



## A TEST OF SEMELPARITY IN THE LONG-TERM POPULATION MONITORING OF THE MARSUPIAL *Marmosops incanus* (DIDELPHIMORPHIA, DIDELPHIDAE)

Priscilla Lora Zangrandi<sup>1\*</sup>, Maja Kajin<sup>2</sup> & Marcus Vinícius Vieira<sup>1</sup>

<sup>1</sup> Universidade Federal do Rio de Janeiro, Instituto de Biologia, Departamento de Ecologia, Laboratório de Vertebrados, Centro de Ciências da Saúde, Av. Carlos Chagas Filho, 373, CEP 21941-902, Rio de Janeiro, RJ, Brasil.

<sup>2</sup> University of Oxford, Department of Biology, 11a Mansfield Road, OX1 3SZ, Oxford, UK.

E-mails: priscillalz@gmail.com (\*corresponding author); majakajin@biology.ox.ac.uk; mvvieira@gmail.com

**Abstract:** Semelparity, the life-history strategy characterized by death after first reproduction, is restricted in mammals to only two marsupial families, Dasyuridae in Australasia and Didelphidae in the Neotropics. Among didelphids, studies suggest a semelparous pattern for mouse opossums of the genus *Marmosops*. These studies have revealed that both sexes may have low survival rates after reproduction in two distinct Atlantic Forest populations. However, the semelparous strategy, which is usually considered a species-specific trait, can also be found in only some populations of Dasyuridae species. Thus, in this study, we aimed to investigate the occurrence of the semelparous life strategy in a population of *M. incanus* in an Atlantic Forest area of the PARNA Serra dos Órgãos, Rio de Janeiro, Brazil, through survival estimates using 13-year capture-mark-recapture data from a long-term population study. We established cohorts, grouping the capture histories of individuals born by the end of the breeding season. We built a global model in which survival and recapture rates vary with time and between sexes, in addition to the interaction between these factors. Model selection and averaged survival estimates were in accordance with the semelparous strategy for this population of *M. incanus*, with survival being affected by both sex and time. Even though we found that the survival of females was higher than that of males as expected, the difference was small. Here we confirm that another population of *M. incanus* displays a semelparous life-history strategy, supporting previous considerations of museum specimens. Nonetheless, the causes and mechanisms of semelparity in didelphid species are still to be understood.

**Keywords:** cohort; life-history strategy; mortality; reproduction; semelparous; survival.

### INTRODUCTION

Semelparity, a life-history strategy first proposed by Cole (1954), is an extreme example of the survival cost of reproduction, where individuals breed only once in their lifetime. While this strategy is more common in plants, invertebrates, and fishes, it is less prevalent in terrestrial vertebrates. Among mammals, semelparity is observed more frequently, or more severely, in males belonging to

the marsupial families Dasyuridae in Australasia and Didelphidae in the Neotropics (e.g., Boonstra 2005, Bradley 2003, Holleley *et al.* 2006, Lorini *et al.* 1994, Oakwood *et al.* 2001, Pine *et al.* 1985). The bulk of our understanding about this mortality pattern in small marsupials comes from studies on two Australian genera, *Antechinus* and *Phascogale*: females exhibit synchronous annual estrous, while males dedicate intensively to locating mates and often die immediately after, in a way that, in some

cases, all males disappear from the population before the offspring are born (Boonstra 2005, Bradley 2003). Some studies claim the semelparous strategy and its variants (partial and facultative semelparity) for some species of the family Didelphidae (review in Zangrandi & Vieira 2022). The research on semelparity in didelphid marsupials suggests that both male and female individuals exhibit reduced survival following reproduction, although males may experience comparatively higher mortality than females (Lorini *et al.* 1994, Martins *et al.* 2006, Leiner *et al.* 2008, Baladrón *et al.* 2012, Barros *et al.* 2015, Lopes and Leiner 2015, Albanese *et al.* 2021).

To date, the semelparous life-history strategy has been observed in nine Neotropical marsupial species so far, including species within the *Marmosops* genus (Zangrandi & Vieira 2022). The gray slender mouse opossum (*M. incanus*) and the Brazilian slender mouse opossum (*M. paulensis*) are partially sympatric species of this genus exhibiting evidence of a semelparous strategy (Lorini *et al.* 1994, Leiner 2005, Macedo 2007, Leiner *et al.* 2008, Barros *et al.* 2015). In a study of over 300 museum specimens, Lorini *et al.* (1994) first suspected *M. incanus* of being semelparous based on external and internal reproductive structures. Later, a field study with *M. paulensis* confirmed the semelparous strategy based on population reproductive patterns (Leiner *et al.* 2008). Breeding seemed to be initiated by a 12L:12D photoperiod and a rapid rate of change in day length, similar semelparous dasyurids. Other field studies observed a high population turnover in populations of *M. incanus*, further supporting the likelihood of semelparity (Macedo 2007, Barros *et al.* 2015). Results also indicated a synchronous reproduction onset driven by photoperiod cues. Zangrandi and Vieira (2022) categorized species of the genus *Marmosops* and five other Neotropical marsupial genera as having reproductive strategy I, following Lee *et al.* (1982). Species classified in this category show seasonal reproduction, with a highly synchronized mating period lasting approximately 2 weeks preceding a long period to reach maturity (about 11 months). In Australasian semelparous marsupials, males die soon after the mating period, but male mortality in didelphid marsupials such as the *Marmosops* genus can occur up to three months after mating, suggesting differences in physiological mechanisms leading to mortality (Boonstra 2005). The semelparous strategy is

usually considered a species-specific trait, but it can also be found in only some populations of particular species as observed in the dasyurids *Parantechinus apicalis* and *Dasyurus hallucatus* (Dickman & Braithwaite 1992). Thus, despite the evidence, not all populations of the *M. incanus* and *M. paulensis* may exhibit a semelparous life history strategy.

Our objective was to investigate the occurrence of semelparity in a *Marmosops incanus* population in southeast Brazil to improve the knowledge of the reproductive pattern of the species. We followed other studies' methodology that evaluated semelparity through survival and recapture estimates for males and females (Leiner *et al.* 2008, Baladrón 2012, Martins *et al.* 2006, Barros *et al.* 2015). We hypothesize that if *M. incanus* has a semelparous life strategy, survival rates will be reduced after the beginning of the breeding season because, during this period, there is a high allocation of resources for reproduction, which reduces the energetic individual reserves (Macedo 2007). In addition, the weaning period is generally long for small marsupials (*i.e.*, with less than 1 kg) compared to eutherian mammals of the same size (Braithwaite & Lee 1979), reducing the chances of small marsupials such as *M. incanus* producing more than one litter within a year. Therefore, the long period of care provided by mothers to their young suggest that adult females to live longer than males during the most critical period, which is the end of the breeding season.

## MATERIAL AND METHODS

### *Study species*

*Marmosops incanus* (Lund 1840) is a small nocturnal marsupial in which females are pouchless, a common characteristic among species of the genus (Rossi *et al.* 2006). It is distributed on the east coast of Brazil, from Bahia to Paraná (Mustringi & Patton 1997), and lives in primary and secondary forests, as well as in the Cerrado and Caatinga biomes near the Atlantic Forest (Câmara *et al.* 2003). *M. incanus* moves on the ground and understory, never using the canopy (Cunha & Vieira 2002, Loretto & Vieira 2008). It is basically insectivorous but has a great proportion of carbohydrates in relation to

proteins and lipids in its diet (Astúa de Moraes *et al.* 2003). In *M. incanus* there is a clear sexual dimorphism in body size, in which males are, on average, 1.5 times the size of females in the study area (Macedo *et al.* 2007). The delimited reproductive activity is related to rainy seasons (Rossi *et al.* 2006), representing periods of resource abundance (Finotti *et al.* 2020). The breeding season in the study area spans from October through February, as indicated by lactation as a measure of reproductive activity (Macedo 2007). The beginning of the breeding period seems to be regulated by changes in the photoperiod (Cerqueira 2005, Macedo 2007, Barros *et al.* 2015).

### **Study area**

The study was carried out in the Serra dos Órgãos National Park, at Garrafão site (22°28'28"S, 42°59'86"W), municipality of Guapimirim, in Rio de Janeiro State, Brazil. The area is in the Atlantic Forest biome and, although it is a region of continuous forest, the study area is surrounded by weekend houses and is influenced of human presence. The canopy of the forest is high and closed, and the understory is dense and structured (details in Gentile *et al.* 2004, Macedo *et al.* 2007 and Finotti *et al.* 2020).

The climate is mild-humid mesothermal (Nimer 1989). During the study period, the mean monthly temperatures varied from 15.7° C to 25° C, the lowest mean minimum temperature recorded was 9.5° C, while the highest maximum monthly temperature 25° C, and the total monthly rainfall ranged between 0.1 and 517.8 mm (Instituto Nacional de Meteorologia 2010). The rainy season was from October/November to March, and the driest months were usually June, July, and August, despite not corresponding to periods of real hydric deficit according to the definition of Walter (1986).

### **Data collection**

Captures were part of the small mammal population monitoring program of the Laboratório de Vertebrados, Universidade Federal do Rio de Janeiro (UFRJ), through the capture-mark-recapture method initiated in April 1997 (Gentile

& Kajin 2015). This study used data collected from April 1997 to December 2009. The trapping sessions were conducted every other month in three 0.64 ha grids at different altitudes (748, 652, and 522 m). The study used a 5 x 5 grid design, with 25 trap stations placed every 20 meters. Each trap station had two live traps on the ground, a Sherman® trap (model XLK, 7.64 cm x 9.53 cm x 30.48 cm) and a Tomahawk® trap (model 201, 40.64 cm x 12.70 cm x 12.70 cm). Additionally, 13 out of 25 trap stations had one trap of each model in the canopy, while 5 larger Tomahawk® traps (model 105, 50.80 cm x 17.78 cm x 17.78 cm) were placed in the farthest and central stations of the grids, resulting in a total of 81 live traps per grid). The bait consisted of oats, bananas, peanut butter, and bacon. Tomahawk® traps on the ground also received pieces of bacon and beef. In each trapping session, traps were baited and checked in the morning for five consecutive days, resulting in a trapping effort of 1215 trap-nights for all three grids combined.

Individuals were marked with numbered ear tags (National Band and Tag Co., Newport, Kentucky, USA) on both ears to minimize loss of marks. All animals were weighed and measured (length of tail and length of head and body). Sex, reproductive condition (lactation and swollen or regressed mammas), presence of ectoparasites and the development of teeth eruption were recorded (following Macedo *et al.* 2006). Only female reproductive condition is informative to the delimitation of breeding seasons because females show signs of breeding such as pregnancy, lactation and swollen or regressed mammas, while males have testicles inside the scrotum for their entire life.

All animals were treated carefully following the standards suggested by the American Society of Mammalogists (Sikes & The Animal Care and Use Committee of the American Society of Mammalogists 2016) and were released at the point of their capture. This study was carried out under license # 02001, 004671/98-51 of the Instituto Brasileiro do Meio Ambiente (IBAMA).

### **Data analysis**

A cohort is defined by a group of individuals who are followed from birth to death or disappearance from the study area. In this study, capture histories of individuals born during the same time period,

specifically by the end of each year's breeding season, were grouped into cohorts. We established cohorts considering a system of age classes based on tooth eruption sequence (following Macedo *et al.* 2006) and body mass. In this way, young and sexually immature individuals were identified by the presence of the 3rd decidual premolars, incomplete molar eruption sequence (until the second functional superior molar), and weight less than 50 g. In Table 1, we identified the 13 cohorts analysed in this study. Cohorts typically spanned from December of the previous year to February of the following year, with one exceptional female who survived until June of her second year. Due to this overlap in the end and beginning of years, it was important to distinguish which individuals belonged to which cohort. For instance, the 1998 cohort represents individuals born in the breeding

season of 1997 and bred in 1998, and therefore lived most of their lives in 1998. Males of the 1998 cohort were first registered in December 1997 as juveniles, while the last male was registered in December 1998 as an adult. Similarly, the 1999 cohort represents individuals born in the breeding season of 1998. Males were first registered in December 1998, while the last male was registered in December 1999. Even though there the overlap between the 1998 and 1999 cohorts (in December 1998), we were able to differentiate individuals based on their unique ear-tag marking and age class. Therefore, we ensured that the following analyses would not mix individuals from different cohorts despite living in the same time period, what could possibly obscure the true mortality rate of adults.

**Table 1.** Time interval of each of the 13 cohorts and the number of individuals (males, females, and total) of *Marmosops incanus* for each cohort from April 1997 to December 2009 in Garrafão, municipality of Guapimirim, Rio de Janeiro state, Brazil.

Cohort	Males		Females		Total
	Time interval	N	Time interval	N	N
1997	Jun/97 - Dec/97	14	Apr/97 - Feb/98	10	24
1998	Dec/97 - Dec/98	13	Feb/98 - Feb/99	12	25
1999	Dec/98 - Dec/99	8	Aug/99 - Feb/00	3	11
2000	Aug/00 - Dec/00	8	Jun/00 - Dec/00	9	17
2001	Feb/01 - Dec/01	14	Apr/01 - Dec/01	9	23
2002	Feb/02 - Oct/02	15	Dec/01 - Dec/02	13	28
2003	Feb/03 - Dec/03	9	Dec/02 - Dec/03	13	22
2004	Apr/04 - Oct/04	9	Feb/04 - Dec/04	6	15
2005	Apr/05 - Dec/05	12	Feb/05 - Feb/06	12	24
2006	Dec/05 - Dec/06	17	Aug/06 - Jun/07	11	28
2007	Dec/06 - Oct/07	13	Dec/06 - Dec/07	11	24
2008	Feb/08 - Feb/09	8	Apr/08 - Dec/08	13	21
2009	Jun/09 - Oct/09	5	Feb/09 - Dec/09	16	21
Total		145		138	283



Survival ( $\phi$ ) and recapture rates ( $p$ ) were modeled under the Cormack-Jolly-Seber model using program MARK, version 9.0 (White & Burnham 1999) in function of sex, time, and constant models. Since we were less interested in inter-annual variation and more interested in the variation over the months of each year, we decided to group all cohorts into one. In this way, all trapping sessions that occurred in a given month of different years were gathered in one session representing that month. Thus, we built a global model with sex and time-dependent survival and recapture rates, as well as interactions between the effects ( $\phi[s*t] p[s*t]$ ).

To assess the goodness of fit for the initial model, we used a parametric bootstrap procedure with 1000 simulations. This involved estimating the distribution of the simulated deviances and fitting the data from the global model (Cooch & White 2007). The initial model is considered fit to the data when the observed deviance is at the core of the distribution of simulated deviances (Johnson & Omland 2004). Additionally, we used the variance inflation factor,  $\hat{c}$ , to adjust the fit of the global and all other models in the candidate model set, correcting for overdispersion (Cooch & White 2007, Lebreton *et al.* 1992, White *et al.* 2001).

Models were selected from the candidate set by their values of QAICc, a corrected form of the Quasi Akaike's Information Criterion, and other related indices. The corrected form is used when a sample is small regarding the number of parameters, and AICc is modified to QAICc (quasi-AICc) when  $\hat{c}$  is calculated. As the value of  $\hat{c}$  increases, QAICc tends to favor models with fewer parameters (Cooch & White 2007). Values of  $\Delta$ QAICc, which represent the difference in the value of the QAICc between the current model and the best-fitting model (the one with the lowest QAICc), and values of QAICc weight, which are the relative evidence of adjustment of a model to the data, proportional to the rest of the candidate models, were obtained for each model (Burnham & Anderson 2002). We used model-averaged estimates obtained from an average value weighted by evidence of each of the selected models to consider model selection uncertainty (Burnham & Anderson 2002).

## RESULTS

During 13 years of study, 283 individuals of *Marmosops incanus* were captured, representing the second most abundant species of small mammal in the study area, after the black-eared opossum, *Didelphis aurita*. We studied thirteen cohorts (Table 1), consisting of 11 to 28 individuals, with the smallest cohort in 1999 and the largest in 2002 and 2006. There was little overlap between generations and both young and adult individuals were captured in December and February.

We built 25 models and adjusted them with  $\hat{c} = 1.347$  ( $p = 0.031$ ). The first two best-ranked models indicated survival was influenced by sex and time, with an additive effect (Table 2). The difference between these models was in the recapture rate: the first indicating a constant rate and the second showing a difference between sexes. These models had an accumulated QAICc weight of evidence of 0.74. When considering the third and fourth models as well, the accumulated weight of evidence increased to 0.92. The third and fourth models had only the effect of time on survival and had  $\Delta$ QAICc equal to 2.82 and 4.18, respectively. Models without time variation had the highest QAICc and were ranked last among the candidate models.

The model-averaged survival rates were the highest in February of the first study year of the cohorts and declined continually. Survival rates were less than 0.5 for both sexes in August, reaching 0.09 (SE = 0.06) for males and 0.14 (SE = 0.08) for females in December (Figure 1a). The estimate for February of the second study year was still low (0.15 [SE = 0.18] for males and 0.23 [SE = 0.24] for females), but the uncertainty was higher than that in December. The survival estimate of the last time interval was invalid because only one female was caught in the last sessions of the present database (April and June of the following year). Females had higher survival rates than males, but the difference was not clear due to an overlap in the confidence intervals between sexes. The model-averaged recapture rates were constant in time and slightly different between sexes: 0.69 (SE = 0.08) for males and 0.73 (SE = 0.06) for females (Figure 1b).

**Table 2.** Model selection for survival ( $\phi$ ) and recapture rates ( $p$ ) of *Marmosops incanus* from April 1997 to December 2009 in Garrafão, municipality of Guapimirim, Rio de Janeiro state, Brazil. Models varied according to sex ( $s$ ) and time ( $t$ ), and with additive (+), interaction (\*), and without effect (.).  $K$  is the number of parameters, QAICc is Akaike's information criteria corrected for small samples,  $\Delta$ QAICc is the difference between the values of QAICc of each model and the first model, and  $w$  is the Akaike weight of the models.

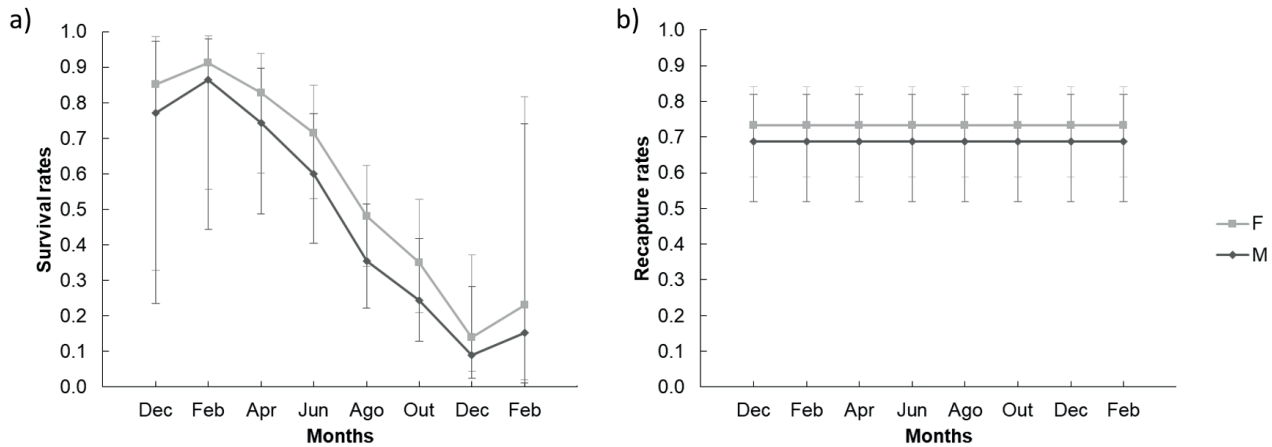
	<b>Model</b>	<b>K</b>	<b>QAICc</b>	<b><math>\Delta</math>QAICc</b>	<b>w</b>
1	$\phi(s+t)p(.)$	11	475.34	0.00	0.51
2	$\phi(s+t)p(s)$	12	476.92	1.58	0.23
3	$\phi(t)p(s)$	11	478.16	2.82	0.12
4	$\phi(t)p(.)$	10	479.52	4.18	0.06
5	$\phi(s+t)p(t)$	19	481.85	6.51	0.02
6	$\phi(s^*t)p(.)$	19	482.01	6.67	0.02
7	$\phi(s^*t)p(s)$	20	483.56	8.22	0.01
8	$\phi(s+t)p(s+t)$	20	483.83	8.49	0.01
9	$\phi(t)p(s+t)$	19	485.08	9.74	0.00
10	$\phi(s)p(s^*t)$	17	485.46	10.12	0.00
11	$\phi(t)p(t)$	18	486.60	11.26	0.00
12	$\phi(s+t)p(s^*t)$	28	487.20	11.86	0.00
13	$\phi(.)p(s+t)$	11	489.16	13.82	0.00
14	$\phi(s^*t)p(t)$	27	489.66	14.32	0.00
15	$\phi(t)p(s^*t)$	27	489.71	14.37	0.00
16	$\phi(.)p(s^*t)$	19	489.85	14.51	0.00
17	$\phi(s)p(s+t)$	12	490.88	15.54	0.00
18	$\phi(s)p(t)$	11	491.15	15.81	0.00
19	$\phi(s^*t)p(s+t)$	28	491.56	16.22	0.00
20	$\phi(.)p(t)$	10	493.68	18.34	0.00
21	$\phi(s^*t)p(s^*t)$	36	502.76	27.42	0.00
22	$\phi(s)p(.)$	3	521.50	46.16	0.00
23	$\phi(.)p(s)$	3	521.61	46.27	0.00
24	$\phi(.)p(.)$	2	521.73	46.39	0.00
25	$\phi(s)p(s)$	4	522.52	47.18	0.00

## DISCUSSION

Our results for the studied population of *Marmosops incanus* were consistent with the pattern expected for the semelparous strategy in didelphid marsupials. The population showed distinct cohorts with little overlap among them, and the recruitment periods of new generations appeared to coincide with months of the senescence periods of the previous generations. The model selection and survival estimates for 13 years of study revealed higher survival rates for females than for males and decreasing survival rates after reproduction events.

According to Lorini *et al.* (1994), the annual age structure and the reproductive indications of

specimens of *M. incanus* in zoological collections strongly characterize the semelparous strategy for this species across a wide geographic range. In a previous analysis of the population dynamics and age distribution for the same data set, Macedo (2007) suggested complete semelparity for *M. incanus*. This strategy has also been indicated for a sister species, *M. paulensis* (Leiner 2005, Leiner *et al.* 2008). However, these studies assumed equal recapture probabilities across different age classes and both sexes, which may not be the case. To investigate semelparity with ecological data more thoroughly, survival and recapture probabilities should be modeled. In a recent study on *M. incanus* based on model selection, Barros



**Figure 1.** Model-averaged estimates and 95% confidence intervals of the monthly survival ( $\phi$ ) and recapture rates ( $p$ ) of females (F) and males (M) of *Marmosops incanus* from April 1997 to December 2009 in Garrafão, municipality of Guapimirim, Rio de Janeiro state, Brazil. Thirteen cohorts were grouped based on the months when the individuals were captured. Since cohorts could start in December of the previous years and end in February of the following year, the grouped cohort represents a time period longer than a regular calendar year.

*et al.* (2015) found that survival was lower during the breeding period for both sexes, and even lower for males. Our results suggest survival rates decreased steadily throughout the months until they get to the bottom in December, the peak of the breeding season. Females had higher survival and recapture probabilities, but the uncertainty of our model-averaged estimates was high. In addition, our method of categorizing capture histories into cohorts enabled us to differentiate between juveniles and adults estimates even when they were captured during the same trapping session.

We expected post-reproductive males to have lower survival probabilities compared to females, who typically survive until the end of the breeding season, which coincides with the lactating period. We found a decline in survival with the beginning of the reproductive activity, with small differences between sexes. The disappearance of both males and females had been observed in other didelphid species, such as *M. paulensis* (Leiner *et al.* 2008), *Monodelphis dimidiata* (Pine *et al.* 1985, Baladrón *et al.* 2012), *Gracilinanus agilis* (Lopes & Leiner 2015), and *Thylamys bruchi* (Albanese *et al.* 2021), although there is variation in this pattern. In a population of *G. agilis*, for example, a small proportion of males survived to a second breeding season, and they were considered partially semelparous (Martins *et al.* 2006). In the case of *T. bruchi*, males showed delayed mortality and died after weaning, similar to females, but without

any sign of second breeding due to severe winters (Albanese *et al.* 2021).

There is a continuum of physiological responses to the stress of reproduction, and life-history strategies of iteroparity and semelparity represent the extremes of this continuum. Partial semelparity would be in an intermediate stage of the continuum when a small proportion of males and females still survive for a while after reproductive activity, allowing a second event of reproduction (Boonstra 2005). In the present study, there was no evidence that individuals of *M. incanus* reproduced more than once because only one female reached the following breeding season, and it did not show reproductive signs. Nevertheless, it is not guaranteed that females produce only one litter because of the prolonged period of reproductive signs observed in the study area from August to February of the following year. Lorini *et al.* (1994) found two breeding seasons within a year in the population of *M. incanus* from Ilhéus (Bahia), a locality without a defined dry season (Nimer 1989), which is similar to our study area. The question of whether to classify species that might produce more than one litter in a breeding season is a matter of debate (Zangrandi & Vieira 2022).

Semelparous species have a reproductive strategy that is synchronized with the period of abundant resources, ensuring greater chances of survival for their offspring (Braithwaite & Lee 1979, Boonstra 2005). The expression of semelparity

appears to be more favored in habitats with stronger seasonality. In contrast, the Atlantic Forest provides a relatively constant habitat in terms of climate and food availability (Instituto Brasileiro de Geografia e Estatística 2019, Finotti *et al.* 2020), which is less seasonal than the habitats of Australasian semelparous marsupials or some didelphid species, such as *M. dimidiata* and *T. bruchi*. In addition to this, *M. incanus* has an insectivore-fructivore diet that may vary seasonally according to the fluctuation of arthropods and fruit availability (Gentile *et al.* 2004), similar to *M. paulensis* (Leiner 2005). Thus, the causes and mechanisms of semelparity in didelphid species are still to be understood. Since research on stress response and physiological mechanisms of semelparity is currently restricted to *Didelphis virginiana* (Woods & Hellgren 2003) and *G. agilis* (Hernandez *et al.* 2018), there is a need for investigation into stress response across a wider range of didelphid marsupial species to understand the drivers of this life-history strategy.

To conclude, we confirmed that this population of *M. incanus* displays a semelparous life-history strategy, even though the phenomenon seems to be less intense, *i.e.*, a gradual decrease in survival rate is observed when compared with the abrupt male die-off observed in many Australasian marsupials. Therefore, to determine where the life history of *M. incanus* is placed inside the continuum between iteroparity and semelparity, it will be essential to evaluate the physiological and endocrinological changes that occur during reproductive activity. These analyses may help shed light on the mechanisms underlying post-reproductive senescence and, ultimately, individual mortality.

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