Nine-year demography of the black-eared opossum *Didelphis aurita* (Didelphimorphia: Didelphidae) using life tables

Maja Kajin [1]; **Rui Cerqueira** [1]; **Marcus V. Vieira** [1] **& Rosana Gentile** [2]

[1] *Laboratório de Vertebrados, Instituto de Biologia, Universidade Federal do Rio de Janeiro. Caixa Postal 68020, 21941-590 Rio de Janeiro, Rio de Janeiro, Brasil. E-mail: maja@biologia.ufrj.br*

[2] *Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, Instituto Oswaldo Cruz, Fundação Oswaldo Cruz. Avenida Brasil 4365, Caixa Postal 926, 21040-360 Rio de Janeiro, Rio de Janeiro, Brasil.*

ABSTRACT. A population of the black-eared opossum, *Didelphis aurita* Wied-Neuwied 1826, was studied during 1997-2006 by capture-mark-recapture in the Atlantic Forest in the state of Rio de Janeiro. Cohorts were established with females marked still in the pouch, classified into five age classes. Population parameters were estimated using life tables. Survival was type III and mortality was greatest in age classes I and II, just after weaning. Fecundity was inversely correlated with survival, reproductive value was inversely correlated with mortality and residual reproductive value was inversely correlated with fecundity. The intrinsic rate of increase was always close to zero and tended to be slightly negative. The black-eared opossum can be considered a good model species for this type of study.

KEY WORDS. Atlantic forest; cohort; intrinsic factors; small mammals; survival.

RESUMO. **Demografia do marsupial *Didelphis aurita* (Didelphimorphia: Didelphidae) durante nove anos utilizando-se tábuas de vida.** Uma população de gambás, *Didelphis aurita* Wied-Neuwied 1826, foi estudada de 1997 a 2006 por captura, marcação e recaptura numa área de Mata Atlântica no Estado do Rio de Janeiro. Foram estabelecidas coortes, incluindo apenas fêmeas marcadas ainda no marsúpio, classificando-as em cinco classes etárias. Os parâmetros populacionais foram calculados através de tábuas de vida horizontais. A maior mortalidade ocorreu entre as classes etárias I e II, logo após o desmame, sendo que a sobrevivência apresentou uma curva do tipo III. A taxa de fecundidade foi inversamente correlacionada com a sobrevida, o valor reprodutivo inversamente correlacionado com a mortalidade e o valor reprodutivo residual inversamente correlacionado com a taxa de fecundidade. A taxa intrínseca de crescimento sempre esteve próxima de zero, porem ligeiramente negativa. O gambá mostrou-se um bom modelo de mamífero para este tipo de estudo.

PALAVRAS-CHAVE. Coorte; fatores intrínsecos; Mata Atlântica; pequenos mamíferos; sobrevivência.

Demographic studies are important to understand factors that influence population ecology as well as for planning conservation and management strategies (SCHWARTZ *et al.* 1998). These studies also permit a better understanding and analysis of trade-off relationships, such as between survival and fecundity (STEARNS 1992). These details are fundamental for understanding life-history strategies, ecology and persistence of populations. Management programs require these kinds of data, especially long-term data, even for wildlife species that are not endangered.

Understanding recruitment and fecundity are the first steps in demographic studies (JULLIARD *et al.* 1999) in which the use of life tables is an important tool (CASWELL 2001). Life table use permits the estimation of age-specific parameters of the population of interest, such as mortality, fecundity and reproductive value. These age specific parameters are very useful for understanding dynamics (MUELLER *et al.* 2004) yet today, life tables are seldom used. Captures may include only females, under the assumption that all females are available for fertilization by the males, since reproduction, and thus demographic data, comes from the females (STEARNS 1992). However, to obtain the demographic parameters, females from all age classes need to be captured.

Life tables permit testing relationships between demographic parameters (EMLEN 1970, ZAMUTTO 1987). For example, negative correlations are often found in mammalian populations between survival and fecundity or between mortality and reproductive value. Also, positive correlations between pairs of variables, such as reproductive value and residual reproductive value, fecundity rate and residual reproductive value, reproductively active female survival rate and residual reproductive value have been reported already (MILLAR & ZAMUTTO 1983, ZAMUTTO 1987).

Demographic studies of small mammals in the Atlantic Forest are almost non-existent and perhaps limited to one (Brito & Fernandez 2000) and few studies of small mammals in Brazil address demography (Quental *et al*. 2001, El Jundi & Freitas 2004, Figueiredo & Fernandez 2004).

The black-eared opossum (*Didelphis aurita* Wied-Neuwied, 1826) is common in the Atlantic Forest from northeastern Brazil in the north, to northern Argentina in the south (Cerqueira 1985, Cerqueira & Lemos 2000). Occasionally arboreal, this mostly terrestrial, generalist species is found in all habitat types of the Atlantic Forest, as well as urban and rural areas and may often be dominant among small mammals (Cerqueira *et al.* 1990, Fonseca & Robinson 1990, Leite *et al.* 1996, Gentile & Fernandez 1999, Cunha & Vieira 2002, Vieira & Monteiro-Filho 2003). *Didelphis* (Linnaeus, 1758) often may be both a predator and competitor of other small mammal species (Cordero & Nicolas 1987, Fonseca & Robinson 1990).

The population dynamics of *D. aurita* has been studied previously with many distinctive objectives (*e.g.* Fonseca & Kierulff 1989, Cerqueira *et al*. 1993, Bergallo 1994, Gentile *et al*. 2000, Gentile *et al*. 2004). The objective of this study was to carry out a nine-year demographic analysis of *D. aurita* based on horizontal life tables. Specifically, we wished to test the following hypotheses: 1) Survival and fecundity are inversely correlated and, therefore, a cost of reproduction exists (Millar & Zammuto 1983, Caswell 1980); 2) reproductive value and residual reproductive value are correlated and highest in the first reproductive age-classes followed by a decline, when fecundity decreases with an increase in mortality (Caswell 2001). The reproductive value indicates an age-specific expectation for future reproduction based on survival and fecundity (Pianka 1974), the residual reproductive value takes into account the female survival until the age considered (Williams 1966). 3) Mortality is inversely correlated with reproductive value, indicating that a high age-specific mortality reduces its contribution to the next generations (Zammuto 1987). 4) Fecundity is inversely correlated with residual reproductive value. This would be the case, if there is a cost to reproduction, such that a large current reproductive effort reduces future reproductive value more than a small current reproductive effort (Zammuto 1987). 5) Residual reproductive value is correlated with survival of reproductive females, since reproductive stress would be avoided and thus mortality woul reduce, if a female delayed her reproduction events for older ages (Zammuto 1987).

MATERIAL AND METHODS

Black-eared opossums were studied in the Serra dos Órgãos National Park, Atlantic Forest, at Garrafão (22º28'S, 42º59'W), Guapimirim municipality, in the state of Rio de Janeiro. Three capture grids were established along an altitudinal gradient (A – 22º28'12"S, 42º59'50"W, 748 m; B – 22º28'29"S, 42º50'08"W, 652 m; C – 22º28'46"S, 42º59'22"W, 522 m) near the margins of the Iconha River. The grids vary in distance from the highway: A – 250 , B – 427 and C – 600 m. Despite it being a national park, the forest in the study area suffers from a variety of human disturbances, such as dirt roads and cottages.

Climate is moderately humid mesothermic (Nimer 1989). During the study, the greatest average maximum temperature was 30.5ºC in February and the minimum average was 10.7ºC in August. Total monthly rainfall varied from a minimum of 0.2 to a maximum of 508.0 mm, with May, June and July being the driest months, and October and February being the wettest.

Animals were captured in the three grids during five days every other month between April 1997-April 2006. Traps (25 stations per grid) were placed every 20 m (total area 0.64 ha). Each trap station had two traps of different sizes on the ground (Sherman®, model XLK, 7.62 cm x 9.53 cm x 30.48 cm; Tomahawk®, model 201, 40.64 cm x 12.70 cm x 12.70 cm, n = 50 per grid). Additional similar traps were placed on 13 platforms in trees (n = 26) and larger Tomahawk traps, model 105 (50.80 cm x 17.78 cm x 17.78 cm), were placed at each corner and in the center of each grid (five per grid). Oats, banana, peanut butter and bacon were used as bait.

Weaned animals were marked with a uniquely numbered ear-tag on first capture (Ear Tags, National Band & Tag Co., Newport, Kentucky, USA). Only young animals still lactating were toe-clipped (Twigg 1975). Upon capture, the location and date were recorded, along with measures of body mass, body size, tail length, reproductive condition and teeth eruption and functionality pattern (following Gentile *et al*. 1995, Macedo *et al*. 2006). All animals were treated carefully following the standards suggested by the American Society of Mammalogists (Animal Care and Use Committee 1998) and were released at the point of their capture. This study was carried out under license # 02001, 004671/98-51 of the Instituto Brasileiro de Meio Ambiente (IBAMA).

Females were used for life table construction and only females that were marked while young and still within the pouch were used, comprising eight cohorts:1997-1998, 1998-1999, 1999-2000, 2000-2001, 2001-2002, 2002-2003, 2003-2004, 2004-2005. Each cohort began in August, the month when females began to be captured with young in the pouch (see results). The 2005 cohort was not analyzed because many were still alive. Animals were included in the analysis until disappearing from the study area. Females were classified into five age classes. Teeth eruption and functionality pattern permit accurate age estimation in this species (Gentile *et al.* 1995, Macedo *et al.* 2006, Tab. I). Thus, age classes of similar time intervals were established, based on teeth and development characters: I) lactant; II) young (reproductively inactive); III) subadults (reproductively active); IV) adults; and V) senescent. Twelve population parameters were calculated for each age class following Williams (1966), Caughley (1977), Zammuto (1987), Stearns (1992) and Krebs (2001) (Tab. II). Hypotheses were tested using Spearman Correlation (Statistica 6.0 StatSoft Inc.), significance level of <0.05.

Table I. Age classes of *D. aurita* following Gentile *et al.* (1995).

Class	Median (in days)	Age (days)	Characteristic
I	50.0	0 - 100	Lactating
II	135.5	101 - 169	Young, dentition dp_xM_x
III	213.0	170 - 255	Subadult, dentition to $P_3M_{3/4}$
IV	296.5	256 - 337	Adults, complete dentition - $P_3M_{4/4}$
V *		> 338	Senescent, teeth worn with use

* The median was calculated using the age of the oldest individual alive in each reproductive season.

Table II. Parameters calculated in the life tables (Williams 1966, Caughley 1977, Zammuto 1987, Stearns 1992, Krebs 2001).

Parameter	Definition
Population size (female)	N females captured
Survival	$l_x = n_x/n_1$
Mortality	$d_x = n_x\text{-}n_{x+1}$
Mortality rate	$q_x = d_x/n_x$
Survival rate	$p_x = l_{x+1}/l_x$ ou $1\text{-}q_x$
Life expectancy	$e_x = \Sigma\ l_y/l_x$
Fecundity rate	m_x = female young/female
Reproductive value	$Vr_x = \Sigma\ l_t/l_x{*}\ m_t$
Residual reproductive value	$Vr_{x*} = (l_{x+1}/l_x){*}\ Vr_{x+1}$
Generation time	$Gc = (\Sigma\ x\ l_xm_x){*}\ R_0^{-1}$
Net reproductive rate	$R_0 = \Sigma\ l_xm_x$
Intrinsic rate of increase of the population	$r_{0est} \approx [\ln(R_0)]/G_c$

RESULTS

Fifty six litters were marked and monitored during this study. The maximum of 12 litters per year was observed in 2004-2005 and the minimum of three litters in 2001-2002. Of these, 189 females were captured, 27 of which were recaptured after weaning and nine of which lived for more than 16 months (Tab. III). The longest lived individual survived 600 days (20 months). In the 2002-2003 cohort, not a single individual marked in the pouch was recaptured and in 2003-2004 only one individual was recaptured after weaning. Thus, it was not possible to establish life tables for these two cohorts.

Survival

The proportion of females recaptured after weaning (l_x) was small in all cohorts (Tab. III). All cohorts showed an accentuated decrease in l_x between first and second age classes, *i.e.* at weaning. Survival also declined after the second age class, but with less intensity (Fig. 1). Similarly, survival rate (p_x) was greatest for the second age class and mortality (d_x) in the first age class (Tab. III). In most cohorts, adult survival was 1.00, since most of the individuals captured as adults were also captured as senescent.

Mortality rate (q_x) was highest in lactant and young, while lowest values were found for adults in most cohorts, since adults were also captured as senescent (Fig. 2). Young had the greatest life expectancy values (e_x), followed by subadults (Fig. 3). After this class, life expectancy declined.

Reproduction

Reproduction in *D. aurita* was seasonal, beginning in July. The first females with young in the pouch were captured in August and by February (end of reproductive period), most females were still lactating, but without young in the pouch. Females began to breed at approximately 5 months (170 days) of age. Average litter size was 7.33 (n = 16, min. = 6, max. = 10). Sex ratio in the pouch was 1:1 (n = 70; $\chi^2 = 39.06$; d.f. = 69, p = 0.99). The 2004-2005 cohort was the largest, with five litters (l). This cohort also included more females previously captured and marked while in the pouch (n = 44, 12 l) that produced these five litters. Females from these cohorts produced one litter per season, except for two females, that each had two litters during one breeding season. Adult females produced 41% of all 56 l, senescent females produced 39%, and subadult females produced 20%.

Fecundity rate increased from subadults to adults, where it reached its maximum (Fig. 4). In the 2001-2002, evidence of reproduction was only found in the senescent age class, therefore fecundity rate was zero in all other age classes. Fecundity rate in the 2000-2001 and 2004-2005 cohorts for the senescent class was zero. Fecundity could not be estimated for the 1999-2000 cohort because the only female in reproductive age showed no signs of reproduction.

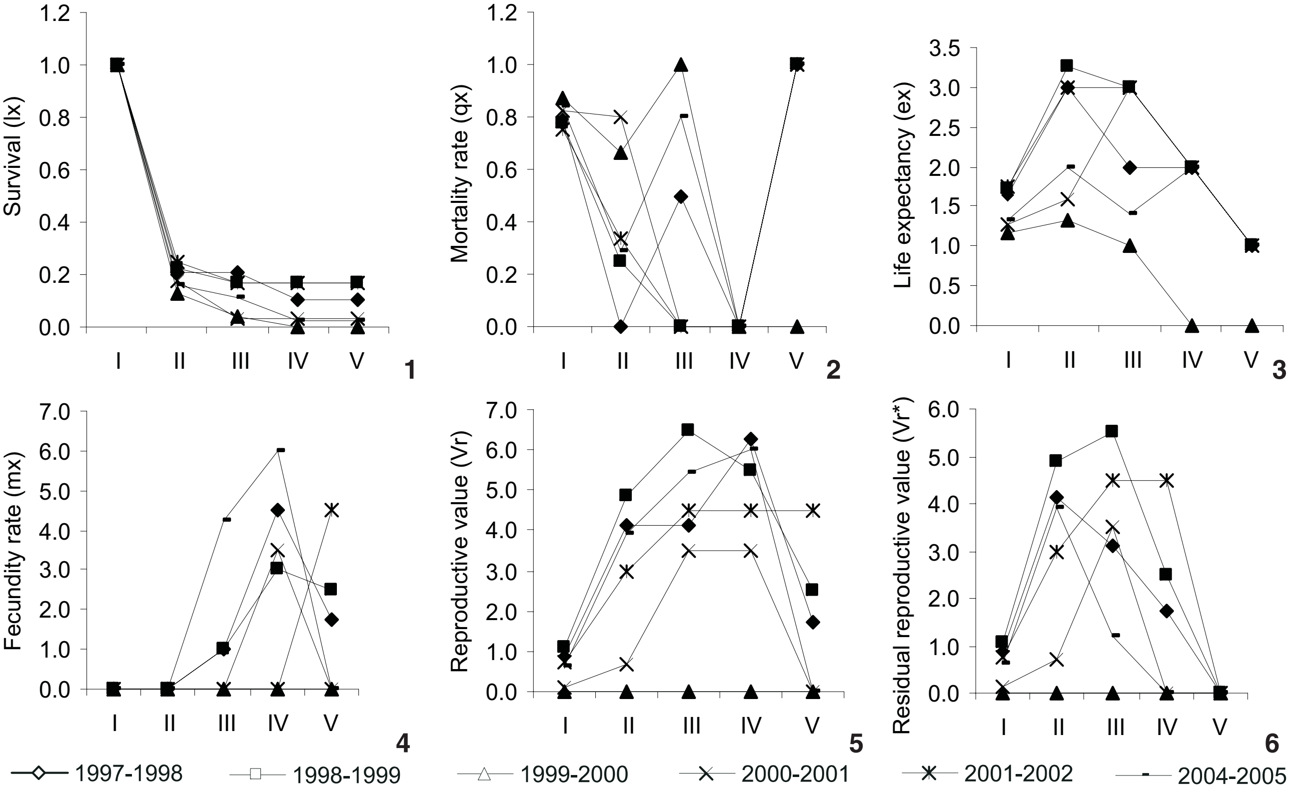
Fecundity rate (m_x) was negatively correlated with survival (r_s = -0.37, p = 0.04), supporting the first hypothesis that increased reproduction reduces survival. Reproductive value and residual reproductive value were strongly correlated (r_s = 0.69, $p < 0.05$), supporting the second hypothesis. Reproductive value increased to the third or fourth age classes, after which it declined (Fig. 5). The greatest residual reproductive values were those of young and subadults (Fig. 6).

Mortality was negatively correlated with reproductive value, supporting the third hypothesis that high mortality rates reduce the contribution to future generations. Fecundity rate was not correlated with residual reproductive value (r_s = -0.14, p = 0.47) and so the fourth hypothesis was not supported. Residual reproductive value was correlated with survival of reproductively active females (r_s = 0.63, $p < 0.05$), supporting the fifth hypothesis.

The 2001-2002 cohort was apparently atypical due to small population size, high survival and low mortality, and fecundity rates. In this cohort, only senescent females reproduced, so reproductive value was constant in the last three age classes (Fig. 5), with a high residual reproductive value until the adult age class (Fig. 6).

General demographic parameters

Generation time (G_c) varied from 231.4 – 469.0 days (Tab. III). Only one female, born in August 2004, reproduced at the



Figures 1-6. Population parameters for five age classes of female *D. aurita* in six cohorts at Garrafão, Rio de Janeiro, between 1997-2006: (1) survival; (2) mortality rate; (3) life expectancy; (4) fecundity rate; (5) reproductive value; (6) residual reproductive value.

end of the same breeding season in which she was born (January 2005). Overall generation time was 330.7 days.

The intrinsic rate of increase, r_0, was close to, and usually somewhat less than zero, suggesting a population decline (Tab. III). The intrinsic rate of increase (r_0) varied between -0.0071 and 0.0002. The $r_0 = 0.0002$ was the single positive value over all cohorts, while the average value was -0.002. Also, the net reproductive rate (R_0) tended to values below 1.00 and varied between cohorts from 0.12 to 1.08 (average = 0.69, Tab. III).

DISCUSSION

The large sample size required for use of life tables is often the major hurdle against their use. Individuals must be followed from birth to death, which can be difficult. The opossum can be considered a good mammalian model for the use of life tables, because of its large population size, especially in disturbed areas and around dwellings, ease of capture and ability to capture and mark young in the pouch.

The survival and mortality curves suggest that the opossum has a type III survival curve due to the accentuated decline in survival after the first age class (PEARL 1928). This is likely because the time period most critical for survival of young is during and soon after weaning (LEE & COCKBURN 1985). A second possibility is related to the reproductive strategy of marsupials, with little investment in gestation and a large investment in lactation. The loss of young at the beginning of lactation should be common, since until this time, the investment of the female was low, also resulting in a type III curve. As a consequence, the life expectancy increases after the young age class and then declines throughout life. High post-weaning mortality is apparently best explained by vulnerability of the recently weaned young. High mortality rates during lactation were also described in *Didelphis virginiana* Kerr, 1792 (see review in KANDA & FULLER 2004), even though some of the studies reviewed show relatively high pouch survival rates (0.78, 0.88 and 0.92).

Generation time for the 2001-2002 cohort was atypical and almost as twice as high compared to the preceding and following years. Perhaps this was an artifact of finding no reproductive females during this year, except among the senescent class. Since birth dates vary along the season and litters may be produced at the beginning or end of the breeding season, this will influence the generation time among cohorts. And, generation time of one cohort can influence that of subsequent cohorts. This is one of the reasons for the need of long-term studies.

Table III. Life tables for six cohorts of *D. aurita* at Garrafão, Rio de Janeiro, during 1997-2006. (n_x) Number of females in age class x, (l_x) survival of age class x, (dx) deaths between age classes x and x + 1, (q_x) death rate for age class x, (p_x) survival rate for age class x, (ex) life expectancy for age class x, (m_x) fecundity rate in age class x, (Vr_x) reproductive value of age class x, (Vr_x*) residual reproductive value of age class x, (R_0) net reproductive rate, (r_0) intrinsic rate of increase, (G_c) generation time.

Cohort	Class	N_x	l_x	d_x	q_x	p_x	e_x	m_x	Vr_x	Vr_x*	G_c	R_0	r_0
1997-1998	I	19	1	15	0.79	0.21	1.63	0	0.87	0.87	306.48	0.87	0
	II		0.21	0	0	1	3	0	4.13	4.13			
	III	4	0.21	2	0.50	0.50	2	1	4.13	3.13			
	IV	2	0.11	0	0	1	2	4.50	6.25	1.75			
	V	2	0.11	2	1	0	1	1.75	1.75	0			
1998-1999	I	18	1	14	0.78	0.22	1.72	0	1.08	1.08	350	1.08	0
	II	4	0.22	1	0.25	0.75	3.25	0	4.88	4.88			
	III	3	0.17	0	0	1	3	1	6.50	5.50			
	IV	3	0.17	0	0	1	2	3	5.50	2.50			
	V	3	0.17	3	1	0	1	2.50	2.50	0			
1999-2000	I	24	1	21	0.88	0.13	1.17	0	0	0	0	0	0
	II	3	0.13	2	0.67	0.33	1.33	0	0	0			
	III	1	0.04	1	1	0	1	0	0	0			
	IV	0	0	0	0	0	0	0	0	0			
	V	0	0	0	0	0	0	0	0	0			
2000-2001	I	29	1	24	0.83	0.17	1.28	0	0.12	0.12	296.50	0.12	-0.01
	II	5	0.17	4	0.80	0.20	1.6	0	0.70	0.70			
	III	1	0.03	0	0	1	3	0	3.50	3.50			
	IV	1	0.03	0	0	1	2	3.50	3.50	0			
	V	1	0.03	1	1	0	1	0	0	0			
2001-2002	I	12	1	9	0.75	0.25	1.75	0	0.75	0.75	469	0.75	0
	II	3	0.25	1	0.33	0.67	3	0	3	3			
	III	2	0.17	0	0	1	3	0	4.50	4.50			
	IV	2	0.17	0	0	1	2	0	4.50	4.50			
	V	2	0.17	2	1	0	1	4.50	4.50	0			
2004-2005	I	44	1	37	0.84	0.16	1.32	0	0.62	0.62	231.39	0.62	0
	II	7	0.16	2	0.29	0.71	2	0	3.89	3.89			
	III	5	0.11	4	0.80	0.20	1.4	4.25	5.45	1.20			
	IV	1	0.02	0	0	1	2	6	6	0			
	V	1	0.02	1	1	0	1	0	0	0			

Few adults survived from one breeding season to the next and turnover rates were high each year. This was most evident in the 2004-2005 cohort, where not a single young produced came from a female of the preceding cohort. The new individuals that formed that cohort had to come outside the study area. Spatial dynamics among females (not studied here) may be an important component in the population turnover each year. However, from a life table perspective, animals that leave the study area or die do not contribute to the measured parameters (SLADEN & BANG 1969) and animals that move into the study area do not contribute to the measurements of the current cohort as well.

Reproduction in *D. aurita* is seasonal, beginning in the middle of the dry season and ending at the end of the rainy season. Thus, the population studied was larger soon after the rains, as is shown by other studies of Neotropical marsupials (FLEMING 1973, TYNDALE-BISCOE & MACKENZIE 1976, O'CONNELL 1989, CERQUEIRA *et al.* 1993, CERQUEIRA & BERGALLO 1993, BERGALLO & CERQUEIRA 1994, CÁCERES & MONTEIRO-FILHO 1998, GENTILE *et al.* 2000, LIMA *et al.* 2001, D'ANDREA *et al.* 2007). Opossums are insectivorous-omnivorous (CÁCERES & MONTEIRO-FILHO 2001) with wide variation in diet, including invertebrates, small vertebrates and fruits (VIEIRA & IZAR 1999). In the case of *D. aurita,* ground-living arthropods in the leaf litter are the major food source

(Santori *et al.* 1996). A strong correlation between leaf litter production and opossum population dynamics was found in a previous study in the same location as this study (Gentile *et al.* 2004). Atramentowicz (1986), and Rademaker & Cerqueira (2006) also related reproduction in *Didelphis* to resource availability (insects, fruits), which in turn, is related to rainfall (Lee & Cockburn 1985). Thus, the reproductive strategy of the opossum is that weaning occurs near the time when food abundance peaks, at the end of the rainy season, therefore, improving the chances of survival of the year's offspring.

The decline in reproductive value at the senescent age class is due to the increased mortality at that time. Thus, senescent females will contribute less to future generations than adult females. This supports the hypothesis that animals less susceptible to mortality will contribute more to future generations (Caswell 1980). On the other hand, it may indicate that those individuals that survive (avoid death) are more able to reproduce as well (Zammuto 1987). The lack of a relationship between fecundity and residual reproductive value indicates that the high fecundity of the females in an age class will not diminish the contribution to future litters (Millar & Zammuto 1983).

The negative relationship between fecundity rate and survival supports the hypothesis that an increasing cost of reproduction in an age class reduces survival in the same and subsequent age classes, due to the stress that reproduction induces (Zamutto 1987, Caswell 1980).

Basic understanding of mammalian demography in tropical forests like the Atlantic Forest requires the study of common and dominant species, such as *D. aurita*. Fonseca & Robinson (1990) reported possible effects of decline of other species in the presence of *D. aurita* in the community. In fragmented forest areas, specifically where large predators are absent, species of *Didelphis* tend to increase in abundance. Consequently, the importance and influence of these opossums on the other species in the community increases (Fonseca & Robinson 1990). Population monitoring and demographic analyses of *Didelphis* may be of fundamental importance to understand community structure, especially in disturbed areas, where they may reach very large population sizes.

ACKNOWLEDGEMENTS

We thank the successive generations of students of the Vertebrate Laboratory of the UFRJ that made this long term study possible. D. Loretto provided valuable observation on earlier versions of the manuscript. N.P. Barros and A.M. Marcondes provided inestimable technical and administrative help. This study was based on the MSc in Ecology (PPGE/UFRJ) by M. Kajin, with support from the Slovenske Zeleznice Company, and finished during doctoral studies in Genetics (PPGEN/UFRJ) with support from CNPq. The study was financed by CNPq, FAPERJ (to R. Cerqueira), PROBIO/MMA/GEF/CNPq and PDA/MMA.

LITERATURE CITED

Animal Care and Use Committee. 1998. **Guidelines for capture, handling, and care of mammals as approved by The American Society of Mammalogists.** Lawrence, The American Society of Mammalogists, 47p.

Atramentowicz, M. 1986. Disponibilités trophiques et rythmes de reproduction chez trois Didelphidés sympatriques de Guyane. **Mémoires du Muséum National D'Histoire Naturelle, Série A, 132**: 123-129.

Bergallo, H.G. 1994. Ecology of a small mammal community in an Atlantic forest area in Southeastern Brazil. **Studies on Neotropical Fauna and Environment 29** (4): 197-217.

Bergallo, H.G & R. Cerqueira. 1994. Reproduction and growth of *Monodelphis domestica* in Northeastern Brazil. **Journal of Zoology 232** (4): 551-563.

Brito, D. & F.A.S. Fernandez. 2000. Metapopulation viability of the marsupial *Micoureus demerarae* in small Atlantic forest fragments in Southeastern Brazil. **Animal Conservation 3**: 201-209.

Cáceres, N.C. & E.L.A. Monteiro-Filho. 1998. Population dynamics of the common opossum, *Didelphis marsupialis* (Mammalia, Marsupialia), in Southern Brazil. **Zeitschrift fur Saugetierkunde 63**: 169-172.

Cáceres, N.C. & E.L.A. Monteiro-Filho. 2001. Diet, home range and activity of *Didelphis aurita* (Mammalia, Marsupialia) in a forest fragment of Southern Brazil. **Studies on Neotropical Fauna and Environment 36** (2): 85-92.

Caswell, H. 1980. On the equivalence of maximizing reproductive value and maximizing fitness. **Ecology 61** (1): 19-24.

Caswell, H. 2001. **Matrix Population Models: construction, analyses and interpretation.** Sunderland, Sinauer Associates Publishers, XXII+722p.

Caughley, G. 1977. **Analysis of vertebrate populations.** New York, John Wiley & Sons, 234p.

Cerqueira, R. 1985. The distribution of *Didelphis* in South America (Polyprodontia, Didelphidae). **Journal of Biogeography 12**: 135-145.

Cerqueira, R. & B. Lemos. 2000. Morphometric differentiation between Neotropical black eared opossums *Didelphis marsupialis* and *Didelphis aurita* (Didelphimorphia, Didelphidae). **Mammalia 64**: 319-327.

Cerqueira, R.; F.A.S. Fernandez & M.F.S.Quintela. 1990. Mamíferos da restinga de Barra de Maricá. **Papeis Avulsos de Zoologia 37**: 141-157.

Cerqueira, R. & H.G. Bergallo. 1993. A possible case of photoperiod controlling the reproduction of a South American Marsupial. **Ciência e Cultura 45**: 140-141.

Cerqueira R.; R. Gentile; F.A.S. Fernandez & P.S. D'andrea. 1993. A five-year population study of an assemblage of small mammals in Southeastern Brazil. **Mammalia 57** (4): 507-517.

Cordero, G.A. & B.R.A.. Nicolas. 1987. Feeding habits of the opossum (*Didelphis marsupialis)* in Northern Venezuela. **Fieldiana Zoology 39**: 125-131.

CUNHA, A.A. & M.V. VIEIRA. 2002. Support diameter, incline, and vertical movements of four didelphid marsupials in the Atlantic forest of Brazil. **Journal of Zoology 258**: 419-426.

D'ANDREA, P.S; R. GENTILE; L.S. MAROJA; F.A.S. FERNANDEZ; R. COURA & R. CERQUEIRA. 2007. Small mammal populations of an agroecosystem in the Atlantic Forest domain, Southeastern Brazil. **Brazilian Journal of Biology 67**: 179-186.

EL JUNDI, T.A.R.J. & T.R.O. FREITAS. 2004. Genetic and demographic structure in a population of *Ctenomys lami* (Rodentia-Ctenomyidae). **Hereditas 140**: 18-23.

EMLEN, J.M. 1970. Age specificity and ecological theory. **Ecology 51** (4): 588-601.

FIGUEIREDO, M.S.L. & F.A.S. FERNANDEZ. 2004. Contrasting effects of fire on populations of two small rodent species in fragments of Atlantic forest in Brazil. **Journal of Tropical Ecology 20**: 225-228.

FLEMING, T.H. 1973. The reproductive cycle of three species of opossums and other mammals in the Panama Canal Zone. **Journal of Mammalogy 53**: 439-455.

FONSECA, G.A.B. & J.G. ROBINSON. 1990. Forest size and structure: competitive and predatory effects on small mammal communities. **Biological conservation 53**: 265-294.

FONSECA, G.A.B. & M.C.M. KEIRULFF. 1989. Biology and natural history of brazilian Atlantic forest small mammals. **Bulletin of Florida Museum of Natural History 34**: 99-152.

GENTILE, R. & F.A.S. FERNANDEZ. 1999. Influence of habitat structure on a streamside small mammal community in a Brazilian rural area. **Mammalia 63** (1): 29-40.

GENTILE, R.; P.S. D'ANDREA & R. CERQUEIRA. 1995. Age structure of two marsupial species in a Brazilian restinga. **Journal of Tropical Ecology 11**: 679-682.

GENTILE, R.; P.S. D'ANDREA; R. CERQUEIRA & L.S. MAROJA. 2000. Population dynamics and reproduction of marsupials and rodents in a Brazilian rural area: a five-year study. **Studies on Neotropical Fauna** and **Environment 35**: 1-9.

GENTILE, R.; R. FINOTTI; V. RADEMAKER & R. CERQUEIRA. 2004. Population dynamics of four marsupials and its relation to resource production in the Atlantic forest in Southeastern Brazil. **Mammalia 68**: 109-119.

JULLIARD, R.; A. PRÉVOT-JULLIARD; H. LIERS; H. STENSETH; N. YOCCOZ; R. VERHAGEN & W. VERHEYEN. 1999. Survival variation within and between functional groups of small mammal, the African multimammate rat *Mastomys natalensis*. **Journal of Animal Ecology 68**: 550-561.

KANDA, L. & T.K. FULLER. 2004. Demographic responses of Virginia opossums to limitation at their northern boundary. **Canadian Journal of Zoology 82**: 1126-1134.

KREBS, C.J. 2001. **Ecology. The experimental analysis of distribution and abundance.** San Francisco, Benjamin Cummings, 695p.

LEE, A.K. & A. COCKBURN. 1985. **Evolutionary ecology of marsupials. Monographs on marsupial biology.** Cambridge, Cambridge University Press, VIII+274p.

LEITE Y.L.R.; L.P. COSTA & J.R. STALLINGS. 1996. Diet and vertical space use of sympatric opossums in a Brazilian Atlantic Forest reserve. **Journal of Tropical Ecology 12**: 453-440.

LIMA, M.; N.C. STENSETH; N.G. YOCCOZ & F.M. JAKSIC. 2001. Demography and population dynamics of the mouse opossum (*Thylamys elegans*) in semi-arid Chile: seasonality, feedback structure and climate. **Proceedings of the Royal Society of London-B 268**: 2053-2064.

MACEDO, J.; D. LORETTO; M.V. VIEIRA & R. CERQUEIRA. 2006. Classes de desenvolvimento em marsupiais: um método para animais vivos. **Mastozoologia Neotropical 13**:133-136.

MILLAR, J.S. & R.M. ZAMMUTO. 1983. Life histories of mammals: an analysis of life tables. **Ecology 64**: 631-635.

MUELLER, H.; J. WANG; J.R. CAREY; E.P. CASWELL-CHEN; C. CHEN; N. PAPADOPOULOS & F. YAO. 2004. Demographic window to aging in the wild: constructing life tables and estimating survival functions from marked individuals of unknown age. **Aging Cell 3**: 125-131.

NIMER, E. 1989. **Climatologia do Brasil.** Rio de Janeiro, IBGE, 421p.

O'CONNELL, M.A. 1989. Population dynamics of neotropical small mammals in seasonal habitats. **Journal of Mammalogy 70**: 532-548.

PEARL, R. 1928. **The rate of living.** New York, Alfred A. Knopf, 185p.

PIANKA, E.R. 1974. **Evolutionary Ecology.** New York, Harper & Row, X+356p.

QUENTAL, T.B.; F.A.S. FERNANDEZ; A.T.C. DIAS & F.S. ROCHA. 2001. Population dynamics of the marsupial *Micoureus demerarae* in small fragments of Atlantic coastal forest in Brazil. **Journal of Tropical Ecology 17**: 339-352.

RADEMAKER, V. & R. CERQUEIRA. 2006. Variation in the latitudinal reproductive pattern of the genus Didelphis (Didelphimorphia, Didelphidae). **Austral Ecology 31**: 337-342.

SANTORI, R.T.; D. ASTÚA DE MORAES & R. CERQUEIRA. 1996. Diet composition of *Metachirus nudicaudatus* (E. Geoffroy, 1803) and *Didelphis aurita* (Wied, 1826) (Marsupialia, Didelphidae). **Mammalia 59**: 511-515.

SCHWARTZ, O.A.; K.B. ARMITAGE & D. VAN VUREN. 1998. A 32-year demography of yellow-bellied marmot (*Marmota flaviventris*). **Journal of Zoology 246**: 337-346.

SLADEN, B.K. & F.B. BANG. 1969. **Biology of populations.** New York, American Elsevier Publishing Company XXII+449p.

STEARNS, S.C. 1992. **The Evolution of Life Histories.** Oxford, Oxford University Press, 249p.

TYNDALE-BISCOE, C.H. & R.B. MACKENZIE. 1976. Reproduction of *Didelphis marsupialis* and *Didelphis albiventris* in Colombia. **Journal of Mammalogy 57**: 249-265.

TWIGG, G.I. 1975. Techniques in mammalogy. 3: Marking mammals. **Mammal Review 5** (3): 101-116.

VIEIRA, E.M. & E.L.A. MONTEIRO-FILHO. 2003. Vertical stratification of small mammals in the Atlantic rain forest of Southeastern

Brazil. **Journal of Tropical Ecology 19**: 501-507.

VIEIRA, E.M. & P. IZAR. 1999. Interactions between aroids and arboreal mammals in the Brazilian Atlantic rainforest. **Plant Ecology 145** (1): 75-82.

WILLIAMS, G.C. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. **American Naturalist 100**: 687-690.

ZAMMUTO, R.M. 1987. Life histories of mammals: analyses among and within *Spermophilus columbianus* life tables. **Ecology 68** (5): 1351-1363.

Submitted: 13.VIII.2007; Accepted: 05.VI.2008.
Editorial responsibility: Lena Geise