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Annual age structure and reproductive patterns in *Marmosa incana* (Lund, 1841) (Didelphidae, Marsupialia)

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Abstract

Investigated were the annual age structure and reproductive indicators in museum specimens of the mouse opossum *Marmosa incana*. Monthly distributions of relative age classes, indexed by tooth eruption and wear, suggest an almost total cohort turnover in an annual cycle (males: one year; females: one year and half). Analysis of tegumentary indicators of reproductive activity, gauged by examination of internal reproductive tracts, demonstrated that all the sexually matured individuals belong to the two oldest age classes. These populational features combined with a three-month seasonal breeding period, detected in the greater part of the geographic range of *M. incana*, apparently result in an unusual life history strategy for this species, characterized by only one "big-bang" reproductive event in a lifetime.

Introduction

Central to the distinction between marsupials and eutherians are the profoundly different morphologies and functions of the reproductive tracts (GRIFFITHS 1978). Likewise, there are marked differences in the early phases of development, marsupials lacking a true trophoblast and apparently not being able to provide prolonged protection for the genetically foreign embryo against the mother's immune system (LILLENGRAVEN et al. 1987). Such features determine a short gestation and a long lactation period, in which a major part of marsupial development is carried out. Together with the characteristically lower rates of development in marsupials (LEE and COCKBURN 1985), these reproductive characters strongly affect aspects of their populational biologies, especially the age of sexual maturation, litter size and litter frequency.

The greater part of what is known about the reproductive biology and life history of marsupials is based on studies focusing on the Australian forms. Contrastingly, detailed specific analyses of wild populations, such as those carried out upon Australian species (e.g. NEWSOME 1965; GUILER 1970; WOOD 1970; GEMMELL 1982), are still rare for the less diversified South American marsupials. To date, most of the reproductive information for the neotropical species comes from small mammal community mark-release studies (e.g. DAVIS 1946; REIG 1964; O'CONNELL 1979; FONSECA and KIERULFF 1989; STALLINGS 1989). In this approach there are usually two difficulties to be faced: the ageing of living specimens in the field and the virtual impossibility of examining the internal reproductive tracts of every individual, making it necessary to use indirect external evidence, such as tegumentary gland activity, to infer the reproductive condition of specimens. The precise correspondence between these indicators and the actual reproductive status, as well as the interspecific variation in their expression, has not yet been investigated.

Herein we propose an alternative approach to the study of reproductive and life history patterns of the didelphid marsupial *Marmosa incana* (mouse opossum), analysing the reproductive indicators in museum specimens for which real reproductive status and relative age are, at least in part, available. *Marmosa incana* shows three pelage types (A, B

and C), unevenly distributed over the year, and apparently related to age, sex and sexual maturity (OLIVEIRA et al. 1992). Such results suggested a detailed investigation of the monthly age structure and reproductive conditions in this species. Notable aspects of the reproductive biology and their bearing on the life history of this marsupial, so revealed, are described in the present contribution.

Material and methods

The total sample analysed in this study is composed of 311 museum specimens from eastern Brazil (Bahia, Minas Gerais, Espírito Santo, Rio de Janeiro and Paraná states), covering the greater part of the geographic range of *Marmosa incana*. Localities, sample sizes and museum acronyms were listed in OLIVEIRA et al. (1992). Date of collecting, sex, body length, weight and conditions of internal reproductive tracts, when available, were taken from original labels. Specimens were aged on the basis of molariform tooth eruption (classes 1 to 6 as established by TRIBE 1990) and five consecutive stages of M1–M4 wear, after complete positioning of PM3. The first two stages were allocated to age class 6 and the last three stages to age class 7 (OLIVEIRA et al. 1992).

As a first step toward understanding the age and seasonal distribution of *M. incana*, we tabulated the occurrence of all individuals with sex and age class available ($n = 225$) by month of collecting.

Regarding the female reproductive condition, color change in the pouch or mammary region is commonly used as an indicator of breeding activity in living didelphids. In some species of *Marmosa* an orange to rust-brown stain around the mammary area is produced during pregnancy and nursing (BARNES 1977). We investigated the occurrence of this stained area and the degree of development and degeneration of nipples in *M. incana* and related these features to reproductive data available from some specimens to infer the females' reproductive condition.

The sternal gland area, a field of hypertrophied apocrine sudoriferous and sebaceous glands (BARNES 1977), was also investigated in each specimen. The activity of these glands has been referred to in the literature as associated with territorial marking and reproductive activity in some species of *Marmosa* (HUNSAKER II and SHUPE 1977); sternal gland activity is characterized by an oily secretion which dries to an amber to dark brown deposition attached to the skin, forming a concretion above the gland field that often glues hairs together.

Results and discussion

Age structure

Analysis of the age composition by month (Fig. 1) reveals that age classes are not homogeneously distributed over the year. Young individuals (classes 3 and 4) are restricted to between January and May in all localities except Ilhéus (state of Bahia), where one additional specimen was collected in September. Class 5 appears in February and occurs until May, with one exception in August for the Ilhéus population. Disregarding these two exceptional individuals from Ilhéus, age classes 3, 4 and 5 are distributed in a restricted and almost coincident period. From class 6 on, differences between sexes are noted in the monthly distributions. Whereas males of class 6 are present from February to October, with higher frequencies between April and May, females appear from April to November, and are more frequent between July and August. Frequency of class 6 increases by the middle of the year, when class 5 declines. Similarly, frequency of class 7 increases in the last months of the year, while frequency of class 6 declines.

Distribution of class 7 over the year extends for ten months for females and eight months for males. Except for two individuals from Ilhéus collected in April, males of age class 7 are absent from February to May. Females of this age class do not occur between July and August, except for one individual from Ilhéus, trapped in July.

It is relevant to note that exceptional individuals reported above comprise only 8 % of the total sample with available data on sex, age and month of capture from Ilhéus ($n = 62$).

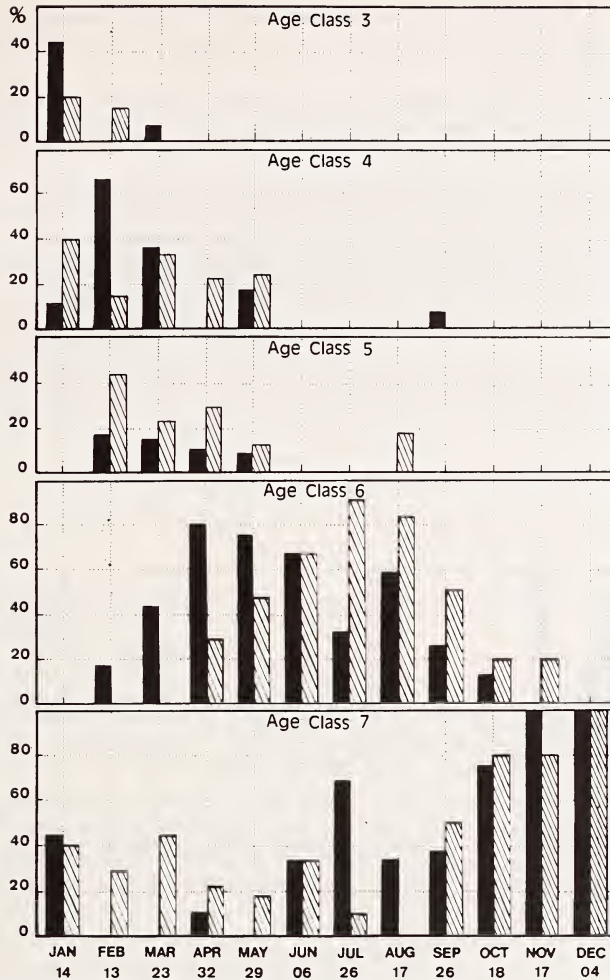


Fig. 1. Monthwise age distribution of *Marmosa incana*. Black bars: males; striped bars: females

Analysis of the mammary region

Analysis of the mammary conditions revealed that females of age classes 3, 4, 5 and 6 with long and soft pelage (type A) did not show indications of reproductive activity. All reproductive females belong to age classes 6 and 7, and have short and coarse pelage (type B).

Six different conditions of the mammary region were identified: a. not stained, indistinguishable from the rest of ventral pelage; b. not stained, but showing glabrous circles without teats; c. stained, showing conspicuous glabrous circles around incipient teats; d. stained, with a homogeneous set of cylindrical nipples up to 1 mm in diameter, each one inside a well-defined glabrous area; e. stained, with a heterogeneous set, containing some lax nipples (more than 1 mm in diameter) and others showing various stages of degeneration, in some cases reduced to a scar; f. stained, showing only darkened scars, with inconspicuous glabrous areas. Reproductive data described in the labels and the analysis of the internal reproductive tracts of recently collected specimens permitted us to

allocate the females, assigning each of the six conditions described above to their respective stages: non-reproductive (a); pre-reproductive (b); pregnant (c), early lactant (d), late lactant (e), and post-lactant (f).

All reproductive females presented a stain in the mammary region. However, even the post-lactants showed the mammary stain, an indication that it remains in the integument as a residual.

This feature has often been employed to determine the reproductive period in *Marmosa incana* (FONSECA and KIELRUFF 1990; STALLINGS 1990). However, this indicator alone does not provide a specific identification of the various reproductive phases of females, since in marsupials the nursing period is extended. Marsupials are born in an exceptionally altricial state, and a large part of their development takes place while fused to or dependent on a nipple.

Monthly rates of reproductive females (Fig. 2) revealed that periods of pregnancy, early and late lactancy, and post-lactancy are consecutive and seasonally distributed over the year. Pregnant females are limited to November, except for one individual collected in

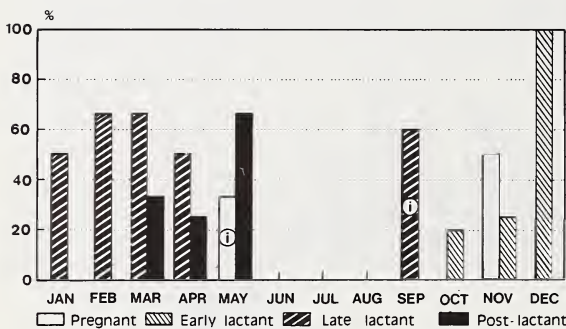


Fig. 2. Monthwise distribution of female reproductive status. Frequency of each status in relation to the total of females showing pelage type B. Bars marked with i denote exceptional individuals from Ilhéus

May in Ilhéus. Early lactant females were captured between October and December, and late lactants between January and April, except for three individuals from Ilhéus collected in September. Post-lactant females are restricted to the period from March to May in the total sample.

Reproductive period

Analysis of the annual distribution of female reproductive status, together with the occurrence of offspring made it possible to identify the reproductive period for *M. incana*. Distributions of pregnant and lactant females suggest that the mating period and subsequent teat attachment phase occur between October and December in the total sample except for part of the Ilhéus population, where a pregnant female was captured in May.

The limited distribution of the youngest individuals in our sample (age class 3) is independent evidence of a single and seasonal three-month reproductive period for the total sample, except the Ilhéus population, where an additional mating period is revealed in May. The distributions of juvenile ages (classes 3 and 4) are coincident with the January–April distribution of late lactant females.

The annual distribution of post-lactant females is coincident with the last months of occurrence of age classes 4 and 5. A comparison of our results with the development data obtained for *Marmosa robinsoni* (EISENBERG 1981; O'CONNELL 1983) makes it possible to relate the juvenile dental age classes 3, 4 and 5 with the rear cycle phases. Age class 3 individuals are probably in the nest phase, when the young of *M. robinsoni* begin to eat solid food and are able to leave the nest alone or following the female (O'CONNELL 1983). Classes 4 and 5 are correlated with the weaning and dispersion events. This conclusion is in

keeping with the attainment of a total crushing surface with four functional molariform teeth at these ages.

The reproductive period is probably more restricted in a given locality than the three months obtained in our analysis, and some asynchrony among localities is not unexpected at all, since reproductive patterns are influenced by local conditions. Among environmental factors that have been recognized in the determination of the reproductive patterns in didelphid marsupials is the seasonality of rainfall (O'CONNELL 1979).

Our total sample comprises several series collected in various parts of the state of Minas Gerais which show a comparable pattern of rainfall, with five to six drier months in the year, and a sample from Ilhéus, in the state of Bahia, a locality characterized by the absence of a dry season (NIMER 1989). Additional records are from localities in Rio de Janeiro, Espírito Santo and Paraná states, in which rainfall distributions show an intermediate pattern as compared to Minas Gerais and Ilhéus.

The reproductive period revealed by our analysis corresponds very well to the rainy season in all localities of Minas Gerais, which compose the greater part of our sample. Remaining localities do not show inconformity to the Minas Gerais pattern, except Ilhéus. In fact, more than one reproductive period in the Ilhéus population is attested by the occurrence of a pregnant female in May and exceptional young individuals of age classes 4 and 5 (August–September), together with a single late lactant female in September.

Consequently, at least two reproductive periods in the year are revealed in the analysis of the Ilhéus sample. A major one, coincident with that shown by the total sample (October–December), and another, revealed by a smaller number of individuals, occurring from March to May.

Sexual maturity

Further interpretation of the results described above, together with that of pelage variation in *Marmosa incana* (OLIVEIRA et al. 1992), permits a determination of the sexually matured individuals. Since TATE (1933), it has been widely accepted that sexual maturity in *Marmosa* is attained at an early stage of life, when the last molariform tooth (third premolar for *M. incana*) is beginning to erupt, a stage that corresponds to class five in our analysis. Our results do not confirm TATE's assertion, at least for *M. incana*. As can be inferred from figure 1, distributions of age class 5 and most of class 6 are not coincident with the reproductive period. Indeed, among females, individuals with reproductive indications were found only in the last two age classes (6 and 7), all showing the short and dull pelage previously described as type B (OLIVEIRA et al. 1992). Almost all males taken during the three months of the reproductive period (October–December) belong to age class 7. The attainment of sexual maturity in males was thought to occur in connection with pelage type C (OLIVEIRA et al. 1992). The monthly prevalence of males with conspicuous type C pattern (modified hairs reaching the middorsum) relative to the total of age class 7 and pelage type C (Fig. 3) demonstrates this relationship. Additional evidence of

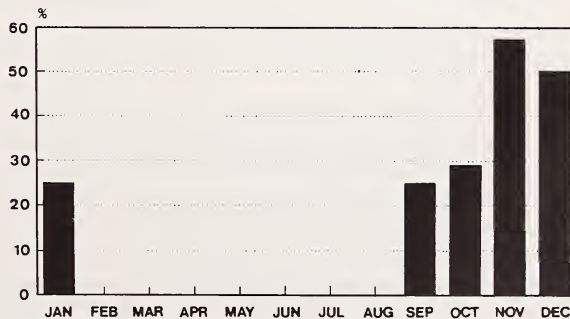


Fig. 3. Frequency of males with modified dorsal hairs reaching the middorsum in relation to the total age class 7 and pelage type C males

the strong correlation between the attainment of sexual maturity and pelage type C is provided by histological analysis of testes. Slides obtained from individuals of age class 7 and pelage type A did not reveal any spermatogenic activity (OLIVEIRA et al. 1992).

The only exceptions to the limited distribution of pelage type C males over the year (July–January) are two individuals from Ilhéus collected in April (OLIVEIRA et al. 1992), precisely during the additional reproductive period at this locality.

Analysis of sternal gland activity

Our results show that the sternal gland is externally discernible in the skins of both sexes at all ages analysed, contrary to TATE's (1933) and HUNSAKER and SHUPE's (1977) assertions that the gland is not present in *Marmosa incana*. Residuals of the oily secretion were detected in specimens of both sexes from class 4 onwards over the year. Frequencies of individuals with sternal secretion by age classes attest to a similar pattern between males and females, with a clear peak in activity at age class 5 and a succeeding decrease at class 6 (Fig. 4). At age class 7, on the other hand, almost all males show glandular activity, whereas females continue with a low percent of individuals showing sternal gland secretion.

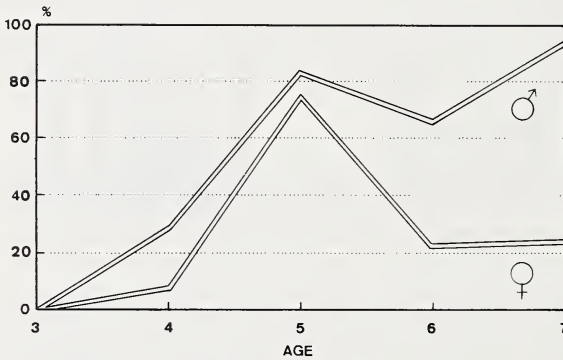


Fig. 4. Frequency by age of individuals showing sternal gland activity

These results do not point to an unequivocal correspondence between the occurrence of sternal gland secretion and reproductive activity. The increasing frequency of sternal secretion in both sexes at classes 4 and 5 (Fig. 4), probable ages of juvenile independence, may be related, rather, to dispersion behavior.

Semelparity

The absence of class 7 males between February and May in all localities except Ilhéus cannot be accounted for by small sample sizes, as even at Além Paraíba (Minas Gerais), where a large sample from these months was assembled ($n = 64$), no males of age class 7 were obtained.

After the absence period (February–May), the only male of class 7 registered in June and most of age class 7 males that were gathered in July show pelage type A. Mean weight of specimens collected between June and August, the first three months after the absence period, is lower than that from the three months before the males' disappearance (November–January). In the same way, molar wear is more accentuated among class 7 before the absence period, suggesting that the males which disappear after January and those collected after June do not belong to the same generation.

In regard to females, the absence of age class 7 in July and August may also be evidence

Descriptive statistics of body weight for samples of supposed cohorts in each sex

Within parenthesis, f-ratio and associated probability (ANOVA) for the null hypothesis of no difference between samples from after (a) and before (b) adults' disappearance

	Males		Females	
	(a) Jun–Aug	(b) Nov–Jan	(a) Sep–Nov	(b) Mar–Jun
n	11	13	16	10
min–max	35–97	50–120	30–62	48–66
mean	60.4	88.4	46.3	58.3
sd. dev.	21.2	18.7	10.2	6.8
(F-ratio)	(11.86)		(10.66)	
(P)	(0.002)		(0.003)	

of a gap between two successive generations. The mean weight of females collected after these months is also lower than that from the first semester, and the molar wear is less accentuated.

Analysis of variance, employed to test the null hypothesis of no differentiation between samples of these supposed cohorts, also revealed that differences in mean weight were significant at the 1 % level ($P < 0.01$) for both sexes (Table).

A probable explanation for the males' absence may be related to a general mortality after the reproductive period. Similarly, the results set forth above also show that females which had already reproduced are not present in a new reproductive period in the following year. Since for females the gap between generations is shorter, it might be supposed that occasionally a female would reach the breeding season of the next year. However, data from *Marmosa robinsoni*, a species of similar habits and size, do not support the hypothesis that such a female would be reproductive, since females of that species are no longer fertile after 17 months.

To date, *M. robinsoni* is the only mouse opossum for which comprehensive reproductive data is available. Young individuals of this species are completely weaned 65 days after birth, and the total time that a female spends rearing a litter, from conception to weaning, totals approximately 80 days (EISENBERG 1981; O'CONNELL 1983). Considering the three-month breeding period of *M. incana* described above, and assuming a rearing cycle similar to that of *M. robinsoni*, a female could only produce a single litter within one reproductive season. This hypothesis is corroborated in our results by the restricted, consecutive and unrepeat occurrence of the female mammary stages for the total sample, aside from the Ilhéus exceptions (Fig. 2). Furthermore, the limited breeding season shown by *M. incana* is also an indication that the female estrous cycle is monoestric, or, at least, seasonally polyestric, in a very limited interval of time.

The above evidence suggests that in *Marmosa incana* each individual takes part in only one reproductive season except in the Ilhéus population, where, occasionally, two independent breeding seasons may occur within a year. Consequently, in localities where there is no additional reproductive season, *Marmosa incana* reproduces only once in a lifetime, which characterizes a semelparous way of life.

Rare among vertebrates, a semelparous strategy was originally demonstrated among mammals in the dasyurid marsupial *Antechinus stuartii*. This species presents a total turnover of the male cohort within consecutive generations owing to the death of all adult males after the reproductive period. A monestrous cycle in the female and a synchronous pattern of breeding within a short interval of time, in a local population, were also documented.

BRAITHWAITE and LEE (1977) suggested that semelparity is the extreme expression of a strategy characterized by an intense and highly synchronized reproductive effort where

juvenile survival is consistently higher during one season of the year. Under this assumption, the development of semelparity in mammals would be favored among species showing a maximum field longevity of approximately one year and an annual optimal period for reproduction of sufficient duration for individuals females to raise successfully one but not two litters (BRAITHWAITE and LEE 1977). These authors considered marsupials weighting less than 1 kg and living in predictable, highly seasonal environments to be the prime candidates for semelparity among mammals.

In keeping with these predictions, all presumptive examples of semelparous mammals suggested since then are small marsupials confined to highly seasonal habitats. Indeed, among New World mammals the only indication of semelparity was obtained in a restricted population of the didelphid marsupial *Monodelphis dimidiata* at Balcarce, Buenos Aires province, Argentina. In this locality none of the adult individuals survive to the first winter, or into the winter, after the reproductive period (PINE et al. 1985). It is noteworthy that records of *M. dimidiata* to the north of Balcarce did not corroborate the semelparous pattern.

Similar to *Monodelphis dimidiata*, *Marmosa incana* also shows a small body size (total weight is less than 120 g in males and 80 g in females). As revealed by the present study however, semelparity seems to be a rather widespread phenomenon in *Marmosa incana*. This species is best known from the humid Atlantic forests of eastern Brazil (STREILEIN 1982), a relatively constant environment, where temperatures do not show extreme variations in the course of the year. Although there is some seasonality in rainfall, especially in the Minas Gerais localities, this cannot be considered a predictable, strongly seasonal environment, as the habitats seem to be of all semelparous mammals reported to date. In the sample analysed, the semelparous pattern was corroborated in all localities except the Ilhéus sample, where it is not impossible that some females take part in more than one breeding period. Although seasonality may constitute an important condition for the evolution of semelparity in mammals, it appears, from our analysis, that this reproductive strategy may also exist in more constant environments than those previously hypothesized.

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Zusammenfassung

Jahreszeitliche Altersstruktur und Fortpflanzung bei Marmosa incana (Lund, 1841)
(Didelphidae, Marsupialia)

Jahreszeitliche Altersstruktur und Fortpflanzungsanzeichen wurden bei 311 Sammlungsexemplaren des Mausopossums *Marmosa incana* studiert. Die monatlichen Häufigkeiten relativer Altersklassen, die nach Zahndurchbruch und -abnutzung festgelegt wurden, deuten auf einen fast vollständigen Wechsel der Population im Jahreslauf (1 Jahr bei Männchen, 1,5 Jahre bei Weibchen). Die Analyse des Fortpflanzungszustandes zeigte, daß alle sexuell aktiven Tiere in die beiden höchsten Altersklassen fallen. Diese Populationsmerkmale und eine im größten Teil des Verbreitungsareals von *Marmosa incana* festgestellte dreimonatige saisonale Fortpflanzungsperiode deuten auf einen ungewöhnlichen Lebenszyklus mit nur einmaliger Reproduktion hin.

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