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Original Investigation

Timing and environmental cues associated with triggering of reproductive activity in Atlantic forest marsupials

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ABSTRACT

Seasonal reproduction during the time when food availability is high is a widespread strategy in marsupials, which maximizes offspring survival. In Australian marsupials, reproduction is commonly synchronous among co-occurring species, the onset of reproduction being triggered by photoperiodic cues. In a subset of these species, partial semelparity with high mortality of males after reproduction is a common pattern. For Neotropical marsupials, however, environmental triggers of reproduction have been poorly studied despite some evidence of a seasonal synchronous reproduction, and semelparity has been described in few species. Using a capture–recapture dataset of co-occurring marsupials in the Atlantic forest sampled for two years, we aim to investigate the timing and triggering of reproductive activity as well as the occurrence of semelparity in Neotropical small marsupials. We evaluated which environmental cues (rainfall, photoperiod and temperature) best explain the age structure of the populations of *Gracilinanus microtarsus*, *Marmosops incanus*, *Marmosops paulensis*, *Monodelphis americana*, *Monodelphis scalops* and *Monodelphis iheringi*. For the most common species we also tested for the occurrence of semelparity by assessing if survival rate is affected by sex and mating period. Our results indicate that reproduction onset seems to be synchronous among species and driven by photoperiod cues. In all species, reproduction is seasonal with juveniles being born and lactation occurring in the period of highest food availability, the warm–wet season. Further, semelparity is likely to be the cause of a high population turnover in *Marmosops incanus*, and probably also in co-occurring marsupials.

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Introduction

A widespread reproductive strategy in marsupials is the coupling of reproduction with the period of maximum offspring survival (Tyndale-Biscoe 2005). As the period of highest energetic costs for female marsupials is lactation (Isaac and Johnson 2005), reproductive success would be higher if this phase of reproduction coincides with the period of highest food availability. Indeed, the beginning of reproduction is commonly synchronous among co-occurring marsupial species, and starts some time before the period of highest food availability (McAllan 2003), usually the period of higher rainfall. An early onset of reproduction would also allow for more than one litter per reproductive period, maximizing annual offspring size (Astúa and Geise 2006; Tyndale-Biscoe 2005).

While the timing and especially the triggering of marsupial reproduction has been the focus of a long-standing debate, photoperiodic cues (either photoperiod length or the rate of change of photoperiod) seem to be widespread as environmental triggers of reproduction in Australian marsupials (Goldman 2001; McAllan et al. 2006; Naylor et al. 2008; Tyndale-Biscoe 2005). In contrast, although two studies suggested that photoperiod length might be the cue triggering reproduction (*Monodelphis domestica*, Cerqueira and Bergallo 1993, *Marmosops paulensis*, Leiner et al. 2008), few studies formally addressed triggers of reproduction in Neotropical marsupials. However, it has been shown that reproduction in this group is seasonal and correlated with rainfall, a proxy for food availability (Bergallo 1994; Bonecker et al. 2009; D'Andrea et al., 2007; Gentile et al. 2000; Graipel et al. 2006; Kajin et al. 2008; Passamani 2000). On the other hand, because temperature also affects the activity of marsupials, with some species entering torpor under unfavorable climatic conditions (high temperature and low rainfall, Bozinovic et al. 2005; or low temperatures, Bozinovic et al. 2004; Geiser and Baudinette 1987), changes in temperature represent another plausible candidate for being a trigger of reproduction in this group.

In small marsupials, in which short lifespan only allows a limited number of reproductive events, terminal investment theory

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Table 1
Number of captures and individuals (in parentheses) for marsupial species captured at the Morro Grande Forest Reserve. Due to the impossibility of separating the species *Monodelphis americana* and *M. scalops* in the field, individuals were counted together. Diet and habit followed Paglia et al. (2012).

Species	Captures (individuals)	Habit
Marmosops incanus	230 (74)	Scansorial
Monodelphis americana, M. scalops	39 (29)	Terrestrial
Monodelphis iheringi	39 (27)	Terrestrial
Gracilinanus microtarsus	23 (21)	Scansorial
Marmosops paulensis	22 (8)	Scansorial
Marmosa paraguayana	13 (4)	Scansorial
Monodelphis sp. nova	12 (9)	Terrestrial
Total	378 (172)	

predicts a benefit from investing in reproduction instead of survival, which would increase mortality after reproduction (Isaac and Johnson 2005). Extreme physiological costs of reproduction that can cause a trade-off between survival and reproduction are linked to compensatory adjustments that divert energy into reproduction, reducing immunocompetence, and affecting hormonal- and thermoregulation (Boonstra 2005; Oackwood et al. 2001; Speakman 2008). The frequency of the die-off after reproduction can be large enough to be defined as semelparity, i.e. each individual takes part in only one reproductive event during its lifetime (Cole 1954). However, semelparity has recently been recognized as part of a continuum rather than a discrete life-history category (Fisher et al. 2013), from negligible survival after reproduction, the die-off of individuals of just one sex, to iteroparity, when individuals participate in multiple reproductive events. In Australian marsupials, male die-offs after reproduction have been observed in most species of three genera of small marsupials (*Antechinus*, *Phascogale* and *Dasykaluta*; Oackwood et al. 2001; McAllan 2003; McAllan et al. 2006). In contrast, the few studies investigating semelparity in Neotropical marsupials indicate that both sexes seem to have low survival after breeding, but sometimes with higher mortality in males compared to females (*Marmosops paulensis*, Leiner et al. 2008; *Marmosops incanus*, Lorini et al. 1994; *Monodelphis dimidiata*, Baladrón et al. 2012; *Gracilinanus microtarsus*, Martins et al. 2006a).

Using capture–recapture data from three 2-ha grids during two years, we here aim at investigating the timing and triggering of reproductive activity, and evaluating the occurrence of semelparity, in co-occurring small marsupials of the Atlantic forest. We first tested and compared alternative hypotheses on which environmental cues (rainfall, photoperiod or temperature) trigger reproduction in the populations of five co-occurring species. We expect that if reproduction is trigged by a particular environmental factor, the proportion of juveniles in the populations will increase at a given level of that factor considering a given time lag (as we are quantifying juveniles instead of reproductive activity). For the most common species, *Marmosops incanus*, we also tested the hypothesis of a semelparous reproductive pattern, by investigating the effect of sex and mating period on survival rates. Survival rate should be lower in the mating period, irrespective of sex, if the species is semelparous.

Material and methods

Studied species

We captured eight species of small marsupials (<100 g), from the commonest to the rarest: *Marmosops incanus*, *Monodelphis americana*, *Monodelphis scalops*, *Monodelphis iheringi*, *Gracilinanus microtarsus*, *Marmosops paulensis*, *Marmosa paraguayana* and *Monodelphis* sp. nova (Table 1). Of those, three species (genus *Monodelphis*) are terrestrial and five are scansorial (Table 1). Most species have an insectivore–omnivore diet (Table 1). We also captured the medium-size marsupial, *Didelphis aurita*. However, data on this species were not included in the analyses due to the exclusive capture of juveniles.

For the analysis of timing and triggering of reproduction, we considered the five most common small marsupials (with more than 20 captures) (Table 1). However, due to the impossibility of separating the species *Monodelphis americana* and *M. scalops* in the field, data from these two congeners were analyzed together. Because a considerable number of recaptures is necessary for reliably estimating survival rates (Williams et al. 2002), semelparity was only analyzed in the most common species *Marmosops incanus*.

Study area

We collected data at the Morro Grande Forest Reserve (23°39′–23°48′ S, 47°01′–46°55′ W, Cotia, São Paulo, Fig. 1), a 9400 ha continuous forest connected to the largest tract of remaining Atlantic forest in Brazil. It is covered by Lower Montane Atlantic Rain Forest in different regeneration stages (Metzger et al. 2006). The altitude in the region varies from 850 to 1100 m above sea level. Mean maximum temperature is 27 °C and mean minimum temperature is 11 °C. Mean annual rainfall is 1339 mm, and the warm–wet season is from September to March (Metzger et al. 2006).

Data collection

We set three 2-ha trapping grids (100 m × 200 m) ~2 km apart within the Reserve (Fig. 1). All of them were located in the same altitude, type of forest, and regeneration stage. Each grid comprised 11,100-m parallel lines, 20 m apart from each other, each composed of 11 trap stations every 10 m. Six alternated lines had only 11 Sherman traps (37.5 cm × 10.0 cm × 12.0 cm or 23.0 cm × 7.5 cm × 8.5 cm) on the ground. The other five lines contained, besides the Sherman traps, 11 pitfall traps (60 l buckets buried at the ground, connected by 50-cm high drift-fences) at the same trap stations, totaling 121 Sherman traps and 55 pitfall traps per grid. In order to reduce accidental mortality at pitfall traps we (1) drilled holes at the bottom of the buckets in order to prevent accumulation of rainwater, (2) placed a piece of styrofoam at the bottom of the buckets for fluctuation in the event of flooding, and (3) put a cover at 50 cm from the ground, working as an umbrella. All traps received daily baits made of a mashed banana, cornmeal, peanut butter and sardines.

We performed 24 five-night capture sessions between March 2008 and January 2010. Interval between sessions varied from 19 to 30 days (mean of 25 days). Captured individuals were marked with tags with unique codes, allowing individual recognition. For each capture we recorded the species, weight, and sex (by external characteristics). Age classes were based on the molar teeth eruption pattern (only M1 or M1 and M2 erupted – juveniles; M3 erupted – subadults; M4 erupted – adults) as described by Macedo et al. (2006). Reproductive activity in females was determined by pregnancy or the presence of swollen teats. Populations of *M. incanus*, the most common species, was monitored during all 24 capture sessions (March 2008 to January 2010), while populations of the remaining small marsupials were monitored during the first 21 capture sessions, till October 2009. Voucher specimens of all species were collected in a pilot sample, identified by experts, and are kept in the Department of Zoology, University of São Paulo.

Photoperiod in São Paulo varies from 10 h 40 min (640 min) in June to 13 h 35 min (815 min) in December (Anuário do Observatório Nacional 2008,2009). Mean monthly rainfall was obtained from SAPESP, the government agency who manages the

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