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ECOLOGY OF TROPICAL FOREST SMALL MAMMAL POPULATIONS: PATTERNS AND PROCESS REVEALED BY THE LONGEST LONG-TERM MONITORING STUDY IN BRAZIL

Mariana Silva Ferreira[1*], *Ana Cláudia Delciellos*[2,3] & *Camila dos Santos de Barros*[1]

[1] Universidade Federal do Rio de Janeiro, Instituto de Biologia, Programa de Pós-Graduação em Ecologia, Av. Carlos Chagas Filho, 373, Cidade Universitária, CEP 21941-590, Rio de Janeiro, RJ, Brasil.

[2] Universidade do Estado do Rio de Janeiro, Instituto de Biologia, Programa de Pós-Graduação em Ecologia e Evolução, Rua São Francisco Xavier 524, Maracanã, CEP 20550-900, Rio de Janeiro, RJ, Brasil.

[3] Universidade do Estado do Rio de Janeiro, Instituto de Biologia, Departamento de Zoologia, Laboratório de Mastozoologia. Rua São Francisco Xavier 524, Maracanã, 20550-900, Rio de Janeiro, RJ, Brasil.

E-mails: msferreira84@gmail.com (*corresponding author); anadelciellos@yahoo.com.br; camilasdebarros@gmail.com

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Abstract: Long-term monitoring studies have spearheaded the development of population ecology as a discipline. Today, the vast amount of information obtained from these studies is concentrated at higher-latitude ecosystems. Here we present the advances achieved by the largest long-term monitoring study of small mammals carried out in a tropical forest in Brazil. Along 22 years, since 1997, the Garrafão project was developed in one of the largest Atlantic Forest remnants, in the southern limit of the Serra dos Órgãos National Park, state of Rio de Janeiro. Most studies developed with this valuable dataset have focused on the most abundant species of marsupials and rodents. In general, this long-term study brought important advances in the understanding of the ecology of mammals in tropical forests, such as: (1) the predominance of population self-regulation in one of the most species-rich environments; (2) the importance of survival for population growth and regulation; (3) seasonal and continuous reproduction in marsupial and rodents, respectively; (4) the positive relationship between body size and space use in marsupials weighing up to 100 g (opposite relationship in species weighing less than 100 g); (5) differences in space use between species, sexes and age classes, and positive (and negative) effects of density; and (6) differences in habitat selection in species living in different forest strata. Several other questions remain to be answered with this dataset and this review aims to stimulate new questions and new long-term monitoring studies in different ecosystems in the tropical region.

Keywords: habitat selection; life history; Long-Term Ecological Research; population dynamics; space use.

INTRODUCTION

Small mammals, belonging to the orders Didelphimorphia and Rodentia, are excellent models for long-term monitoring studies (Krebs 2013). Their small size, short longevity, and easy trappability mean that individuals can be captured and marked repeatedly and for multiple generations in a short time period. Through monitoring individuals over their lifespan, we can access information on their demography, life history, and population dynamics. With long-term studies, we can easily access a very large number of generations and thus unravel the main factors affecting individuals and populations, and the long-term consequences to their viability.

Long-term monitoring studies have spearheaded the development of population ecology as a discipline (Elton 1924, Elton & Nicholson 1942, Krebs 2013). Following the seminal work of Elton (1924), many other long-term monitoring studies were conducted in order to identify the main causes of population variation over time and space. These studies have identified both trophic interactions (food and/or predation) and seasonality as the main drivers of population dynamics of small mammals at higher-latitude temperate forests (Yoccoz *et al.* 2001), deserts (Lima *et al.* 2001), and grasslands (Aars & Ims 2002). Aside from these well-known studies, most studies evaluating small mammal population dynamics in tropical environments to date have been short-term, which undermine the understanding of population patterns and processes (Cerqueira *et al.* 1993, Barros *et al.* 2015, but see da Rosa *et al.* 2021, Rossi & Leiner 2022).

Long-term monitoring studies are also necessary to understand the effects of large-scale climatic changes on the population dynamics that would otherwise go unnoticed. This is especially true for tropical forest areas where long-term dynamics of animal populations are still lacking (Krebs 2013), and where most threats to biodiversity are concentrated on (Barlow *et al.* 2018).

One of the most important long-term monitoring studies to date on small mammals in a tropical forest was conducted uninterruptedly for 22 years in Brazil (Gentile & Kajin 2015). Located at one of the largest Atlantic Forest remnants, the study site is locally known as Garrafão (22º29`S, 43º00`W) – which is the name of the valley the study area is inserted in, within the limits of the Serra dos Órgãos National Park, in the state of Rio de Janeiro. The small mammal monitoring study occurred from April 1997 to February 2019 in three 5 x 5 trapping grids established along an elevation gradient in trapping sessions of five consecutive nights (see Gentile *et al.*, 2023, for more details on study site and the monitoring study). Along these 22 years, many studies were conducted evaluating the demography, population dynamics, life history, and behavior of marsupials and rodents. Here we review these studies and summarize their main findings, highlighting the main advances achieved in the study of tropical forest small mammals, and the questions that remain to be answered.

In this review, we evaluated the studies on (1) small mammal community, (2) demography and life-history, (3) population dynamics, (4) habitat selection, (5) space use, vertical stratification, and movements, (6) activity patterns, (7) population genetics, and (8) method development, carried out in the Garrafão by researchers at the Laboratório de Vertebrados (LabVert) from Universidade Federal do Rio de Janeiro. The literature used was obtained in LabVert and composed by one bachelor's dissertation, 20 master dissertations, four thesis, and 39 peer-reviewed articles in English and Portuguese (Supplementary Material 1).

SMALL MAMMAL COMMUNITY

Eight marsupials and 11 rodent species from five different families (Didelphidae, Sciuridae, Cricetidae, Muridae, and Echimyidae) were recorded in the study area (Cronemberger *et al.* 2019; Supplementary Material 2). *Didelphis aurita* was the most abundant and dominant species in the small mammal community, followed by *Marmosops incanus* (Ferreira *et al.* 2016a). Six other species were regularly captured, such as *Marmosa paraguayana*, *Metachirus myosuros*, *Philander quica*, *Trinomys dimidiatus*, *Rhipidomys itoan*, and *Euryoryzomys russatus*, while *Caluromys philander* and *Gracilinanus microtarsus* were captured less frequently in the live traps, but more often in the artificial nests (Loretto & Vieira 2011). Other species were considered rare in the study area, including: *Juliomys pictipes*, *Monodelphis sp.*, *Akodon cursor*, *Oligoryzomys nigripes*, *Phyllomys pattoni*, and *Guerlinguetus brasiliensis*.

The large and dominant *D. aurita* was considered a key species, being an occasional intraguild predator, with a pervasive interference and clear avoidance by four other didelphid species, which may have resulted from indirect signs as scent marks (Moura *et al.* 2009). Possible hypotheses explaining the high abundance of *D. aurita* include the mesopredator release hypothesis (Soulé *et al.* 1988), due to the absence of large predators in the study area, and additional food resources provided by garbage of the local human population (Moura *et al.* 2009). In a comparison of species composition among Garrafão and other four rural areas (*i.e.*, three farms and a fragmented landscape with small rural properties) on its surroundings, Olifiers *et al.* (2005) revealed that the distance of the study site to human residences is a determinant of species composition; species of the genus *Akodon* and *Oligoryzomys*, which are common in agrosystems, were rarely captured in Garrafão, while others, such as *D. aurita*, were captured in both forested and rural areas.

Vegetation structure and weather had also a fundamental role in structuring small mammal community. Detection probabilities for arboreal species (*M. paraguayana* and *R. itoan*) were affected by the preceding six months rainfall, while for the scansorial and terrestrial species, *P. quica*, *M. incanus*, and *M. myosuros*, detection probability varied over time and was more affected by the microhabitat surrounding trapping stations; rock cover negatively influenced the probability of detection and occupancy of *M. myosuros*, while the probability of occupancy of *P. quica* and *M. incanus* was negatively affected by canopy cover. These results showed the importance of considering imperfect detection and provided evidence that the processes responsible for community structure are not entirely neutral or random (Costa 2014).

DEMOGRAPHY & LIFE HISTORY

Life History

At Garrafão, small mammals have a suite of life-history traits that position them towards the fast end of the life history continuum. Overall, marsupials in the study area have short gestation time (~13 days; Kajin *et al.* 2008), large litter sizes (max. 11 young; Santana 2012), low generation time (330.7 days; Kajin *et al.* 2008), and short life span (max. 2 years, Kajin *et al.* 2008). Most marsupials are iteroparous, *i.e.*, reproduce more than once in a lifetime, and seasonal reproducers, except for *M. incanus*. The low survival rate of males after the mating period supports the hypothesis that *M. incanus* is semelparous, *i.e.*, reproduce only once in a lifetime (Zangrandi *et al.* 2023). After mating, females live longer to rear their young, and only few survive to a second year (no recorded reproduction), which explains the high population turnover for this species in the study area (Zangrandi 2011). For this species, senescence, observed by a significant decrease in body condition (see the sub-item “Body condition”), is coincident with periods of high food resource availability, thus mortality is probably not related to environmental conditions, but health weakening caused by intense reproduction (Macedo 2007). Another potential semelparous species at Garrafão is *G. microtarsus*. This assumption is based on the congener, *G. agilis*, which was classified as partially semelparous at Cerrado biome (Martins *et al.* 2006). However, this hypothesis was not evaluated with the Garrafão dataset.

Among iteroparous species, *C. philander* has probably the slowest life history. They have monoecious reproduction (unique among marsupials that live more than a year), late sexual maturity (12-13 months), small litter size (4.32 ± 0.6 pouch young), long parental care (6-7 months), and long life span (max. 4.75 years) (Loretto 2012). Others, such as *D. aurita*, *M. myosuros*, and *P. quica*, reproduce twice in the breeding season, mature at approximately eight months old, produce larger litters (7.04, 7.59 and 5.5 young, respectively) with at most four months of parental care, living usually no more than two years (Kajin *et al.* 2008, Ferreira *et al.* 2020).

Knowledge of life-history traits can help us identify the life-history strategy adopted by populations and species, and its effects on population growth rate (λ) (Ferreira 2016). Based on studies with eutherian mammals, it is expected that species that mature early, have large litters, and short life spans (“fast species”) have higher potential contribution of reproduction to λ (Oli & Dobson 2003). Three studies so far which evaluated the potential contribution of life-history traits to λ at Garrafão showed that marsupials may not follow the eutherian pattern described above. For *M. incanus*, survival components had higher potential contribution to λ mainly in the dry season (Zangrandi 2011), while juvenile survival and age at first reproduction had a higher potential contribution to λ in *D. aurita* and *M. paraguayana*, respectively, in an annual analysis (Kajin 2008, Ferreira 2016). These studies have now opened a new research venue on the life history of marsupials, focusing on the peculiarities and differences between the Theria subclass.

Trade-offs between life-history traits, the core of the life-history theory, were also evaluated for *D. aurita*. Kajin *et al.* (2008) identified two trade-offs: (1) fecundity and survival, and (2) mortality and reproductive value. The first showed that there is a cost of reproduction in the *D. aurita* population. However, high female fecundity in an age class will not reduce their contribution to future litters, but delaying reproduction reduces opossum mortality, probably through the reduced energy spent by reproductive demands. The second trade-off indicated that high age-specific mortality reduces individual's contribution to future generations.

Survival

Survival differed strongly between sexes and seasons in most marsupials. Overall, higher rates were estimated for females and in the dry season (Ferreira *et al.* 2020). For *C. philander*, survival was comparatively high and constant through the year, with no difference between sexes (Loretto 2012). Differences in survival among age classes were also evaluated in *D. aurita* (Kajin *et al.* 2008). Survival rate was low for both pouch young and juveniles revealing it as the most critical period in opossum's life (Kajin *et al.* 2008). High post-weaning mortality is best explained by vulnerability of juveniles; they must explore the environment in search for food and to establish a home range, becoming susceptible to predators, diseases, and other potential hazards (Kajin *et al.* 2008, Ferreira *et al.* 2013). However, the challenges faced by these young opossums are not all the same. Silva *et al.* (2023) have shown that individuals born in the first breeding period (August - October) of the season had higher survival rates than those born in the second breeding period (December - February). These first cohort opossums are weaned in the wet season, a period with greater resource abundance and lower population density. Thus, the environment faced by these juveniles affect its lifetime survival.

Survival has often been regarded as one of the most important demographic rates for understanding population dynamics, but what role do changes in population size play in causing changes in survival? Ferreira *et al.* (2020) revealed that survival was negatively affected by population size in three marsupial species (*D. aurita*, *M. myosuros*, and *M. paraguayana*); high population sizes in a given year reduced survival rates in the following year. Thus, density-dependent survival was the mechanism regulating population size of marsupials, either through a reduction in survival or an increase in emigration rates.

Marsupial survival was also affected by weather; an increase in accumulated rainfall and mean minimum temperature in the wet season led to high survival rates in the following dry season for *D. aurita* and *M. incanus*, respectively (Ferreira *et al.* 2020). Kajin (2008) also found a positive effect of *El Niño Southern Oscillation* (hereafter, *El Niño*) on *D. aurita* annual survival, but not rainfall. Future studies with long term datasets should investigate the relationship between *El Niño* and associated changes in temperature and rainfall in southeastern Brazil, and the consequences to small mammal demography and population dynamics.

Reproduction

Seven marsupial populations analyzed until now (*D. aurita*, *M. incanus*, *M. paraguayana*, *M. myosuros*, *P. quica*, *C. philander*, and *G. microtarsus*) followed the expected seasonal pattern of reproduction (Loretto 2006, Kajin *et al.* 2008, Loretto 2011, Ferreira *et al.* 2016b, 2020), usual for Didelphidae and Dasyuridae marsupials (Voss & Jansa 2021). Based on pouch young appearance and gestation time, breeding starts in the middle of the driest season (July), with juveniles weaned at the beginning of the wettest season (October), when food is most reliably abundant (Kajin *et al.* 2008, Loretto 2012, Ferreira *et al.* 2016b, 2020, Bernardo *et al.* 2023). For some species (*M. incanus* and *M. paraguayana*), reproduction started latter, in September (Macedo 2007, Santana 2012). Two reproductive events at the same breeding season were usually observed, as well as the same female reproducing in two consecutive breeding seasons (Santana 2012, Ferreira *et al.* 2020, Silva *et al.* 2023). Rodents, on the other hand, tend to reproduce all year long in the Neotropics (Larcher Jr 1992). At Garrafão, only one species had its reproductive activity evaluated. *Rhipidomys itoan* breeds predominantly from August to February and it was negatively affected by critical temperatures (maximum and minimum) and positively affected by rainfall with a four-month time lag (Simas 2016).

Body condition

Body condition, a proxy for the amount of energy (lipids) reserves accumulated in an individual, has been used as a surrogate of fitness (Schulte-Hostedde *et al.* 2005). For *M. incanus*, body condition was calculated as an allometric relation between body mass and body size following Braga (1986). No correlation between monthly variation in body condition and population abundance, rainfall, and fruit availability were observed; an immediate relationship was only detected with litterfall (Macedo 2007). However, the highest body condition values were recorded in 1997, 1998 and 1999, which could be related to a strong *El Niño* that occurred from 1997 to mid-1998, which apparently provided more stable environmental conditions in the study area (Macedo 2007).

Body condition analyses also revealed the negative effects of habitat loss and fragmentation on two marsupials (Delciellos *et al.* 2018), considering another allometric metric also based on the relationship between body mass and body condition (Peig & Green 2009). Overall, body condition of *D. aurita* and *P. quica* was lower in nearby forest fragments compared to Garrafão, but only in the super-humid season for *D. aurita* and in the humid ("dry") season for *P. quica* (Delciellos *et al.* 2018). However, the authors have warned that body condition should not be used as a direct indicator of animal fitness or habitat quality, since different responses were observed for each species at the forest fragments and at Garrafão, suggesting that body condition can also be affected by other factors such as reproductive stage and parasite load.

POPULATION DYNAMICS

Six species had their population dynamics analyzed at Garrafão. Overall, small mammals exhibited large interannual variation in population sizes (Kajin 2008, Zangrandi 2011, Santana 2012, Brigatti *et al.* 2016, Ferreira *et al.* 2016a, 2016b, Simas *et al.* this volume). Populations were strongly regulated by a first-order negative feedback (Kajin 2008, Zangrandi 2011, Santana 2012, Ferreira *et al.* 2016a, 2016b, Simas *et al.* 2023), in which the population is self-regulated, probably by intraspecific competition for food and/or space (Zangrandi 2011, Ferreira *et al.* 2016a, 2016b). In a modelling exercise, Brigatti *et al.* (2016) found that the 13-year time series of *D. aurita* population size was partially explained by the opossum's mode of reproduction. The authors suggested a possible time delay in the density effect on natality and revealed the crucial importance of the time of attaining sexual maturity for the dynamics of the population.

Inter-seasonal density feedback was also detected in both dry and wet seasons, with compensation processes in just one season being sufficient to allow population persistence (Ferreira *et al.* 2016a). *Didelphis aurita* and *M. myosuros* populations were primarily regulated in the dry season, while *M. incanus* and *P. quica*, in the wet season. This direct negative density feedback in both seasons rather than primarily in the dry season as expected suggests that didelphids respond differently to similar environmental pressures despite sharing similar life histories and phylogeny. Rainfall and minimum and maximum temperatures had more pronounced effects on reproductive rates (*i.e.*, recruitment, fecundity, and proportion of reproductive females) than in survival, which suggest that species may respond to changes in the weather through changes in reproduction. Temperature, in fact, had marked effects on small mammal population dynamics and demography (Ferreira *et al.* 2016a, Simas 2016, Ferreira *et al.* 2020). An increase in mean minimum temperature in a six-month interval negatively affected *D. aurita* reproduction, due to a reduction in the proportion of reproductive females and fecundity, which negatively affected recruitment. With the reduction in the number of new individuals in the population, an increase in survival was observed in the dry season after years of increased mean minimum temperature in the previous wet season (Ferreira *et al.* 2020). Negative effects of temperature variation on reproduction were also detected in *M. paraguayana*, *M. incanus*, *M. myosuros* (Ferreira et al. 2020), and *R. itoan* (Simas 2016).

Rainfall, a proxy for food availability, also have an important role in marsupial population dynamics (Gentile *et al.* 2004, Ferreira *et al.* 2016a, 2016b). Litterfall increases at the end of the dry season (Finotti *et al.* 2020), and fruit production and biomass of arthropods were larger between December and February (Macedo 2007). For *M. myosuros*, rainfall may operate as a nonlinear perturbation effect influencing the strength of density dependence (intraspecific competition and intraguild predation) or as a lateral perturbation effect influencing the carrying capacity of the environment (Ferreira *et al.* 2016b, Ferreira *et al.* 2020).

Total annual rainfall at Garrafão was not directly linked to *El Niño* (Kajin 2008, Zangrandi 2011, Ferreira *et al.* 2016b), probably because of the shape and position of the study area, a valley in a sea-facing slope of the mountain range. Orographic clouds and fog are frequent, leading to high local rainfall, probably overcoming the effects of *El Niño* events. However, *El Niño* had a clear effect on both *D. aurita* and *M. incanus* populations (Kajin 2008, Zangrandi 2011) and the main mechanism is still unclear, with possible effects trough temperature. Cunha *et al.* (2023) observed that in periods of high *El Niño* intensity, the regional temperature increased from 1 to 1.5 ºC and reduces ≈1 ºC in periods of intense *La Niña*.

Biomass variation over time may also reveal different aspects of the dynamics of populations (Mendel *et al.* 2008, Sá 2013). Rainfall and litterfall are major determinants of resource availability for *D. aurita*. Female density increased without an associated increase in biomass, suggesting regulation by resource availability combined with a density-dependent process (Mendel *et al.* 2008). Such a trend was not observed in males, which may be more influenced by the stochasticity resulting from their high vagility (Mendel *et al.* 2008). At least for *D. aurita*, population biomass is more stable than abundance especially for females, and there is an increasing trend in abundance and biomass over fifteen years, possibly primarily related to an increase in rainfall (Sá 2013).

HABITAT SELECTION

Each species perceives the habitat in different ways depending primarily on its morphology, physiology, and behavior (Morris 1987). Thus, it is expected that each species selects certain habitat characteristics to be used disproportionate over others also available in the environment to fulfil its resources requirements (Morris 1987). At Garrafão, habitat selection was studied at two spatial scales: microhabitat and mesohabitat. Overall, no pattern was identified at the microhabitat scale for *D. aurita*, *M. myosuros*, and *P. quica*, although few individuals avoided or preferred certain habitat characteristics. While, at the mesohabitat scale, *D. aurita* actively selected places with more rock cover, *M. myosuros*, with less canopy cover, and *P. quica*, with more rock and less litter (Moura *et al.* 2005) (Supplementary Material 3).

In general, the small mammals species that had their habitat selection evaluated in Garrafão (Supplementary Material 3) preferred microhabitats with: (i) few rocks and seedlings, and low understory obstruction from the ground to ≈1 m height, *i.e.*, areas with less obstacles to movements since the evaluated species are mostly terrestrial or scansorial; (ii) larger amount of litter, which suggests favorable places to encounter arthropods that are part of their diet, as well as material for building nests (Loretto *et al.* 2005); and (iii) higher canopy cover and leaf obstruction in the understory (1 m and 1.5 m in height), which suggests that most studied species avoid clearings (Freitas 1998, Aprigliano 2003, Moura *et al.* 2005, Ferreira *et al.* 2023).

Arboreal microhabitat preference was evaluated for three didelphid species (Supplementary Material 3). The scansorial *P. quica* actively selected larger (> 5.0 cm) and steeper supports (> 10°; only females) used during its arboreal locomotion (Delciellos *et al.* 2020). *Marmosops incanus*, an arboreal species of the understory (*i.e.*, does not use the canopy), selected thin (diameters between 0.9 and 1.7 cm) and less inclined (near the horizontal) supports (Loretto & Vieira 2008). *Caluromys philander,* an arboreal specialist that uses the forest canopy, preferred more open canopy and understory, with fewer fruit trees, bromeliads and lianas, more dead trees, and taller trees with a larger diameter, in places with flatter terrain (Cobra *et al.* 2023).

SPACE USE, VERTICAL STRATIFICATION AND MOVEMENTS

Animal movement is a key process to understand population dynamics and community structure (Morales *et al.* 2010). Movements encompass from large-scale displacements (*e.g.*, migrations; Hobson & Norris 2008) to fine-scale space use (*e.g.*, choice of which diameters and inclinations of arboreal supports to use; Delciellos *et al.* 2020). Different aspects of space use (*e.g.*, home range - HR, daily home range - DHR, movement tortuosity and aboveground locomotion) were approached for five didelphid marsupials at Garrafão (Cunha & Vieira 2002, Papi 2011, Delciellos *et al.* 2017, Supplementary Material 4).

Body mass is one of the main intrinsic factors that determines how individuals use the space (Carbone *et al.* 2005). Organisms with larger body mass often have higher energy requirements and, consequently, the more the organism has to move to obtain enough resources, implying larger HR or DHR (*i.e.*, daily measure of space requirements to fulfill food and other resources; Carbone *et al.* 2005). At Garrafão, this positive scaling was found for the DHR of *D. aurita*, *M. myosuros*, and *P. quica* (Vieira & Cunha 2008, Delciellos *et al.* 2017). However, Vieira *et al.* (2019) found the opposite (*i.e.*, longer movements with decreasing body mass) for species weighing less than 100 g as *M. incanus* and suggested that this negative relationship of body mass with HR or DHR was due to rising costs of thermoregulation in species below a specific body mass.

The percentage of the total path performed aboveground (understory and canopy) was also affected by body mass for *P. quica* – higher estimates for individuals with smaller body mass (Delciellos *et al.* 2017), but not for *D. aurita* – no difference between age classes in the choice of arboreal supports (Cunha & Vieira 2005) and *M. incanus* – no difference between sexes in space use despite the sexual dimorphism in body mass (Loretto & Vieira 2008). Additionally, body mass effects were not detected for another aspect of space use, path tortuosity (*i.e.*, a measure of how individuals explore the space, from tortuous to straight movements) in *P. quica* (Delciellos *et al.* 2017).

Sex and climatic seasons also affected space use of didelphids. In general, males invest in traveling longer distances and establish larger HRs and DHRs in the reproductive season, possibly searching for mates, while females present this pattern in the dry season, possibly to cover the energetic expenses with lactation. In Garrafão, these different patterns between sexes in DHR were found for *D. aurita* (Loretto & Vieira 2005, Almeida 2007) and *M. incanus* (Vieira *et al.* 2019), but not for *M. myosuros* (Ferreira *et al.* 2017). DHR of *M. myosuros* did not differ between sexes but was affected only by climatic seasons; DHR was larger in the dry season as expected, which again was attributed to compensate for the reduced availability of food resources in that season (Ferreira *et al.* 2017). As for *M. myosuros*, the DHR of *P. quica* did not differ between sexes and was larger in the dry season, but the percentage of the total path performed aboveground was higher for females than males (Delciellos *et al.* 2017).

Age effects on space use were evaluated for *D. aurita*, with juveniles using more aboveground supports (*i.e.*, vertical strata of the forest) than subadults and adults, which was attributed to the small body mass and an escape predation behavior (Cunha & Vieira 2005). Path tortuosity also differed according to age and sexual maturity, with young and sexually immature individuals showing less tortuous paths than adults (Almeida 2007). This pattern was attributed to juveniles' lack of experience in exploring the habitat (Almeida 2007).

Effects of population density on use of space were found only for path tortuosity of *D. aurita* (Almeida 2007, Almeida *et al.* 2015). Individuals used its DHR more intensively (*i.e.*, with more tortuous paths) at high population densities, probably to avoid intraspecific competition (Almeida *et al.* 2015). However, no effect of population density on path tortuosity was observed for *P. quica* (Delciellos *et al.* 2019), and DHR and intensity of habitat use (*i.e.*, the time spent per unit area) of *M. myosuros* (Ferreira *et al.* 2017). In general, the lack of density dependence in space use was attributed to the low abundance of these species, as well as the study site is in a large continuous area, probably providing no limit in space use for this population (Ferreira *et al.* 2017, Delciellos *et al.* 2019).

Finally, an ecologically relevant aspect regarding the use of space is how the interaction between species in the small mammal's community takes place. Some studies have highlighted the role of vertical stratification of species in the locality in providing coexistence between species (Prevedello *et al.* 2008), possible reducing competition for resources (Moura *et al.* 2009) and enabling escape from predation (Cunha & Vieira 2005). Overall, species do not have strictly arboreal or strictly terrestrial niches, but rather use different forest stratum to some degree (Cunha & Vieira 2002, Prevedello *et al.* 2008). These results became more evident when data from trapping grids, artificial nests, and measurements of space use with radiotelemetry and with the spool-and-line device were analyzed together (Prevedello *et al.* 2008).

ACTIVITY PATTERNS

The activity pattern of a species corresponds to the hours during the period of a day in which it carries out its activities (Bennie *et al.* 2014). As well as the use of space, activity pattern will play a role in population dynamics and community structure, because it is one of the mechanisms by which coexistence between species can be achieved (Bennie *et al.* 2014). At Garrafão, activity pattern was evaluated for two didelphids - *D. aurita* and *M. myosuros*, and one rodent species – *T. dimidiatus*; all nocturnal at some degree (Ferreira & Vieira 2014a, Ferreira & Vieira 2015, Motta 2021). *Didelphis aurita* was mostly nocturnal, but with eventual diurnal records (12%) (Ferreira & Vieira 2014a). During the night, two activity peaks were identified, one around the sunset and other around sunrise. This bimodal activity pattern was explained by minimum temperature (*i.e.*, species more active at colder temperatures), indicating that low temperatures apparently do not limit the species activity (Ferreira & Vieira 2014a). The second peak of activity was also explained by age and moonlight, with adults being more captured than juveniles and subadults (Ferreira & Vieira 2014a), and with a reduction in activity in bright moon nights, probably as a strategy to avoid potential predators (Tripodi *et al.* 2023).

The activity pattern of *D. aurita* was also evaluated using camera traps (Motta 2021) instead of time devices on the traps (Ferreira & Vieira 2014a,b), and covering not only Garrafão, but the entire Serra dos Órgãos National Park (Motta 2021). The activity pattern described was similar to Ferreira & Vieira (2014a), with most records of activity at night (85%), followed by 15% at dusk (Motta 2021). However, only one peak of activity was observed (23:00h and 00:00h), differing to the bimodal pattern previously observed. The activity pattern differed: (i) between dry and wet seasons, with more intense activity at the beginning and at the end of the night during the dry season; and (ii) between the continental and oceanic slopes of the park, with more intense activity in the early evening and sharper drop at the end of the night on the continental slope (Motta 2021). Additionally, activity was affected by altitude, with the range of activity decreasing with increasing altitude, suggesting again that the variation in temperature may be a determining factor of the daily cycle of *D. aurita* (Motta 2021).

POPULATION GENETICS

Didelphis aurita was the only species with studies evaluating the level of population genetic diversity (Gentile 2000, Kajin 2008). Although Garrafão study site was composed by three trapping grids (maximum distance of 1,426 m), it was found a single population with seven identified haplotypes (Kajin 2008). When compared to other five nearby forest fragments, small, but significant genetic differences between haplotypes were found, supporting the hypotheses of a metapopulation structure, considering a fine time scale, with restricted gene flow and possible isolation by distance (Gentile 2000, Kajin 2008). The number of immigrants was high and indicated that dispersal is a determining factor in structuring populations on a regional scale, which is enough to reduce or prevent differentiation between populations (Gentile 2000). Genetic as well as ecological analyses also showed a tendency to population demographic equilibrium, rejecting hypotheses of past population expansion or bottleneck effect (Kajin 2008).

METHODS DEVELOPMENT

Long-term field studies are a great opportunity to develop new methods, as well as to test those proposed in other environments and with other species. During this long-term monitoring study, five new methods were developed or adapted from previous ones. In the small mammal community, arboreal species were present, but rarely captured in live traps placed in the canopy. Loretto (2006) identified this sampling gap and installed artificial nests (AN), modified from Tubelis (2000). Indeed, the combination of AN and live traps produced more accurate data on population dynamics and community structure of arboreal species (Loretto & Vieira 2011).

Along with gathering data on population and community numbers, long-term monitoring studies rely also on the collection of data on the environment (*e.g.*, weather, habitat structure) and intrinsic characteristic of species (*e.g.*, age classes, habitat preference, activity patterns). At Garrafão, researchers (i) proposed a pre-sampling method to estimate the minimum number of litter traps to estimate litterfall (Finotti *et al.* 2003); (ii) developed a method to determine age classes of marsupials in the field (Macedo *et al.* 2006); (iii) improved time devices attached to Tomahawk live traps to record activity patterns (Ferreira & Vieira 2014b); and (iv) tested a new method for the analysis of microhabitat and mesohabitat selection by small mammals (Freitas 1998).

Comparison between different methods were also present. Mendel & Vieira (2003) compared two methods for estimation of movement distance, the spool-and-line device and trapping grids, to determine the boundary stripe and effective sample area to obtain population density. The spool-and-line device provided more accurate movement distance and density estimates than trapping grids. Loretto (2012) also evaluated how different baits (banana, mixed-bait, fresh meat, and pineapple) affected the trappability of small arboreal mammals.

FUTURE DIRECTIONS AND CHALLENGES

Many years of uninterruptedly monitoring are necessary to acquire the valuable results summarized here. Considerable amount of time, human, and financial resources must be invested in order to maintain such an ambitious long-term project. More than 100 people among undergrad students, graduated students, postdoctoral researchers, professors, and laboratory technician were part of these 22-years of research, that was supported by six different long term financial projects, among other individual ones. The team of researchers leading the project were successful in maintaining funding and consistent data collection over the 22 years. One solution found by the team of researchers involved at Garrafão was to keep the monitoring ongoing while other side projects, as the microhabitat evaluation, were conducted in the study area and with the same monitored species. Often self-funded, these individual studies answered questions that emerged from the long-term monitoring helping to increase comprehension of the biology of the species and the process involved in the pattern of population dynamics identified over the years.

The impact of the research originated from long-term monitoring studies increase with time. This is probably the largest trade-off faced by researchers; high investment in the first years of monitoring and considerably low return on investment in terms of publication impact in academia at the same period (Clutton-Brock & Sheldon 2010). At Garrafão, results that brought the main novelties in the field of population ecology were conducted with more than 10 years of data gathering. Thus, only long-term monitoring studies will enable us to unravel the patterns of population dynamics over time and to assess the impact of environmental changes such as climate change on populations and species.

Despite its great importance, this long-term monitoring study focused on evaluating population fluctuation of small mammals only. Today, after identifying the patterns of population fluctuation of six species of small mammals, data on potential predators and resource availability would provide new insights on the processes behind it. Proxies of resource availability, as the amount of rainfall and the Normalized Difference Vegetation Index (NDVI), can be used but these will only reflect part of the resource dynamics that take place in the study area. A solution for future studies that will enter this endeavor is to establish collaborations with other research groups to collect relevant data (*e.g.*, plant phenology, abundance of potential competitors, predators and parasites, and local climate), thus building a collaborative network that may in the future intercross and enable a better understanding of the studied system.

Finally, several questions remain to be answered with this dataset and this review is just a start to stimulate the construction of new ones. Experimental demographic studies such as feeding manipulation are desirable and can be viewed as the next step for the full comprehension of the system. The application of new developed methods in population ecology and life history will also open an array of research, and the combination of different sources of data in the same analysis is now a possibility. Ultimately, we also need to uncover how changes in climate affect the small mammal populations and the mechanisms behind it. We hope that this review will stimulate future further long-term monitoring studies with wild populations in tropical wet and dry forests in the Neotropics.

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SUPLEMENTARY MATERIAL

1 - List of references used in this review

2 - List of small mammals captured along the 22-year long-term monitoring study at Garrafão, in the Serra dos Órgãos National Park, state of Rio de Janeiro, Brazil.

3 - Studies that evaluated habitat selection at Garrafão, Serra dos Órgãos National Park, state of Rio de Janeiro, Brazil, during a 22-year long-term monitoring study of non-volant small mammals.

4 - Studies that evaluated use of space by didelphid marsupials at Garrafão, Serra dos Órgãos National Park, state of Rio de Janeiro, Brazil, during a 22-year long-term monitoring study of non-volant small mammals.

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