REARING CYCLE AND OTHER REPRODUCTIVE PARAMETERS OF THE XEROPHITIC MOUSE OPOSSUM Marmosa xerophila (Didelphimorphia: Didelphidae) IN THE PENINSULA OF PARAGUANA, VENEZUELA

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SUMMARY

Some reproductive parameters were measured in 60 adult females of Marmosa xerophila to infer the significance of some adaptations to a semi-arid ecosystem when compared to M. robinsoni, a filogenetically closely related species inhabiting more humid environments. The study was carried out in a tropical thorny woodland in the Peninsula of Paraguaná, Falcon State, Venezuela. Field data were collected by two methods: capture-mark-recapture and radioactive tagging. A reproductive peak occurred in June and July, during the dry season. Post-lactating females were detected from July to February. There was no reproductive activity from March to May. The rearing cycle lasted 60 days and the mean litter size was 7.9 young. The reproductive strategy of M. xerophila is similar to the rainforest species M. robinsoni, reflecting a great plasticity that allows Marmosa species to adapt successfully to different Neotropical ecosystems.

Introduction

The genus *Marmosa* consists of nine living species (Wilson and Reeder, 2005) distributed throughout Neotropical terrestrial habitats, with *M. robinsoni* being the most widespread and *M. xerophila* restricted to the semi-arid coastal ecosystem extending over northwestern Venezuela and northeastern Colombia (Handley and Gordon, 1979; Eisenberg, 1989).

Handley and Gordon (1979) suggested a close phylogenetic relationship between *M. robinsoni* and *M. xerophila*, whereby the latter is probably the result of adaptations to xeric conditions. *M. xerophila* is smaller than *M. robinsoni*, even in the sympatric area where the smallest specimens of *M. robinsoni* occur (López-Fuster *et al.*, 2002). This agrees with Bergmann's rule that in hot and dry climates the high surface-to-volume ratio of smaller animals facilitates heat loss through the skin and helps cooling of the body (Ashton *et al.*, 2000; Millien *et al.*, 2006).

As reproductive strategies are influenced by environmental conditions (Sadleir, 1969) it could be expected that reproductive parameters of M. xerophila also reflect adaptations to semiarid environments, especially in one characterized by low and unpredictable precipitation (Díaz and Granadillo, 2005), if compared to those of M. robinsoni. For example, a tendency to a lower parental investment, especially early in pregnancy, and/or a higher degree of iteroparity (Low, 1978; Morton et al., 1982) would be expected for M. xerophila rather than for M. robinsoni.

The goal of this study was to measure some reproductive parameters of *M. xerophila* as

an initial approach to the natural history of this relatively new species, and to infer the significance of some adaptations to semi-arid ecosystems when comparing the data to the information available from field specimens and colonies of *M. robinsoni*.

Materials and Methods

The study was carried out in a tropical thorny woodland (Ewell et al., 1976; Matteucci, 1987) in the Peninsula of Paraguaná (12°02'N, 70°03'W), Falcon State, Venezuela (Figure 1). Local climate is biseasonal, with a long dry season from January to August, followed by a short wet season in September-December. Mean annual precipitation is 467mm, mean annual temperature 27.4 ±1.2°C (Hijmans et al., 2005), and evaporation is >2000mm/ year (Veillon, 1995).

Field data were collected by two methods: capturemark-recapture and radioactive tagging. For the first one, an 11×11 (2.25ha) trapping grid with 121 trapping stations located 15m apart from each other was established. At each station, two Sherman live traps were placed on the ground. Trapping was run for eight consecutive nights each month for 13 months. from June 1994 to June 1995. Despite the expected effort of 25168 trap-nights (i.e., 13 months \times 8 nights \times 121 traps \times 2 traps/station), only 23842 trap-nights were placed because of occasional logistical problems. General morphometric (body weight; body, tail and rear foot lengths) were recorded for each female and young captured, providing a continuous record of individual development. Each adult female was included in one of the following four reproduc-

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CICLO DE CRIA Y OTROS PARÁMETROS REPRODUCTIVOS DE LA COMADREJITA XEROFÍTICA Marmosa xerophila (Didelphimorphia: Didelphidae) EN LA PENÍNSULA DE PARAGUANÁ, VENEZUELA

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RESUMEN

Algunos de los parámetros reproductivos fueron medidos en 60 hembras adultas de Marmosa xerophila para inferir el significado de algunas de sus adaptaciones a ecosistemas semiáridos cuando se comparan con aquéllas de M. robinsoni, una especie presente en sistemas más húmedos y a la que está estrechamente relacionada filogenéticamente. El estudio se llevó a cabo en un arbustal seco espinoso en la Península de Paraguaná, Estado Falcón, Venezuela. Los datos de campo se colectaron a través de dos métodos: captura-marcado-recaptura y marcado con radioisótopos. Un pico reproductivo se presentó en la estación seca, entre junio y julio. Las hembras con señales de haber destetado sus crías eran más evidentes entre julio y febrero. No se observó actividad reproductiva en las hembras entre marzo y mayo. El ciclo reproductivo duró 60 días y el tamaño promedio de la camada fue 7,9 crías. La estrategia reproductiva de M. xerophila es similar a la de M. robinsoni que habita selvas tropicales, lo que refleja una gran plasticidad que permite a estas especies adaptarse exitosamente a diferentes ecosistemas neotropicales.

CICLO DE CRIAÇÃO E OUTROS PARÂMETROS REPRODUTIVOS DA CUÍCA XERÓFILA Marmosa xerophila (Didelphimorphia: Didelphidae) NA PENÍNSULA DE PARAGUANÁ, VENEZUELA

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RESUMO

Foram medidos alguns parâmetros reprodutivos de 60 fêmeas adultas de M. xerophila para inferir sobre o quão significativas são algumas adaptações ao ecossistema semi-árido comparando-os com M. robinsoni. O estudo foi realizado em um bosque espinhoso tropical na Península de Paraguaná, Estado Falcon, Venezuela. Os dados de campo foram coletados usando-se dois métodos: captura-marcação-recaptura e uso de etiquetas radioativa. Um pico de reprodução ocorreu em junho e julho, durante a estação seca. Fêmeas pós-lactantes foram detectadas de julho a fevereiro. Não houve atividades reprodutivas de março a maio. O ciclo de criação dura 60 dias e o tamanho médio da ninhada foi de 7,9 jovems. A estratégia reprodutiva de M. xerophila é similar a de M. robinsoni de floresta tropical, refletindo uma grande plasticidade que permite às espécies do gênero se adaptarem com êxito em diferentes ecossistemas Neotropicais.

tive categories: young attached to teats (with young, WY), milk secretion and/or orange mammary area (lactating, LAC), no milk secretion and pale orange mammary area (postlactating, PL), and none of the previous categories (non-reproductive, NR). For young still clinging to the teats, crown to rump length was measured.

Radioactive tagging was performed by using a 1.9×0.9mm tag containing Ir-192 with 1mCi of activity, placed subcutaneous in the individual's dorsum with a 15-gauge needle. Four reproductive females were tagged and traced

with a Geiger-Müller detector from the "teat-attachment phase" to weaning. The detector was placed close to the nest; it sent a signal to a por-



Figure 1. Location of study area at the Peninsula of Paraguaná, Falcon State, Venezuela.

table computer allowing a 24h recording of the presence of tagged individuals. Continuous monitoring of tagged females and daily inspections of their

nests and young provided information about "nest phase" evolution, young development, and weaning dynamics. This information plus available data from the capture-recapture method were used to study the "nest phase" (Thielen, 1996).

Results

Data presented here come from 60 different adult females, out of which 38 were recaptured at least once. Monthly captures averaged 16.1 (12-25) adult females. A seemly weather synchronized peak of females with young attached to the

teats occurred in June and July, during the dry season, a couple of months prior to the beginning of the rainy season (Figure 2). The proportion of females with young decreased gradually until December. Post-lactating females were detected from July to February. No reproductive activity was recorded from March to May.

Observations of 55 litters, of 42 females, in the same reproductive season showed a 60 days rearing cycle (time from birth to weaning). Thirty-one females produced one litter; nine had two and two three litters. Mean number of litters per reproductive female was 1.3 per year, and mean litter size was 7.9 ± 2.1 (mean \pm SD), ranging from 3 to 11 young. By multiplying these two values, a reproductive season productivity of 10.4 ± 2.7 (mean \pm SD) young per female was obtained.

Morphometric, reproductive and developmental differences between *M. xerophila* and *M. robinsoni* are shown in Table I. *M. xerophila* had a shorter time from birth to



Figure 2. Relative abundance of adult females of *Marmosa xerophila* in different reproductive categories. WY: with young attached to teats, LAC: lactating young at "nest phase", PL: post-lactating (i.e. weaned and dispersed offspring), and NR: non-reproductive. pp: precipitation

weaning, shorter dispersal time and smaller birth body size than *M. robinsoni*. On the other hand, *M. xerophila* had a longer teat-attachment phase, dorsal pigmentation and dorsal fur were completed later and nest phase started at an older age. Finally, litter size in *M. xerophila* was similar to that registered in *M. robinsoni* inhabiting forested habitats, but lower than that from *M. robinsoni* from the Venezuelan Llanos.

Discussion

There is limited information available for many species of mouse opossums (Hayssen *et al.*, 1993), former genus Marmosa, and therefore little is known on the reproductive patterns of such species. Walker (1975) suggested that several mouse opossum species breed from one to three times per year in cool habitats and throughout the year in areas with tropical climate. Indeed, available data show great variation among species, with M. canescens reproducing all over the year (Ceballos and Miranda, 1986; Ceballos, 1990) and other species showing marked seasonality in reproduction, most of them having their reproductive activity correlated to precipitation (O'Connell, 1979; Fleck and Harder, 1995; Martins

et al., 2006). On the other hand, some other species as Marmosops incanus (Lorini et al., 1994) and Thylamys elegans (Mann, 1978) breed in the driest season of the year.

M. xerophila and *M. robinsoni* show a seasonal reproductive biology. In both species, reproduction starts at the end of the dry and beginning of the wet seasons (Enders, 1966; Fleming, 1973; August, 1984; O'Connell, 1989). Although beginning of rainfall could trigger reproduction, Fleming (1973, 1975) reported that synchronization

of reproduction depends on more complex factors, such as a strong selective pressure for the young to wean when there is greater food availability and adults being energetically more active; that is, adults being more capable to allocate more energy for those events related to reproduction (Gittleman and Thompson, 1988). In this sense, in the area of the present study, Thielen et al. (1997b) reported a peak of ripe fruits and invertebrates corresponding with the breeding season and weaning of young, respectively.

In marsupials, litter size is inversely correlated and duration of maternal care is

 TABLE I

 REPRODUCTIVE AND DEVELOPMENTAL DATA OF M. robinsoni AND M. xerophila

Reproductive and developmental data	M. robinsoni*	M. xerophila*
Time from birth to weaning	65 days	60 days
Litter size	6-13 in rainforest; 13-15 in the Venezuelan Llanos; 8 in colonies	3-11
Birth body size	8-12 mm	6-7 mm
Teat-attachment phase	20 days	23 days
Dorsal pigmentation	20 days	23 days
Dorsal fur completed	34 days	36 days
Open eyes	39-40 days	40 days
Dispersal	70 days	60 days
Nest-phase starts	28 days	30-32 days
No. litters/♀/year	1-2	1-3
Productivity/2/year	10 in rainforest; 19.6 in the Venezuelan Llanos	10.4
Gestation time	13-14 days	14 days

* Fleming, 1973; O'Connell, 1989; Eisenberg and Maliniak, 1967. ** This study.

directly correlated to body mass, especially for small didelphids, in which larger litter size seems to be more important than shortened age at weaning or earlier maturation (Thompson, 1987). The present data diverges from this tendency, as litter size and body size of M. xerophila were smaller than M. robinso*ni* from the Venezuelan Llanos (O'Connell, 1983; López-Fuster et al., 2000), and young M. xerophila developed slower than M. robinsoni (Eisenberg and Maliniak, 1967; Collins, 1973; O'Connell, 1979; Eisenberg, 1983). However, dispersal was reached faster than in *M. robinsoni* and in a gradual manner, probably when young follow their mother to foraging excursions and accidentally or intentionally, walk away.

Fleming (1973, 1975) and O'Connell (1989) found that *M. robinsoni* produced up to two litters in the same year, but tendency is to have only one. Mean litter size was 10 young (6-13, n=7) in the rainforest (Fleming, 1973), and 14 young (13-15, n=13) in the Venezuelan Llanos (O'Connell, 1979, 1989), so annual productivity for these two ecosystems is 10.0 and 19.6 young, respectively. This difference is in concert with the López-Fuster et al. (2000) report that individuals of M. robinsoni coming from second growth habitats, such as the Venezuelan Llanos, are bigger and heavier than those found in primary forests, owing to the higher Llanos annual productivity. M. xerophila from the present study area and M. robinsoni from the rainforest showed comparable values of productivity per female, and data of both species could have been influenced by the low productivity registered in these habitats.

Spencer and Steinhoff (1968) and O'Connell (1979, 1989) reported a selective pressure on didelphids in highly variable habitats where the tendency is to produce few big litters during the most favorable season. Thielen (1996), Thielen *et al.* (1997a), Hunsaker (1977) and O'Connell (1979, 1989) considered this factor as an adaptive mechanism to compensate for the short reproductive life of females and high mortality of young in these areas.

Thielen (1996) and Thielen et al. (1997a) reported females of M. xerophila becoming sexually mature at nine months old and surviving for a short time after a year of age. O'Connell (1989), in the Venezuelan Llanos, found that females of M. robinsoni became sexually mature as young as six months of age; however, Hunsaker (1977) and Godfrey (1975) suggested a minimal period of 8-9 months to reach sexual maturity. O'Connell's findings could be due to a long wet season favorable influence. Fitch and Sandidge (1953) interpreted Didelphis virginiana semelparity by saying that either females are preyed upon after first breeding or they remain too exhausted to breed for a second time. Climate and diet could be important factors affecting multiparity (Hunsaker, 1977).

The adaptive strategy of these closely related species of *Marmosa* is similar, reflecting a plasticity that helps the species overcome the differences that characterize each ecosystem. Further studies would be necessary to confirm that this plasticity makes the genus *Marmosa* not only the most diverse of the Didelphidae family, but also a mammal group distributed successfully in the different Neotropical ecosystems.

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REFERENCES

- Ashton KG, Tracy MC, de Queiroz A (2000) Is Bergmann's Rule Valid for Mammals? *Am. Nat.* 156: 390-415.
- August PV (1984) Population ecology of small mammals in the Llanos of Venezuela. *Spec. Publ. Mus. Texas Tech. Univ.* 22: 71-104.
- Ceballos G (1990) Comparative natural history of small mammals from tropical forest in western Mexico. J. Mammal. 71: 263-266.
- Ceballos G, Miranda A (1986) Los Mamíferos de Chamela, Jalisco. Instituto de Biología. Universidad Nacional Autónoma de México. México DF, México. 436 pp.
- Collins LR (1973) Monotremes and Marsupials, a Reference for Zoological Institutions. Smithsonian Institution Press. Washington, DC, USA. 323 pp.
- Díaz M, Granadillo E (2005) The significance of episodic rains for reproductive phenology and productivity of trees in semiarid regions of northwestern Venezuela. *Trees Struct. Funct. 19*: 336-348.
- Eisenberg JF (1983) The Mammalian Radiations: Analysis of Trends in Evolution, Adaptation and Behavior. University of Chicago Press. Chicago, IL, USA. 610 pp.
- Eisenberg JF (1989) Mammals of the Neotropics. Vol. 1. The Northern Neotropics: Panama, Colombia, Venezuela, Guyana, Suriname and French Guiana. University of Chicago Press. Chicago, IL, USA. 449 pp.
- Eisenberg JF, Maliniak E (1967) Breeding the murine opossum Marmosa sp. in captivity. Int. Zool. Yb. 7: 78-79.
- Enders RK (1966) Attachment, nursing, and survival of young in some didelphids. *Symp. Zool. Soc. London 15*: 195-203.
- Ewell JJ, Madriz A, Tosi JA (1976) Zonas de Vida de Venezuela. MAC-FONAIAP. Caracas, Venezuela. 265 pp.
- Fitch HS, Sandidge LL (1953) Ecology of the opossum on a natural area in northeastern Kansas. *Publ. Mus. Nat. Hist. Univ. Kans.* 7: 305-338.
- Fleck DW, Harder JD (1995) Ecology of marsupials in two Amazonian rain forests in northeastern Peru. *J. Mammal.* 76: 809-818.
- Fleming TH (1973) The reproductive cycles of three species of opossums and other mammals in the Panama Canal Zone. J. Mammal. 54: 439-455.
- Fleming TH (1975) The role of small mammals in tropical ecosys-

tems. En Golley F, Petrusewicz K, Ryszkowski L (Eds.). *Small Mammals: Their Productivity and Population Dynamics*. Cambridge University Press. Cambridge, UK. pp. 269-298.

- Gittleman JL, Thompson SD (1988) Energy allocation in mammalian reproduction. *Am. Zool.* 28: 863-875.
- Godfrey GK (1975) A study of oestrus and fecundity in a laboratory colony of Mouse opossums (Marmosa robinsoni). J. Zool. Lond. 175: 541-555.
- Handley CO Jr, Gordon LK (1979) New species of mammals from Northern South America, Mouse opossum, Genus Marmosa Gray. En Eisenberg JF (Ed.) Vertebrate Ecology in the Northern Neotropics. Smithsonian Institution Press. Washington, DC, USA. pp. 65-72.
- Hayssen V, Tienhoven A van, Tienhoven A van (1993) Asdell's Patterns of Mammalian Reproduction: A Compendium of Species-Specific Data. Cornell University Press. Ithaca, NY, USA. 1023 pp.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25: 1965-1978.
- Hunsaker D II (1977) Ecology of the New World Marsupials. En Hunsaker D (Ed.) *The Biology of Marsupials*. Academic Press. New York, NY, USA. pp. 95-156.
- López-Fuster MJ, Pérez-Hernández R, Ventura J, Salazar M (2000) Effect of environment on skull-size variation in *Marmosa robinsoni* in Venezuela. *J. Mammal. 81*: 829-837.
- López-Fuster MJ, Salazar M, Pérez-Hernández R, Ventura J (2002) Craniometrics of the orange mouse opossum *Marmosa xerophila* (Didelphimorphia: Didelphidae) in Venezuela. *Acta Theriol.* 47: 201-209.
- Lorini ML, de Oliveira JA, Perssom VG (1994) Annual age structure and reproductive patterns in Marmosa incana (Lellund, 1841) (Didelphidae, Marsupialia). Z. Saeugetierkd 59: 65-73.
- Low BS (1978) Environmental uncertainty and the parental strategies of marsupials and placentals. *Am. Nat.* 112: 197-213.
- Mann G (1978) Los pequeños mamíferos de Chile. *Gayana, Zoología* 40: 1-342.
- Martins EG, Bonato V, da-Silva CQ, Reis SF (2006) Seasonality in reproduction, age structure and density of the Gracile Mouse Opossum *Gracilinanus microtarsus* (Marsupialia: Didelphidae) in a Brazilian cerrado. J. Trop. Ecol. 22: 461-468.
- Matteucci S (1987) The vegetation of Falcon State, Venezuela. Vegetatio 70: 67-91.

- Millien V, Lyons KS, Olson L, Smith FA, Wilson AB, Yom-Tov Y (2006) Ecotypic variation in the context of global climate change: revisiting the rules. *Ecol. Lett.* 9: 853-869.
- Morton SR, Recher HF, Thompson SD, Braithwaite RW (1982) Comments on the Relative Advantages of Marsupial and Eutherian Reproduction. Am. Nat. 120: 128-134.
- O'Connell MA (1979) Ecology of didelphid marsupials from Northern Venezuela. En: Eisenberg JF (Ed.) Vertebrate Ecology in the Northern Neotropics. Smithsonian Institution. Washington, DC, USA. pp. 73-87.
- O'Connell MA (1983) Marmosa robinsoni. Mammal. Species 203: 1-6.
- O'Connell MA (1989) Population dynamics of Neotropical small mammals in seasonal habitats. J. Mammal. 70: 532-548.
- Sadleir RMFS (1969) *The Ecology* of *Reproduction in Wild and Domestic Animals.* Methuen and Company LTD. London, UK. 321 pp.
- Spencer AW, Steinhoff HW (1968) An explanation of geographic variation in litter size. J. Mammal. 49: 281-286.
- Thielen DR (1996) Ecología Poblacional de Marmosa xerophila (Marsupialia: Didelphidae) en un Ecosistema Semiárido del Norte de Venezuela. Master thesis. Universidad de Los Andes, Venezuela. 233 pp.
- Thielen DR, Arends A, Segnini S, Fariñas MR (1997a) Population ecology of *Marmosa xerophila* (Marsupialia: Didelphidae) in a semiarid ecosystem of the northern Venezuela. *Zoocriaderos 2(1)*: 1-19.
- Thielen DR, Arends A, Segnini S, Fariñas MR (1997b) Food availability and the variations on the diet and the population ecology of *Marmosa xerophila* (Marsupialia: Didelphidae). *Zoocriaderos* 2(2): 1-10.
- Thompson SD (1987) Body size, duration of parental care, and the intrinsic rate of natural increase in eutherian and metatherian mammals. *Oecologia (Berlín)* 71: 201-209.
- Veillon JP (1995) Los bosques Naturales de Venezuela. Parte III. Los Bosques Xeróphilos de las Zonas de Vida: Bosque Espinoso Tropical (BET) y Bosque Muy SecoTropical (BMST). Universidad de Los Andes, Mérida, Venezuela. 55 pp.
- Walker EP (1975) Mammals of the World. Vol 1. Johns Hopkins University Press, Baltimore, MD, USA. 644 pp.
- Wilson DE, Reeder DM (2005) Mammal Species of the World: A Taxonomic and Geographic Reference. 3rd ed. Vol. 1. Johns Hopkins University Press. Baltimore, MD, USA. 743 pp.