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Population dynamics of *Dromiciops gliroides* (Microbiotheriidae) in an austral temperate forest

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Dromiciops gliroides is an arboreal marsupial endemic to the southern temperate forest located between 36°S and 43°S in both Chile and Argentina. This species is a key seed disperser of many native plants, including the keystone mistletoe, *Tristerix corymbosus*. We studied the population fluctuation of *D. gliroides* and the possible effects of natural disturbances on the population. We estimated density, abundance, survival, and recruitment ratios for 7 years (2009–2011 and 2013–2016) at Reserva Llao Llao, Argentina, using capture–recapture techniques. A Jolly–Seber model with robust design was fitted using a hierarchical Bayesian approach. The estimated mean abundance during these 7 years was 81 individuals. The highest abundances were observed in 2009, 2010, 2011, and 2014 (98 individuals on average). The years with lowest abundance were 2013, 2015, and 2016 (60 individuals on average), which coincided with the occurrence of natural disturbances in the study area (eruption of the Puyehue-Cordón Caulle volcano, the flowering of Chusquea bamboo and a subsequent rodent outbreak, and an unusually dry summer). These results suggest that the observed population fluctuations of *D. gliroides* could be related to natural forest disturbances.

Dromiciops gliroides es un marsupial arborícola endémico del bosque templado austral ubicado entre los 36 ° S y 43 ° S tanto en Chile como en Argentina. Esta especie es clave en la dispersión de semillas de muchas plantas nativas, incluyendo al muérdago austral *Tristerix corymbosus*. En este trabajo estudiamos las fluctuaciones poblacionales de *D. gliroides*, estimando densidad, abundancia, tasa de supervivencia y de reclutamiento durante 7 años (2009–2011 y 2013–2016) en la Reserva Llao Llao, Argentina. Usamos 50 trampas separadas en dos grillas desde Enero a Abril, completando 800 trampa-noche por año. Para analizar los datos ajustamos el modelo de Jolly–Seber con un diseño robusto usando un enfoque bayesiano jerárquico. El promedio de la densidad estimada durante los 7 años fue de 18 individuos/ha. Las densidades mayores se observaron en 2009, 2010, 2011 y 2014 (22 individuos/ha en promedio). Los años con densidades menores fueron 2013, 2015 y 2016 (14 individuos/ha en promedio) los cuales coincidieron con disturbios naturales ocurridos en el área de estudio (la erupción del volcán Puyehue-Cordón Caulle, la floración de la caña Colihue (*Chusquea culeou*) y la posterior "ratada," y la ocurrencia de veranos muy secos). Estos resultados sugieren que las fluctuaciones poblacionales observadas en la población de *D. gliroides* podrían estar relacionadas con los disturbios naturales ocurridos en el bosque. Monitoreos futuros determinarán si las densidades de esta población se recuperan a valores pre-disturbio.

Key words: capture–recapture, hierarchical Bayesian analysis, natural disturbance, Patagonia

Dromiciops gliroides is an arboreal marsupial endemic to the southern temperate forest, located between 36°S and 43°S in both Chile and Argentina (Hershkovitz 1999; Martin 2010). This marsupial belongs to the family Microbiotheriidae (Hershkovitz 1999) along with 2 recently described species: *D. bozinovici* and *D. mondaca* (D´Elia et al. 2016). It is closely associated with mature forests dominated by native and exotic species (Rodriguez-Cabal and Branch 2011; Salazar and

Fonturbel 2016). *Dromiciops gliroides* is an important member of the ecological community, with low redundancy because it plays a key role in these forests (Rodriguez-Cabal et al. 2013; Fonturbel et al. 2014).

Dromiciops gliroides disperses seeds of many temperate forest species with fleshy fruits (Amico et al. 2009), and is the main seed disperser of the mistletoe, *Tristerix corymbosus* (Amico et al. 2011). For this reason, *D. gliroides* is an essential player in the conservation of biodiversity in the temperate forests of Patagonia (Rodriguez-Cabal et al. 2013; Fonturbel et al. 2014). However, *D. gliroides* has been classified as "near-threatened" by the IUCN due to the loss and fragmentation of its natural habitat (IUCN 2010). In Argentina, it is classified as vulnerable (Diaz and Ojeda 2000), and as "insufficiently known" in Chile (Fonturbel et al. 2012). Given the important ecological role played by this species, it was necessary to study its population dynamics and sensitivity to natural disturbances, which have not been reported previously, although other studies have investigated the species' abundance (Franco et al. 2011; Celis-Diez et al. 2012; Fonturbel et al. 2012).

Natural disturbances such as fire, earthquakes, droughts, population outbreaks, and volcanism occur frequently in the northern region of Patagonia (Veblen et al. 1996; Gonzalez and Donoso 1999; Veblen et al. 2011). Many studies of the effects of natural disturbances on animal populations have been carried out on mammals (e.g., Previtali et al. 2009; Linzey et al. 2012; Swan et al. 2016), and the consequences can sometimes be severe (Jones et al. 2001; Zwolak 2009). Some species characteristics may influence how sensitive they are to a disturbance. Endemic species, such as *D. gliorides*, tend to be more prone to extinction when facing severe disturbances (Cardillo et al. 2006). Describing typical fluctuations in abundance and identifying factors that might critically impact small or isolated populations of *D. gliroides* can facilitate its conservation. The objective of this work therefore was to assess the population dynamics of *D. gliroides* and the possible effects of natural disturbances on its abundance.

Materials and Methods

Study site.—Our study was conducted at the Reserva Municipal Llao Llao, located 30 km west from the city of San Carlos de Bariloche, Rio Negro, Argentina (41°8′S, 71°19′W). The area lies within the southern temperate forest in the biogeographic region of the sub-Antarctic province (Cabrera 1976; Mermoz and Martin 1986). The annual rainfall is ~1,800 mm and the annual average temperature is 9°C (Mermoz and Martin 1986). The canopy forests are dominated by Coihue (*Nothofagus dombeyi*—Nothofagaceae) and Ciprés (*Austrocedrus chilensis*—Cupressaceae), while Colihue bamboo (*Chusquea culeou*—Poaceae), Maqui (*Aristotelia chilensis*—Elaeocarpaceae), Maitén (*Maytenus boaria*—Celastraceae), and Chin-Chin (*Azara microphylla*—Salicaceae) are dominant plants in the shrub layer (Mermoz and Martin 1986; Garcia et al. 2009).

Capture of individuals.—We estimated the abundance of *D. gliroides* using capture–recapture techniques. We had in place 2 grids of 25 traps for 7 years (2009, 2010, 2011, 2013, 2014, 2015, and 2016). We did not sample during 2012, when a rodent outbreak occurred following a massive bamboo flowering during the previous year. The trapping grids sampled a total area of 2.5 ha, and were separated from each other by at least 150 m. We used Tomahawk traps (30 × 14 × 14 cm; Tomahawk Live Trap, Hazelhurst, Wisconsin), baited with banana and apple.

In 2009, the traps were placed in a grid design, whereas in other years we used a web arrangement because it provides better estimates of population abundance (Parmenter et al. 2003). For 2009, the distance between traps was 10 m, whereas in the following years it was 15 m. Traps were placed on branches of understory shrubs, between 1 and 2 m above ground. We sampled for 4 consecutive nights per month during January, February, March, and April of each year (total sampling effort of 800 trap-nights per year). Traps were checked at dawn and captured individuals were marked with PIT tags (model TXP148511B; Biomark, Boise, Idaho; 8.5 × 2.12 mm, 134.2 kHz ISO, 0.067 g) and released as soon as possible in the same area where they were captured. All capture and handling methods were performed according to the guidelines of the American Society of Mammalogists (Sikes et al. 2016) and approved by the authorities of the Reserva Municipal Llao Llao and by state officials of the Province of Rio Negro.

Data analysis.—We estimated abundance, survival, and recruitment using the Jolly–Seber model with robust design (Pollock 1982). Following this design, we considered the population to be open between primary periods (years) but closed during the secondary sampling periods (trap-nights) within a year (Royle et al. 2013). To consider those individuals that are part of the population but were not captured, we used data augmentation (Royle and Kery 2007). Under the concept of "data augmentation," we added "pseudo-individuals" that were never captured (their capture history is all zeros). Incorporating these zeros into the data, we introduced a latent variable that links them with the probability of being part of the population under study (Gardner et al. 2009). The model also included the effect of trap competition considering that the capture probability varies according to the number of traps open per night. The model was fitted using WinBUGS 1.4 (Bayesian analysis Using Gibbs Sampler—Spiegelhalter et al. 1996) and R 2.15.3 (R Core Team 2012). The R packages used were "coda" and "R2WinBUGS." We ran 3 Markov chains (MCMC), with 100,000 iterations, and discarded the first 50,000. The initial values for all the parameters were assigned by random functions, and we used vague priors. We checked the convergence and autocorrelation of the 3 MCMC. Model specification is provided in Supplementary Data SD1. The population densities were calculated from the estimated population abundance, and the effective sampling area estimated as the grid area plus a buffer area of a width half of the largest recapture distance (Parmenter et al. 2003).

Results

A total of 556 captures of *D. gliroides*, including 280 recaptures and corresponding to 276 individuals, was obtained during the

7 years of trapping (Table 1). Total capture success (captures/trap-nights * 100) was 13.9% (Table 1). The total number of captures fluctuated throughout the years, being highest in 2011 (n = 168) and fewest in 2013 (n = 45; Table 1). Captures of rodents were less than 10 in every year except 2010, when more than 60 rodents were captured (Table 1).

The highest abundances of *D. gliroides* were recorded in 2009, 2010, 2011, and 2014. The mean values of posterior distributions for the abundance of these 4 years were 111, 92, 105, and 84 individuals, respectively. The 95% highest density probability (HPD) intervals were 92–130 individuals in 2009, 74–111 individuals in 2010, 89–122 individuals in 2011, and 71–99 individuals in 2014, showing overlap between these years (Fig. 1). The lowest abundances were recorded in 2013, 2015, and 2016, with the overall lowest abundances observed in 2013. The mean values of the posterior distributions of the abundance for those years were 56, 58, and 65 individuals, respectively. The HPD intervals overlap between years; there were 42–68 individuals in 2013, 47–72 individuals in 2015, and 54–77 individuals in 2016 (Fig. 1; Table 1).

Survival rate showed a similar pattern to that observed for the rate of captures and abundance. During the seasons 2011–2013 and 2014–2015, survival rate was lower than in other seasons (Fig. 1). Survival rate increased a little between 2013–2014, and 2015–2016, reaching the same rate as that in the 2009–2010 season. In the 2010–2011 season, the survival rate was higher than in all other seasons. However, recruitment did not show the same pattern as survival and abundance. The values were constant in most years with an increase from 2013 to 2014 and 2015 to 2016 (Fig. 1).

Discussion

Abundance of *D. gliroides* varied between 56 and 111 individuals between years. Previous studies on *D. gliroides* carried out in Chile and Argentina indicated that the continental population has densities between 19 ± 6 and 27 ± 4 individuals/ha (Fonturbel et al. 2012). The densities estimated for our study site in 2009, 2010, 2011, and 2014 were similar to densities reported previously in other studies; however, for 2013, 2015, and 2016, the densities were reduced to between 12 and 15 individual/ha. The decrease in density found for these years could be related to a series of associated natural disturbances and ecological factors.

Several natural disturbances—the eruption of the Puyehue-Cordón Caulle volcano, the flowering of the bamboo and subsequent rodent outbreak, or dry summers—occurred between 2009 and 2015 in the study area. The major disturbances were the volcano eruption during the fall of 2011, and the massive bamboo flowering with the subsequent rodent outbreak that occurred during the springs of 2010 and the summer of 2012, respectively. Between 2011 and 2013, *Dromiciops* populations decreased dramatically, from around 100 individuals to near 50 individuals. The bamboo flowered in the spring (October–December) of 2010, generating a great source of food in the fall of 2011 (≈ 3,000 seeds/m^2, or 18 g/m^2; R. D. Sage, Sociedad Naturalista Andino Patagónica, pers. comm.). The great source of food was followed by a rodent outbreak that peaked in the summer of 2012. The increased number of rodents was associated with an increased number of avian predators (particularly, the owls *Tyto alba* and *Strix rufipes*) in the area. The rodents and *D. gliroides* share avian predators such as *S. rufipe*s. The low abundance of the marsupial observed in 2013 could be explained as a case of apparent competition (Sinclair et al. 1998).

Another ecological factor associated with bamboo flowering is the change in understory structure. Bamboo dies after flowering (during 2011), decreasing the "connectivity" between plants in the understory. Particularly for *D gliroides*, connectivity plays an important role in the conservation of the species (Fonturbel and Jimenez 2011; Tiribelli 2014). Since forest connectivity influences animal dispersal, habitat loss caused by the death of the bamboo will have an important effect on population dynamics (Koprowski 2005; Lancaster et al. 2011). Habitat loss can cause lost shelters, reduced foraging areas, and greater exposure to predation for *D. gliroides*. Also, the loss of connectivity could influence the mobility of individuals and therefore reduce the probability of capture observed at 2013. In addition to bamboo flowering, the volcano Puyehue-Cordón Caulle (40°02′S, 70°14′W) erupted in 2011, covering the study area with ash. Puyehue-Cordón Caulle dispersed about 100 million metric tons of ash, covering about 7.5 million ha in Patagonia, Argentina (Gaitan et al. 2011). Concurrent studies to ours showed that volcanic ash affected the abundance of insects in the area (Masciocchi

Table 1.—Number of captures, recaptures, individuals captured, percentage recaptures, capture success, rodent captures, abundance estimated with the model, and density (abundance/area) estimated for each year for *Dromiciops gliroides* in Reserva Municipal Llao Llao, Argentina, during 7 sampling seasons.

Year	Number of captures	Number of recaptures	Individuals captured	% recaptures	Capture success	Rodents captured	Abundance estimated with the model	Density (Individuals/ha)
2009	152	80	72	53	19.25	2	111 ± 10	25 ± 2.22
2010	95	43	52	45	11.87	66	92 ± 10	20 ± 2.22
2011	168	100	68	60	21	7	105 ± 9	23 ± 2.00
2013	45	12	33	27	5.63	6	56 ± 7	12 ± 1.55
2014	96	45	51	47	12	3	84 ± 7	19 ± 1.55
2015	67	32	35	48	8.37	7	58 ± 7	13 ± 1.55
2016	77	32	45	42	9.625	6	65 ± 6	15 ± 1.33
Total	556	280	276	50	13.9	91		

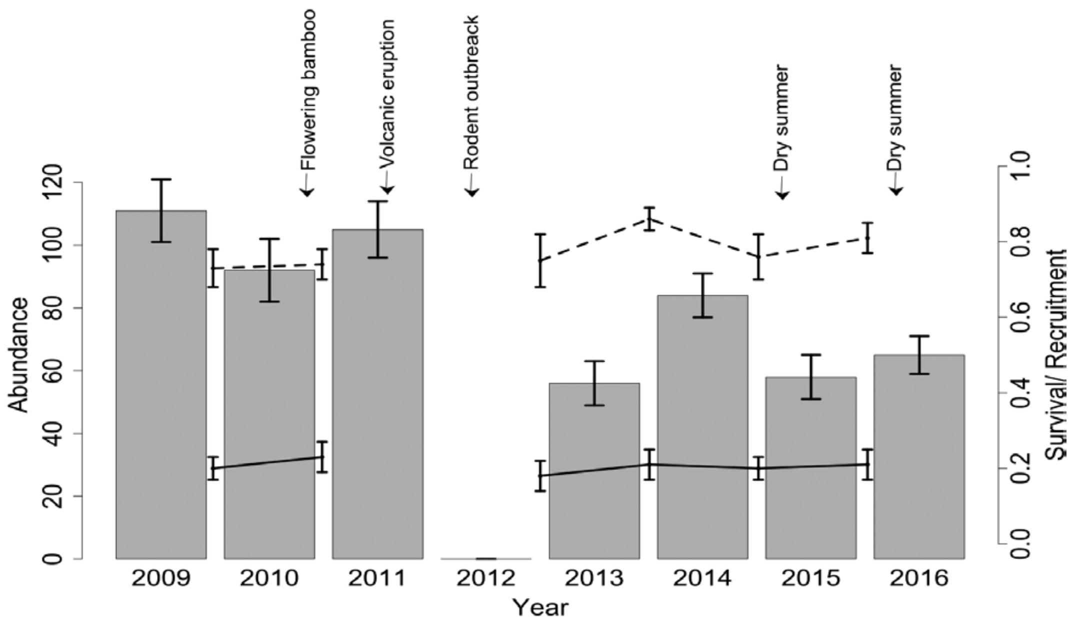

Fig. 1.—Population fluctuation of *Dromiciops gliroides* at Llao Llao Reserve, Argentina, in relation to disturbances and extreme climatic events. Abundance (bars), survival (continuous line), and recruitment (dotted line).

et al. 2013). Other studies reported that volcanic ash adheres to the body cuticle of insects and is toxic to them (Buteler et al. 2011). Insects, mainly Lepidoptera and Coleoptera, are important items in the diet of *D. gliroides* (Amico et al. 2009). The effect of ash on insect populations may have affected food availability for *D. gliroides* and hence their abundance. The combination of these 3 events (bamboo flowering, rodent outbreak, and volcanic eruption), operating individually or together, may be the cause of the decline in the abundance of the marsupial in 2013.

The abundance of *D. gliroides* increased after these events, and by 2014 reached values similar to previous seasons. These values could indicate that the population recovers after the disturbances. However, in 2015 and 2016, the population declined again. The 2nd reduction may be related to the drought that occurred in the study area during these seasons (Supplementary Data SD2). Droughts can directly increase the deaths of individual animals (Gould et al. 1999), and this may have happened in this marsupial population. Droughts can affect the growth and maturity of fruits (Ogaya and Peñuelas 2007). Fruits of several plant species are important in the diet of *Dromiciops* (Amico et al. 2011), and if changes in the growth and maturation of these fruits occur, then declining food availability may adversely affect *Dromiciops* abundance.

The pattern of survival and recruitment rates was similar to the pattern observed in the number of captures and abundance (Table 1). Studies of recruitment and survival rates of *Dromiciops* have not been carried out before. However, there are studies that have evaluated survival rates and recruitment of other small mammals. Most studies show great variability by species regarding these rates (Lima et al. 2003; Marescot et al. 2015; Larsen et al. 2016). There are several cases, mainly in rodents, where rates increase in the year following disturbances similar to those that occurred in the study area for *D. gliroides* (Fisher and Wilkinson 2005; Banks et al. 2010; Griffiths and Brook 2015).

This study shows that fluctuation in the population of *D. gliroides* over the years could be related to effects of natural disturbances on population abundance. Although *Dromiciops* have shown a great ability to recover from such disturbances, the occurrence of multiple and consecutive disturbances could affect their populations. There are few long-term studies that evaluate the population dynamics of marsupials, and it is important to conduct studies where the population can be evaluated over time, particularly in species that play a key role in the ecosystem such as *D. gliroides*.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Description of model (Jolly–Seber) used in this work.

Supplementary Data SD2.—Annual and summer rainfall during the last 20 years in the study site.

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