Chapter 2
South American Living Metatherians: Physiological Ecology and Constraints

Abstract South American living metatherians are relatively inconspicuous and comprise ca. 10 % of the region's mammal species richness. Most of them are small-sized (<150 g), with long tails and grasping hands and feet, and resemble one another in their general appearance. Individuals are solitary, nocturnal or crepuscular, and most of them are arboreal or scansorial. Two orders are exclusive of South America (Microbiotheria and Paucituberculata), while a third (Didelphimorphia) ranges from Patagonia (Argentina) to the border between USA and Canada. The ecology, physiology, and reproductive traits of living South American marsupials have been poorly studied. This chapter describes several aspects of their natural history and how they influence their recent distribution, as they probably did so throughout the Cenozoic. Physiological constraints include variable energetic costs for regulating metabolic processes, due to low rates of metabolism, the possibility to enter torpor/hibernation, and the storage of different types of fat tissues available for those varied processes. Reproduction, which can be characterized by a short gestation period and long, energy-demanding, breeding period, shows specific differences in strategies (e.g., semelparity, partial semelparity, iteroparity) and their main traits (e.g., litters per year and litter size, teat number). South American marsupials make a complete use of the habitat available to them and have a broad, generally opportunistic and omnivorous diet. These adaptations, combined with a general small size, small energy expenditure on foraging and other daily activities, limit their distribution. Despite these constraints, South American marsupials seem to thrive in environments where competition with other animals might be strong (e.g., tropical and subtropical climates), or where a few small mammals can survive (e.g., temperate and temperate-cold climates) due to several environmental limitations.

Keywords Marsupialia · South America · Physiology · Ecology · Distribution · Reproductive strategy · Life histories · Ecological constraints

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2.1 Introduction

Our knowledge of the natural history of South American living metatherians is still very incomplete, despite a long history since their discovery (Hershkovitz 1987). Living New World marsupials were some of the first animals to receive the attention of naturalists after the early voyages of exploration to central and northern South America, back in the 1500s (Hershkovitz 1987; Tyndale-Biscoe and Renfree 1987). Taking into account their size and habits, they are relatively inconspicuous components of the mammal fauna of this continent, comprising ca. 10 % of the region's species richness (Streilen 1982; Birney and Monjeau 2003). Most of them are solitary, nocturnal or crepuscular, live in tropical and subtropical ecosystems (Tyndale-Biscoe 2005; Gardner 2008), and are arboreal or scansorial (Eisenberg 1981; Vieira 2006a, b). They are generally small-sized (<150 g), with long tails and grasping hands and feet, and resemble one another in their general appearance (Nowak 1999; Tyndale-Biscoe 2005).

Of the three currently recognized orders of new World marsupials, two are exclusive to South America (Microbiotheria and Paucituberculata) (Figs. 2.1 and 2.5b, c). The remaining one, the Didelphimorphia (Figs. 2.2, 2.3, 2.4 and 2.5a), is distributed throughout all of South and Central America, and the southern and eastern portion of North America to the border between USA and Canada. The Order Microbiotheria includes a single living species, the "*monito del monte*" *Dromiciops gliroides* Thomas, which is restricted to the Valdivian Temperate Rainforest (sensu Olson et al. 2001; Martin 2010) (Fig. 2.5b). The Order Paucituberculata includes six or seven species allocated in three genera: *Caenolestes*, *Lestoros* and *Rhyncholestes*, with a distribution concentrated in the Andean "*páramos*" and "*subpáramos*", the upper stratum of the *Yungas* in Perú, Bolivia and adjacent areas (for *Caenolestes* and *Lestoros*), and the Valdivian Temperate Rainforest (for *Rhyncholestes*; Brown 2004; Martin 2008, 2011; Myers and Patton 2008; Patterson 2008; Timm and Patterson 2008) (Fig. 2.5c). Recent didelphimorphs are grouped in the family Didelphidae , which has been recently subdivided into four subfamilies: Glironiinae, Caluromyinae, Hyladelphinae, and Didelphinae (Voss and Jansa 2009). The subfamily Didelphinae is distributed from 48°N to 48°S, with the highest diversity in tropical and subtropical South America (Brown 2004; Birney and Monjeau 2003; Martin 2012; Fig. 2.6a). Species of the subfamily Caluromyinae range from 18°N to 30°S (Fig. 2.6b), in forested habitats of the Neotropical Region (sensu Morrone 2004, 2006; see Chap. 4). A few records fall within the South American Transition Zone (sensu Morrone 2004, see Chap. 4), representing low altitude localities (<2000 m) in Venezuela, Colombia and Ecuador, which have a Neotropical affinity (Brown 2004). The distribution of representatives of the subfamilies Glironiinae and Hyladelphinae is restricted to South America, ranging from 10°N to 15°S and 0° to 17°S, respectively (Bernarde and Machado 2008; Voss et al. 2001; Astúa 2006; Fig. 2.6c, d, respectively).

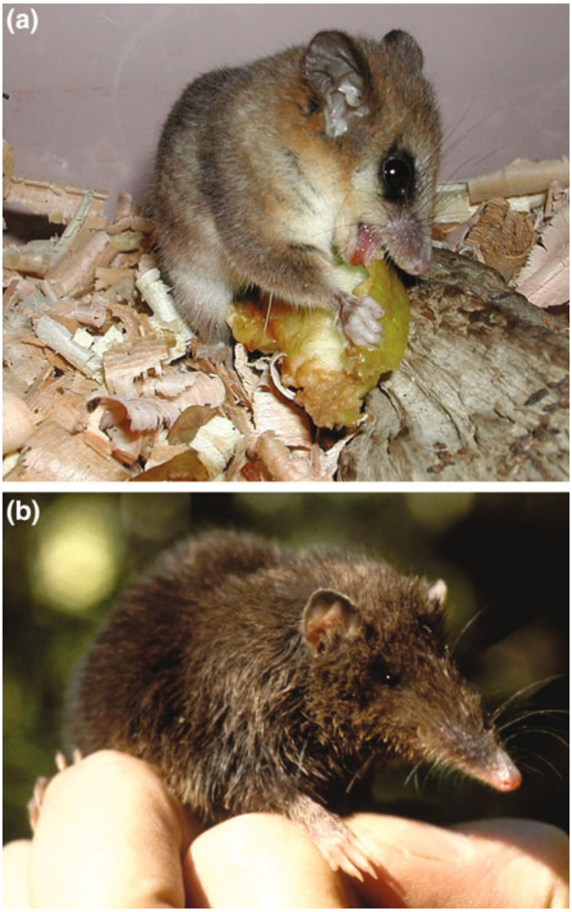
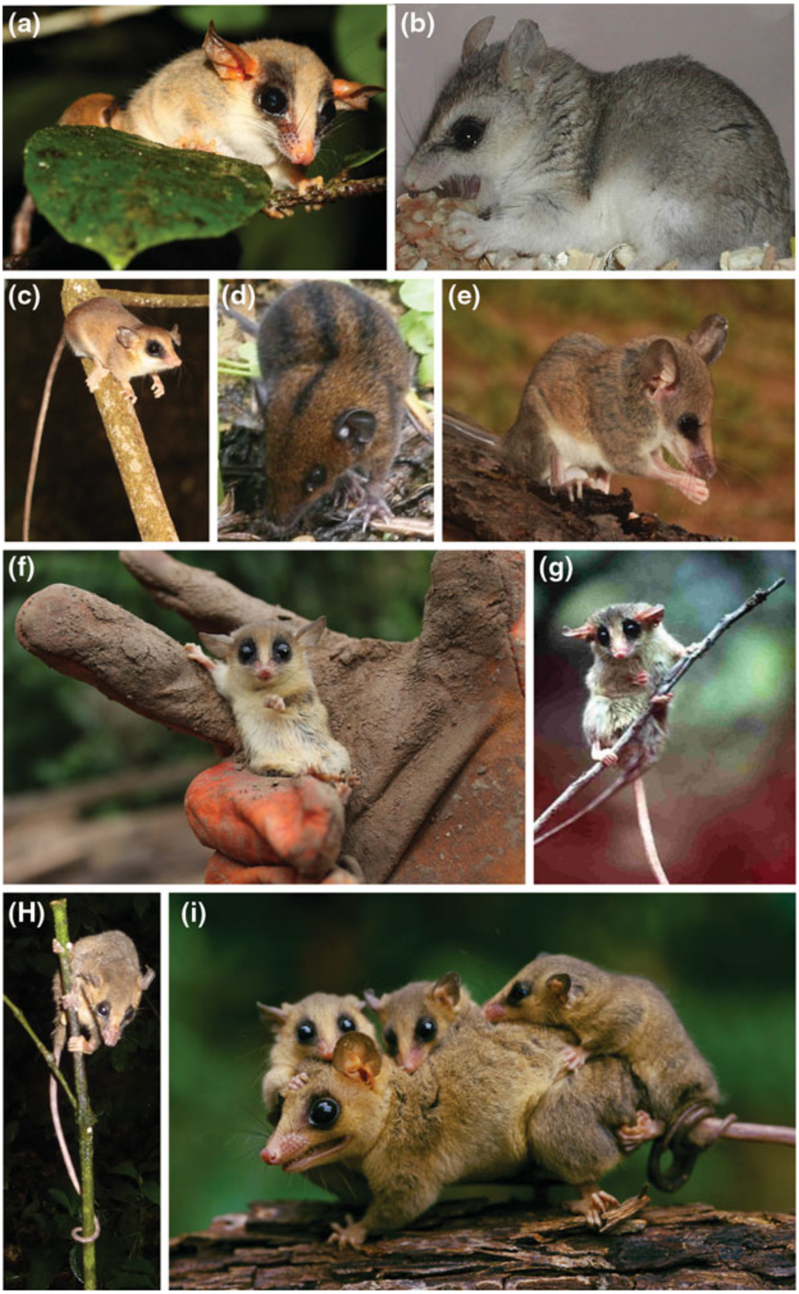


Fig. 2.1 Non-didelphid South American marsupials: **a** *Dromiciops gliroides* (Microbiotheria, Microbiotheriidae), northwestern Patagonia, Argentina (photograph by Gabriel Martin). **b** *Rhyncholestes raphanurus* (Paucituberculata, Caenolestidae), La Picada, Chile (photograph by Peter Meserve, Brian Lang, and Bruce Patterson)

The ecology, physiology, and reproductive traits of living South American marsupials have been poorly studied for most species (e.g., Eisenberg and Wilson 1981; Willig and Gannon 1997; Birney and Monjeau 2003; Martin in preparation), although an increasing number of works has been produced in the last 30 years (e.g., O'Connell 1979; Atramentowicz 1986; Monteiro-Filho and Cáceres 2006).

This chapter introduces several aspects of the physiology and ecology of living South American marsupials. It illustrates how these constraints limit their distribution in South America and, probably, did so throughout the Cenozoic (see also Chap. 6). The taxonomic arrangement follows mostly that of Voss and Jansa (2009), with the exception of recently described species.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◀ **Fig. 2.2** South American small-sized marsupials referable to the family Didelphidae (Didelphimorphia) : **a** *Hyladelphys kalinowskii*, La Trinidad Mountains, French Guiana; **b** *Lestodelphys halli*, central Patagonia, Argentina; **c** *Gracilinanus emiliae*, Petit-Saut, Sinnamary, French Guiana; **d** *Monodelphis gardneri*, Central Andes, Perú; **e** *Marmosops parvidens*, Tresor Natural Reserve (Kaw-Roura), French Guiana; **f** *Marmosa murina*, Ecuador; **g** *Gracilinanus microtarsus*, southeastern Brazil; **h**, **i**, *Micoureus demerarae*, Tresor Natural Reserve (**h**), and Madidi National Park, Bolivia (**i**). Photographs by Sylvain Pincebourde (**a**), Gabriel Martin (**b**), Mael Dewynter (**c**), Fabrice Schmitt (**d**), Jean-Francois Szpigel (**e**), Max Bernal Montes (**f**), Vitor Rademaker (**g**), Francois Catzeflis (**h**), Andre Baertschi (**i**). Drs. Francois Catzeflis and Sergio Solari facilitated several of the photos here displayed

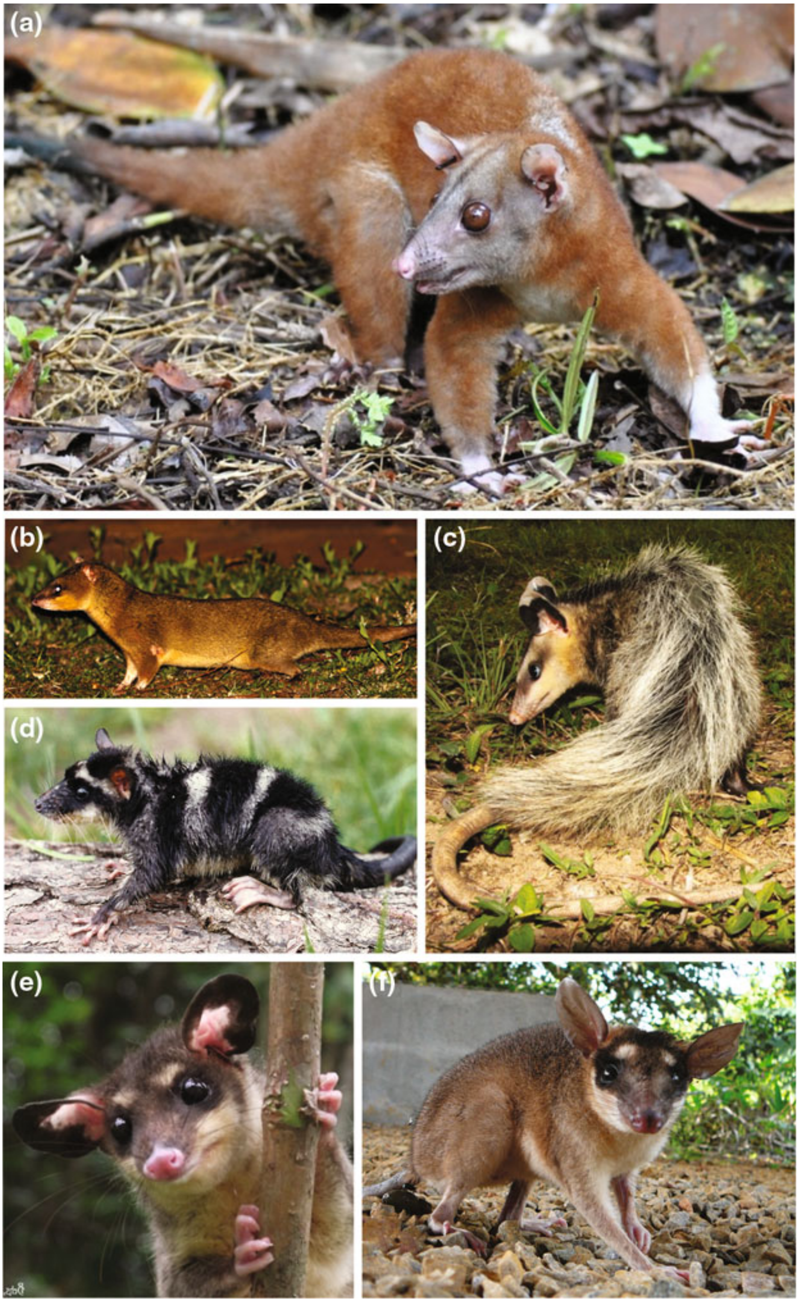
2.2 Thermal Constraints

Most South American living marsupials are nocturnal and/or crepuscular, being active during the coldest part of the day and facing high thermoregulatory costs during foraging, feeding, and other physiologically demanding activities (Geiser 2003). Despite this, a few studies on the thermal biology of South American marsupials have documented a high capacity for thermal regulation and the ability to achieve metabolic rates higher than most placentals (Dawson and Olson 1987; Bozinovic et al. 2004, 2005; Ribeiro and Bicudo 2007).

Marsupials can be characterized as having low basal metabolic rates (BMR), high thermal conductance due to a large surface area/volume ratio, and low body temperatures (McNab 1982; Hume 1999; Geiser 2003; Tyndale-Biscoe 2005). Several studies have found different correlation values between BMR and ambient temperature, climate, substrate use, and the ability to enter torpor and/or hibernation (McNab 2005), with body mass being pointed out as the main determinant in the ability of New World marsupials to thermoregulate (Harder and Fleck 1997; McNab 2005). Feeding preferences and/or diet show little or no direct relationship to BMR (Hume 1999).

Apart from this, marsupials have been found to use different mechanisms for thermogenesis than those of placentals (Riek and Geiser 2014). The main source for non-shivering thermogenesis in placentals is brown adipose tissue (BAT) (Jastroch et al. 2008; Riek and Geiser 2014). However, some studies in marsupials show that BAT is absent, while others show BAT is present but nonfunctional (Hope et al. 1997; Rose et al. 1999). Therefore BAT and its adaptive use in marsupials remains controversial. Also, marsupials are able to use vasoconstrictor-induced non-shivering and shivering thermogenesis in skeletal muscles (Geiser et al. 2003 and literature cited therein), which in turn might represent the most common adaptation as a response to cold exposure. Several of these adaptations have been documented for Australian marsupials but little or no information is available for South American species.

Despite differences in size, habitat use and diet, data on BMR has been found to be similar among marsupials in general (Dawson and Hulbert 1970; Hulbert and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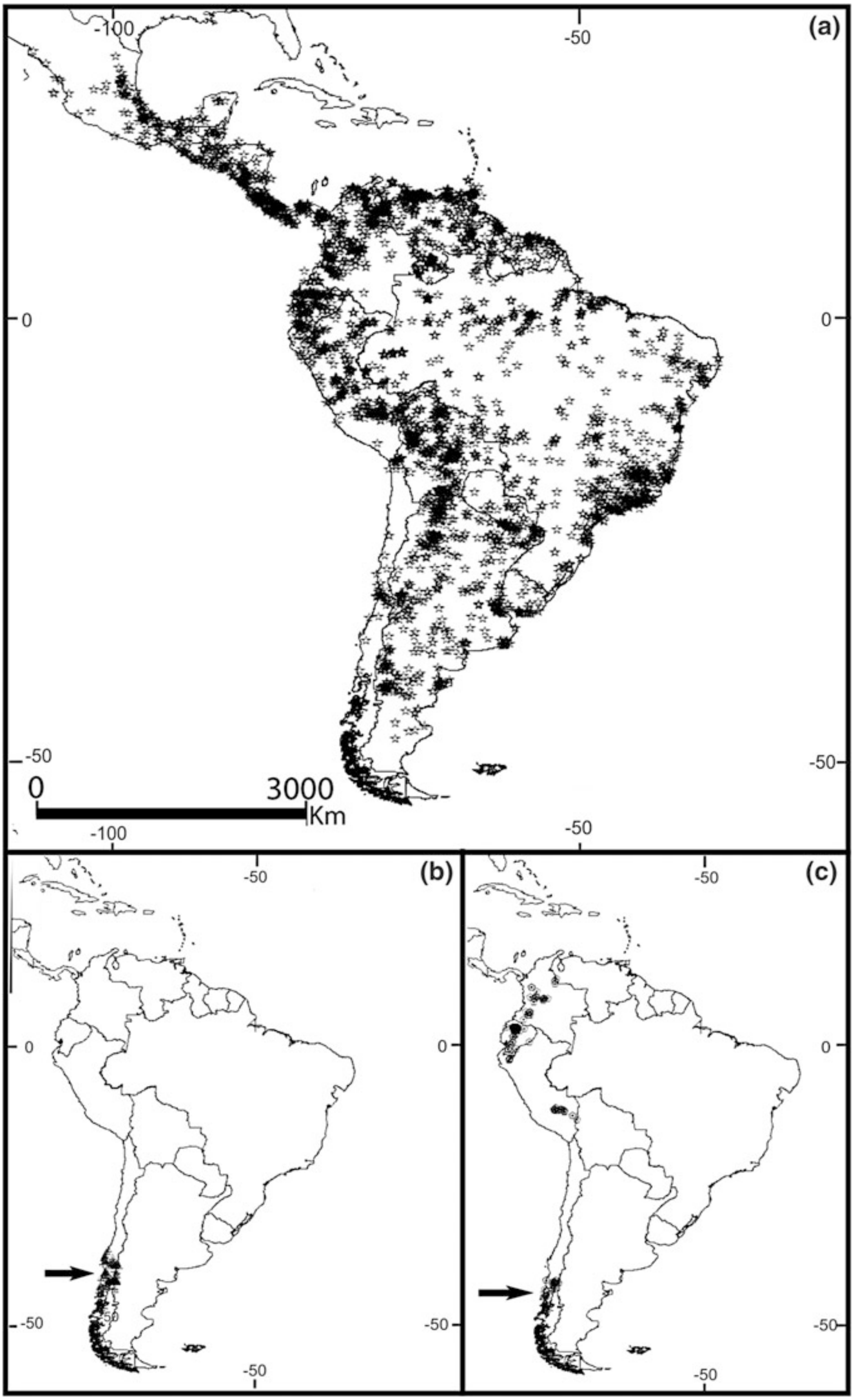
◀ **Fig. 2.3** South American medium-sized marsupials referable to the Family Didelphidae (Didelphimorphia): **a** *Caluromys derbianus*, Costa Rica; **b** *Lutreolina crassicaudata*, Corrientes Province, Argentina; **c** *Didelphis imperfecta*, Petit Saut (Sinnamary), French Guiana; **d** *Chironectes minimus*, Mata Atlantica, southeastern Brazil; **e** *Philander frenatus*, Santa Catarina, Brazil; **f** *Metachirus nudicaudatus*, Cacao, French Guiana. Photographs by Joseph Rupert (**a**), Guillermo Gabriel Soteras (**b**), Sebastien Barrioz (**c**), Maurício E. Graipel (**d**), "danybehs" (Project Noah) (**e**), Francois Catzeflis (**f**). Michael Butcher, Francois Catzeflis and Karen Loughrey (Project Noah) facilitated several of the photos here displayed

Dawson 1974; Dawson and Wolfers 1978; McNab 1978, 1986; Thompson 1988; Wallis and Farrell 1992; Ribeiro and Bicudo 2007). The BMR of South American marsupials varies from 50.6 to 99.1 % of that expected for mammals, with only one species showing a marginally high basal rate by mammalian standards (i.e., *Didelphis marsupialis* with 105 %) (McNab 2005). Predicted values of BMR from allometric equations show that marsupials have substantially lower BMR than similar sized placentals living in similar environments, especially at small body masses (Geiser 2003; McNab 2005). Low BMRs have often been described as a poor adaptation to tolerate temperate-cold climates and, hence, a factor limiting the distribution of marsupials on a continental scale. It has also been argued that low BMRs reflect primitive thermoregulatory characteristics of ancestral mammals. Recently, and in contrast to this, it has been suggested that a low BMR in marsupials might be influenced by physiological and ecological constraints (e.g., water balance, feeding, predation), or climate unpredictability (e.g., daily and/or seasonal temperature variation, rainfall) (Geiser 2003 and literature cited therein). Lovegrove (2000) has argued that BMR is mainly determined by resource availability during certain periods of time, and throughout a limited space (i.e., the areas where individuals forage for food). Clearly, several factors might influence energy balance in marsupials depending on their size, thermoregulation ability, environmental constraints, and phylogenetic affinities (Geiser 2003; McNab 2005; Riek and Geiser 2014).

Most studies show that American marsupials are similar in physiology and metabolism to Australian marsupials, especially dasyurids (Hume 1999; McNab 2005; Tyndale-Biscoe 2005). Several studies point to a relationship between thermal regulation and BMR, especially for Australian marsupials which are very competent homeotherms, but these studies have not been replicated in American marsupials (Dawson and Dawson 1982). In general, New World marsupials show a higher BMR than Old World marsupials (McNab 1978), an exception being *D. gliroides*, which seems to be closer in physiological ecology to Australian marsupials (Bozinovic et al. 2004). This particular fact could be a result of the phylogenetic affinities of Microbiotheria with Australian marsupials, adding support to the idea in which critical temperatures, as measured by thermoneutral zones (in turn, highly related to BMR), are all influenced by phylogeny (Riek and Geiser 2014).

Fig. 2.4 **a**–**c** A female specimen of *Lutreolina crassicaudata* showing seven pouch-young attached to its nipples. **a** handling of the specimen by researchers for sexing and measuring; **b** a view of its ventral side; **c** the same specimen and view, with completely relaxed pouch. The specimen was captured at Fazenda Experimental da Ressacada (Universidade Federal do Santa Catarina), Florianópolis, Santa Catarina, Brazil. Photographs by Laise Orsi Becker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◀ **Fig. 2.5** Distribution (known localities) of the three orders of New World marsupials: Didelphimorphia (**a**), Microbiotheria (**b**), and Paucituberculata (**c**). Didelphimorphia does not include North American localities, referrable to *Didelphis virginiana*

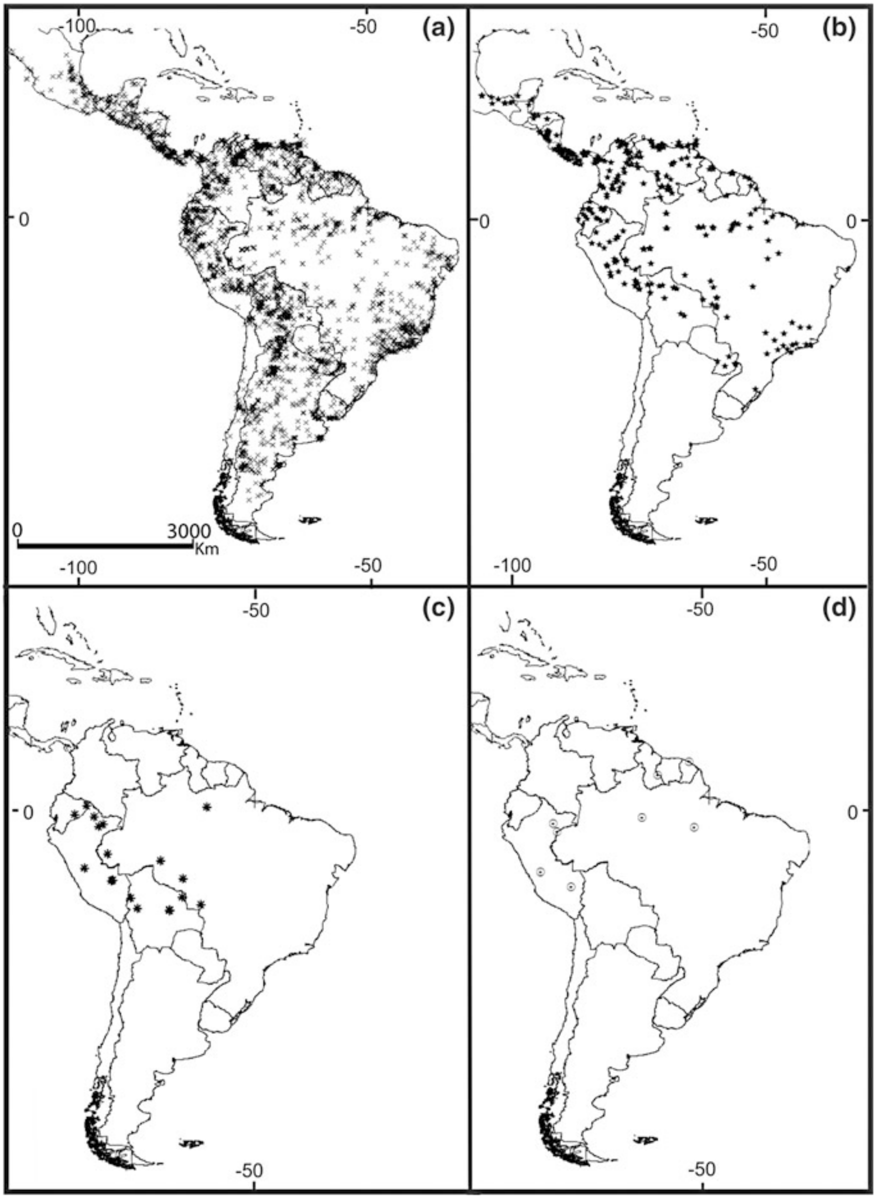

Fig. 2.6 Distribution of the four subfamilies of Didelphidae: Didelphinae (**a**), Caluromyinae (**b**), Glironiinae (**c**), and Hyladelphinae (**d**). Didelphimorphia does not include North American localities, referrable to *Didelphis virginiana*

2.3 Feeding Constraints

Feeding habits of South American marsupials were, until recently, mostly based on qualitative data and, to certain extent, are still poorly known (Cordero and Nicolas 1987, Lee and Cockburn 1987, Hume 1999, 2003). Traditionally considered to represent the ancestral and generalized omnivore/insectivore pattern of food consumption (Lee and Cockburn 1987), recent quantitative studies have revealed a large variation in the preferences of living New World marsupial diets (e.g., Carvalho et al. 1999; Astúa de Moraes et al. 2003; Ceotto et al. 2009; García et al. 2009).

Studies on the diet of South American marsupials conform to a series of feeding categories (Eisenberg 1981, Martin in preparation), ranging from predominantly frugivorous to a diet that can be mostly characterized as animalivorous, with several species which can be included in animalivore/omnivore and animalivore/frugivore categories. Proportionately, the diets of South American marsupials show that 14 genera (63.6 %) fall into the animalivore/frugivore category, three (13.6 %) in the animalivore/omnivore category, three (13.6 %) in the frugivore/animalivore category, one (4.5 %) in the animalivore category (*Lestodelphys*), and one (4.5 %) in the omnivore category (*Didelphis*) (Table 2.1). Diet information is available, mainly from tropical/subtropical environments, for medium/large-sized species and a few small-sized ones (e.g., Atramentowicz 1988; Busch and Kravetz 1991; Freitas et al. 1997; Carvalho et al. 1999; Fernandes et al. 2006; Ceotto et al. 2009; Pires et al. 2009; Bocchiglieri et al. 2010; Macedo et al. 2010). However, it is not clear whether data on a single species from polytypic genera can be extrapolated to the rest of the species (e.g., *Monodelphis domestica* to some *Monodelphis* spp.), especially considering the variation in habitats, latitude, and altitude in many of them (e.g., *Monodelphis*, *Thylamys*). Also, several of these polytypic genera conform to a similar craniodental and anatomically conservative pattern of mastication, despite living in different environments, showing how versatile and efficient the tribosphenic molar and food processing in these marsupials is. Despite the information presented above, the inclusion of species in feeding categories should be used with caution due to overlaps in general consumption patterns (Astúa de Moraes et al. 2003).

In recent years, the role of marsupials as seed dispersers especially in tropical and subtropical environments has been acknowledged (Thielen et al. 1997; Amico and Aizen 2000; Cáceres 2000; Cáceres and Monteiro-Filho 2000; Cáceres et al. 2002; Amico et al. 2009; García et al. 2009; Cantor et al. 2010), a role which was previously attributed to birds, bats, monkeys, and some rodents. In order to be a good disperser, seeds must pass undamaged through the digestive tract and be deposited at places favorable to germination (Cáceres 2006). Under some circumstances, the passage through the gut is critical in the development of a “holdfast” mechanism which affects the seed’s attachment to the host plant (Amico and Aizen 2000;

Table 2.1 Feeding and foraging categories of South American marsupial genera (n = number of species within each genera)

Genus (*n*)	Feeding category	Foraging category
Caluromys (3)	Frugivore/animalivore[a]	Arboreal
Caluromysiops (1)	Frugivore/animalivore	Arboreal
Chacodelphys (1)	Animalivore/frugivore	Scansorial
Chironectes (1)	Animalivore/frugivore	Semiaquatic
Cryptonanus (5)	Animalivore/frugivore	Scansorial
Didelphis (6)	Omnivore[a]	Scansorial
Glironia (1)	Frugivore/animalivore	Arboreal
Gracilinanus (6)	Animalivore/frugivore[a]	Arboreal
Hyladelphys (1)	Animalivore/frugivore	Scansorial
Lestodelphys (1)	Animalivore	Scansorial
Lutreolina (1)	Animalivore/frugivore[a]	Terrestrial
Marmosa (15)[b]	Animalivore/frugivore[a]	Arboreal
Marmosops (15)	Animalivore/frugivore[a]	Arboreal
Metachirus (1)	Animalivore/frugivore[a]	Terrestrial
Monodelphis (22)	Animalivore/frugivore[a]	Terrestrial
Philander (7)	Animalivore/frugivore	Scansorial
Thylamys (13)	Animalivore/frugivore	Scansorial
Caenolestes (5)	Animalivore/omnivore	Terrestrial
Lestoros (1)	Animalivore/omnivore	Terrestrial
Rhyncholestes (1)	Animalivore/omnivore	Terrestrial
Dromiciops (1)	Animalivore/frugivore[a]	Arboreal

Adapted from Eisenberg (1981) and Martin (in prep.)

[a] Species involved in seed dispersion

[b] *Marmosa* includes species in the subgenus *Micoureus* sensu Voss and Jansa (2009)

Nickrent and Musselman 2004). Seasonal fruit availability in tropical and subtropical environments is directly related to the use of these resources as food items, fluctuating from high to low proportions during humid and dry periods, respectively (Cáceres et al. 2002; Cáceres 2006; Leiner and Silva 2007). Nine genera of New World marsupials (ca. 41 %) have been reported as seed dispersers, eight of them from tropical and/or subtropical environments (Table 2.1). In the only study made in a southern temperate environment (i.e., *D. gliroides* in the Valdivian ecoregion), fruit availability was found to be related to summer temperature, becoming a highly seasonal resource (Amico and Aizen 2000).

Through the study of marsupial feeding, Hume (1999) proposed a relationship between food quality and digestibility, and described a series of constraints: (1) optimal digestion time will vary depending on the type of food ingested (i.e., longer for poor quality items like adult insects, shorter for high-quality items like larvae, earthworms, or soft fruits); (2) animals with longer digestion times will have longer digestive tracts than those eating easily/quickly digestible food; (3) young animals with limited gut capacity will consume only high-quality food items; (4) animals should maximize food retention in order to extract the most energetic value out of the consumed items. Studies of the alimentary tract in South American marsupials show a relationship between relative length of the stomach, caecum and colon, with species' feeding habits (Hume 1999; Astúa de Moraes et al. 2003 and literature cited therein). The observed variation in craniodental anatomy and diet is directly related to differences in the species' digestive tracts, but only subtle differences were found between them (Santori and Astúa de Moraes 2006).

According to the information presented above, most South American marsupials can be considered, within certain limits and a few exceptions, opportunistic omnivores in a broad sense. This generalization has a strong influence on both ecological and physiological traits. For example, species might present seasonal variations related to food availability (e.g., feeding on fruits and insects during the rainy and dry seasons, respectively), and individual development (e.g., young individuals might feed on insects at one point in life, and shift to feeding on vertebrates as adults). This in turn, would influence their reproductive strategy (e.g., seasonal, aseasonal), energetic balance (e.g., use of torpor bouts, tail incrassation), reproduction and habitat use (see below).

In comparison to Australian marsupials, New World species occupy relatively broad ecological niches when it comes to feeding categories, with only a few of them showing feeding specializations (Vieira and Astúa de Moraes 2003; Tyndale-Biscoe 2005). The consumption of variable proportions of animal material and fruits in their diet is comparable, in many cases, to Australian dasyurid species (Strahan 1991; Hume 1999). Species within Caluromyinae are similar in feeding preferences to ringtails, gliders, brushtails and cuscuses (Petauridae and Phalangeridae), while *D. gliroides* can be easily compared to pygmy possums (Burramyidae; Strahan 1991). Noticeably, Caenolestids have feeding preferences that resemble (or are similar to) that of shrews (Soricidae) (Vaughan et al. 2011). The generalized feeding habits of living New World marsupials contrast with those inferred for extinct metatherian lineages, which included several types of hypercarnivorous, granivorous, strictly frugivorous, and even folivorous forms (see Chap. 6).

2.4 Reproductive Constraints

The reproduction pattern found in marsupials differs consistently from that of placentals with respect to gestation length, lactation, and neonate size (Cockburn and Johnson 1988). Originally considered primitive, recent studies have shown that the "marsupial mode of reproduction" is a highly derived condition, and not the ancestral pattern of a primitive Therian mammal (Hayssen et al. 1985). Marsupials are born in a much earlier stage of development and have a shorter duration of gestation relative to lactation, with a general average of $\sim 12\ \%$ (Hayssen et al. 1985;

Tyndale-Biscoe and Janssens 1988). Despite their small size (usually weighing less than 0.01 % of the mother's weight at birth) and poorly developed appearance, newborn marsupials show a mixture of well-developed functional organs and embryonic structures (Clark and Smith 1993; Tyndale-Biscoe 2005). Amongst the first well-developed organs are a relatively large head with large mouth and tongue, well-developed shoulders and forelimb skeleton. Embryonic or poorly developed structures include comparatively small hind legs and hip, a short and poorly developed tail, and ears and eyes concealed by membranes (or shut; Tyndale-Biscoe 2005). The well-developed structures are crucial during what is considered the most vulnerable period for the newborn marsupial (i.e., the transition from an intrauterine life to an external world), where it migrates from the vagina to the teat, mostly unaided. The young are wholly dependent on the mother during this period, and remain attached to the teat for a variable period of time (e.g., 48 days in *Didelphis virginiana*; 20 days in *Marmosa robinsoni*; 14 days in *M. domestica*), or detach briefly during this period (Tyndale-Biscoe and Renfree 1987 and literature cited therein, R. Cerqueira, personal communication).

The common name given to marsupials implies the presence of a pouch/marsupium enclosing the teat area (Fig. 2.4). In the Didelphimorphia , this morphological feature is present only in some of the larger (i.e., Didelphini) and medium-sized species (i.e., Caluromyinae), but is not developed in the remaining taxa (e.g., Glironiinae, Hyladelphinae, Marmosini, Metachirini, Thylamyini), which includes all small and a few medium-sized species (Voss and Jansa 2009). The absence or poor development of a pouch in most groups is probably the ancestral condition for New World species, and might be related to a nesting phase in the development of the young, with a well-developed pouch being a derived feature (Tyndale-Biscoe and Renfree 1987; Merritt 2010). The pouch opening in Didelphini is medially oriented, except in *Chironectes* where it opens posteriorly, an adaptation that has been related to its peculiar semiaquatic lifestyle (Nowak 1999). A pouch is not present in the Caenolestidae and Microbiotheria, where lateral folds of skin tend to enclose the teat area, at least partially (Tyndale-Biscoe and Renfree 1987; Hershkovitz 1999).

Only a few studies have documented the gestation period in South American marsupials, most of them from tropical/subtropical environments and from large/medium-sized didelphids, with the exception of *Lutreolina crassicaudata*, *M. robinsoni,* and *Monodelphis dimidiata* (Table 2.2). The gestation period found for most species is of 13–15 days, with the exception of *Caluromys philander* in which data of up to 20 days was recorded (Table 2.2).

South American marsupials have a variable number of teats, ranging from 4 to 19 (Table 2.2). The plesiomorphic number within American marsupials appears to be 4 teats, as found in Microbiotheria, Paucituberculata (e.g., *Lestoros inca*), and three subfamilies within Didelphidae (i.e., Caluromyinae, Glironiinae and Hyladelphinae). Small species from the tribes Marmosini and Thylamyini show most of the variation, with some genera having smaller teat numbers (e.g., *Marmosops* spp. with 5–9 teats) and others with the highest amongst New World marsupials (*Cryptonanus* spp., *Gracilinanus* spp., and *Thylamys* spp. with 9–15

Table 2.2 Reproductive information on South American marsupials

Species	Gestation (days)	Average litter size	Teat number	Litters/Year	References
Caluromys derbianus	–	3.3 (2–4)	–	2?	Biggers (1967), Phillips and Knox Jones (1968)
Caluromys lanatus	–	3.7	–	–	Cáceres (2000)
Caluromys philander	14–20+	3.6–6	4–7	2–3	Davis (1947), O'Connell (1979), Atramentowicz (1986), Perret and Atramentowicz (1989), Julien-Lafèrriere and Atramentowicz (1990), Cáceres and Monteiro-Filho (1997), Emmons and Feer (1997)
Chironectes minimus	–	2–4.5	5	–	Enders (1966), Hunsaker (1977), Marshall (1978b), Eisenberg (1980), Crespo (1982), Hershkovitz (1997), Cáceres (2000)
Cryptonanus chacoensis	–	12	9	–	Massoia and Fornes (1972), Voss et al. (2005), but see Gardner (2008)
Cryptonanus guahybae	–	–	15	–	Tate (1933)
Didelphis albiventris	–	4.2–9.1	8–13	–	Hershkovitz (1997), Tyndale-Biscoe and Mackenzie (1976), Streilen (1982), Monteiro-Filho (1987), Rigueira et al. (1987), Regidor and Gorostiague (1996), Catzeflis et al. (1997)
Didelphis aurita	–	6.5–8.1	11	–	Hill (1918), Davis (1947), Cerqueira et al. (1993), Bergallo and Cerqueira (1994), Cherem et al. (1996), Cáceres and Monteiro-Filho (1997), D'Andrea et al. (1999)
Didelphis marsupialis	–	4–9	9–13	–	Fleming (1973), Tyndale-Biscoe end Mackenzie (1976), O'Connell (1979), Eisenberg (1980), Atramentowicz (1986), Julien-Lafèrriere and Atramentowicz (1990), Hershkovitz (1997)

(continued)

Table 2.2 (continued)

Species	Gestation (days)	Average litter size	Teat number	Litters/Year	References
Gracilinanus agilis	–	–	13	–	Tate (1933)
Gracilinanus marica	–	–	11	–	Hershkovitz (1992a)
Gracilinanus microtarsus	–	–	15	–	Tate (1933)
Hyladelphys kalinowskii	–	–	4	–	Voss et al. (2001)
Lutreolina crassicaudata	13–15	5–11	9–11	2	Monteiro-Filho and Dias (1990), Hershkovitz (1997), Regidor et al. (1999), Iodice et al. (2010)
Marmosa lepida[a]	–	–	7	–	Tate (1933)
Marmosa murina[a]	–	–	7–13	–	Thomas (1888), Tate (1933), Hershkovitz (1992a)
Marmosa quichua[a]	–	–	11	–	Hershkovitz (1992a)
Marmosa robinsoni[a]	14	10–14	15 (11–19)	–	Barnes and Barthold (1969), Fleming (1973), Godfrey (1975), O'Connell (1979), Eisenberg (1980), Eisenberg and Wilson (1981), Hershkovitz (1992a)
Marmosa rubra[a]	–	–	7–9	–	Hershkovitz (1992a)
Marmosa tyleriana[a]	–	–	4	–	Tate (1933)
Marmosa xerophila[a]	14	7.9 (3–11)	–	1–3	Thielen et al. (1997)
Marmosa alstoni[b]	–	–	9–11	–	Tate (1933)
Marmosa cinerea[b]	–	–	9–15	–	Tate (1933), Hershkovitz (1992a)
Marmosa constantiae[b]	–	–	15	–	Tate (1933)
Marmosa demerarae[b]	–	10	9–11	–	Hershkovitz (1992a), Monteiro-Filho and Cáceres (2006)

(continued)

Table 2.2 (continued)

Species	Gestation (days)	Average litter size	Teat number	Litters/Year	References
Marmosa phaea[b]	–	–	9	–	Hershkovitz (1992a)
Marmosops bahiensis	–	–	7	–	Tate (1933)
Marmosops carri	–	–	7–9	–	Tate (1933)
Marmosops caucae	–	–	7–9	–	Tate (1933)
Marmosops handleyi	–	–	9	–	Hershkovitz (1992a)
Marmosops impavidus	–	–	9	–	Tate (1933), Hershkovitz (1992a)
Marmosops incanus	–	–	7	–	Tate (1933)
Marmosops noctivagus	–	–	5–9	–	Tate (1933), Hershkovitz (1992a)
Marmosops parvidens	–	–	7–9	–	Pine (1981), Hershkovitz (1992a)
Marmosops paulensis	–	–	–	1	Leiner et al. (2008)
Metachirus nudicaudatus	–	4–9	9	–	Fonseca and Kierulff (1989), D'Andrea et al. (1999), Cáceres (2000), Gardner and Dagosto (2008)
Monodelphis americana	–	–	15	–	Thomas (1888)
Monodelphis brevicaudata	–	7.5	11	–	Thomas (1888), O'Connell (1979), Eisenberg and Wilson (1981)
Monodelphis dimidiata	–	11	16	–	O'Connell (1979), Eisenberg (1980)
Monodelphis domestica	14	7–8	13–16	–	Thomas (1888), VandeBerg (1983), Kraus and Fadem (1987), Bergallo and Cerqueira (1994), Pfiegler and Cabana (1996), Harder and Fleck (1997)
Monodelphis sorex	–	–	13	–	Carlsson (1903)
Philander andersoni	–	–	4–7	–	Hershkovizt (1997)

(continued)

Table 2.2 (continued)

Species	Gestation (days)	Average litter size	Teat number	Litters/Year	References
Philander frenatus	13–14	4.5–5.4	7	–	Davis (1947), Crespo (1982), Fonseca and Kierulff (1989), Cerqueira et al. (1993), Hingst et al. (1998), D'Andrea et al. (1999), Cáceres (2000)
Philander opossum	–	4–5	7	–	Fleming (1973), Eisenberg (1980), Atramentowicz (1986), Julien-Lafèrriere and Atramentowicz (1990), Hershkovizt (1997)
Thylamys elegans	–	17 (embryos)	11–15	–	Tate (1933), Mann (1958)
Thylamys janetta	–	–	15		Tate (1933)
Thylamys karimii	–	–	–	2?	Carmignotto and Monfort (2006)
Caenolestes fuliginosus	–	3.4	–	–	Osgood (1921), Kirsch and Waller (1979), Tyndale-Biscoe (1980)
Lestoros inca	–	–	4	–	Osgood (1924)
Rhyncholestes raphanurus	–	–	7	1	Patterson and Gallardo (1987)
Dromiciops gliroides	–	1–4	4	1	Philippi (1893), Krieg (1924), Osgood (1943), Mann (1955), Greer (1965), Muñoz-Pedreros et al. (2005)

[a]Subgenus *Marmosa*
[b]Subgenus *Micoureus*

teats; *Monodelphis* spp. with 11–16 teats; *Marmosa* spp. with 7–19; Mann 1958; Hershkovitz 1992a; Bergallo and Cerqueira 1994; Voss et al. 2005; Martin in preparation). Large- to medium-sized species of the tribes Didelphini and Metachirini show intermediate numbers, between 4–13 and 9 teats, respectively (Julien-Lafèrriere and Atramentowicz 1990; Catzeflis et al. 1997; Cáceres 2000). Despite variation in teat number, two reproductive strategies appear to be common: one in which more young are born than the available number of teats (e.g., *Didelphis*), and one in which young are less or equal to the number of teats (e.g., *Caluromys*) (Tyndale-Biscoe 2005). Unfortunately, no information on this aspect of reproduction in species with higher teat numbers is available.

Information on the average litter size is available for less than 20 species (Table 2.2), but this data should be taken carefully as it has been demonstrated that wide ranging species (in latitude) have variable litter sizes, with smaller ones registered toward the periphery of their distribution (Fleming 1973; Rademaker and Cerqueira 2006). The available information has a high bias toward medium/large-sized marsupials from tropical environments, with little information on specialized taxa (e.g., *Caluromysiops*, *Glironia*, *Lestodelphys*) and species-rich genera (e.g., *Marmosops*, *Monodelphis*, *Thylamys*) (Table 2.2).

Another reproductive aspect that has been poorly studied in South American marsupials is the number of litters per year (Table 2.2). Two litters per year have been documented for *Caluromys philander*, *Didelphis albiventris, D. aurita* and *L. crassicaudata* (Catzeflis et al. 1997; Emmons and Feer 1997; D'Andrea et al. 1999; Regidor et al. 1999). One litter per year has been documented for *Philander frenatus*, *D. gliroides* and *Rhyncholestes raphanurus* (Patterson and Gallardo 1987; Cáceres 2000; Muñoz-Pedreros et al. 2005). Because semelparity or partial semelparity (see below) has been described as the reproductive strategy for *M. dimidiata*, *Gracilinanus microtarsus*, *Marmosops incanus* and *Marmosops paulensis,* a single litter per year can be inferred for all these species. In the same context, and given that many species of South American marsupials inhabit highly seasonal habitats, it could be argued that most species would reproduce once a year, and conform to a semelparous or partially semelparous life cycle. From an energetic/metabolic point of view, this would represent a substantial advantage over species with multiyear life cycles (especially in small species), in which individuals should have to regulate and/or balance their energy input to cope with significant seasonal fluctuations in food availability, energy storage (e.g., in the form of interstitial and inner body fat reserves), and resuming reproductive activities on a year-round basis. A reproductive "strategy" that has been recorded for Australian diprotodonts , shows that at least two different aged young can be found at any one time inside the pouch. This has not been documented for New World marsupials, even in species with two or three breeding cycles throughout a year.

The first stages in the life of newborn marsupials were reviewed by Tyndale-Biscoe (2005), who divided postnatal development in three consecutive phases in which different processes take place: (1) acquisition of immune competence, eyes, ears, whiskers and cerebral cortex differentiate, functions of the nervous system develop, and the brain grows fast; (2) acquisition of homeothermality with the increased growth of fur, the development of the thyroid, liver, kidney, and the hormones that control each organ's function; and (3) facultative detachment from teats until they are weaned, changes in diet from milk to other "adult" items, changes in energy balance and metabolism, modifications of the stomach and intestine, and the need for water as the young becomes physiologically independent. Different studies in New World marsupials contribute to validate these phases (e.g., Pine et al. 1985; Muñoz Pedreros et al. 2005; Krause and Krause 2006; Monteiro-Filho and Cáceres 2006), phases which have been based on studies of mostly large-sized Australian marsupials.

When young start detaching from the teat and enter into phase 3, they are left in a den or nest while the mother forages, and later on cling to her back until they are weaned (Tyndale-Biscoe and Renfree 1987). A nesting phase was reported for

D. gliroides (Mann 1955), *M. paulensis* (Leiner et al. 2008) and *Metachirus nudicaudatus* (Loretto et al. 2005), showing this might be a more common feature of South American marsupials than previously thought, even in medium/large sized species.

The reproductive strategies of South American marsupials have been poorly studied, and have been mostly concentrated on a few small-sized species from tropical/subtropical environments (Martins et al. 2006; Leiner et al. 2008), and *M. dimidiata* from temperate grasslands (Pine et al. 1985). In didelphids, different reproductive strategies have been documented, from multiyear cycles with no post-reproductive die-off to complete semelpartity (e.g., Pine et al. 1985; Hingst et al. 1998; Martins et al. 2006; Leiner et al. 2008). Semelparity, also known as senescence, involves a post mating die-off (generally of males), and/or a decline in reproductive fecundity (generally of females) after one reproductive cycle (Braithwaite and Lee 1979; Lee and Cockburn 1987). In semelparous species reproduction occurs once in a lifetime and leads to nonoverlapping discrete generations (Cole 1954; Martins et al. 2006). This reproduction mode has been intensively studied in many Australian species (e.g., *Antechinus* spp., *Phascogale* spp., *Dasyurus hallucatus*) showing some variation in life histories, from complete to partial semelparity (Lee et al. 1982; Cockburn 1997; Oakwood et al. 2001, but see Pine et al. 1985). In South American marsupials, complete semelparity has been inferred based on seasonal weight and marked sexual dimorphism in *M. dimidiata* (Pine et al. 1985). Well-marked sexual dimorphism has been correlated with a high reproductive effort and semelparity (Williams 1966), which relates to males investing in growth associated to reproductive success (and therefore aging at a faster speed and shorter time), and females growing at a slower rate due to breeding and raising the young (Gardner 1973, fide Pine et al. 1985). Complete semelparity has been also inferred based on age classes of museum specimens in *M. incanus* (Lorini et al. 1994), and has been recently reported in an ecological study of *M. paulensis* where both males and females did not survive to breed for a second season (Leiner et al. 2008). Partial semelparity, a different strategy in which males die-off after reproduction but females survive over a period of time, albeit gradually disappearing from the population, has been documented for *G. microtarsus* (Martins et al. 2006).

Braithwaite and Lee (1979) noted a predominance of semelparous marsupials in coastal regions of Australia, and associated this strategy with highly seasonal and predictable environments. If this hypothesis was true, one would expect semelparity as the predominant reproductive strategy in highly dimorphic species that inhabit seasonal environments. Unfortunately, our present knowledge on the reproductive strategies in species living in seasonal environments (both warm and temperate-cold) is very limited, and most South American marsupials are not highly dimorphic. This does not allow for a good interpretation of how climatic factors are involved (or not) in their life cycles. A recent approach proposed by Bradley (2003), involves the study of physiological changes that are likely to occur before males die, those of which could indicate a semelparous reproductive strategy. Although these studies are lacking for most South American marsupials, the combination of environmental and physiological factors at different levels could provide answers onto why semelparity evolved convergently in such different lineages (i.e., Marmosini and Thylamyini in America; Dasyuridae in Australia).

Even though several aspects of New World marsupial reproductive strategies are still poorly understood, different studies show that species tie their reproduction to photoperiod, rainfall or food availability (Julien-Laferrière and Atramentowicz 1990; Bergallo and Cerqueira 1994; Cerqueira 2004). Comparisons between different sized species of didelphid marsupials from Brazil show that photoperiod appears to be the most important proximal factor to influence the onset of the reproductive cycle, instead of meteorological events like rainfall (Cerqueira 2004).

Despite the available data, it is not clear how these factors would influence species with a broad latitudinal distribution (e.g., *Thylamys pallidior, D. albiventris*). For these species, shortening of their reproductive cycle, growth period, and a delay in the onset of the breeding season should be associated to a faster sexual maturity rate and an increase in developmental timing, for which we lack information. The effects of a broad latitudinal range on litter size have been partially explored for the genus *Didelphis* by Rademaker and Cerqueira (2006), showing a positive correlation, and a negative one between breeding season and latitude. This pattern of reproduction and growth would also have consequences in the development of the young, which should have a faster growing curve from tropical to more temperate climates. The time in which species attain sexual maturity would also be critical and should decrease with the distance from the equator (i.e., shorter lived species living far from the equator should reach sexual maturity faster, especially if they were to live for shorter periods of time). Many questions remain to be answered in this respect. For example, what would happen in species that inhabit temperate environments exclusively (e.g., *D. gliroides*, *Lestodelphys halli*), where differences in photoperiod are highly marked in comparison to tropical and subtropical environments studied so far? Would species of widespread distribution along a longitudinal pattern (east-west) show the same reproductive pattern throughout their range despite other variables like rainfall and altitude (e.g., *D. albiventris* from eastern Brazil and eastern Perú or Bolivia)? Would feeding resources influence any of these parameters? As with many of the subjects treated before, our knowledge of the reproductive strategies of South American marsupials is still fragmentary, with no information for caenolestids and very scarce, anecdotal information for *D. gliroides* and most of the species living in temperate ecosystems.

2.5 Size and Anatomical Constraints, Locomotion and Habitat Use

South American marsupials range in size from ca. 10 g to 1.4 kg (*Chacodelphys formosus* and *D. albiventris/D. marsupialis,* respectively) (Gordon 2003; Voss and Jansa 2009). Compared to other living mammals, they are somewhat externally homogeneous, their main morphological variation being body size, with subtle variations in general form, tail and limb proportions, and toe disposition patterns (Voss and Jansa 2009). Of the three extant South American orders, Didelphimorphia shows the largest variation in size, habitat use, and anatomical adaptations (Palma 2003; Tyndale-Biscoe 2005; Gardner 2008). Despite this variation, most didelphids have a surprisingly similar body plan: grasping hindfeet with opposable thumbs and a prehensile or semiprehensile tail (Szalay 1994; Martin 2008). The only living microbiotheriid, *D. gliroides*, is very similar to small didelphids (e.g., *Marmosa* s.l.) in body form, and is highly arboreal. Caenolestids are clearly different from didelphids in their shrew-like appearance, mostly terrestrial (semifossorial?) adaptations and procumbent lower incisors.

Morphological variation in didelphids is also accompanied by subtle variations in postural behavior, locomotion and locomotor performance, with posterior limbs more developed than anterior ones, even in arboreal species (Vieira 1997, 2006a, b). When comparing body and limb weights, hindlimb muscle weight was found to be highest in *Metachirus* and *Chironectes*, two species living in clearly different substrates (i.e., terrestrial and semiaquatic, respectively) (Carvalho et al. 2000; Argot 2001, 2002, 2003). Differences between scansorial/arboreal from generally terrestrial species have also been found in the use and shape of the pelvic girdle (Argot 2002, 2003; Vieira 2006a, b). Terrestrial forms show a larger development of muscular insertions with a somewhat reduced mobility, while arboreal/scansorial forms have more muscular mobility and greater articulation (Argot 2002). The vertebral column, especially in the lumbar region, has also become different in relation to the species' habits: arboreal forms tend to have a thinner and narrower vertebral column, with plenty of freedom in movement (e.g., *Caluromys*, *Marmosa*; Works 1950; Grand 1983), while terrestrial species show more robust muscular insertions and a more developed lower back musculature (e.g., *Metachirus*; Argot 2003). Two main patterns in the scapulae of living New World marsupials were found, one with a triangular shape, present in arboreal species and also in small-sized marsupials (e.g., *Caluromys*, "*Marmosa*" [=*Micoureus*], *Dromiciops*); and the other with a quadrangular shape, present in terrestrial and generalist species (e.g., *Metachirus*, *Didelphis* , *Monodelphis*; Argot 2001, Martin pers. obs.). This difference can be related to the rotation of the anterior limbs and protraction/retraction of the humerus, which is in turn related to muscular mass and therefore to locomotion (Vieira 1997, 2006a, b; Argot 2001).

A primitive pattern of foot morphology is characteristic of didelphids and microbiotheriids, with minor deviations related to toe size and predominance (Szalay 1982a, b, 1994; Voss and Jansa 2003). The hand of didelphids and *Dromiciops* do not reflect major differences in locomotor habits, and are used in a similar stereotyped behavior common to most species, especially the smaller sized ones (e.g., *Dromiciops*, *Lestodelphys*, *Monodelphis*; Streilen 1982; Martin 2008; Martin and Udrizar Sauthier 2011). Extant caenolestids deviate from this pattern, probably in response to a scansorial way of life, by having a reduced hallux (*contra* Szalay 1994).

Studies on foot articulation have led to the assumption that living metatherians (especially Didelphidae) are, in general, highly arboreal (e.g., Szalay 1982a, b, 1994; Szalay and Sargis 2001); and were therefore considered plesiomorphic in their locomotor adaptations. This view has been challenged by recent work (e.g., de Muizon and Argot 2003), supporting the idea that living New World marsupials appear to be more specialized than their Paleogene ancestors, especially in relation to their climbing abilities. Most didelphids and *Dromiciops* share a hindfoot with a powerful grasping mechanism and scansorial adaptations (Grand 1983; Szalay 1994), including the use of the tail as a “fifth member” (see below). Exceptions to this generalized pattern include *Chironectes, Metachirus,* and caenolestids, which are clearly distinct from the rest by having a unique foot morphology with more terrestrial adaptations. Toe length is also directly related to differences in substrate locomotion, where arboreal species (e.g., *Marmosa*, *Caluromys*, *Dromiciops*) have longer ones than terrestrial species (e.g., *Monodelphis*, *Metachirus*).

Locomotion presents different constraints depending on substrate use and the individual’s size, especially when moving in inclines (Pridmore 1992, 1994; Hildebrand 1995; Santori et al. 2005; Delciellos and Vieira 2006; Vieira 2006a, b). Terrestrial environments, on one hand, are perceived in different ways by small or medium/large animals, with smaller individuals having to sort out larger obstacles and longer, more sinuous paths when moving around, in proportion to larger ones (Vieira 2006a, b). Arboreal environments, on the other hand, pose considerable constraints to size in mammals, which are related to living in a highly complex three-dimensional habitat which includes gathering food, escaping from predators, and moving through different sized branches and open spaces, amongst others (Szalay 1994; Hildebrand 1995).

Marsupial locomotion has been described as mostly quadrupedal (also called grasp climbing by Szalay 1994), both on terrestrial and arboreal substrates (Grand 1983; Vieira 2006a, b). South American marsupials move at a slow pace, regardless of the substrate, exploring with their heads up and “sensing” the environment (Streilen 1982; Martin and Udrizar Sauthier 2011). Despite this common pattern, differences between lineages show most didelphids move in a lateral sequence (Pridmore 1992; Hildebrand 1995), while *D. gliroides* and *Caluromys philander* use a diagonal sequence, which has been associated (mostly) with locomotion on narrow substrates (Pridmore 1994; Lemelin et al. 2003). The pattern of lateral sequence changes to a diagonal one when starting to run or trot (McManus 1970; Pridmore 1992; Vieira 2006a, b), which is typical for arboreal mammals (Hildebrand 1995; Lemelin et al. 2003). Diagonal sequencing apparently produces a more stable stride in arboreal mammals, probably due to the fact that lateral sequences make thin branches shake in an uncontrolled manner (sideways for the animal). Both diagonal and lateral sequences are symmetrical in Didelphidae (Lemelin et al. 2003; Vieira 2006a, b), meaning that limbs move in pairs. This is also true for the diagonal sequence found in *Caluromys philander* (Caluromyidae) and the microbiotheriid *D. gliroides* (Pridmore 1994; Lemelin et al. 2003). All studied species (except *C. philander*) move to an asymmetrical half-bound and transverse gallop or trot when fleeing (Pridmore 1992, 1994; Lemelin et al. 2003).

These changes in locomotion patterns have been recorded in substrates resembling trees, even with different inclination angles (Vieira 1997, 2006a, b). What does this locomotion pattern imply, and does it resemble the ancestrally inferred pattern of locomotion? It is interesting to note that two lineages of arboreal South American marsupials which are not related (*Caluromys* and *Dromiciops*), share the same diagonal pattern of locomotion, and that this pattern is found in running Didelphidae. Although further studies are required, this could mean that living Didelphidae evolved from an arboreal species with a diagonal sequence, and that a lateral sequence derived when animals ventured onto the ground, with the diagonal sequence retained by “older” lineages.

Compared to other arboreal/scansorial mammals, marsupials move slowly when in trees, grasping the surface and positioning themselves as vertical to the substrate as they can. Also, the position of their limbs is distinct from other arboreal mammals, placing the forefeet close to each other and supporting much of the weight, using the head and tail as balancing organs, and placing the hindfeet a little apart from the gravity center as a way to support the moving individual. Most New World marsupials have long and well-developed tails, with the exception of caenolestids and some terrestrial forms in which the tail is clearly shorter than head-body length (e.g., *Monodelphis*). The presence of a long tail plays an important role as a balancing organ in which the center of gravity is moved backwards and allows for quick movements on uneven substrates without the use of the forelimbs (Argot 2003; Muizon and Argot 2003). Anatomically, arboreal forms are characterized by caudal bones with well-developed neural and mammillary processes, coupled with robust transverse processes and strong abductors at the base of the tail (Argot 2003). In these species, the tail is heavy and muscular at its base, with a lengthening of the posterior caudals and prehensility toward the posteriormost end, where the development of a series of plicas add to the grasping capacity (Hershkovitz 1992b, 1997, 1999). In terrestrial forms, the distal caudal vertebrae are much more slender, presumably not able to support the body weight of the animal (Argot 2003, but see Martin 2008). The use of the tail as a “fifth member,” even in highly terrestrial species like *L. halli* (Szalay 1994, but see Argot 2002; Martin and Udrizar Sauthier 2011), would add support to this arboreal ancestry in living didelphids (Enders 1935; McManus 1970).

Although marsupials (with the exception of *Chironectes*) use water habitats only on rare occasions (i.e., when fleeing from predators, encounter them as obstacles during foraging activities or floods), they can be active swimmers. Locomotion in water has been studied for *D. virginiana*, *Chironectes minimus,* and *L. crassicaudata* (Fish 1993; Santori et al. 2005). Main differences were found in the propulsion of these species, *Chironectes* using only its hindfeet while the other two use underwater paddling, which is different between them as well. The use of hindlimbs for swimming in *Chironectes* also has the advantage of leaving the forelimbs free for foraging, capturing, and manipulating prey (Hamrick 2001). *Lutreolina* has a higher stride frequency than *Didelphis*, similar buoyancy and swimming posture to *Chironectes*, but swimming speed similar to that of *Didelphis.* As opposed to that of *Didelphis*, the fur of *Chironectes* and *Lutreolina* is non-wettable and provides a certain degree of buoyancy (Fish 1993; Marshall 1978a), which is associated with a more efficient control of swimming movements. Anecdotal information on swimming capabilities is available for *M. nudicaudatus, P. frenatus, D. albiventris, D. aurita,* and *M. domestica* (Hershkovitz 1997; Santori et al. 2005 and literature cited therein). Mammals with semiaquatic adaptations are not very common due to thermal (and also anatomical) restrictions, especially those with low BMRs (McNab 2005). Heat loss in water through convection is probably a strong limitation and other than *Chironectes*, no other marsupial has "ventured" into this niche.

Although marsupials comprise ca. 10 % of the mammal species of South America, our knowledge on their ecology and behavior is mostly anecdotal. South American marsupials can be found throughout all the region's biomes, and occupy different ecological niches while making use of a variety of substrates (Eisenberg and Wilson 1981; Streilen 1982; Corvalán 2004; Cáceres 2006; Vieira 2006a, b; Martin 2008; Martin and Udrizar Sauthier 2011).

Habitat use has been studied in tropical and subtropical species, most of them from forested biomes (e.g., Charles-Dominique et al. 1981; Charles-Dominique 1983; Pires and Fernandez 1999; Vieira 2006a, b). A few exceptions include *D. albiventris* and *M. domestica* in the Cerrado and Caatinga (Streilen 1982); *M. dimidiata* in the Pampa (Pine et al. 1985); *T. pallidior* in the Monte (Corvalán 2004) and *D. gliroides* in the Temperate Rainforest (Patterson et al. 1990; Rodríguez-Cabal et al. 2007). Studies show that most species make a "complete" use of the habitat by moving throughout most of the space available to them, even if they are mostly arboreal, scansorial or mostly terrestrial. Smaller species, with the exception of *Monodelphis* spp. and *L. halli*, are arboreal or scansorial, and those from tropical or subtropical forests can be found living in microsympatry with similar body-sized species and sharing the same resources (Eisenberg and Wilson 1981; Emmons and Feer 1997; Pires and Fernández 1999; Delciellos and Vieira 2006; Vieira 2006a, b). This has provided unique opportunities to test for hypothesis of vertical stratification and resource partitioning. Comparing different areas in the Brazilian Atlantic Forest, Vieira (2006a, b) found that substrate use was influenced by: (1) seasonal patterns related to food availability, (2) intraspecific segregation (e.g., young from adults, males from females), (3) changes in patterns of community composition according to substrate, and (4) ecological processes involving habitat use in relation to the species' daily activities (e.g., foraging, resting). Many of these factors are influenced by others mentioned above, some of them intrinsic (e.g. diet , reproduction, locomotion, and population density), others extrinsic (e.g., climate, type, and condition of habitat). Two separate studies on *M. incanus* and *M. paraguayanus* in the Brazilian Atlantic forest have shown space use to be the same for both males and females in the former but different in the latter, with females of *M. paraguayanus* exploring the vertical strata of the forest more frequently than males (Loretto and Vieira 2008; Prevedello et al. 2009). Unfortunately, these are the only studies documenting space use at this scale and for one ecoregion, with no information on other spatially/vertically complex environments. Species living in somewhat "simpler" environments (i.e., less vertically stratified) still show a complex habitat use (e.g., *T. pallidior* in the Monte desert of Argentina, Corvalán 2004).

The behavior of South American marsupials is generally comprised of anecdotical accounts in works with a broad scope that might include one or several species. Streilen (1982) presented a lengthy description of activity patterns in *D. albiventris* and *M. domestica*, including activity period, exploration, sleeping, prey manipulation, grooming, and other socially related behavior. Both species have nocturnal and crepuscular activity patterns, concentrated during the first hours after dawn and with bouts throughout the night, depending on foraging activities and food intake. In relation to this, both species move with their noses close to the substrate, stopping for brief moments and sniffing the air, to continue moving with their noses close to the substrate. When an item is located, a moment is spent calculating distance and possible movements, and followed by a quick grasp with its mouth. If the item is a live vertebrate, it is bitten in the neck and immobilized. After this, a semierect feeding position is assumed. Manipulation of the prey is generally done by one or both paws, depending on its size. Grooming of the head and forepaws is often a previous activity to prey manipulation and consumption. Grooming patterns start with the forepaws around the head, which have been previously and extensively licked, and then proceed onto the rest of the body. The hindfeet are used to scratch the body and head, in a similar manner as the forefeet, but with restricted mobility. These stereotyped patterns were found typical, with minor variations, for other species [e.g., *M. dimidiata* (González and Claramunt 2000), *Philander* spp. (Hershkovitz 1997), *D. gliroides* (Mann 1955, 1958; Martin 2008), *Thylamys fenestrae* (Bruch 1917), *Thylamys elegans* (Palma 1997), *L. halli* (Martin and Udrizar Sauthier 2011)].

A combination of anatomical features including size and locomotion, along with a series of common patterns of behavior, results in minor differences between habitat use and other related adaptations in South American marsupials. Most species show variable levels of integration with the habitat in which they live, and the way they use it. Vertical stratification in structurally complex habitats is mostly related to resource availability, while species mobility might influence habitat use in simpler environments.

2.6 Integrating Physiological and Ecological Constraints

As described above, several factors appear to be relevant when analyzing the physiological and ecological constraints of South American marsupials. The BMR and other physiological adaptations (e.g., field metabolic rate), diet and food availability, foraging activities and habitat use, are all related and can be indicative of how different species cope with the availability of food resources and climatic variations (Tyndale-Biscoe and Renfree 1987; Green 1997; Hume 1999; McNab 2005). Apart from the direct relationship to food items, energy expenditure during foraging activities is a critical factor that should maximize, ideally, the net rate of energy balance (Townsend and Hughes 1981). One of the strategies documented in both New and Old World old world marsupials is related to the way in which animals make use of their energetic resources, and includes hibernation and/or daily torpor (McNab 1978, 2005; Geiser 1994, 2003; Bozinovic et al. 2004, 2005), and the storage of those accumulated resources, both as body or caudal fat (Morton 1980; Krause and Krause 2006; see below). Torpor and/or hibernation are common (but not exclusive) adaptations in mammals that experience seasonal food shortages and sometimes low environmental temperatures, to counterbalance the negative results between foraging activities and food intake (Geiser 2003; Bozinovic et al. 2004). While hibernation in New World marsupials is only known to occur in *D. gliroides* (Bozinovic et al. 2004), daily torpor appears to be a common strategy, especially in smaller species (e.g., *L. halli*, *Monodelphis brevicaudata*, *T. elegans*; Morrison and McNab 1962; McNab 1978; Bozinovic et al. 2005; Martin 2008; Geiser and Martin 2013). Torpor can be induced by food deprivation and low ambient temperatures, proving this adaptation is an opportunistic (and facultative) response to unpredictable biotic and abiotic conditions (Geiser 1994; Bozinovic et al. 2004, 2005; Martin 2008; Martin and Udrizar Sauthier 2011; Geiser and Martin 2013). Torpor may also occur in tropical or subtropical environments, even when food is available, as a way of maximizing energy use (Geiser 1994). This has only been documented in small species (e.g., *G. microtarsus*, *M. robinsoni*), suggesting a strong relationship between size (i.e., body mass) and heterothermy (McNab 2005). Recent work on torpor and hibernation in marsupials shows that torpor intensity varies from juveniles to adults, being longer in the former (Geiser et al. 2008). This appears to be an important adaptation in growing individuals to survive periods of energy shortage, and may facilitate somatic growth because valuable nutrients are not wasted in thermoregulation (Geiser et al. 2008). No indication of torpor or hibernation was found in recent observations of several individuals of *Caenolestes fuliginosus*, maintained in captivity during variable periods of time (1 to 12 consecutive days; Martin and González Chávez, in prep.).

A complimentary behavior to torpor that was recently discovered to occur in Australian marsupials is basking (Geiser et al. 2008). A few species of desert dasyurids employ this strategy during rewarming from torpid states, a process that can reduce the energy costs of this process by 85 % (Geiser et al. 2008). Although this behavior is yet to be recorded in South American marsupials, species living in highly seasonal environments (e.g., Patagonian Steppe, Puna, Cerrado, Caatinga) could be expected to show this adaptation as well.

Caudal fat storage has been documented as an adaptation to highly seasonal environments acting as energy reserves during periods of food shortage (Morton 1980). This feature is common in many of the small dasyurids living in central Australia, and is also present in some rodents, insectivores, and lemurs. It has also been found to occur in small didelphids from xeric environments (e.g., *L. halli, Thylamys* spp.) and, convergently, in *D. gliroides* and *R. raphanurus*, both from the Valdivian Temperate Rainforest (Morton 1980; Birney and Monjeau 2003; Solari 2003; Martin 2008). Even though *Caenolestes* spp. and *L. inca* inhabit extreme environments (the *páramos* and *subpáramos* above 1800 m) there is no record of tail incrassation in these species (Albuja and Patterson 1996, Tyndale-Biscoe 2005). Tail incrassation has been mentioned in *D. virginiana*

(Krause and Krause 2006), and might also occur in other didelphids that live in highly seasonal environments (e.g., Caatinga, Cerrado, Chaco). Unfortunately, little is known about the occurrence of this adaptation in other didelphids and no information is available on the total amount of energy stored as caudal fat. Also, the speed at which this fat is consumed or metabolized remains unknown. In specimens of *L. halli* maintained in captivity for over two months and with a constant food supply, the tail quickly became incrassated changing its shape from dorsoventrally flattened to "carrot-like" in less than a week (Martin and Udrizar Sauthier 2011). When deprived of food, caudal fat was consumed in a matter of 7–10 days, which is indicative of a quickly available energy resource. High-energy resources like this might provide an important advantage when rewarming from daily or multiday torpor, an adaptation that could also maximize energy use for short foraging activities during harsh environmental conditions. These adaptations would be directly related to the need to prolong fat reserves, keeping the body functioning with a minimum waste of energy to maintain vital processes needed to survive (Morton 1980; Geiser 1994, 2003; Bozinovic et al. 2004, 2005).

The occurrence of physiological adaptations as those mentioned above are generally combined with a selective habitat use. Many species also rely on tree cavities, burrows, and other protected locations during the day and between foraging bouts. While these areas within the environment can be used as resting places and would provide protection from predators, they are also important for buffering thermal extremes (Geiser 2003). In many ways, these adaptations are somewhat related and are a direct consequence of most South American species being small-sized (Lee and Cockburn 1987; Geiser 2003). Locomotor and anatomical features characteristic of New World marsupials influence the species' habitat use and preferences, resulting in most species being arboreal or scansorial. This in turn, can be associated with a generally opportunistic and omnivorous diet , giving these species the capacity to cope with fluctuating resources due to different environmental constrains, including those related to seasonality and complex habitats. While moving away from multi-stratified habitats into simpler ones, resource availability also decreases. Marsupials living in more simple and sometimes extreme habitats should therefore "concentrate" on strategies to minimize energy use during physiological processes (e.g., homeothermy) and foraging activities by entering torpor (daily or multiday bouts), while maximizing energy input by shifting their feeding preferences and fat storage. Most South American marsupials are nocturnal, which represents an additional energetic problem. It is during the night that lowest temperatures are recorded, increasing heat loss and energy expenditure to maintain a constant internal temperature. It is also during the night that "mobile" food resources (mainly arthropods and rodents) are active and easily available, while "static" resources might be available due to other animals not being active during the night (e.g., frugivorous monkeys and birds in tropical and subtropical environments). Another critical factor, especially for species living in xeric environments, is related to hydric balance (Díaz and Cortés 2003). Concentrating foraging activities during the night would maximize the chances of finding food items quicker and with less energy expenditure, while the water balance remains positive avoiding evapoperspiration (Schmidt-Nielsen 1964).

The reproductive strategies of South American marsupials are most likely to be influenced by these ecological and physiological constraints as well. As a result, different strategies might evolve, resulting in species that live for more than one year and reproduce seasonally or throughout the year, and species that only reproduce once in their life (i.e., are truly semelparous). Although our information is very limited in this respect, species with broader distributions appear to have marked seasonal reproduction patterns, especially toward their distribution extremes. These species tend to produce one litter per year and/or reduce their litter size when away from their optimal range, especially towards the South. Thermal constraints would have a direct influence on the reproductive cycles of these broad-ranging species, while resource availability and other ecological factors (i.e., intraspecific competition) might influence tropical and subtropical species more acutely. The advantage of a single reproductive cycle in non-semelparous species living in temperate environments would allow individuals to reduce the energy expenditure related to breeding and allocate resources into metabolic processes for surviving to reproduce yet another season.

The distribution of living South American marsupials is a result of all these constraints, along with historical factors. In this context, two separate lineages (i.e., Microbiotheria and Paucituberculata) adapted to living in temperate or temperate-cold environments would be remnants of once diverse groups, while a separate, and highly diversified lineage (i.e., Didelphimorphia) mainly lives in humid tropical/subtropical environments and has recently adapted to (colonized?) a diversity of habitats (e.g., warm-dry habitats like the Chaco and Caatinga; cold-dry habitats like Patagonia and Puna; cool-humid habitats like the Humid Pampas). Due to this combination of physiological ecology and historical factors, the area between 40°S/70° 30′W and 41° 30′S/72° 30′W (Fig. 2.7) is the only one where the three extant New World marsupial Orders coexist (with five species): Didelphimorphia (*L. halli*, *T. pallidior* and *D. albiventris*); Microbiotheria (*D. gliroides*); and Paucituberculata (*R. raphanurus*) (Martin 2008, 2010, 2011).

South America shows unique environmental conditions, including steep environmental gradients mostly due to acute altitudinal differences, which have no correlation in Australia, providing a magnificent opportunity to study the anatomical and physiological adaptations of these marsupials. Intrinsic (i.e., physiological, ecological) and extrinsic (i.e., climatic) thermal constraints strongly influence their feeding preferences and reproductive strategies, which are bounded within several anatomical constraints, and related to habitat use and, ultimately, their distribution patterns. Several constraints appear to be critical as part of the life strategies of South American marsupials: (1) variable energetic costs for regulating metabolic processes, due to a low rate of metabolism, the possibility to enter torpor/hibernation, and the storage of different types of fat tissues available for those varied processes; (2) a broad, generally opportunistic and omnivorous diet; (3) a reproduction cycle that shares a short gestation period and long, energy-demanding, breeding period, but with specific differences in reproductive strategies

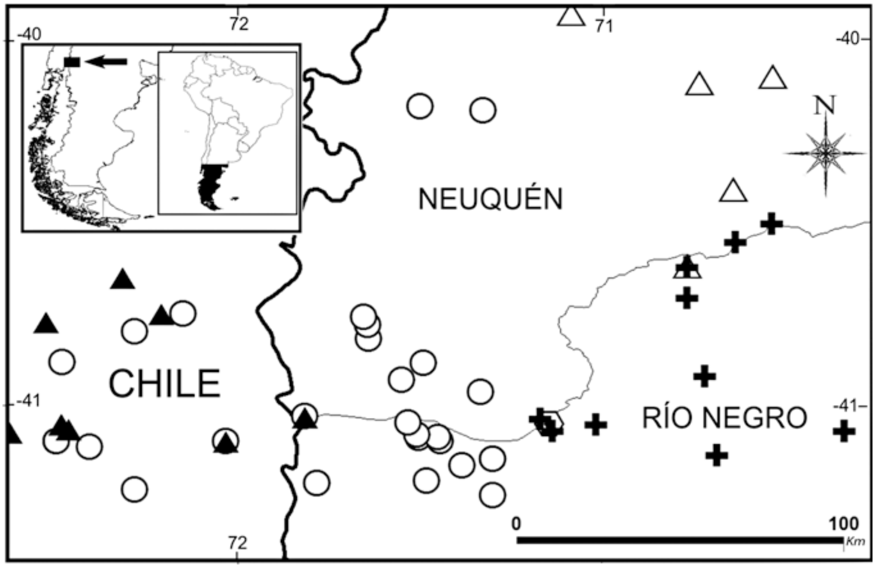

Fig. 2.7 Map of the area between 40°S/70° 30′W and 41° 30′S/72° 30′W where representatives of the three extant New World marsupial orders coexist: Didelphimorphia [*Lestodelphys halli*, black crosses; *T. pallidior*, open triangles; *Didelphis albiventris*, open hexagon]; Microbiotheria [*Dromiciops gliroides*, open circles]; and Paucituberculata [*Rhyncholestes raphanurus*, black triangles]

(e.g., semelparity, partial semelparity, iteroparity), and their main traits (e.g., litters per year and litter size, teat number); (4) arboreal/scansorial habits and a complete use of the available habitat. These adaptations, added to a generally small size, small energy expenditure on foraging and other daily activities, most of which take place during night hours, allow South American marsupial species to thrive in environments where competition with other animals might be strong (e.g., tropical and subtropical climates), or where a few small mammals can survive (e.g., temperate and temperate-cold climates), due to several environmental limitations.

Future studies should aim at filling the many gaps in our knowledge of their natural history, and integrate them into a body of work which should provide some insight on the evolutionary history of these peculiar groups of mammals.

References

Albuja L, Patterson BD (1996) A new species of northern shrew-opossum (Paucituberculata: Caenolestidae) from the Cordillera del Cóndor, Ecuador. J Mammal 77:41–53

Amico G, Aizen MA (2000) Mistletoe seed dispersal by a marsupial. Nature 408:929–930

Amico G, Rodríguez-Cabal MA, Aizen MA (2009) The potential key seed-dispersing role of the arboreal marsupial *Dromiciops gliroides*. Acta Oecol 35:8–13

Argot C (2001) Functional-adaptive anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J Morphol 247:51–79

Argot C (2002) Functional-adaptive analysis of the hindlimb anatomy of extant marsupials, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J Morphol 253:76–108

Argot C (2003) Functional-adaptive anatomy of the axial skeleton of some extant marsupials and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus*. J Morphol 255:279–300

Astúa de Moraes D (2006) Range extension and first Brazilian record of the rare *Hyladelphys kalinowskii* (Hershkovitz, 1992) (Didelphimorphia, Didelphidae). Mammalia 70:174–176

Astúa de Moraes D, Santori RT, Finotti R, Cerqueira R (2003) Nutritional and fibre contents of laboratory-established diets of neotropical opossums (Didelphidae). In: Jones M, Dickman C, Archer M (eds) Predators with pouches: The Biology of Carnivorous Marsupials. CSIRO Publishing, Victoria

Atramentowicz M (1986) Dynamique de population chez trois marsupiaux didelphidés de Guyane. Biotropica 18:136–149

Atramentowicz M (1988) La frugivorie opportuniste de trois marsupiaux didelphidés de Guyane. Rev Ecol (Terre et Vie) 43:47–57

Barnes RD, Barthold SW (1969) Reproduction and breeding behavior in an experimental colony of *Marmosa mitis* Bangs (Didelphidae). J Reprod Fertility 6:477–482

Bergallo HG, Cerqueira R (1994) Reproduction and growth of the opossum *Monodelphis domestica* (Mammalia: Didelphidae) in northeastern Brazil. J Zool 232:551–563

Bernarde PS, Machado RA (2008) Mammalia, Didelphimorphia, Didelphidae, *Glironia venusta* Thomas, 1912: Distribution extension to the state of Acre, Brazil. Checklist 4:151

Biggers JD (1967) Notes on reproduction of the woolly opossum (*Caluromys derbianus*) in Nicaragua. J Mammal 48:678–680

Birney EC, Monjeau JA (2003) Latitudinal variation in South American marsupial biology. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Bocchiglieri A, Mendonca AF, Campos JB (2010) Diet composition of *Gracilinanus agilis* (Didelphimorphia, Didelphidae) in dry woodland areas of Cerrado in central Brazil. Mammalia 74:225–227

Bozinovic F, Ruiz G, Rosenmann M (2004) Energetics and torpor of a South American "living fossil", the microbiotheriid *Dromiciops gliroides*. J Comp Physiol (B) 174:293–297

Bozinovic F, Ruiz G, Cortés A, Rosenmann M (2005) Energetics, thermoregulation and torpor in the Chilean mouse-opossum *Thylamys elegans* (Didelphidae). Rev Chilena Hist Nat 78:199–206

Bradley AJ (2003) Stress, hormones and mortality in small dasyurid marsupials. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Braithwaite RW, Lee AK (1979) A mammalian example of semelparity. Amer Nat 113:151–155

Brown B (2004) Atlas of new world marsupials. Fieldiana Zool NS 102:1–308

Bruch C (1917) La Comadrejita *Marmosa elegans*. Rev Jard Zool Buenos Aires 51(52):208–214

Busch M, Kravetz FO (1991) Diet composition of *Monodelphis dimidiata* (Marsupialia, Didelphidae). Mammalia 55:619–621

Cáceres NC (2000) Dieta, adaptações morfológicas à alimentação e dispersão de sementes por marsupiais do Sul do Brasil. PhD thesis, Univ Fed Paraná

Cáceres NC (2006) O papel de marsupiais na dispersão de sementes. In: Cáceres NC, Monteiro Filho ELA (eds) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. UFMS Editora, Campo Grande

Cáceres NC, Monteiro-Filho ELA (1997) Reproductive biology of the common opossum *Didelphis marsupialis* (Mammalia: Marsupialia), in southern Brazil. Brenesia 47–48:97–104

Cáceres NC, Monteiro-Filho ELA (2000) The common opossum, *Didelphis aurita*, as a seed disperser of several plants in south Brazil. Ciência e Cultura 52:41–44

Cáceres NC, Ghizoni-Jr IR, Graipel ME (2002) Diet of two marsupials, *Lutreolina crassicaudata* and *Micoureus demerarae*, in a coastal Atlantic Forest island of Brazil. Mammalia 66:331–340

Cantor M, Ferreira LA, Silva WR, Setzl EZF (2010) Potential seed dispersal by *Didelphis albiventris* (Marsupialia, Didelphidae) in highly disturbed environment. Biota Neotropical 10:45–51

Carlsson A (1903) Beitrage zur Anatomic der Marsupial Region bei den Beuteltherien. Zoologische Jahrbiicher, Abteilung Anatomic und Ontogenie der Thiere 80:489–505

Carmignotto AP, Monfort T (2006) Taxonomy and distribution of the Brazilian species of *Thylamys* (Didelphimorphia, Didelphidae). Mammalia 70:126–144

Carvalho FMV, Fernandez FAS, Nessimian JL (1999) Diet of small mammals in Atlantic forest fragments in southeastern Brazil. Rev Brasilera Zoociências 1:91–101

Carvalho RVC, Delciellos AC, Vieira MV (2000) Medidas externas dos membros de marsupiais didelfídeos: una comparção com medidas do esqueleto pós-craniano. Bol Mus Nac NS Zool 438:1–8

Catzeflis F, Richard-Hansen C, Fournier-Chambrillon C, Lavergne A, Vié JC (1997) Biométrie, reproduction, et sympatrie chez *Didelphis marsupialis* et *D. albiventris* en Guyane française (Didelphidae: Marsupialia). Mammalia 61:231–243

Ceotto P, Finotti R, Santori R, Cerqueira R (2009) Diet variation of the marsupials *Didelphis aurita* and *Philander frenatus* (Didelphimorphia, Didelphidae) in a rural area of Rio de Janeiro State, Brazil. Mastozool Neotropical 16:49–58

Cerqueira R (2004) Fatores ambientais e a reprodução de marsupiais e roedores no leste do Brasil1. Arqu Mus Nac 63:29–39

Cerqueira R, Gentile R, Fernandez FAS, D'Andrea PS (1993) A five year study of an assemblage of small mammals in southeastern Brazil. Mammalia 57:507–517

Charles-Dominique P (1983) Ecology and social adaptations in didelphid marsupials: comparison with eutherians of similar ecology. Amer Soc Mammal Sp Publ 7:395–422

Charles-Dominique P, Atramentowicz M, Charles-Dominique M, Gérard H, Hladik A, Hladir CM, Prévost MF (1981) Les memifères frugivores arboricols nocturnes d'une forêt guyanaise: interrelations plantes-animaux. Rev Ecol (Terre et Vie) 35:341–435

Cherem JJ, Graipel ME, Menezes ME, Soldateli M (1996) Observações sobre a biologia do gambá (*Didelphis marsupialis*) na Ilha de Ratones Grande, Estado de Santa Catarina, Brasil. Biotemas 9:47–56

Clark CT, Smith KK (1993) Cranial Osteogenesis in *Monodelphis domestica* (Didelphidae) and *Macropus eugenii* (Macropodidae). J Morpholgy 215:119–149

Cockburn A (1997) Living slow and dying young: senescence in marsupials. In: Saunders NR, Hinds LA (eds) Marsupial biology: recent research, New perspectives. Univ New South Wales Ltd, Sydney

Cockburn CN, Johnson A (1988) Patterns of Growth. In: Janssens PA (ed) Tyndale-Biscoe CH. The developing marsupial. Models for biomedical research. Springer, Berlin

Cole LC (1954) The population consequences of life history phenomena. Quart Rev Biol 29:103–137

Cordero AG, Nicolas RA (1987) Feeding habits of the opossum (*Didelphis marsupialis*) in northern Venezuela. In: Patterson BD, Timm RM (eds) Studies in neotropical mammalogy, essays in honor of Philip Hershkovitz. Fieldiana Zool NS 39:125–131

Corvalán VE (2004) Uso del hábitat y ecología poblacional de pequeños mamíferos del desierto del monte central, Mendoza, Argentina. PhD thesis, Univ Nacional de La Plata

Crespo JA (1982) Ecología de la comunidad de mamíferos del parque Nacional Iguazú, Misiones. Rev Mus Arg Cs Nat "B. Rivadavia" Ecol 3:45–162

D'Andrea PS, Gentile R, Cerqueira R, Grelle CEV, Horta C, Rey L (1999) Ecology of small mammals in a Brazilian rural area. Rev Bras Zool 16:611–620

Davis DE (1947) Notes on the life histories of some Brazilian mammals. Bol Mus Nac 76:1–8

Dawson TJ, Dawson WR (1982) Metabolic scope and conductance in response to cold of some dasyurid marsupials and Australian rodents. Comp Biochem Physiol 71:59–64

Dawson TJ, Hulbert AJ (1970) Standard metabolism, body temperature, and surface areas of Australian marsupials. Am J Phys 218:1233–1238

Dawson TJ, Olson JM (1987) Thermogenic capacities of the opossum *Monodelphis domestica* when warm and cold acclimated: similarities between American and Australian marsupials. Comp Biochem Physiol 89:85–91

Dawson TJ, Wolfers JM (1978) Metabolism, thermoregulation and torpor in shrew sized marsupials of the genus Planigale. Comp Biochem Phy A 59:305–309

Delciellos AC, Vieira MV (2006) Arboreal walking performance in seven didelphid marsupials as an aspect of their fundamental niche. Austral Ecol 31:449–457

Díaz GB, Cortés A (2003) Pequeños mamíferos en ambientes desérticos: los problemas de conservación de agua. In: Bozinovic F (ed) Fisiología Ecológica y Evolutiva, Teoría y casos de estudio en animales. Univ Católica de Chile, Santiago

Eisenberg JF (1980) The density and biomass of tropical mammals. In: Soulé ME, Wilcox BA (eds) Conservation biology. Sinauer Associates, Sunderland

Eisenberg JF (1981) The mammalian radiations: an analysis of trends in evolution, adaptation and behavior. Univ Chicago Press, Chicago

Eisenberg JF, Wilson D (1981) Relative brain size and demographic strategies in didelphid marsupials. Amer Nat 118:1–15

Emmons LH, Feer F (1997) Neotropical rainforest mammals: a field guide, 2nd edn. Univ Chicago Press, Chicago

Enders AC (1966) Attachment, nursing, and survival of young in some Didelphids. In: Rowlands JW (ed) Comparative biology of reproduction in mammals. Academic Press, New York

Enders RK (1935) Mammalian life-histories from Barro Colorado Island, Panama. Bull Mus Comp Zool 78:385–497

Fernandes MEB, Andrade FAG, Silva Júnior JS (2006) Dieta de *Micoureus demerarae* (Thomas) (Mammalia, Didelphidae) associada às florestas contíguas de mangue e terra firme em Bragança, Pará, Brasil. Rev Bras Zool 23:1087–1092

Fish FE (1993) Comparison of swimming kinematics between terrestrial and semiaquatic opossums. J Mammal 74:275–284

Fleming TH (1973) The reproductive cycles of three species of opossum and other mammals in the Panamá Canal Zone. J Mammal 54:439–455

Fonseca GAB, Kierulff MCM (1989) Biology and natural history of Brazilian Atlantic forests of different sizes. Bull Florida Mus Nat Hist Biol Sci 34:99–152

Freitas SR, Astúa de Moraes D, Santori RT, Cerqueira R (1997) Habitat preference and food use by *Metachirus nudicaudatus* and *Didelphis aurita* (Didelphimorphia, Didelphidae) in a restinga forest at Rio de Janeiro. Rev Bras Biol 57:93–98

García D, Rodríguez-Cabal MA, Amico GC (2009) Seed dispersal by a frugivorous marsupial shapes the spatial scale of a mistletoe population. J Ecol 97:217–229

Gardner AL (1973) The systematics of the genus *Didelphis* (Marsupialia: Didelphidae) in North and Middle America. Spec Publ Mus Texas Tech Univ 4:1–81

Gardner AL (2008) Mammals of South America, Volume 1: marsupials, xenarthrans, shrews, and bats. Univ Chicago Press, Chicago

Gardner AL, Dagosto M (2008) Tribe Metachirini. In: Gardner AL (ed) Mammals of South America, Vol 1: marsupials, xenarthrans, shrews, and bats. Univ Chicago Press, Chicago

Geiser F (1994) Hibernation and daily torpor in marsupials: a review. Aus J Zool 42:1–16

Geiser F (2003) Thermal biology and energetics in carnivorous marsupials. In: Jones M, Dickman C, Archer M (eds), Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Geiser F, Martin GM (2013) Torpor in the Patagonian opossum (*Lestodelphys halli*): implications for the evolution of daily torpor and hibernation

Geiser F, Drury RL, McAllan BM, Wang DH (2003) Effects of temperature acclimation on maximum heat production, thermal tolerance, and torpor in a marsupial. J Comp Phyisiol 173:437–442

Geiser F, Christian N, Cooper CE, Körtner G, McAllan BM, Pavey CR, Turner JM, Warnecke L, Willis CKR, Brigham M (2008) Torpor in marsupials: recent advances. In: Lovegrove BG, McKechnie AE (eds) Hypometabolism in animals: hibernation, torpor and cryobiology. Univ KwaZulu-Natal, Pietermaritzburg

Godfrey GK (1975) A study of oestrus and fecundity in a laboratory colony of mouse opossums (*Marmosa robinsoni*). J Zool 175:541–555

González EM, Claramunt S (2000) Behavior of captive short-tailed opossums, *Monodelphis* dimidiata (Wagner, 1847) (Didelphimorphia, Didelphidae). Mammalia 64:271–285

Gordon CL (2003) A first look at estimating body size in dentally conservative marsupials. J Mammal Evol 10(1–2):1–21

Grand TI (1983) Body weight: relationships to tissue composition, segmental distribution of mass, and motor function. III. The Didelphidae of French Guyana. Aust J Zool 31:299–312

Green B (1997) Field energetics and water fluxes in marsupials. In: Saunders NR, Hinds LA (eds) Marsupial biology: recent research, new perspectives. Univ New South Wales Ltd, Sydney

Greer JK (1965) Mammals of Malleco Province, Chile. Publ Mus Mich State Univ Biol Ser 3: 81–149

Hamrick MW (2001) Morphological diversity in digital skin microstructure of didelphid marsupials. J Anatomy 198:683–688

Harder JD, Fleck DW (1997) Reproductive ecology of New World marsupials. In: Saunders NR, Hinds LA (eds) Marsupial biology: recent research, new perspectives. Univ New South Wales Ltd, Sydney

Hayssen V, Lacy RC (1985) Basal metabolic rates in mammals: taxonomic differences in the allometry of and body mass. Comp Biochem Physiol 81:741–754

Hershkovitz P (1987) A history of the recent mammalogy of the Neotropical region from 1492 to 1850. In: Patterson BD, Timm RM (eds) Studies in neotropical mammalogy essays in honor of Philip Hershkovitz. Fieldiana Zool NS 39:11–98

Hershkovitz P (1992a) The South American gracile mouse opossums, genus *Gracilinanus* Gardner and Creighton, 1989 (Marmosidae, Marsupialia): a taxonomic review with notes on general morphology and relationships. Fieldiana Zool NS 70:1–56

Hershkovitz P (1992b) Ankle bones: the Chilean opossum *Dromiciops gliroides* Thomas, and marsupial phylogeny. Bonner Zool Beitr 43:181–213

Hershkovizt P (1997) Composition of the family Didelphidae Gray, 1821 (Didelphoidea: Marsupialia), with a review of the morphology and behavior of the included four-eyed opossums of the genus *Philander* Tiedemann, 1808. Fieldiana Zool NS 86:1–103

Hershkovitz P (1999) *Dromiciops gliroidesThomas*, 1894, last of the Microbiotheria (Marsupialia), with a Review of the family Microbiotheriidae. Fieldiana ZoolNS 93:1–60

Hildebrand M (1995) Analysis of vertebrate structure. Wiley, New York

Hill JP (1918) Some observations on the early development of *Didelphis aurita* (contributions to the embryology of the marsupialia V). Quart J Microsc Sci 63:93–139

Hingst E, D'Andrea PS, Santori R, Cerqueira R (1998) Breeding of *Philander frenata* (Didelphimorphia, Didelphidae) in captivity. Lab Anim 32:434–438

Hope PJ, Pyle D, Daniels CB, Chapman I, Horowitz M, Morley JE, Trayhurn P, Kumaratilake J, Wittert G (1997) Identification of brown fat and mechanisms for energy balance in the marsupial, Sminthopsis crassicaudata. Am J Physiol 273:161–167

Hulbert AJ, Dawson TJ (1974) Standard metabolism and body temperature of perameloid marsupials from different environments. Comp Biochem Phys A 47:583–590

Hume ID (1999) Marsupial nutrition. Cambridge University Press, Cambridge

Hume ID (2003) Nutrition of carnivorous marsupials. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Hunsaker D (1977) Ecology of New World marsupials. In: Hunsaker D (ed) The biology of marsupials. Academic Press, New York

Iodice OH, Cervino CO, Affanni JM (2010) Manejo y reproducción de *Lutreolina crassicaudata* (Marsupialia, didelphidae) en condiciones de bioterio. Rev Electrón Vet 11:1695–7504

Jastroch M, Withers KW, Taudien S, Frappell PB, Helwig M, Fromme T, Hirschberg V, Heldmaier G, McAllan BM, Firth BT, Burmester T, Platzer M, Klingenspor M (2008) Marsupial uncoupling protein 1 sheds light on the evolution of mammalian nonshivering thermogenesis. Physiol Genomics 32:161–169

Julien-Laferrière D, Atramentowicz M (1990) Feeding and reproduction of three didelphid marsupials in two neotropical forests (French Guiana). Biotropica 22:404–415

Kirsch JAW, Waller PF (1979) Notes on the trapping and behavior of the Caenolestidae (Marsupialia). J Mammal 60:390–395

Kraus DB, Fadem BH (1987) Reproduction, development, and physiology of the gray short-tailed opossum (*Monodelphis domestica*). Lab Animal Sci 37:478–482

Krause WJ, Krause WA (2006) The opossum: its amazing story. Department of Pathology and Anatomical Sciences, School of Medicine, University of Missouri

Krieg H (1924) Biologische Reisestudien in Südamerika. III. Chilenische Beutelratten. Z Morphol Okol Tiere 3:169–176

Lee AK, Cockburn A (1987) Evolutionary ecology of marsupials. Monographs on marsupial biology. Cambridge University Press, Cambridge

Lee AK, Wooley P, Braithwaite RW (1982) Life history strategies of dasyurid marsupials. In: Archer M (ed) Carnivorous Marsupials. Royal Zoological Society of New South Wales, Sydney

Leiner NO, Silva WR (2007) Seasonal variation in the diet of the Brazilian slender opossum (*Marmosops paulensis*) in a montane Atlantic forest area, southeastern Brazil. J Mammal 88:158–164

Leiner NO, Setz EZF, Silva WR (2008) Semelparity and factors affecting the reproductive activity of the Brazilian slender-opossum (*Marmosops paulensis*) in southeastern Brazil. J Mammal 89:153–158

Lemelin P, Schmitt D, Cartmill M (2003) Footfall patterns and interlimb co-ordination in opossums (Family Didelphidae): evidence for the evolution of diagonal-sequence walking gaits in primates. J Zool 260:423–429

Loretto D, Vieira MV (2008) Use of space by the marsupial *Marmosops incanus* (Didelphimorphia, Didelphidae) in the Atlantic Forest, Brazil. Mamm Biol 73:255–261

Loretto D, Ramalho E, Vieira MV (2005) Defense behavior and nest architecture of *Metachirus nudicaudatus* Desmarest, 1817 (Marsupialia, Didelphidae). Mamm 69(3–4):417–419

Lorini ML, Oliveira JA, Persson VG (1994) Annual age structure and reproductive patterns in *Marmosa incana* (Lund, 1841) (Didelphidae, Marsupialia). Z Sauegetierkunde 59:65–73

Lovegrove BG (2000) The zoogeography of mammalian basal metabolic rate. Am Nat 156:201–219

Macedo L, Fernandez FAS, Nessimian JL (2010) Feeding ecology of the marsupial *Philander frenatus* in a fragmented landscape in Southeastern Brazil. Mamm Biol 75:363–369

Mann G (1955) Monito del Monte. Dromiciops australis Philippi. Invest Zool Chilenas 2:159–166

Mann G (1958) Reproducción de *Dromiciops australis* (Marsupialia, Didelphydae). Invest Zool Chilenas 4:209–213

Marshall LG (1978a) *Lutreolina crassicaudata*. Mamm Sp 91:1–4

Marshall LG (1978b) *Chironectes minimus*. Mamm Sp 109:1–6

Martin GM (2008) Sistemática, Distribución y Adaptaciones de los Marsupiales Patagónicos. PhD thesis, Univ Nacional de La Plata

Martin GM (2010) Geographic distribution and historical occurrence of *Dromiciops gliroides* Thomas (Marsupialia, Microbiotheria). J Mammal 91:1025–1035

Martin GM (2011) Geographic distribution of *Rhyncholestes raphanurus* Osgood, 1924 (Paucituberculata: Caenolestidae), an endemic marsupial of the Valdivian Temperate Rainforest. Aust J Zool 59:118–126

Martin GM (2012) Distribución geográfica de marsupiales americanos. II Congreso Latinoamericano de Mastozoología y XXV Jornadas Argentinas de Mastozoología, Buenos Aires

Martin GM (in preparation) Living New World marsupials. What do we know? In: Goin FJ, Forasiepi A (eds) New World Marsupials and their Extinct Relatives: One Hundred Million Years of Metatherian Evolution. Springer, Berlin

Martin GM, Udrizar Sauthier DE (2011) Observations on the captive behavior of the rare Patagonian opossum *Lestodelphys halli* (Thomas, 1921) (Marsupialia, Didelphimorphia, Didelphidae). Mammalia 75281–286

Martins EG, Bonato V, da-Silva CQ, Reis SF (2006) Partial semelparity in the Neotropical didelphid marsupial *Gracilinanus microtarsus*. J Mammal 87:915–920

Massoia E, Fornes A (1972) Presencia y rasgos etoecológicos de *Marmosa agilis chacoensis* Tate en las provincias de Buenos Aires, Entre Ríos, y Misiones (Mammalia-Marsupialia-Didelphidae). Rev Invest Agropec, Ser 1. Biol Prod Animal 9:71–82

McManus JJ (1970) Behavior of captive opposums, *Didelphis marsupialis virginiana*. Amer Midland Nat 84:144–169

McNab BK (1978) The comparative energetics of neotropical marsupials. J Comp Physiol 125:115–128

McNab BK (1982) The physiological ecology of South American mammals. In: Mares MA, Genoways HH (eds) Mammalian biology in South America. Pymatuning Lab of Ecol, Spec Publ Ser 6. Univ Pittsburgh

McNab BK (1986) Food habits, energetics, and the reproduction of marsupials. J Zool 208: 595–614

McNab BK (2005) Uniformity in the basal metabolic rate of marsupials: its causes and consequences. Rev Chilena Hist Nat 78:183–198

Merritt JF (2010) The biology of small mammals. Johns Hopkins Press, Baltimore

Monteiro-Filho ELA (1987) Biologia reprodutiva e espaço domiciliar de Didelphis albiventris em uma área perturbada na região de Campinas, Estado de São Paulo. Master thesis, Universidade Estadual de Campinas

Monteiro-Filho ELA, Cáceres NC (2006) Biología Reproductiva de Fêmeas de Marsupiais Didelfídeos. In: Caceres NC, Monteiro-Filho ELA (eds) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. Ed Univ Federal do Paraná, Curitiba

Monteiro-Filho ELA, Dias VS (1990) Observações sobre a biologia de *Lutreolina crassicaudata* (Mammalia: Marsupialia). Rev Bras Biol 50:393–399

Morrison PR, McNab BK (1962) Daily torpor in a Brazilian murine opossum (*Marmosa*). Comp Physiol Biochem 6:57–68

Morrone JJ (2004) Panbiogeografía, componentes bióticos y zonas de transición. Rev Bras Entomol 48:149–162

Morrone JJ (2006) Biogeographic areas and transition zones of Latin America and the Caribbean Islands based on panbiogeographic and cladistic analyses of the entomofauna. Ann Rev Entomol 51:467–494

Morton SR (1980) Ecological correlates of caudal fat storage in small mammals. Aust Mammal 3:81–86

Muizon C, Argot C (2003) Comparative anatomy of the didelphimorphs marsupials from the early Palaeocene of Bolivia (*Pucadelphys*, *Andinodelphys*, and *Mayulestes*). Palaeobiologic implications. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Muñoz Pedreros A, Lang BK, Bretos M, Meserve PL (2005) Reproduction and development of *Dromiciops gliroides* (Marsupialia: Microbiotheria) in the temperate rainforests of Southern Chile. Gayana 69:225–233

Myers P, Patton JL (2008) Genus *Lestoros* Oehser, 1934. In: Gardner A (ed) Mammals of South America, vol 1. Marsupials, Xenarthrans, Shrews, and Bats. Univ Chicago Press, Chicago

Nickrent DL, Musselman LJ (2004) Introduction to parasitic flowering plants. The Plant Health Instruct. doi:10.1094/PHI-I-2004-0330-01

Nowak RM (1999) Walker's mammals of the World, 6 edn, 2 vols. The Johns Hopkins Univ Press, Baltimore

O'Connel MA (1979) The ecology of didelphid marsupials from northern Venezuela. In: Eisenberg JF (ed) Vertebrate ecology in the northern neotropics. Smithsonian Inst Press, Washington

Oakwood M, Bradley AJ, Cockburn A (2001) Semelparity in a large marsupial. Proc R Soc London 268:407–411

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the world: a new map of life on earth. Bioscience 51:933–938

Osgood WH (1921) A monographic study of the American marsupial *Caenolestes*. Field Mus Nat Hist Zool Ser 16:1–162

Osgood WH (1924) Review of living caenolestids with description of a new genus from Chile. Field Mus Nat Hist Zool Ser 14:165–173

Osgood WH (1943) The mammals of Chile. Field Mus Nat Hist Zool Ser 30:1–268

Palma RE (1997) *Thylamys elegans*. Mammal Sp 572:1–4

Palma RE (2003) Evolution of American marsupials and their phylogenetic relationships with Australian metatherians. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Patterson BD (2008) Genus *Rhyncholestes* Osgood, 1924. In: Gardner A (ed) Mammals of South America, Vol. 1: Marsupials, Xenarthrans, Shrews, and Bats. Univ Chicago Press, Chicago

Patterson BD, Gallardo MH (1987) *Rhyncholestes raphanurus*. Mammal Sp 286:1–5

Patterson BD, Meserve PL, Lang BK (1990) Quantitative habitat associations of small mammals along an elevational transect in temperate rain-forests of Chile. J Mammal 71:620–633

Perret M, Atramentowicz M (1989) Plasma concentrations of progesterone and testosterone in captive woolly opossums (*Caluromys philander*). J Reprod Fert 85:31–41

Pfiegler JF, Cabana T (1996) The vestibular primary afferents and teh vestibulospinal projections in the developing and adult opossum, *Monodelphis domestica*. Anat Embryol 194:75–88

Philippi F (1893) Un nuevo marsupial chileno. Anales de la Universidad de Chile 85:31–34

Phillips CJ, Knox Jones J (1968) Additional comments on reproduction in the woolly opossum (*Caluromys derbianus*) in Nicaragua. J Mammal 49:320–321

Pine RH (1981) Reviews of the mouse opossums *Marmosa parvidens* Tate and *Marmosa invicta* Goldman (Mammalia: Marsupialia: Didelphidae) with description of a new species. Mammalia 45:55–70

Pine RH, Dalby PL, Matson JO (1985) Ecology, postnatal development, morphometrics, and taxonomic status of the short-tailed opossum, *Monodelphis dimidiata*, an apparently semelparous annual marsupial. Ann Carnegie Mus 54:195–231

Pires AS, Fernandez FAS (1999) Use of space by the marsupial *Micoureus demerarae* in small Atlantic forest fragments in southeastern Brazilian. J Tropical Ecol 15:279–290

Pires MM, Cruz LD, Fernandes FR, Martins EG, dos Reis S (2009) Omnivory by *Micoureus paraguayanus* (Didelphimorphia: Didelphidae) in a Brazilian Cerrado remnant: diet composition and dietary seasonality. Ann, 3 Congr Latino Americano de Ecol, São Lourenço, Minas Gerais

Prevedello JA, Rodrigues RG, Monteiro-Filho ELA (2009) Vertical use of space by the marsupial *Micoureus paraguayanus* (Didelphimorphia, Didelphidae) in the Atlantic forest of Brazil. Acta Theriol 54:259–266

Pridmore PA (1992) Trunk movements during locomotion in the marsupial *Monodelphis domestica* (Didelphidae). J Morphol 211:137–146

Pridmore PA (1994) Locomotion in *Dromiciops australis* (Marsupialia: Microbiotheriidae). Aust J Zool 42:679–699

Rademaker V, Cerqueira R (2006) Variation in the latitudinal reproductive patterns of the genus *Didelphis* (Didelphimorphia: Didelphidae). Austral Ecol 31:337–342

Regidor HA, Gorostiague M (1996) Reproduction in the white-eared opossum (*Didelphis albiventris*) under temperate conditions in Argentina. Stud Neotropical Fauna Environ 31:133–136

Regidor HA, Gorostiague M, Sühring S (1999) Reproduction and dental age classes of the little water opossum (*Lutreolina crassicaudata*) in Buenos Aires, Argentina. Rev Biol Tropical 47 (1–2):271–272

Ribeiro P, Bicudo EPW (2007) Oxygen consumption and thermoregulatory responses in three species of South American marsupials. Comp Biochem Physiol A 174:658–664

Riek A, Geiser F (2014) Allometry of thermal variables in mammals: consequences of body size and phylogeny. J Zool 292:74–85

Rigueira SE, Valle CMC, Varejão JBN, Albuquerque PV, Nogueira JC (1987) Algumas observações sobre o ciclo reproductivo anual de fêmeas do gambá *Didelphis albiventris* (Lund, 1841) (Marsupialia, Didelphidae) em populações naturais no Estado de Minas Gerais, Brasil. Rev Bras Zool 4:129–137

Rodríguez-Cabal MA, Aizen MA, Novaro A (2007) Habitat fragmentation disrupts a plant–disperser mutualism in the temperate forest of South America. Biol Conservation 139:195–202

Rose RW, West AK, Ye JM, McCormack GH, Colquhoun EQ (1999) Nonshivering thermogenesis in a marsupial, the Tasmanian bettong (Bettongia gaimardi) is not attributable to brown adipose tissue. Physiol Biochem Zool 72:699–704

Santori RT, Astúa de Moraes D (2006) Alimentação, nutrição e adaptações alimentares de marsupiais brasileiros. In: Caceres NC, Monteiro-Filho ELA (eds) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. Ed Univ Federal do Paraná, Curitiba

Santori RT, Rocha-Barbosa O, Vieira MV, Magnan-Neto JA, Loguercio MFC (2005) Locomotion in aquatic, terrestrial, and arboreal habitat of the thick-tailed opossum, *Lutreolina crassicaudata* (Desmarest 1804). J Mammal 86:902–908

Schmidt-Nielsen K (1964) Animal physiology, 2nd edn. Prentice Hall Inc, London

Solari SA (2003) Diversity and distribution of *Thylamys* (Didelphidae) in South America, with emphasis on species from the western side of the Andes. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Strahan R (1991) Complete book of Australian mammals. Cornstalk Publishing, New South Wales

Streilein KE (1982) Behavior, ecology, and distribution of South American marsupials. In: Mares MA, Genoways HH (eds) Mammalian biology in South America. Special Publications Series, Vol. 6. Pymatuning Laboratory of Ecology, Univ Pittsburgh

Szalay FS (1982a) Phylogenetic relationships of the marsupials. In: Buffetant E, Janvier P, Rage JC, Tassy P (eds) Philogenie et palengeographie: livre jubilaire de Robert Hoffstetter. Géobios Mém Spéc 6:177–190

Szalay FS (1982b) A new appraisal of marsupial phylogeny and clasification. In: Archer M (ed) Carnivorous marsupials. R Zool Soc of New South Wales, Sydney

Szalay FS (1994) Evolutionary history of the marsupials and an analysis of osteological characters. Cambridge Univ Press, New York

Szalay FS, Sargis EJ (2001) Model-based analysis of postcranial osteology of marsupials from the Palaeocene of Itaborai (Brazil) and the phylogenetics and biogeography of Metatheria. Geodiversitas 23:139–302

Tate GHH (1933) A systematic revision of the marsupial genus *Marmosa*, with a discussion of the adaptive radiation of the murine opossums (*Marmosa*). Bull Amer Mus Nat Hist 66:1–250

Thielen DR, Arends A, Segnini S, Fariñas M (1997) Food availability and population dynamics of *Marmosa xerophila* Handley and Gordon 1979 (Marsupialia: Didelphidae). Zoocriaderos 2:1–15

Thomas O (1888) Catalogue of the Marsupialia and Monotremata in the collection of the British Museum of Natural, History edn. Trustees of the British Museum, London

Thompson SD (1988) Thermoregulation in the water opossum (*Chironectes minimus*): an exception that "proves" a rule. Physiol Zool 61:450–460

Timm RM, Patterson BD (2008) Genus *Caenolestes* O. Thomas, 1895. In: Gardner A (Ed), Mammals of South America, vol. 1. Marsupials, Xenarthrans, Shrews, and Bats. Univ Chicago Press, Chicago

Townsend, CR, Hughes RN (1981) Maximizing net energy returns from foraging. In: Townsend CR, Calow P (eds) Physiological ecology: an evolutionary approach to resource use. Sinauer Associates, Sunderland Massachusetts

Tyndale-Biscoe CH (1980) Observations on the biology of marsupials in Colombia and Venezuela. Nat Geogr Soc Res Report 12:711–720

Tyndale-Biscoe CH (2005) Life of marsupials. CSIRO Publishing, Victoria

Tyndale-Biscoe CH, Janssens PA (1988) The developing marsupial. Models for biomedical research. Springer, Berlin

Tyndale-Biscoe CH, MacKenzie RB (1976) Reproduction in *Didelphis marsupialis* and *Didelphis albiventris* in Colombia. J Mammal 57:249–265

Tyndale-Biscoe CH, Renfree MB (1987) Reproductive physiology of marsupials. Cambridge Univ Press, Cambridge

VandeBerg JL (1983) The gray short-tailed opossum: a new laboratory animal. Inst Lab Animal Resources News 26:9–12

Vaughan TA, Ryan JM, Czaplewski NJ (2011) Mammalogy, 5th edn. Jones and Bartlett Publishers, Sudbury, Massachusetts

Vieira MV (1997) Body size and form in two neotropical marsupials, *Didelphis aurita* and *Philander opossum* (Marsupialia: Didelphidae). Mammalia 61(2):245–254

Vieira EM (2006a) Padrões de Uso Vertical do Habitat por Marsupiais Brasileiros. In: Caceres NC, Monteiro-Filho ELA (eds) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. Ed Univ Federal do Paraná, Curitiba

Vieira MV (2006b) Locomção, Morfologia e Uso do Habitat em Marsupiais Neotropicais: Uma Abordagem Ecomorfológica. In: Caceres NC, Monteiro-Filho ELA (eds) Os Marsupiais do Brasil: Biologia, Ecologia e Evolução. Ed Univ Federal do Paraná, Curitiba

Vieira EM, Astúa de Moraes D (2003) Carnivory and insectivory in Neotropical marsupials. In: Jones M, Dickman C, Archer M (eds) Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing, Victoria

Voss RS, Jansa SA (2003) Phylogenetic studies on didelphid marsupials II. Nonmolecular data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. Bull Am Mus Nat Hist 276:1–82

Voss RS, Jansa SA (2009) Phylogenetic relationship and classification of Didelphid marsupials an extant radiation of New World metatherian mammals. Bull Amer Mus Nat Hist 332:1–177

Voss RS, Lunde DP, Simmons NB (2001) The mammals of Paracou, French Guina: a Neotropical lowland rainforest fauna. Part. 2 nonvolant species. Bull Amer Mus Nat Hist 263:1–236

Voss RS, Lunde DP, Jansa SA (2005) On the contents of *Gracilinanus* Gardner and Creighton, 1989, with the description of a previously unrecognized clade of small didelphid marsupials. Amer Mus Novit 3482:1–34

Wallis IR, Farrell DJ (1992) Energy metabolism in potorine marsupials. J Comp Physiol B 162:478–487

Williams GC (1966) Adaptation and natural selection. Princeton Univ Press, Princeton

Willig MR, Gannon MR (1997) Gradients of species density and turnover in marsupials: a hemispheric perspective. J Mammal 78:756–765