

# The ecology and evolution of the Monito del monte, a relict species from the southern South America temperate forests

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## Abstract

The arboreal marsupial Monito del Monte (genus *Dromiciops*, with two recognized species) is a paradigmatic mammal. It is the sole living representative of the order Microbiotheria, the ancestor lineage of Australian marsupials. Also, this marsupial is the unique frugivorous mammal in the temperate rainforest, being the main seed disperser of several endemic plants of this ecosystem, thus acting as keystone species. *Dromiciops* is also one of the few hibernating mammals in South America, spending half of the year in a physiological dormancy where metabolism is reduced to 10% of normal levels. This capacity to reduce energy expenditure in winter contrasts with the enormous energy turnover rate they experience in spring and summer. The unique life-history strategies of this living Microbiotheria, characterized by an alternation of life in the slow and fast lanes, putatively represent ancestral traits that permitted these cold-adapted mammals to survive in this environment. Here we describe the ecological role of this emblematic marsupial, summarizing the ecophysiology of hibernation and sociality, actualized phylogeographic relationships, reproductive cycle, trophic relationships, mutualisms, conservation and threats. This marsupial shows high densities, despite presenting slow reproductive rates, a paradox that is explained by the unique characteristics of its three-dimensional habitat. We finally suggest immediate actions to protect these locally abundant but globally threatened species.

## Introduction: relictual lineages, marsupials and *Dromiciops*

The discovery of living representatives of groups that were thought long extinct opens a window in time to improve our understanding of their biology, as they represent invaluable material to test evolutionary hypotheses on adaptation. These relict species (sensu Habel, Assman, Schmidtt, & Avise, 2010) generate an enormous amount of valuable knowledge regarding ecological, morphological, and physiological traits of past lineages, as they could serve as a ‘window to the past’ that allow us to understand the conditions that allowed them to survive for so long (Habel et al., 2010; Tan, Kelly, & Jiang, 2013; Yoder et al., 2010). Here we address one of these cases, the relict monito del monte (“little mountain monkeys”, with two recognised species, *Dromiciops gliroides* Thomas 1894 and *D. bozinovici* D’Elia et al. 2016), an outstanding

mammal from southern South America. From fossil evidence (Goin & Abello, 2013) and ancestral habitat reconstruction of present-day marsupials (Mitchell et al., 2014), this marsupial (*Dromiciops*, hereafter) seems to have retained the ecological niche of its Gondwanan marsupial ancestors.

The ancestors of Marsupialia (crown-clade Metatheria) diverged from placental mammals (crown-clade Eutheria) at least 125 Mya in Laurasia (Bi et al., 2018; Luo, Yuan, Meng, & Ji, 2011), originating in today's China and spreading to North America, where the earliest evidence of true marsupials is known (O'Leary et al., 2013). Those early mammals remained confined to Laurasia until the late Cretaceous, when they dispersed to Gondwana, following a North America – South America path. About the same time, they suffered particularly dire consequences of the KT extinction in Laurasia, which ultimately drove them to extinction on the supercontinent (Case, Goin, & Woodburne, 2005; Sanchez-Villagra, 2013). In South America, marsupials thrived and diverged, eventually spreading further south and reaching Antarctica about 65–70 Mya (Mitchell et al., 2014), presumably via dispersal of Microbiotherians (Nilsson et al., 2010; Prevosti, Forasiepi, & Zimicz, 2013). This order reached Australia through Antarctica and gave origin to Australasian marsupials, which dominated the continent and adjacent islands, occupying much the same ecological niches that placental mammals did in every other continent (Long, Long, Archer, Flannery, & Hand, 2002; Mitchell et al., 2014).

Today, marsupials are taxonomically less diverse than placental mammals, but their long and often isolated evolutionary history has resulted in a comparable morphological and ecological diversity (Sanchez-Villagra, 2013). Extant marsupials are grouped into three American (Didelphimorphia, Microbiotheria, and Paucituberculata) and four Australasian orders (Dasyuromorphia, Diprotodontia, Notoryctemorphia, and Peramelemorphia). The evolutionary relationships among marsupial orders have long been assessed using a wide range of methods that have often yielded contradictory and intensively debated results. Particularly puzzling is the position and origin of Microbiotheria. In this regard, Szalay (1982) proposed that Microbiotheria is nested within the modern Australasian clade: Australidelphia (Meredith, Westerman, Case, & Springer, 2008; Nilsson et al., 2010). The revolution of genetic and genomic methods during the last couple of decades has helped to disentangle the topology of the marsupial phylogeny (Eldridge, Beck, Croft, Travouillon, & Fox, 2019), clearly positioning *Dromiciops* within Australidelphia, the sister group of all living Australasian marsupials (Euaustralidelphia) and confirming the monophyly of the rest of American marsupials (Duchêne et al., 2018; Mitchell et al., 2014).

### Updated phylogeographic affinities within *Dromiciops*

*Dromiciops* distribution extends from the Chilean Pacific Coast in the west to the slopes of the Chilean Andes in the east and from the Maule Province at the north (35°S) to the Palena Province at the South (44°S) (Mejías et al., 2021; Oda, Rodríguez-Gómez, Fontúbel, Soto-Gamboa, & Nespolo, 2019). In Argentina, *Dromiciops* is distributed along the Andes, from Neuquén to Chubut provinces (Figure 1). A small fraction of these habitats (7%, according to Martin, 2010) corresponds to the central valley of Chile (shrubland-type or Maulino forest habitats); while the temperate rainforest represents the remaining 93% of its distribution (Lobos, Charrier, Carrasco, & Palma, 2005; Martin, 2010; Saavedra & Simonetti, 2001; Uribe, Chiappe, & Estades, 2017). In addition to being drier than the typical wet rainforest, the habitats occupied in the Chilean central valley receive more sunlight and have more fruits available during the summer (Fontúbel, Salazar, & Medel, 2017a). This distribution is much smaller than the past distribution of Microbiotheria, which encompassed Bolivia, Rio de Janeiro (Middle Palaeocene), Argentinian Patagonia, and the Seymour Island in Antarctica (Hershkovitz, 1999). Such distributional shrinking likely reflects major climatic changes, as the original Microbiotheria distribution (during the Miocene) was dominated by a subtropical-humid climate, similar to the present-day *Dromiciops* habitat.

<Figure 1 about here>

The first phylogeographic analysis of *Dromiciops* populations was performed using two mitochondrial genes (Himes, Gallardo, & Kenagy, 2008), identifying three main clades that displayed geographic structure (northern: clade "A", central: clade "B", and southern: clade "C" clades). Most interestingly, this study reported

sequence divergence between clades A and C of 11.3%, 15.1% between A and B, and 8.2% between B and C, markedly differentiated northern and southern clades later confirmed by Valladares-Gómez et al. (2019) using microsatellite markers. According to Himes et al. (2008), *Dromiciops* populations could have diverged in the Quaternary (1–1.8 Myr) before the last glacial maximum (~20,000 yr ago), but the deep divergence based on mitochondrial DNA suggests that these could be even older and paleontological evidence appears to agree with older divergences. Fossil evidence indicates that *Dromiciops* may be morphologically indistinguishable with *Microbiotherium*, a genus that lived between the late Oligocene and early Miocene (~29–16 Myr; Goin & Abello, 2013), which includes at least four extinct species and is considered the sister group of *Dromiciops* (Figure 2). Therefore, if *Dromiciops* is as old as these extinct lineages, this would suggest that the whole clade is as old as the Andes mountain range (Charrier, Pinto, & Rodríguez, 2006), and older than the scission of the Chiloé island (ca. 10,000 years ago; Watters & Fleming, 1972). This would explain the similarities between insular and continental populations and between Argentinean and Chilean populations. The time-calibrated phylogenetic reconstruction of these clades provided recently by Quintero-Galvis et al. (2021) confirmed the paleontological dating of Goin and Abello (2013) and the Miocene origin of the genus.

<Figure 2 about here>

The pronounced differentiation of *Dromiciops* north-south populations together with the important morphological differentiation observed across this range have even inspired the proposition of new *Dromiciops* species (D'Elía, Hurtado, & D'Anatro, 2016). This idea, however, sparked an immediate debate based on species delimitation criteria, morphological comparisons, and genetic evidence (Martin, 2018; Valladares-Gómez, Celis-Diez, Palma, & Manríquez, 2017). Two subsequent studies (Suárez-Villota et al., 2018; Valladares-Gómez et al., 2019) contributed new genetic data and confirmed the existence of the “Northern” and “Southern” clusters of *Dromiciops*, but differentiation between these groups was not sufficient to warrant recognition as different species. Still, these studies covered a small percentage of this species large (~1200 km) geographic range. The most complete geographic sampling of *Dromiciops* populations to date was provided by Quintero-Galvis et al. (2021), who resolved genetic distances for 31 localities covering the whole geographic range for the genus. Using two mtDNA and four nuclear genes, these authors proposed four clades, being the northernmost clade different enough from the other three to be considered as a different species (*Dromiciops bozinovici*). Another study by the same authors, using RAD sequencing (1856 variant SNPs), confirmed these results and proposed that the clade “C”, defined by D'Elía et al. (2016) as *D. mondaca*, to be redefined as a subspecies of *D. gliroides* (Quintero-Galvis et al., 2022).

Phenotypically, the two *Dromiciops* species differ mainly in the fur coloration, and the size of muzzle and ears. In general, *D. bozinovici* has fur that is lighter in coloration and shorter muzzle and ears than *D. gliroides* (see Figure 3). Behaviorally, *D. bozinovici* appears to have lower activity levels and reactivity to human presence and perhaps lower resting metabolism (RFN, personal observation) (Mejías et al., 2021). Both species are small (20–30 g, 110 mm snout-vent length) arboreal mammals (~30 g, 110 mm snout-vent length), with broad carnivorous-frugivorous habits (Vazquez, Rodríguez-Cabal, Gonzalez, Pacheco, & Amico, 2018; Vazquez, Zamora-Nasca, Rodriguez-Cabal, & Amico, 2021), social, sexually non-dimorphic, and are found on trees as high 30 m high in mature broadleaf forests (Godoy-Güinao, Díaz, & Celis-Diez, 2018). As with other marsupials, they accumulate fat reserves in the body and tail, which is also prehensile. *Dromiciops* individuals are well adapted to arboreal life; they have opposable thumbs on all four limbs, exhibiting great precision and agility when they move through the canopy. They can run vertically up the bark of the *Nothofagus* at speeds of up to 1 m/s and can leap with enormous precision between distant branches up to one meter far (Balazote-Oliver, Amico, Rivarola, & Morales, 2017; Mejías et al., 2021). This is attained by visual and cerebellar adaptations to discriminate distances in absolute darkness (di Virgilio, Amico, & Morales, 2014; Gurovich & Ashwell, 2020), and most likely given their Australidelphia trichromate condition (colour vision in the ultraviolet-infrared spectrum; (Arrese, Hart, Thomas, Beazley, & Shand, 2002). The recent discovery that *Dromiciops* fur fluoresce pink with UV light supports this idea. This is also possible to adapt for inter-individual recognition in the dark (Y. Gurovich and R. Nespolo, personal observation). Thus, it is highly probable that *Dromiciops* can identify the colour of the fruits in almost complete darkness, and in turn, detect each other with visible colouration patterns in the ultraviolet zone, as in platypuses and

springhares (Anich et al., 2021; Olson et al., 2021).

<Figure 3 about here>

### The “conservative” reproduction of *Dromiciops*

Although the basic biology of *Dromiciops* has been historically considered poorly known, this situation has drastically changed in the last decades, as several populations have been studied in detail by Latin American researchers (e.g., Balazote-Oliver et al., 2017; Celis-Diez et al., 2012; Fontúrbel, Franco, Rodríguez-Cabal, Rivarola, & Amico, 2012; Franco, Quijano, & Soto-Gamboa, 2011; Kelt, Meserve, Patterson, & Lang, 1999; Meserve, 1981; Meserve, Lang, & Patterson, 1988; Patterson, Meserve, & Lang, 1989). Inappropriate capture methods (Fontúrbel, 2010; Fontúrbel & Jiménez, 2009), but also lack of knowledge about its seasonal activity patterns led to a large underestimation of its densities (Fontúrbel & Jiménez, 2011; Franco et al., 2011; Nespolo, Verdugo, Cortes, & Bacigalupe, 2010). For example, captive *D. gliroides* individuals seem to be more active during summer than during other seasons (Aizen, 2003; Kelt & Martínez, 1989), but only recently, several authors have studied *Dromiciops* activity in the field. For instance, Fontúrbel, Candia, and Botto-Mahan (2014) found that this species presents a nocturnal activity (from 19:00 h to 07:00 h), with a significant monthly variation related to resource abundance and distribution, closely related to fleshy fruit availability (di Virgilio et al., 2014; Fontúrbel, Salazar, & Medel, 2017b).

Historical descriptions (Hershkovitz, 1999; Mann, 1978; Muñoz-Pedreros, Lang, Bretos, & Meserve, 2005) indicate that *Dromiciops* is relatively long-lived, with reports of 5–6 years-old individuals captured in the field (Balazote-Oliver et al., 2017). According to Muñoz-Pedreros et al. (2005), *D. gliroides* reproductive cycle is divided into seven stages. They attain sexual maturity at the second year of age and start reproducing in August-September (stage I: pair formation), then producing 1–4 pups (females have four nipples) that develop in the uterus for about a month (stage II: intra-uterine development), and approximately in early November they migrate to the marsupium (stage III: parturition) and start lactation (stage IV: intra-marsupium development). Most Australian marsupials are characterised by secreting milk of different compositions from different mammary glands, in close concordance to the development stage of the young (Pharo, 2019; Renfree, 1981), which is unknown for this marsupial. During the austral summer (December–January), pouched young abandon the marsupium for short exploratory excursions. However, they do not stop suckling and use the nest as a centre for home-range activities (stage V: extra-marsupium development) (Figure 4). Finally, juveniles join family excursions during February (stage VI: nocturnal family excursions), coinciding with the elevated trapping success usually reported. Then, juveniles become independent in March (Stage VII: juvenile independence) and start preparing for hibernation (see below). A summary of *Dromiciops* annual cycle is presented in Figure 5.

<Figures 4 and 5 about here>

This extended *Dromiciops* breeding (i.e., 20 days of gestation and 70 days lactating), which is also energetically very extenuating and energy consuming, is combined with a low reproductive output. For instance, a female *Dromiciops* individual can produce a maximum of four offspring in a single reproductive event each year and become fertile at the second year. This represents a reproductive output of two new individuals per year (Nespolo et al., 2022). In comparison, opossums (*Thylamys elegans*, for instance, which is sympatric with *D. bozinovici* in its northern distribution range) produce up to 16 individuals per reproductive event, which attain sexual maturity at the first year. This translates into a (a maximum) reproductive output of 16 individuals per year, eight times the value for *Dromiciops* (assuming only one breeding period per year). Similarly, the poorly known sympatric marsupial *Rhyncholestes raphanurus* (Caenolestidae) has been described to have continuous reproduction at any moment of the year, with a maximum litter size of seven young individuals (Iriarte, 2008). Reproduction in *Dromiciops* is followed by a fattening period in which animals forage frenetically to gain weight for hibernation, which starts in autumn. The peak of energy expenditure occurs during lactation, which is the longest recorded in marsupials and in *Dromiciops* extends from December to January. To compensate for the high energy expenditure of this extravagant way of life, *Dromiciops* must reduce energy expenditure in the cold period, which is achieved by hibernation.

## Daily, seasonal, and “hot” torpor in *Dromiciops*

The seasonal regulation of energy balance is a key concept in mammalian life histories (Harvey, Pagel, & Rees, 1991), and hibernation—a distinctive characteristic of *Dromiciops*—represents the evolution of “slow” life histories (Turbill, Bieber, & Ruf, 2011). *Dromiciops* spend six months a year in this lethargic condition, constraining the activity period to spring and summer (Figure 5). In eutherian hibernators, there is a marked cycle of adiposity, where animals accumulate fat during summer to be consumed during hibernation, without ingesting any food during this period (Humphries, Kramer, & Thomas, 2003; Humphries, Thomas, & Speakman, 2002; Toien et al., 2011). In *Dromiciops*, this cycle is unclear as they ingest food whenever they find it, which can happen even during interbout arousals when hibernating (Franco, Contreras, Place, Bozinovic, & Nespolo, 2017; Nespolo et al., 2020). In this section, we discuss distinctive aspects of seasonality and energetics of *D. gliroides*: its capacity for daily, seasonal torpor and aestivation (torpor in response to hot and dry conditions).

Hibernation (also known as “seasonal torpor”; Geiser & Ruf, 1995) was first described in placental mammals of the northern hemisphere (e.g., squirrels, marmots, hamsters, bears; Melvin & Andrews, 2009), where a clear pattern of seasonal metabolic depression in autumn and winter is distinguished from continuous periods of activity in spring and summer (Geiser, Currie, O’Shea, & Hiebert, 2014; Heldmaier, Ortmann, & Elvert, 2004). This is functionally different from daily torpor, which consists of short and shallow bouts of metabolic depression of a few hours that occur at any moment of the year and is characteristic of several bat and marsupial species (Geiser, 2013; Ruf & Geiser, 2015). *Dromiciops* seems to do both, as was confirmed recently by a set of experiments under semi-natural enclosures, indicating that in winter, animals experience seasonal torpor with multiday torpor episodes lasting 5 to 10 days, which together represents a net energy savings of 90% compared to animals that did not hibernate (Mejías, Sabat, Franco, Bozinovic, & Nespolo, 2022). This complemented older studies indicating that *Dromiciops* experiences a dynamic form of torpor, including daily torpor of a few hours, at any moment of the year, whenever food or water is scarce (Nespolo, Fontúbel, et al., 2021). A novel aspect of *Dromiciops* torpor was recently revealed when animals under hot torpor (also known as aestivation: metabolic depression under hot and dry conditions) were discovered in the field (Nespolo, Fontúbel, et al., 2021). These authors described torpor in summer, with temperatures above 25°C and water was scarce. The same study described torpor in females with pups at the marsupium (pups were also in torpor, see Fig 2 in Nespolo, Fontúbel, et al., 2021). When entering into winter torpor, animals experience a metabolic shut-down followed by passive cooling, to a limit of about -0.5°C in the tissues, and then they start thermoregulating in torpor in order to avoid freezing (Mejías et al., 2022; Nespolo, Fontúbel, et al., 2021). The whole transition from normothermia to torpor lasts 4-6 hours (Cortés, Franco, Moreno-Gómez, Barrientos, & Nespolo, 2014), and happens in the nest, normally in groups of two to five individuals (Franco et al., 2011; Nespolo, Fontúbel, et al., 2021), but arousal can be as rapid as in 30–150 minutes, depending on ambient temperature (Mejías et al., 2022; Nespolo, Fontúbel, et al., 2021). These costly rewarming events are bursts of aerobic activity that could account for 25% of the energy consumed during hibernation (Mejías et al., 2022). Rewarming during hibernation have a typical frequency in winter of about twice a month (Nespolo, Fontúbel, et al., 2021; Nespolo, Mejías, et al., 2021), which explains why long-term energy savings during hibernation (90%) are lower than the energy reduction estimated from a single torpor bout (96%, see Mejías et al., 2022). The extreme capacity to endure under-zero temperatures of hibernating *Dromiciops* explains its presence in high Andean locations such as Altos de Lircay at the northern edge of the distribution (Mejías et al., 2021), Llao Llao in Argentina (Rodríguez-Cabal, Amico, Novaro, & Aizen, 2008) or Futaleufú at the southern limit (Oda et al., 2019). The seasonal cycle of hibernation-activity of *Dromiciops* define an annual energy budget with profits and loss, that the animal modulates precisely in order to give an overall positive balance (Figure 6).

<Figure 6 about here>

## Social thermoregulation and communal nesting

Extensive fieldwork has shown that *D. gliroides* nests and hibernates communally, in tree holes or bamboo stems but, in some cases, nesting occurs with animals individually curled up instead of grouped in the nest

(Figure 7a). Nests built by *D. gliroides* are spherical, with a single entrance, built with plant materials from *Chusquea*spp. leaves, *Hymenophyllum* spp. ferns, and lined with many moss species (Figure 7b). Occasionally, nests are used more than once, although they prefer to build new ones. Based on these observations, Franco et al. (2012; 2011) and Celis-Diez et al. (2012) showed that communal nesting is common in *D. gliroides* using nest-boxes in two localities of southern Chile (near Valdivia and in Chiloe), with a mean of 2.3 animals per nesting box. Monitoring of nest boxes suggested that *D. gliroides* is resident throughout the year and uses torpor during cold seasons. Ageing negatively correlates with *D. gliroides* communal nesting, as juveniles usually nest in groups (17% are found nesting solitary), whereas adults usually nest solitary (83% found nesting solitary; Celis-Diez et al., 2012). Neither sex nor body mass seems to influence communal nesting in *D. gliroides*. Several Australian marsupials (Baker & Dickman, 2018), American rodents (Arnold, 1988; Boyles, Storm, & Brack, 2008; Bustamante, Nespolo, Rezende, & Bozinovic, 2002; Edelman & Koprowski, 2007; Schradin, Schubert, & Pillay, 2006; Viñals, Bertolino, & Gil-Delgado, 2017; Wilson, O'Riain, Hetem, Fuller, & Fick, 2010), and Neotropical bats (Roverud & Chappell, 1991) obtain significant energetic savings by hibernating in groups (Gilbert et al., 2010). This phenomenon remains little explored in *D. gliroides*. Preliminary laboratory measurements indicate, however, that grouped individuals do not benefit from thermoregulatory savings during torpor (Franco et al., 2012), which suggests that for *D. gliroides*, the energetic benefits of communal nesting are secondary to the benefits of sociality itself (Boix-Hinzen & Lovegrove, 1998; Ebensperger, 2001; Schradin et al., 2006). These observations were confirmed by recent mesocosms experiments performed in hibernating individuals in the field using thermographic images, which suggest that clustered *D. gliroides* do not conserve heat better than animals hibernating in isolation (Nespolo, Fontúbel, et al., 2021; Figure 7c). These individuals were not related, discards the idea that communal nesting is driven by kin relatedness or parental care (Franco et al., 2011; see Figure 7d).

<Figure 7 about here>

### The “all-purpose” trophic strategy of *Dromiciops*

The common name “monito del monte” refers to the arboreal habits of this marsupial, which includes opposable thumbs and a prehensile tail, resembling a small primate. They move relatively long distances (home range:  $1.6 \pm 0.6$  ha) (Fontúbel et al., 2012), across the canopy, reaching 30 meters of height (Godoy-Güinao et al., 2018), and speeds of 1 m/s (3.7 km/h, see Mejías et al., 2021), which for a 20–30 g mammal is extremely fast (e.g., Djawdan & Garland, 1988). Their agility in forest canopies permits these animals to forage efficiently on a variety of food items, for which qualitative descriptions exist, based on faecal analysis and laboratory preference trials (Amico, Rodríguez-Cabal, & Aizen, 2009; Celis-Diez et al., 2012; Cortés, Franco, Sabat, Quijano, & Nespolo, 2011; di Virgilio et al., 2014; Meserve et al., 1988; Quijano, 2008). These studies have shown that *D. gliroides* does not appear to be selective (contrarily to other mammals, which select food items with specific nutrient composition, see Torres-Contreras & Bozinovic, 1997; Woods, 2009), but rather opportunistic (i.e., dietary composition follows environmental availability, see Bozinovic, Muñoz, Naya, & Cruz-Neto, 2007; Cortés et al., 2011; Quijano, 2008). However, *Dromiciops* cannot fulfil its nutritional requirements only from fruits or insects. Contrarily, it needs a mixed diet of fruits and insects to maintain a healthy body condition and a proper energy balance (Cortés et al., 2011). It is well established that differences in the digestive physiology of vertebrates reflect the historic levels of specific substrates of the natural diets, linking digestive enzyme activity, dietary flexibility, and digestive plasticity in an evolutionary context (Ramirez-Otarola, Narvaez, & Sabat, 2011; Sabat, Lagos, & Bozinovic, 1999; Sabat, Novoa, Bozinovic, & del Rio, 1998). Therefore, the digestive physiology of *D. gliroides* supports the hypothesis that digestive capabilities are a necessary—but not an essential—component for explaining dietary selection (Bozinovic & Martínez del Río, 1996; Cortés et al., 2011; Silva, Jaksic, & Bozinovic, 2004; Veloso & Bozinovic, 2000).

Fruit availability represents a strong driver of *Dromiciops* dietary habits. They select individual fruits according to their size and colour, exerting important selective forces on plant populations (Fontúbel & Medel, 2017), performing long foraging trips to disturbed forest stands to consume fleshy fruits (Amico, Rodríguez-Cabal, & Aizen, 2011; di Virgilio et al., 2014; Mora & Soto-Gamboa, 2011; Salazar & Fontúbel, 2016). In

fact, *Dromiciops* consumes fruits from at least 16 species of shrubs, trees, vines, and particularly from the hemiparasite mistletoe *Tristerix corymbosus* (see Table 1 in Amico et al., 2009). Then, considering the assorted nutrient content on *Dromiciops*' diet, an interesting set of questions arises, such as how these requirements vary among individuals at different ontogenetic stages (Maldonado et al., 2016), or if they exhibit ontogenetic trophic niche shifts as a logic outcome (Araujo, Bolnick, & Layman, 2011; Schoener, 1971). Furthermore, considering that male and female marsupials invest energy differently during the reproductive period, ecological sexual dimorphism in diet selection could be expected (Araujo et al., 2011; Schoener, 1971). This is an interesting avenue that can be explored, for instance, using the most recent technologies in stable isotope analysis (Maldonado, Bozinovic, Newsome, & Sabat, 2017).

### Frugivory: A Retained Characteristic of Microbiotheria?

The mutualistic relationships between *Dromiciops* and several endemic plants can be traced back in time to their ancestors. These facts furnish fascinating ideas about the trophic habits of past Microbiotheriids and their eco-evolutionary relationships with the temperate flora of southern South America, which may have coevolved during millions of years. Highly specific and asymmetric (i.e., uneven dependence between the plant and the animal) interactions have appeared, such as the seed dispersal relationships between *Dromiciops* and the hemiparasitic mistletoe *Tristerix corymbosus* (Aizen, 2003; Amico & Aizen, 2000).

Recent work suggests an inter-dependence between *Dromiciops* and *Tristerix*, which may also reflect an ancient association between microbiotheriids and mistletoes. Successive phylogenetic reconstructions have pushed the origin of mistletoes back further in time (Liu et al., 2018; Nickrent, Malécot, Vidal-Russell, & Der, 2010), with the growth habit now estimated to have transitioned from root parasite to aerial parasite in the Loranthaceae during the early Eocene (approximately 50 million years ago). Based on fossil reconstructions and the modern-day distribution of lineages on either side of this transition, it is estimated that the shift from understorey up to the canopy occurred in western Gondwanaland. This time is 20 to 30 million years prior to the origin of the modern frugivorous birds, the main dispersers of Loranthaceae mistletoes today (Liu et al., 2018). This temporal mismatch between the origins of mistletoes and their seed dispersers has been previously noted, as early Microbiotheriids are invoked as the most probable agents of mistletoe dispersal prior to the diversification of songbirds (Amico & Aizen, 2000; Restrepo, Sargent, Levey, & Watson, 2002). Recently, this idea has been taken one step further by Watson (2020), who suggested Microbiotheriids may have been indeed the selective agents responsible for the transition within Loranthaceae from root-parasitic shrubs to stem-parasitic mistletoes. By consuming fruits from understorey shrubs and dispersing them up to the canopy, *Dromiciops* ancestors catalysed the switch in growth habit to the upper canopy, where transitional forms likely parasitised the roots of vascular epiphytes like the present-day *Gaiadendron* (Restrepo et al., 2002).

### Ecological Role and Interactions

Seed dispersal by Didelphid marsupials has been widely reported in tropical forests (Cáceres, 2002; Santori, De Moraes, & Cerqueira, 1995, 2004). A few marsupial species have also been involved in seed dispersal interactions in Australia (Ballardie & Whelan, 1986; Bass, 1990; Dennis, 2003) and even in New Zealand, where they are non-native (Dungan, O'Cain, Lopez, & Norton, 2002; Williams, Karl, Bannister, & Lee, 2000). The high incidence of frugivory and seed dispersal on *Dromiciops* is remarkable among American and Australian marsupials, posing interesting questions about the coevolutionary processes that shaped the temperate rainforest's native flora. Recent work in Madagascar has uncovered comparable inter-dependence between mistletoes and mouse lemurs (Cheirogaleidae). As with *Dromiciops*, these small mammals are active throughout the canopy and act as principal dispersers of mistletoe seeds in their habitats. They also undergo prolonged periods of torpor/hibernation during periods of low resource availability (Génin & Rambeloarivony, 2018 and references therein).

Mistletoes are shrubby stem-parasitic plants with more than 1600 species for which dispersal represents a critical link in their life cycle (Mathiasen, Nickrent, Shaw, & Watson, 2008; Nickrent et al., 2010; Norton & Carpenter, 1998). Most of these plants depend on animal vectors for transporting their seeds from the

parent plant to the branches of competent host plants. Mistletoes produce ripe green fruits within the South American temperate rainforests, which are not easily detected by birds (as they depend on chromatic contrast). Nevertheless, *Dromiciops* are nocturnal and locate their food primarily by scent, hearing, and vision (Amico et al., 2011). Together with their capacity for colour vision at the ultraviolet-infrared spectrum (the trichromacy, discussed before), permit them to be excellent foragers at night. Seed passage through *Dromiciops* digestive tract is critical for *T. corymbosus* germination (Amico & Aizen, 2000; Amico, Sasal, Vidal-Russell, Aizen, & Morales, 2017), as revealed by experimental germination trials (close to 100% of successful germination; Amico et al., 2017). Furthermore, seed establishment is strongly favoured by *Dromiciops*' climbing behaviour, defecating seeds within suitable hosts and at adequate branch sizes (Amico et al., 2017), in turn impacting positively on the mistletoe regeneration rate in the forest (Amico et al., 2017; García, Rodríguez-Cabal, & Amico, 2009). Consequently, *T. corymbosus* abundance and distribution is spatially correlated with the presence of *Dromiciops*, both at different spatial scales (Fontúbel et al., 2017a; García et al., 2009; Rodríguez-Cabal & Branch, 2011).

The cascade of ecological services provided by *D. gliroides* extends to the whole forest community in different ways, one being the important relationship between the mistletoe *T. corymbosus* and the hummingbird *Stephanoides sephaniodes* for pollination (Aizen, 2003). This hummingbird is responsible for pollinating several species of the highly endemic woody flora in this biome (Aizen, Vázquez, & Smith-Ramírez, 2002; Armesto, León-Lobos, & Arroyo, 1996). In contrast to most temperate forests where hummingbirds migrate to warmer climates in winter, this species is resident (Aizen & Ezcurra, 1998) when *T. corymbosus* is present, serving as its principal food during this period. Hence, the mutualistic relationship between the marsupial and the mistletoe determines the distribution of the plant and may have broader evolutionary consequences. The marsupial might have allowed the mistletoe *T. corymbosus* to retain green colouration in mature fruits, a condition to which it is preadapted by a slower ripening process in temperate forest populations (Amico et al., 2011).

### Conservation, Threats, and Future Trends

As an arboreal marsupial, a key issue for *Dromiciops* persistence is its dependence on forest habitats with certain structural features (Fontúbel, Candia, Salazar, et al., 2014). Even though the IUCN updated its threat category from Vulnerable to Near Threatened in 2011, the main problem persists: habitat loss. The southern South America temperate rainforests are rapidly being cleared due to land-use change (Echeverría et al., 2006; 2007). Therefore, suitable habitat for *D. gliroides* is not only reduced but also becoming increasingly fragmented and degraded. Habitat fragmentation has a negative effect on *Dromiciops* abundance, causing local extinction in small fragments (Rodríguez-Cabal, Aizen, & Novaro, 2007), and collapsing seed dispersal services (Amico & Aizen, 2000; Amico et al., 2011). Fragmentation threatens this marsupial as it is unable to disperse through open habitats (e.g., pastureland), remaining confined to the extant forest fragments (Fontúbel, Silva-Rodríguez, Cárdenas, & Jiménez, 2010).

Although some authors have recorded *D. gliroides* in exotic plantations (Fontúbel, Candia, & Botto-Mahan, 2014; Uribe et al., 2017), a fragment of a native forest was always found in the vicinity, where they maintain their nesting sites (Salazar & Fontúbel, 2016). As a strict arboreal mammal, *D. gliroides* require a dense forest with a complex three-dimensional architecture covering the whole vertical matrix. In fact, the discovery of *Dromiciops* as high as 30 m above ground in the canopy using camera traps were expected but difficult to document precisely (Godoy-Güinao et al., 2018; Tejo & Fontúbel, 2019). Forest requirements, together with frugivorous habits, configure a strong dependence on a very special kind of ecosystem characterised by the combined presence of the native bamboo (*Chusquea* spp.) and *Nothofagus* spp. and Myrtaceae plants (Rodríguez-Cabal & Branch, 2011), influencing the particularities of *Dromiciops* nest. Nests are considered part of an organism's 'extended phenotype' (Rubalcaba, Polo, Maia, Rubenstein, & Veiga, 2016), imprinted by the same combination of environmental and genetic factors of standard phenotypic variation. In the case of Microbiotheria, several lines of evidence suggest that the nest is fundamental for their survival (Franco, Contreras, & Nespolo, 2013; Hershkovitz, 1999; Honorato et al., 2016). *Dromiciops* nests are built as an oval cavity covered by a scaffold of tightly interwoven bamboo leaves combined with mosses and *Hymenophyllum*

ferns (Celis-Diez et al., 2012). This structure is impermeable and well insulated. Some authors have also attributed antimicrobial properties to it (Honorato et al., 2016), as its thick structure and the acid pH of the *Chusquea*spp. leaves may protect from predators and have a biocidal effect against parasites and pathogens.

Since *D. gliroides* distribution and abundance are influenced by several factors (particularly bamboo and mistletoe abundance; Rodríguez-Cabal & Branch, 2011), transformed habitats can give valuable insights on *D. gliroides* persistence probabilities in a changing world. A telemetry-based study (Salazar & Fontúbel, 2016) showed that *D. gliroides* movement behaviour was similar between native and transformed habitats (and consistent with other locations reported by Fontúbel et al., 2012). However, its occurrence in transformed habitats was mainly determined by neighbouring native remnants in the landscape where *D. gliroides* nests. Animals loaf in these native patches during the day, but perform foraging trips to abandoned plantations during the night (Salazar & Fontúbel, 2016), attracted by many shade-intolerant plant species that provide abundant fruits, such as *Aristotelia chilensis*, *Rhaphithamnus spinosus*, or *Ugni molinae* (Fontúbel et al., 2017a).

Another major threat to this species is climate change. Given its hibernating habit, even a slight increase in winter temperatures can drastically affect them. In this case, heterothermy is *Dromiciops* normal condition, and it needs to hibernate during the winter to survive with the energy reserved collected during the summer (Nespolo, Mejías, et al., 2021). Thus, climate change emerges as a critical threat to this species as warmer temperatures necessitate extra energy expenditure, resulting in a lower survival probability (Nespolo, Fontúbel, et al., 2021). Furthermore, severe and prolonged droughts are a consequence of climate change and can cause moisture stress in plants. Such moisture stress causes significant reductions in flower and fruit production (Fontúbel, Lara, Lobos, & Little, 2018), indirectly reducing *Dromiciops* energy reserves. Altogether with the destruction of its habitats, climate change may relegate this species and, with it, the entire order to the fossil record if no actions are taken in the short term. Thus, *Dromiciops* local extinctions may have cascade effects in the community as a result of the loss of the seed dispersal services that this marsupial performs.

## Concluding Remarks

According to the metabolic theory of ecology (Brown, Gillooly, Allen, Savage, & West, 2004), populations that maintain a sustained (positive) rate of nutrient conversion into new individuals will persist compared to those that do not (Sibly & Calow, 1986; Sibly & Hone, 2002). This could be attained either by maximising the annual reproductive rate, which in mammals is represented by small, short-lived species (Shattuck & Williams, 2010), and in marsupials characterised by the smallest Didelphimorphia (i.e., the “fast” extreme, see Fisher, Owens, & Johnson, 2001). The “slow pace” marsupial extreme is represented by large herbivorous forms such as Vombatidae and Phalangeridae (Fisher et al., 2001). Hence, the small living Microbiotheriids, with a reproductive output of two individuals per year (Nespolo et al., 2022), fall in the “slow” extreme. In terms of the allometric predictions for life histories in marsupials, given by the equation: age at first reproduction =  $5.75 * M_B^{0.10}$  provided by Hamilton et al. (2011), a 30 g marsupial such as *Dromiciops* should have an age of first reproduction of 243 days (but it attains sexual maturity at 720 days). A similar computation for a maximum lifetime ( $=0.041 * M_B^{0.20}$ , Hamilton et al. (2011) gives 2.5 years (but in *Dromiciops*, this parameter is above 4–5 years) (Nespolo et al., 2022). Then, the high observed densities of *Dromiciops* can only be explained by low mortality and an extended reproductive period during their lifetime, an aberrant life history which can only be achieved in a complex three-dimensional habitat, such as mature temperate rainforests.

Hershkovitz (1999) proposed that Microbiotheriids’ life history is intimately associated with a combination of *Nothofagus* trees and *Chusquea* native bamboos (i.e., the *Chusquea* -*Nothofagus* -*Microbiotheria* association, CNF), which allowed them to build their sophisticated and impermeable nests that, in turn, are fundamental for hibernating in such a humid and cold forest. Thus, (according to Hershkovitz, 1999) what eventually extinguished all other Microbiotheriids was the disruption of the CNF by desertification at the northern edge of their distribution and freezing temperatures at the South (including Antarctica) (Hershkovitz, 1999, p10). Such phylogenetic conservatism (sensu Buckley et al., 2010) of Microbiotheriids niche is consistent with

the paleontological evidence, which describes the oldest and largest Microbiotheriid known (*Woodbounodon casei*) as “a generalised non-microbiotheriid Microbiotherian” that “resembles other frugivorous marsupials” (Goin et al., 2007).

Contemporary reconstructions also suggest that habitat preference is highly conserved across the marsupial phylogeny, as ancestral trait reconstruction of basal marsupial nodes is assigned to wet-closed environments with large posterior probabilities (i.e., rainforests, see Fig. 1 in Mitchell et al., 2014). These observations are also supported by recent evidence suggesting that mutualistic associations of microbiotheriids with aerial mistletoes dates back to the Cretaceous (Liu et al., 2018; Watson, 2020). The ancestral marsupial that colonised Australia from Antarctica was probably little different from the present-day Microbiotheriid, *Dromiciops* —an arboreal, nest-building, social, omnivorous-frugivorous mammal with adaptations to the cold, seasonal and humid canopy of the rainforest. This generalised all-purpose animal had the potential for adapting and specialising to the new ecological niches opened by the isolation of Australia and would explain the success of colonisation and posterior diversification of Australasian marsupials.

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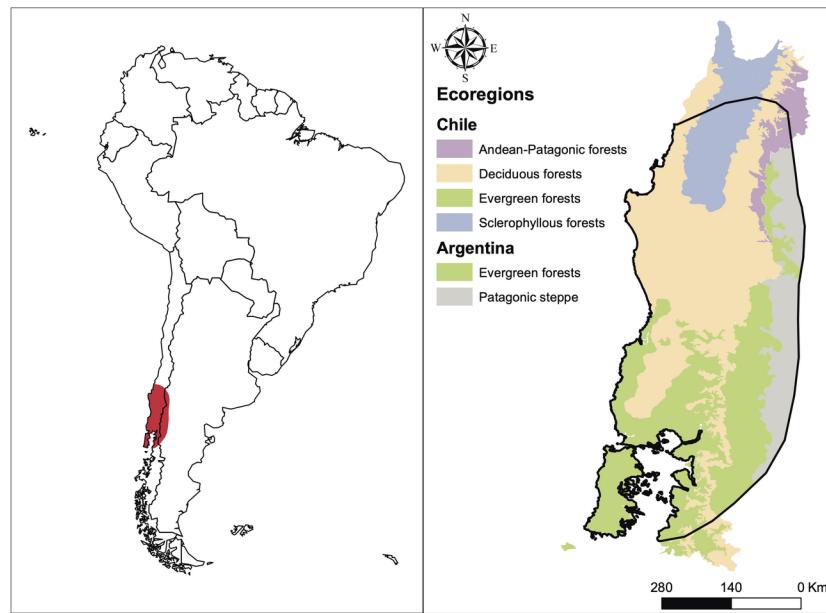
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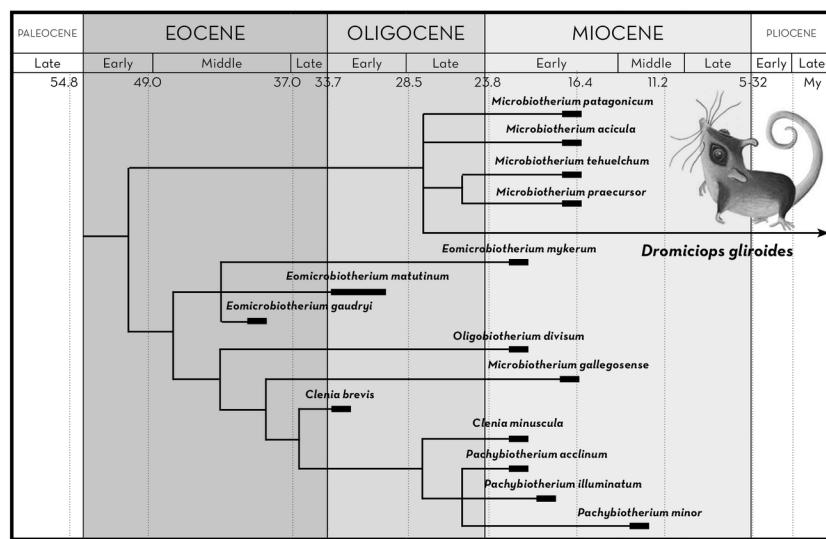
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## Figures

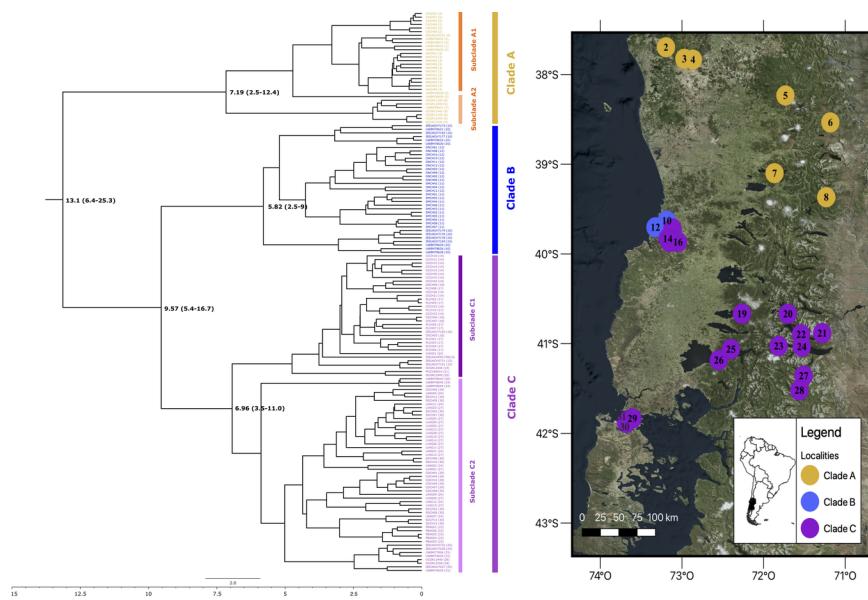


**Figure 1.** Updated *Dromiciops gliroides* distribution, including the new records extending the range to the South (based on Oda et al. 2019 and Mejías et al. 2021).



**Figure 2.** Calibrated fossil phylogeny of Microbiotheria modified from Goin and Abello (2013), show-

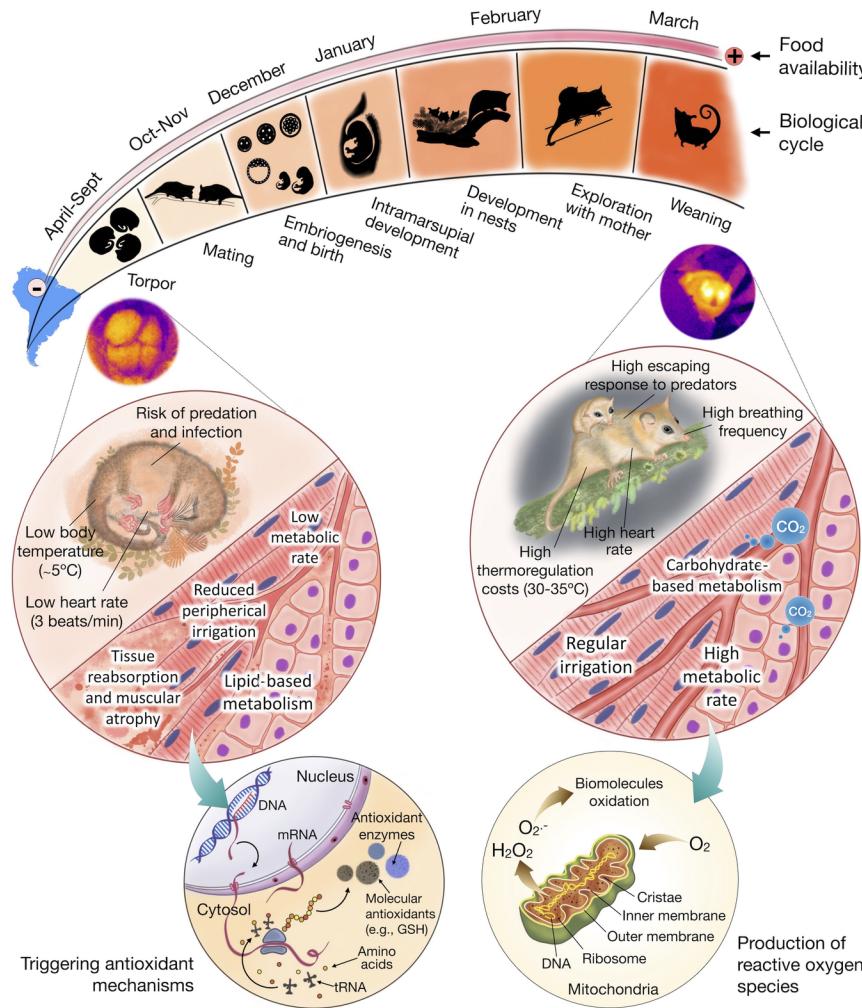
ing the closeness of *D. gliroides* and *Microbiotherium*. According to these authors, both *Dromiciops* and *Microbiotherium* are morphologically indistinguishable.



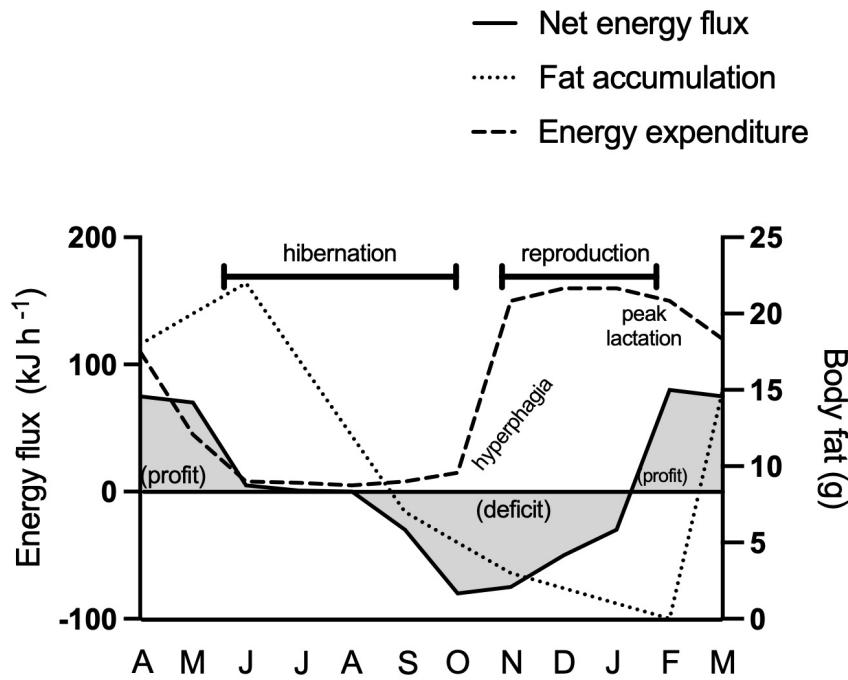
**Figure 3.** *Dromiciops* phylogenetic tree showing the support of two different species: *Dromiciops bozinovici* in the northern clade (A) and *Dromiciops gliroides* in the two southern clades (B and C). Colours show the correspondence of genetic distances and the locations in map. This figure was adapted from Quintero-Galvis et al. (2021).



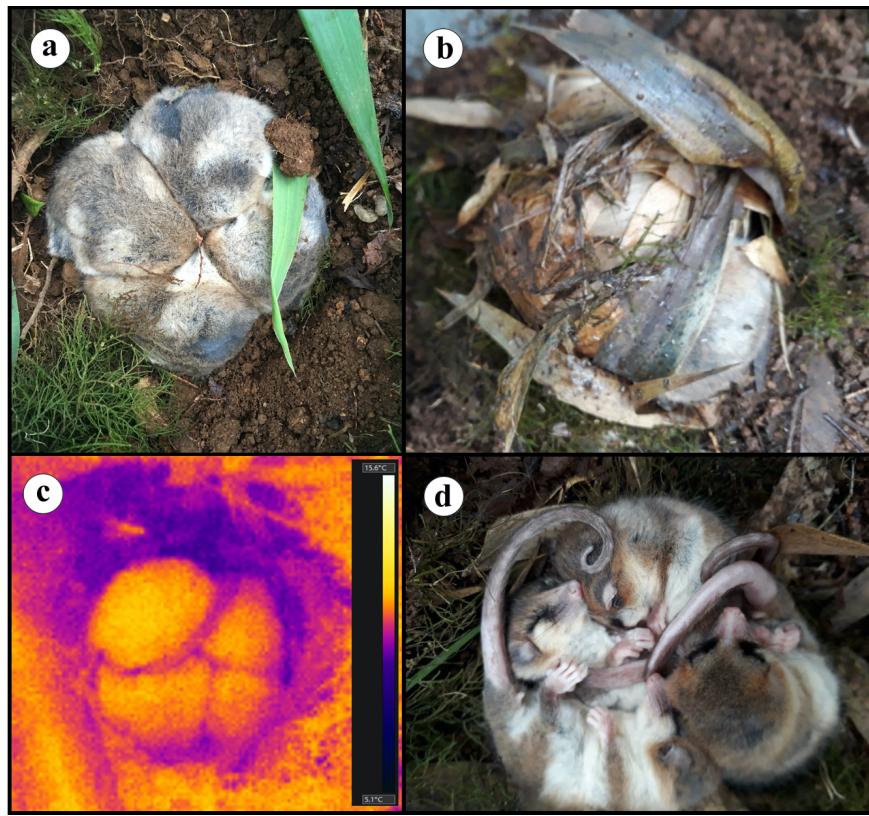
**Figure 4.** *Dromiciops* developmental stages. Panels *a* and *b* correspond to lactation in the pouch I, panels *c* and *d* correspond to lactation in the pouch II, panels *e* and *f* correspond to lactation outside the pouch, panel *g* corresponds to juveniles, and panel *h* corresponds to adults. Photos: R. Nespolo.



**Figure 5.** Annual cycle of *Dromiciops gliroides* showing its physiological, tissue, and biochemical changes during torpor and activity periods. Particular cellular alterations involve oxidative homeostasis by increasing molecular and enzymatic scavengers in torpor to inactivate reactive oxygen species generated during the activity period. The stages of the cycle were modified from Muñoz-Pedreros et al. (2005), according to a field experiment (Nespolo, Fontúrbel, et al., 2021).



**Figure 6.** A hypothetical (but realistic) annual budget of energy and activity of a  $M_B=40\text{g}$  (lean mass) *Dromiciops gliroides*, summarized from descriptions of the reproductive cycle (Muñoz-Pedreros et al., 2005), seasonal variations in activity, adiposity, and body mass (Celis-Diez et al., 2012; Franco et al., 2017) and food availability (di Virgilio et al., 2014; Franco et al., 2011; Quijano, 2008). After reproduction, *D. gliroides* reduce activity and energy expenditure and accumulate almost twice their body size in fat (Franco et al., 2017). Fat accumulation was estimated from body mass fluctuations using quantitative magnetic resonance, which indicated that animals could double their body mass in autumn (Mejías et al., 2022).



**Figure 7.** Photos of hibernating *D. gliroides* taken from an outdoor facility near Valdivia in May (austral autumn). (a) Four clustered individuals packed to minimise heat loss in a nest (uncovered). (b) a single individual within a typical nest built on bamboo (*Chusquea quila*) leaves and mosses. (c) A thermography of four clustered individuals showing their body temperature (~10°C, according to the colour bar scale to the right). Ambient temperature is 5.2°C. (d) Lateral view of hibernating individuals. Photo credits: panel (a): R. Nespolo, panel (b): C. Mejias, panel (c): E. Oda, panel (d): P. Gutiérrez.