°04'	12
24	Contulmo [Valdivian] (FT18)	38°00'	73°13'	12
25	Jauja [Matorral] (FT17)	38°04'	71°55'	12
26	Laguna Malleco [Valdivian] (FT5)	38°13'	71°49'	12
27	Lonquimay [Valdivian] (FT16)	38°26'	71°14'	12
28	Pino Hachado pass [Valdivian] (FT15)	38°40'	70°54'	12
29	Río Ranquil [Valdivian] (FT5)	38°16'	71°18'	12
30	Selva Oscura [Matorral] (FT18)	38°22'	72°11'	12
31	Troyo [Valdivian] (FT5)	38°15'	71°18'	12
32	Cerro Nielol [Matorral] (FT17)	38°40'	72°38'	14
33	Nahuelbuta NP [Valdivian] (FT5)	37°51'	73°05'	14
34	Tolhuaca NP [Valdivian] (FT5)	38°10'	71°43'	14
35	Conguillío NP [Valdivian] (FT2)	38°39'	71°38'	14
36	Antillanca (2 km NW of sky area), Puyehue NP [Valdivian] (FT15)	40°45'	72°09'	15
37	Antillanca (6 km NW of sky area), Puyehue NP [Valdivian] (FT15)	40°45'	72°09'	15
38	Lago Paraíso, Puyehue NP [Valdivian] (FT6)	40°48'	72°17'	15
39	15 km S of Quellón, near mouth of Yaldad River [Valdivian] (FT16)	43°04'40"	73°44'59"	15
40	Río Itata [Valdivian] (FT18)	36°23'	72°52'	16 (see also 27)
41 (see Fig. 1b)	5 km NW of Pampa Linda [Valdivian] (FT8)	41°13'	71°47'	17 (see also 23)
42	Concepción (corresponds to a place near Curanilahue) [Valdivian] (FT17)	37°26'	73°19'	18
43	Osorno [Valdivian] (FT19)	40°34'	73°09'	18 ^b
44	La Picada [Valdivian] (FT20)	41°06'	72°30'	19 (see also 20, 21, 27)
45 (see Fig. 1b)	Puerto Blest [Valdivian] (FT5)	41°02'	71°49'	22 (see also 23)
46 (see Fig. 1b)	2 km E, 1 km S of Cerro Catedral [Valdivian] (FT8)	41°12,58'	71°28,92'	23
47 (see Fig. 1b)	Reserva Municipal Llao-Llao (also as Municipal Park) [Valdivian] (FT5)	41°03'	71°32'	24
48	Reserva Nacional Los Queules [Valdivian] (FT17)	35°59'	72°41'	25
49	Lago Puelo [Valdivian] (FT16)	42°03'52"	71°36'53"	26
50	Catamutún [Valdivian] (FT16)	40°07'	73°07'	27
51	Máfil [Valdivian] (FT16)	39°39'	72°57'	27
52 (see Fig. 1b)	Río Castaño Overo, W of Bariloche [Valdivian] (FT5)	41°12'	71°48'	27
53	Termas de San Luis, 30 km E of Pucón [Valdivian] (FT6)	39°16'	71°42'	27
54	Arroyo T[i]jerras Coloradas, Lago Huechulafquen, near Cerro del Chico (Castillo?) [Valdivian] (FT5)	39°44'54"	71°27'19"	27
55 (see Fig. 1b)	Hotel Tunquelén, 25 km W of Bariloche (erroneously cited near Río Castaño Overo) [Valdivian] (FT19)	41°09'	71°20'	27
56	Lago Quillén [Valdivian] (FT2)	39°25'	71°18'	27

TABLE 1.—Continued.

Locality no.	Locality	Latitude	Longitude	Reference ^a
57 (see Fig. 1b)	Refugio Neumeyer, SSW of Bariloche [Valdivian] (FT8)	41°15'	71°18'	27
58	Cocauque, opposite shore of Yaldad [Valdivian] (FT7)	43°06'35"	73°44'06"	27
59 (see Fig. 1b)	Cascada Diana, 16 km WNW Villa La Angostura [Valdivian] (FT19)	40°45'39"	71°39'19"	27
60	32 km SSE of Osorno and 14.5 km NNW of Pto. Octay [Valdivian] (FT16)	40°40'	73°01'	27
61	Río Negro, 12.4 km WNW [Valdivian] (FT16)	41°58'	72°29'	27
62 (see Fig. 1b)	Refugio, 3.5 km N, 1.5 km E of Estancia Paso Coihue [Valdivian] (FT4)	40°58'	71°20'	27
63	Lago Todos los Santos [Valdivian] (FT7)	41°06'58"	72°24'31"	27
64	Lago Lácar, Lanín NP [Valdivian] (FT5)	40°11'	71°30'	27
65	Mouth of Río Inio [Valdivian] (FT14)	43°21'	74°07'	27
66	Cucao [Valdivian] (FT16)	42°37'59"	74°06'25"	27
67	Maicolpué [Valdivian] (FT19)	40°35'39"	73°44'5"	27
68	Puerto Cármen [Valdivian] (FT7)	43°08'15"	73°46'13"	27
69	Seno Reloncaví (Quillaipe?) [Valdivian] (FT7)	41°36'52"	72°50'13"	27
70	Contao, 19.7 km N Río Negro and 26.7 km S Contao [Valdivian] (FT7)	41°57'45"	72°42'10"	27
71 (see Fig. 1b)	Valle de Chalhucaco [Valdivian] (FT8)	41°15'	71°16'	28
72	Reserva Nacional Los Ruiles [Valdivian] (FT10)	35°50'	72°30'	29
73	Cholila/Lago Rivadavia [Valdivian] (FT4)	42°32'58"	71°37'56"	30
74	Comuna Curanilahue [Valdivian] (FT17)	37°26'	73°21'	30
75	Comuna Valdivia, Sto. Domingo [Valdivian] (FT5)	39°50'	72°45'	30
76	Rupanco, Piedras Negras [Valdivian] (FT16)	40°53'	72°29'	30
77	Comuna Valdivia, Huellethue [Valdivian] (FT16)	39°44'	73°06'	30
78	Fundo San Martín [Valdivian] (FT16)	39°38'	73°07'	30
79	Santa Bárbara [Valdivian] (FT18)	37°40'	71°58'	30
80	54 km SSE of Osorno and 13.5 km E of Pto. Octay [Valdivian] (FT16)	41°00'7"	72°40'6"	30
81	Coipomó [Valdivian] (FT14)	42°03'	73°58'	30
82	Ancud [Valdivian] (FT19)	41°52'11"	73°49'13"	30
83 (see Fig. 1b)	Piscicultura Beveraggi, Colonia Suiza [Valdivian] (FT5)	41°05'	71°30,5'	30
84 (see Fig. 1b)	Lago Moreno, Colonia Suiza [Valdivian] (FT5)	41°05,5'	71°30,2'	30
85 (see Fig. 1b)	Ladera Sur Cerro Otto, Villa Arelauquen [Valdivian] (FT8)	41°10'	71°23'	30
86 (see Fig. 1b)	Bustillo Ave. km 13, Bariloche [Valdivian] (FT19)	41°06'	71°26,6'	30
87 (see Fig. 1b)	Bustillo Ave. km 14, Bariloche [Valdivian] (FT5)	41°05,4'	71°27'	30
88	4.5 km N, 0.5 km E of Cerro Falkner, Lago Lácar [Valdivian] (FT9)	40°11'13"	71°19'12"	30

^a 1, Cunningham (1871); 2, Philippi (1893); 3, Thomas (1894); 4, Wolffsohn and Porter (1908); 5, Thomas (1919); 6, Wolffsohn (1921); 7, Krumbiegel (1941); 8, Osgood (1943); 9, Santos Gollan (1946); 10, Schneider (1946); 11, Mann (1955); 12, Greer (1965); 13, Reig et al. (1977); 14, Jiménez and Rageot (1979); 15, Pine et al. (1979); 16, Tamayo and Frassinetti (1980); 17, Pearson and Pearson (1982); 18, Patterson and Gallardo (1987); 19, Meserve et al. (1988); 20, Patterson et al. (1989); 21, Patterson et al. (1990); 22, Birney et al. (1996); 23, Mares and Braun (2000); 24, Amico and Aizen (2001); 25, Saavedra and Simonetti (2001); 26, Martín (2003); 27, Brown (2004); 28, Trejo and Ojeda (2004); 29, Lobos et al. (2005); 30, this work.

^b Corrected according to *Global Gazetteer* (<http://www.fallingrain.com/world> Accessed March 2008).

high values of area under the curve: All = 0.991 ± 0.002 SD and 1950 = 0.984 ± 0.003 SD, respectively. Similar values in fractional predicted area and significant *P*-values were recovered for both models (Table 3).

Distribution and forest types.—The distribution of *D. gliroides* is mainly included within the limits of the Andean region, Subantarctic subregion, and Valdivian Temperate Forests ecoregion (Morrone 2001; Olson et al. 2001). A few marginal records are located in the Central Chilean subregion (Morrone 2001) or Chilean Matorral ecoregion (Olson et al. 2001), the dominant ecosystem in the central regions of Chile (Regions IV–VII) that extend as a relatively broad wedge between the Cordillera de la Costa and the Andes to approximately 38°30'S. This area is known as the central valley (valle o llano central—Donoso 1995, 1996) or intermediate depression (depresión intermedia—Murúa 1997), and has suffered from severe anthropogenic modifications (Donoso 1995). Between approximately 39° and 36°S these ecoregions (Olson et al. 2001) form an ecotone, in both latitudinal and altitudinal patterns, where components of the Valdivian Temperate Forests ecoregion (e.g., *Maytenus boaria*

and *Laurelia sempervirens*) and Chilean Matorral ecoregion (e.g., *Acacia caven*, *Jubaea chilensis*, and *Quillaja saponaria*) reach their northernmost and southernmost distributions, respectively (Donoso 1995). *D. gliroides* reaches its northernmost extension in the west at Los Queules and Los Ruiles National Reserves. These sites are located within FT10, with remnants of FT12 and surrounded by exotic tree plantations (FT17; Table 1; Appendix I).

Most (93.2%) of the recorded localities are included in the Valdivian Temperate Forests ecoregion ($n = 82$), whereas only 6 (6.8%) are located in the central valley. Of the 22 categories mapped for the Valdivian Rain Forest ecoregion by Lara et al. (1999), *D. gliroides* is present in 15 of them (Table 1; Appendix I). The most important FTs are FT5 with 21.6% ($n = 19$) of the records, FT16 with 17% ($n = 15$), and FT19 with 14.8% ($n = 13$), which constitute >53% ($n = 47$) of all known localities. Other important FTs where the species has been collected includes FT7 ($n = 8$, 9.1%), FT18 ($n = 6$, 6.8%), and FT17 ($n = 6$, 6.8%). FTs with <5 records include 21 localities scattered throughout the Valdivian Temperate Forests ecoregion (Table 1; Appendix I). Localities within

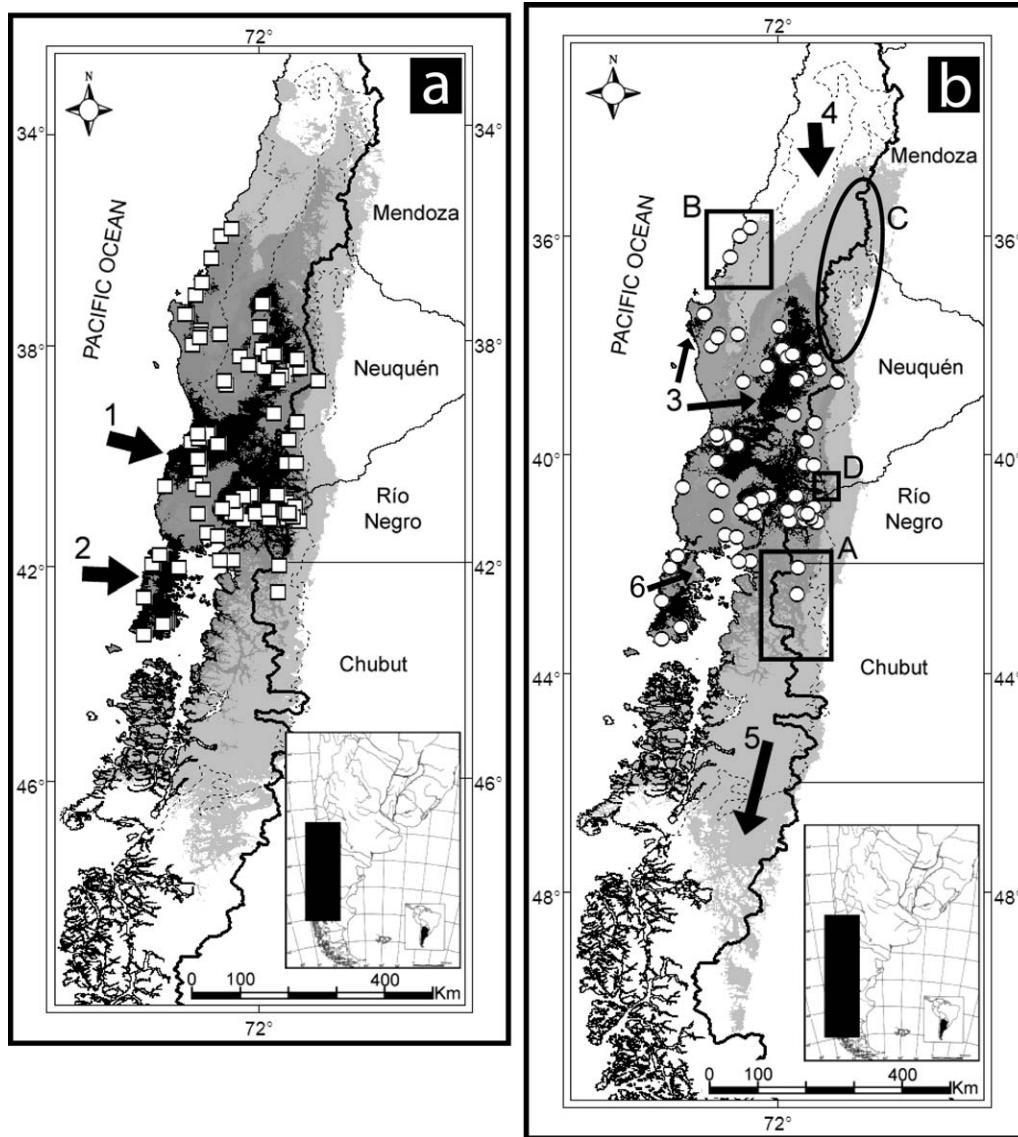


FIG. 2.—Potential distribution models generated for *Dromiciops gliroides* using a) all known localities ($n = 86$), and b) those recorded after 1950 ($n = 69$). High prediction values (100–51) are shaded black, medium values (50–11) dark gray, and low values (10–1) light gray. White was used for areas having 0 probabilities of species presence. Important changes are marked by arrows or selected areas in the models (see “Potential distribution” in the “Results” and “Discussion” sections). Dashed lines represent the limits of the Valdivian Temperate Forests ecoregion (Olson et al. 2001).

FT16 and FT19 are, in general, due to the presence of forest remnants within cities or towns (e.g., Valdivia, Chile, and San Carlos de Bariloche, Argentina) or location of towns within a matrix of native forest with variable degrees of human impact (e.g., Villa La Angostura, Argentina). The presence of the species in different-sized forest remnants surrounded by plantations of exotic species (e.g., *Eucalyptus* spp. and *Pinus* spp.; FT17) or agricultural areas (FT18), which are generally connected by riparian corridors and vegetation growing at the sides of roads and hedges between plots, also is common.

DISCUSSION

The numbers of localities recorded for *D. gliroides* are evenly distributed throughout most of what is likely to be the

species range and suitable habitat. The number of records per decade is highly variable, and most of them come from concentrated collecting efforts and their successive publication, followed by long periods of poor field sampling (e.g., the periods between 1920 and 1939—Osgood 1943). Also, the documented range might be influenced partially by the trap bias of *D. gliroides*, which is rarely caught in Sherman traps (HB Sherman, Tallahassee, Florida—Patterson et al. 1989, 1990). Almost half of the occurrence records come from the last 9 years of research, when the number of studies using different trap types (e.g., snap traps and Tomahawk traps, Tomahawk Live Trap Co., Tomahawk, Wisconsin), or those that were specifically designed to check for the presence of the species, increased (Table 1). Although most of the localities come from Chile, recent fieldwork in Argentina has

TABLE 2.—Heuristic estimates of relative contributions of the environmental variables and results of the jackknife test of variable importance to the MaxEnt models generated for *Dromiciops gliroides*. WorldClim (Hijmans et al. 2005a) environmental variables were used to generate the models. Values are indicated as percentages.

Variable	All	1950
July precipitation	50.0	42.9
Mean temperature of wettest quarter	23.4	26.6
Precipitation seasonality (coefficient of variation)	12.6	12.3
Precipitation of driest quarter	—	5.2
June precipitation	3.9	2.2
August precipitation	1.2	2.2
September minimum temperature	—	1.8
May precipitation	—	1.6
June mean temperature	1.3	—
March minimum temperature	1.2	—
Total	93.6	94.8
Jackknife test of variable importance		
Variable with highest explanatory power	July precipitation	July precipitation
Variable with most “unique” information	Maximum September temperature	September precipitation

contributed almost one-third of the species' records, including the southernmost continental record (locality 73; Table 1; Fig. 1a).

In Chile collecting records appear concentrated in 2 areas north and south of the species' continental distribution (Table 1; Fig. 1a), and in Chiloé they appear concentrated in the south and north of the Island, and many areas remain unsurveyed. In Argentina the known distribution is more confined than in Chile and mostly concentrated near Bariloche (Fig. 1), whereas a few localities are scattered north and only 2 south of this area. Although the species has not been captured in continental Chile east of Chiloé Island despite intensive sampling (Elgueta et al. 2006; Kelt 1994; Kelt and Martínez 1989; Murúa 1997), recent findings in western Chubut Province (Argentina; Fig. 1a) have increased its continental extension toward the south (Martin 2003, 2008). Further studies in these areas should be aimed at specifically finding the species by using selective trapping methods.

In most of the literature *D. gliroides* has been considered to be an exclusive inhabitant of the very humid portions of the Valdivian Temperate Rain Forest, with dense and very humid forests, dense bamboo (*Chusquea* spp.) understory, over well-drained soils, and at lower altitudes (Cunningham 1871; Greer 1965; Hershkovitz 1992, 1999; Mann 1955; Osgood 1943; Pine et al. 1979; Santos Gollan 1946). In contrast, more recent specimens from the last 20 years have been captured in a variety of environments, showing a broader tolerance of the species to different habitats, which include transitional areas between the Valdivian Temperate Forests ecoregion and drier ecosystems, such as the Patagonian steppe in Argentina and the central Chilean matorral (Donoso 1996; Lara et al. 1999); and patches of native “Maulino” forest in a matrix of pine

TABLE 3.—Results of equalized predicted areas for cumulative threshold values of 1, 5, and 10 for both models generated, and significance values of the binomial probabilities of test points used in the analyses.

Cumulative threshold	All		1950	
	Fractional predicted area	P-value	Fractional predicted area	P-value
1	0.062	3.68E-023	0.063	2.66E-022
5	0.036	4.81E-028	0.029	1.04E-018
10	0.029	4.13E-030	0.02	2.32E-018

(*Pinus* spp.) or eucalyptus (*Eucalyptus* spp.), or both, plantations, probably as remnants of a past distribution that extended north along the Andes and the coastal mountains of Chile (Lobos et al. 2005; Saavedra and Simonetti 2001). Of particular interest is the presence of the species in small forest patches inside towns (e.g., locality 17; Table 1) and in narrow corridors that traverse through cultivated and other highly disturbed areas (e.g., the central valley of Chile in Regions VIII–X). Its presence also has been documented in different-sized forest remnants of native vegetation, but no information is available as to how patch size relates to species occurrence (Kelt 2000). These records might be remnants of larger populations or dispersing individuals and could represent interesting ecological case studies, especially because habitat fragmentation has been shown to affect the abundance of this species (Rodríguez-Cabal et al. 2007).

Only 1 quantitative work has dealt with the microhabitat preferences of *D. gliroides* in the context of a much broader study on temperate rain-forest small mammals (Patterson et al. 1990), and future studies could test these preferences by applying a similar methodology to new localities. *D. gliroides* seems to be associated most commonly with tree species of *Nothofagus*, and *Nothofagus dombeyi* in particular. This species has a mutualistic relationship, as a seed disperser, with the mistletoe *Tristerix corymbosus* (Amico and Aizen 2000), an association that can be extrapolated to other fleshy-fruited species of the temperate rain forest (Amico et al. 2009). Although the presence of *T. corymbosus* could be used as an indicator for the occurrence of *D. gliroides*, the marsupial also occurs in other areas (Martin 2008).

The MaxEnt models represent the 1st attempt to approximate the potential distribution for this species at a regional scale. Both models are reasonable representations of the distribution of *D. gliroides* and the environments present in the area.

Several differences were found between the models using all records and those after 1950. In theory, a larger number of evenly distributed records used in any analysis should result in a better model, with reduced numbers implying a smaller area or worst discrimination between prediction values, or both (i.e., coarser resolution in the predicted model). In this case, and because of the temporal association between the climatic database and localities, the use of a smaller number of records produces a better model. This is shown by a more-detailed

discrimination between prediction values, as an increase in medium prediction values to the south and east (e.g., area A; Fig. 2b), toward the limit of the Valdivian Temperate Forests ecoregion (dashed line in Fig. 2). Also, the 1950 model shows areas where the species has not been recently trapped (e.g., arrow 3 in Fig. 2b) and that require further exploration. The reduction in potential distribution to the north of the Valdivian Temperate Forests ecoregion could be interpreted as an overprediction of the model generated with all known localities, including areas where the species might not be found today because of an absence or reduction of suitable habitats caused by human intervention. Therefore, these northernmost localities (area B; Fig. 2b) could represent remnant populations in danger of extinction and of high conservation value for the species (Lobos et al. 2005; Saavedra and Simonetti 2001). However, the southward extension in the 1950 model could represent an expansion of the species to more suitable (recent) environments. Both of these processes might have been triggered by a decrease in precipitation and an increase in temperature toward the northern portion of Valdivian Temperate Forests ecoregion, as shown by the trends of precipitation and temperature for periods between 1901 and 1995 (Watson et al. 1998).

A few areas of similar environmental conditions to where the species already occurs but has yet to be found can be identified for further exploration (Fig. 2b): area C, where broad-leaved deciduous *Nothofagus* reach their northernmost extension (Donoso 1996); area D, where isolated forests of *Nothofagus* spp. and *Athyonidium chilensis* are found and where rodents considered typical of the Valdivian Temperate Forests ecoregion are known to occur (e.g., *Irenomys tarsalis*, *Oligoryzomys longicaudatus*, and *Chelemys macronyx*—Pardiñas et al. 2003; Pearson and Pearson 1993).

Both models also show high to medium prediction values in the Juan Fernández archipelago (not shown), a group of islands located 670 km west of South America between 33°36' and 33°47'S and 80°47' and 78°47'W (Rodríguez et al. 1983). Although these islands have what appear to be suitable environmental conditions for *D. gliroides*, it is not likely that the species could have dispersed to them because they are relatively recent in origin (~3 million years ago) and do not support any native mammal (Poulin 2006).

Precipitation and precipitation-related variables appear to be the biggest determinants in the potential distribution models generated for *D. gliroides* at a regional scale. Both the heuristic estimates of environmental variable contributions and the jackknife test of variable importance show July precipitation as the most important explanatory variable in the models. It is noteworthy that although models were generated with 68 environmental variables—all variables of the WorldClim database (Hijmans et al. 2005a)—only 7 in All and 8 in 1950 account for >90% of the contributions in each model. Although winter–late autumn precipitation might not have a direct influence on *D. gliroides*, which has periods of torpor and hibernation during these months triggered by food deprivation and low ambient temperatures (Bozinovic et al.

2004), it affects the environment. Winter precipitation regulates moisture availability in the soil during the drier spring–summer months, which are concurrent with plant growing–flowering–fruiting seasons, and, therefore, has an influence on food and shelter availability when the species is highly active. Also, both variables with unique information occur in the same month (September), implying a causal relationship on the generated models with some aspect that highly contributes to the distribution of *D. gliroides*. Similar results, despite a smaller number of localities used, were found in Martin (2008).

Of all the FTs recognized for the Valdivian Rain Forests ecoregion by Lara et al. (1999), *D. gliroides* has not been recorded in only a few: FT1, FT3, FT11, FT12, and FT13 (not considering FT20, FT21, and FT22; Appendix I). The presence of *D. gliroides* in most of the FTs could be related to a tolerance of the species to different environments with varied coverage and plant species diversity. As can be observed in the predictive models (Fig. 2), the northern distribution of the species reaches 35°S where extensive areas of different FTs are located (including FT5, isolated remnants of FT4, FT10, FT8, FT9, and FT12), all of them inserted in a large shrub matrix of anthropogenic origin (FT16), rocks and high Andean vegetation (FT15), and agricultural lands (FT18).

At a habitat scale, *D. gliroides* has been associated, with different levels of persistence, with native species of bamboo (*Chusquea* spp.) and southern beech trees (*Nothofagus* spp.) in what Hershkovitz (1999) termed the *Nothofagus–Chusquea–Dromiciops* association. This association would be part of a long evolutionary process between extinct species of Microbiotheriidae and *Nothofagus–Chusquea* forests that has persisted since the early Cenozoic and where *D. gliroides* replaced the extinct marsupials. Recent studies by Amico et al. (2009) have supported this hypothesis documenting the ability of *D. gliroides* to consume fruits and disperse seeds of several species of plants that are part of *Nothofagus* forests. The presence of *D. gliroides* in most of the habitats and FTs of the Valdivian Rain Forests ecoregion also can be explained by a broad set of feeding requirements, which probably evolved in response to temporal fluctuations in food availability similar to those experienced in the southern temperate rain forests (Amico et al. 2009; Murúa 1997).

Future studies probably will increase the number of localities throughout the known range of the species, providing new and complementary information on FTs and smaller scale occurrence, habitat preferences, and other ecological aspects at different levels (i.e., population and community). Also, other work should concentrate on trying to find the limits to the distribution of the species, especially toward the south, by sampling areas in which the models predict the existence of suitable habitats for *D. gliroides*.

RESUMEN

Las localidades de registro de una especie son esenciales para comprender patrones de distribución y son importantes a

la hora de planificar esfuerzos de conservación y generar modelos de distribución potencial. En este trabajo analicé la ocurrencia histórica y geográfica de *Dromiciops gliroides*, un marsupial endémico de los bosques templados del sur de Chile y Argentina, único representante viviente del orden Microbiotheria. Las localidades de registro fueron tomadas de trabajos previos y ejemplares en colecciones, e integradas en un sistema de información geográfica. La distribución de la especie fue analizada en un contexto histórico, geográfico y biogeográfico, mediante el uso de mapas a diferentes escalas (región, subregión, provincia, ecoregión, y tipos forestales). Se usó el software MaxEnt para generar 2 modelos potenciales de distribución usando datos ambientales. Se reconocen 88 localidades para la especie con un rango latitudinal y longitudinal de 7°31' (~850 Km) y 3°13' (~350 Km), respectivamente. Los modelos generados muestran una contracción y expansión hacia el norte y sur, respectivamente, de su distribución potencial; con una variación de ambientes apropiados para la especie en todo el rango de distribución. Las variables que más influyeron en los modelos generados fueron la precipitación y unas pocas variables relacionadas con la temperatura. La distribución de la especie se encuentra contenida en la región Andina, subregiones Subantártica y de la Patagonia, y en las provincias del Maule, Valdiviana y Subandina. A una escala menor, la mayoría de los registros se ubican en la ecoregión Valdiviana y en la mayoría de los tipos forestales, implicando requerimientos ecológicos más amplios que los esperados para una especie de estas características. La identificación de áreas críticas a partir de los modelos de distribución potencial podrían tener implicancias en la conservación de la especie y su biogeografía.

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APPENDIX I

Forest types (Lara et al. 1999). Translations and scientific names are given in square brackets.

- FT1. Alerce [southern larch tree, *Fitzroya cupressoides*]
 FT2. Araucaria [monkey-puzzle tree, *Araucaria araucana*]
 FT3. Ciprés de las Guaitecas [*Pilgerodendron uviferum*]
 FT4. Ciprés de la Cordillera [Chilean cedar, *Austrocedrus chilensis*]
 FT5. Roble–Raulí–Coihue [*Nothofagus obliqua*–*Nothofagus nervosa*–*Nothofagus dombeyi*]
 FT6. Coihue–Raulí–Tepa [*Nothofagus dombeyi*–*Nothofagus–Laureliopsis philipiana*]
 FT7. Valdiviano [Valdivian, evergreen forest]
 FT8. Lenga (Incluye las formaciones con porte arbóreo y achaparrado) [*Nothofagus pumilio*, includes formations of tree- and shrub-size]
 FT9. Ñire o ñirre (Incluye formaciones dominadas por ñire/ñirre y matorrales mixtos en Argentina) [*Nothofagus antarctica*, includes stands dominated by *N. antarctica*–*N. antarctica* and mixed shrubland in Argentina]
 FT10. Roble–Hualo [*Nothofagus obliqua*–*Nothofagus glauca*]
 FT11. Coihue de magallanes [Magellanic coihue or coigüe, *Nothofagus betuloides*]
 FT12. Esclerófilo mixto [mixed sclerophytic, characterized by the presence of *Peumus boldus*, *Quillaja saponaria*, *Lithraea caustica*, and *Cryptocarya alba*]
 FT13. Estepa patagónica [Patagonian steppe]
 FT14. Humedales [locally called mallines, wetlands or marshlands]
 FT15. Vegetación altoandina y otras áreas con vegetación rala [high Andean vegetation and other areas with low plant cover]
 FT16. Praderas y matorrales de origen antrópicos [prairies and shrublands of anthropogenic origins]
 FT17. Plantaciones [plantations, mostly of *Pinus* spp. and *Eucalyptus* spp.]
 FT18. Terrenos Agrícolas [cultivated lands]
 FT19. Urbano [urban]
 FT20. Nieves y glaciares [snow and glaciers]
 FT21. Cuerpos de agua [water bodies]
 FT22. Areas no reconocidas [unrecognized or uncharted areas]