Reproductive ecology of the invader species gekkonid lizard *Hemidactylus mabouia* in an area of southeastern Brazil

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ABSTRACT. *Hemidactylus mabouia* Moreau de Jonnés, 1818 is a "fixed" clutch size exotic species well established in Brazil. In this paper we investigate some reproductive strategies adopted to minimize the costs of invariant clutch size to this invader species living in an environment with marked climatic seasonality in Southeastern Brazil (22°56'S; 46°55'W). The study was carried out from April 2002 to March 2003. Females and males attain maturity at 47.9mm and 46.9mm SVL, respectively. Larger females tended to produce larger eggs. The reproduction occurred throughout the year, but only at the wet season the females increase the clutch frequency. There was a significant variation in mean testis volume among the months throughout the year and the largest means were recorded between August and December. Maternal investment on egg size, increase on clutch frequency and seasonal increase on testis volume can represent important reproductive strategies of this invader species living in an non-urban habitat whit climatic seasonality (dry and cold weather season).

KEYWORDS. *Hemidactylus*, exotic species, reproduction, egg size relationships.

RESUMO. Ecologia reprodutiva da espécie de lagarto gekkonídeo invasora *Hemidactylus mabouia* em uma área do sudeste do Brasil. *Hemidactylus mabouia* Moreau de Jonnés, 1818 é uma espécie exótica, com tamanho fixo de ninhada e bem estabelecida no Brasil. Neste estudo foram investigadas algumas estratégias reprodutivas adotadas no sentido de minimizar os custos do tamanho fixo de ninhada nesta população que vive em uma região onde há uma marcada sazonalidade climática. O estudo foi realizado entre abril de 2002 e março de 2003 em Valinhos (22°56'S; 46°55'W; sudeste do Brasil). Os resultados indicaram que as fêmeas atingem a maturidade sexual com 47,9mm enquanto que os machos com 46,9mm. As fêmeas maiores tendem a produzir ovos maiores. A reprodução ocorre ao longo do ano todo, mas somente durante a estação úmida as fêmeas aumentam a freqüência reprodutiva. O tamanho médio dos testículos sofre uma variação ao longo do ano e as maiores médias foram registradas entre os meses de agosto e dezembro. Investimento maternal no tamanho do ovo, aumento na freqüência reprodutiva e aumento sazonal no volume médio dos testículos podem representar uma importante estratégia reprodutiva desta espécie invasora que habita um campo ruderal com sazonalidade climática marcada (estação fria e seca bem definida).

PALAVRAS-CHAVE. *Hemidactylus*, espécie exótica, reprodução, tamanho de ovo.

The total reproductive output of an individual during its reproductive season is a function of offspring number, offspring size, and clutch frequency. As an individual has a finite amount of energy to spend on reproduction, the female must do a trade-off among these reproductive parameters (SELCER, 1990). Some lizard species of different families (e. g. Gekkonidae, Gymnophtalmidae and Polychrotidae) exhibit "fixed" clutch size, producing always one or two eggs per clutch (ANDREWS & RAND, 1974; VITT, 1986; SELCER, 1990). The "fixed" clutch size can limit these species in size and mass of offspring and/or frequency of clutches (SELCER, 1990). Lizards presenting a "fixed" clutch size tend to maximize their reproductive outcome by increasing the frequency of clutches, increasing egg size, or investing in vitellogenic nutrients (ANDREWS & RAND, 1974; VITT, 1986; DOUGHTY, 1997; SELCER, 1990).

Hemidactylus mabouia Moreau de Jonnès, 1818 is a successful colonizer (MESHAKA, 2000; MESHAKA *et al.*, 1994) well established in Brazil (VANZOLINI *et al.*, 1980) and, nowadays it is quickly colonizing the North American Continent (LAWSON *et al.*, 1991; BUTTERFIELD *et al.*, 1993; MESHAKA *et al.*, 1994; MESHAKA, 2000). A well-established population of *H. mabouia* was found living in an outcrops non-urban environment of Valinhos municipality (22°56'S; 46°55'W), in state of São Paulo, Brazil. The knowledge about the reproductive process of an invasive species is the key to understand its success as an invader, as well as to control established populations (WHITTIER & LIMPUS, 1996). *Hemidactylus mabouia* has a "fixed" clutch size, producing two eggs per clutch, with a year-round reproduction (VITT, 1986; MESHAKA, 1994; but see BONFIGLIO *et al.*, 2005). Some authors point out that *H. mabouia* has a high fertility (BOCK, 1996; MESHAKA *et al.*, 1994); nevertheless there is no accurate data on reproductive frequency or longevity for this invader species. In this paper we investigate some reproductive aspects, such as extension of the reproductive period, minimum size at maturity, frequency of clutches and parental investment of a population living in a non-urban area (Valinhos) with marked climatic seasonality in southeastern Brazil.

MATERIAL AND METHODS

This study was carried out between April 2002 and March 2003 in a grassland area in Valinhos municipality (22º56'S; 46º55'W), state of São Paulo, southeastern Brazil, at an elevation of approximately 700m. The area has abundant granite boulders surrounded by grassy and shrubby vegetation. Rainy season occurs from October to March and the dry one from April to September; the mean annual temperature (±sd) and total annual rainfall are 20.7 ± 2.2ºC and 1,379 mm, respectively

(VAN SLUYS *et al*., 1994). During the period of this study, rainfall totaled 230mm in the dry season and 1,047mm in the wet season [all climatic data were obtained from the Centro de Pesquisas em Agricultura (CEPAGRI) of the Universidade Estadual de Campinas] (Fig. 1).

Lizards were collected with a noose or by hand. Immediately after capture, each lizard was transferred to a plastic sac containing cotton embedded in ether, in order to euthanasia them. We collected 295 lizards, of which 88 were adult males, 88 adult females, and 119 juveniles.

In the laboratory, lizards were fixed with 10% formalin solution and stored at 70% alcohol solution. After that, they were dissected and their gonads were removed for posterior analysis. In females we measured the longer and the shorter length of the eggs in each oviduct, and, when present, the largest follicle in each ovary, registering the condition of those vitellogenic follicles [enlarged yolked ovarian follicles are yellow colored, and this coloration indicate the secondary vitellogenic follicle condition, according to BLANCO & ACOSTA (1998)]. The criterion used to determine the minimum size of an adult female was the smallest female containing enlarged yolked ovarian follicles (diameter ≥ 1.9mm). In males, we measured the longer and the shorter length of the largest testis. All measurements were taken with a caliper (at the precision of 0.01mm). To determine the minimum size of adult males, slides were made of both testis and epididymis of each male. The gonads were embedded in paraffin, sectioned in transversal axis at 5µm, and stained with hematoxylin-eosin. Males containing sperm in epididymis were considered adult.

In the field, upon the sand soil and covered by grass that grows besides rocky walls we collected three clutches, with two eggs each. The first two clutches were collected on August 2002 and the third clutch was collected on September 2002. Clutches were carefully removed and stored in a plastic recipient containing a small amount of substrate (sandy soil) from the site where the eggs were removed. Clutches were taken to the laboratory and kept in similar conditions of temperature and humidity to those encountered in the field, until they hatched. During these period the monthly mean temperature, at the laboratory, ranged from 22.4°C to 26.5°C (similar values to that registered at the field (Fig. 1)). The collection and maintenance of eggs in captivity aimed to development and hatching of eggs in order to obtain some information about the size of newborns on this population studied.

For estimation of testis volume (mm^3) we used the ellipsoid formula: $V = \frac{4}{3} \times \pi \times \left(\frac{L}{2}\right) \times \left(\frac{W}{2}\right)^2$

where, V = volume, L = higher length and W = lesser length. We used a regression analysis to evaluate the effect of lizard body size (snout-vent length) on testis/follicle or egg volume. When the data set did not fit the normal distribution, or were a heterocedastic, data were log-transformed (ZAR, 1999). Residual analysis between reproductive structures (i.e. testis, follicle and egg volumes) and lizard size (snout-vent length) was also performed (ZAR, 1999). An ANOVA was performed to test whether there was a significant difference between the residuals of testis volume throughout the year (ZAR, 1999). We used an *a posteriori* test, least square deviation (LSD), to investigate in which months the mean of residuals was different from the other ones (ZAR, 1999). We also used ANOVA to test for differences on the residuals of egg volume between dry and wet seasons. The proportion of gravid females in the wet and the dry seasons was analyzed by a Z test for proportion (ZAR, 1999).

RESULTS

The SVL of the smallest male with sperm in testis or epididymis was 46.9mm. The mean adult male SVL was 56.7 ± 5.0mm (range = 46.9-68.2mm, n = 88). The SVL of the smallest adult female was 47.9mm. Mean adult female SVL was 56.6 ± 5.2mm (range = 47.9-67.2mm, n = 88). There was no significant difference (t = - 0.231; df = 173; p = 0.818) in the mean SVL between adult males and adult females.

Females containing oviductal eggs were collected in almost every month of the studied period (Fig. 2) and

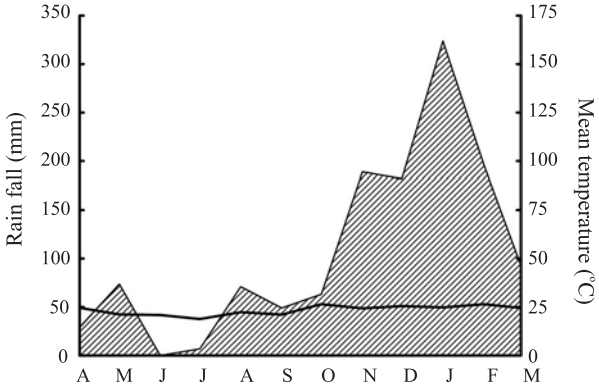

Fig. 1. Monthly mean temperature (in ºC, solid black line) and rainfall (in mm, hachured area) in Campinas-Valinhos region, southeastern Brazil from April 2002 to March 2003. Data were provided by Centro de Pesquisa em Agricultura (CEPAGRI) of the Universidade Estadual de Campinas.

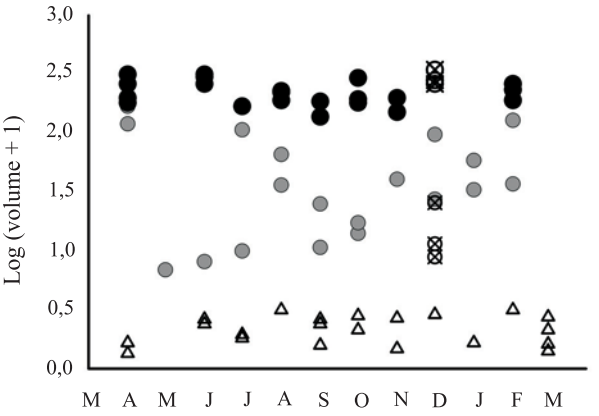

Fig. 2. Log-transformed volumes of larger non-vitellogenic ovarian follicles (triangles), larger enlarged yolked ovarian follicles (grey circles), and larger oviductal eggs (solid circles) of females *Hemidactylus mabouia* Moreau de Jonnés, 1818 captured in Valinhos, southeastern Brazil, between April 2002 and March 2003. Open circles marked with X represent the three females with both oviductal eggs and enlarged yolked follicles.

in December 2002 we recorded three females containing both oviductal eggs and enlarged yolked follicles (Fig. 2). There was no significant difference in the proportion of gravid females captured between dry (27.7%) and wet (26.8%) seasons (Z-test: $Z_C = 0.52$; df = 1; p = 0.603).

Female body size affected egg volume ($R^2 = 0.57$; $F_{1,20} = 26.57$; $p < 0.001$; Fig. 3). Nevertheless the maternal investment in volume of oviductal eggs, after removed the female size, did not differ between wet and dry seasons (ANOVA; $F_{1,22} = 0.95$; p = 0.66; Fig. 4).

With regard to males, there was a significant variation in mean testis volume (independent of male size) among the months throughout the year (ANOVA; $F_{11,76} = 3.99$; $p < 0.001$). The largest testes were recorded between August and December 2002 (Fig. 5).

The viability on development and hatching of eggs collected at the field was 100%, and the incubation period ranged between 22 and 68 days. The hatchlings' mean SVL for the each one of the three clutches were 24.3 ± 0.04mm (mean mass = 0.3 ± 0g); 22.6 ± 0.28mm (mean mass = 0.23 ± 0.04g); and 22.3 ± 0.07mm (mean mass = 0.20 ± 0g). The overall hatchling SVL was 23.1 ± 1.0mm (range = 22.2 – 24.4mm) and overall mean hatchling mass was 0.24 ± 0.05g (range = 0.2 – 0.3g). We collected juveniles with body size close to that of newborns hatched at the laboratory in all months throughout the year (Fig. 6).

DISCUSSION

We found no difference in the body size between males and females of the population of *H. mabouia* studied in Valinhos. Sexual dimorphism in body size may result from sexual selection (TRIVERS, 1972, 1976; STAMPS, 1977). If an increase on female body size influences clutch size increase and these characteristics reflect on a lizard's reproductive success, then natural selection would favor continuous growth in females, they being larger than

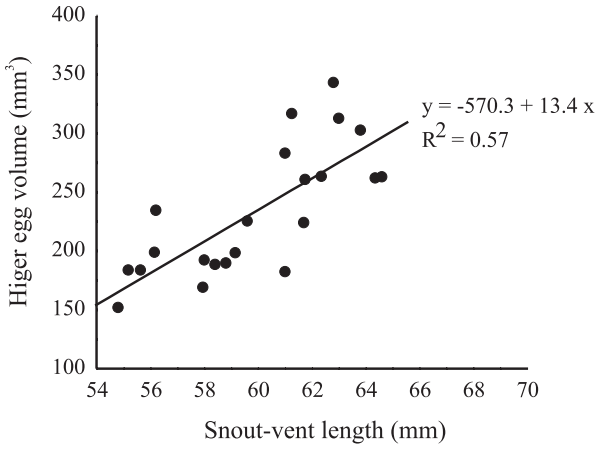

Fig. 3. Relationship between Snout-vent length (mm) and larger egg volume of female *Hemidactylus mabouia* Moreau de Jonnés, 1818 captured monthly at Valinhos, southeastern Brazil, between April 2002 and March 2003 ($R^2 = 0.57$; $F_{1,20} = 26.57$; $p < 0.001$).

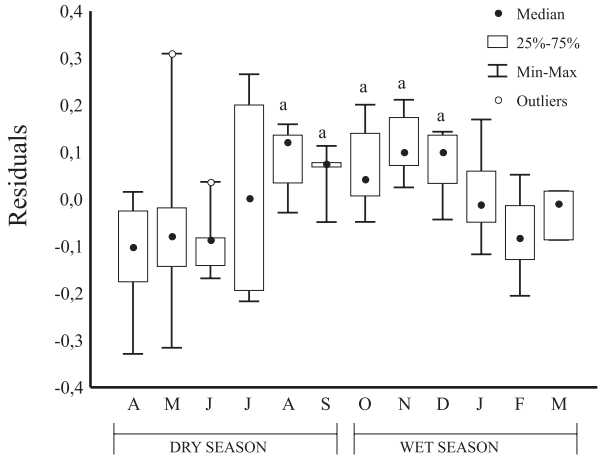

Fig. 5. Residuals of testis volume (mm³) of adult male *Hemidactylus mabouia* Moreau de Jonnés, 1818 captured at Valinhos, southeastern Brazil from April 2002 to March 2003. Letter "a" denotes months with non significant differences between residuals mean value.

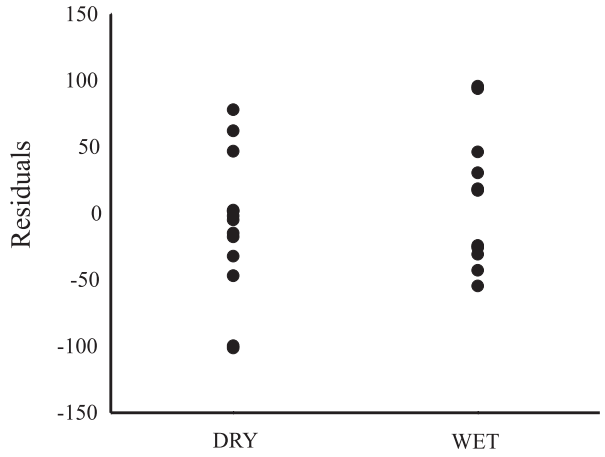

Fig. 4.Residuals of egg volume (mm³) of *Hemidactylus mabouia* Moreau de Jonnés, 1818 captured during dry (April to September) and wet season (October to March) at Valinhos, southeastern Brazil (ANOVA; $F_{1,22} = 0.945$, p = 0.657).

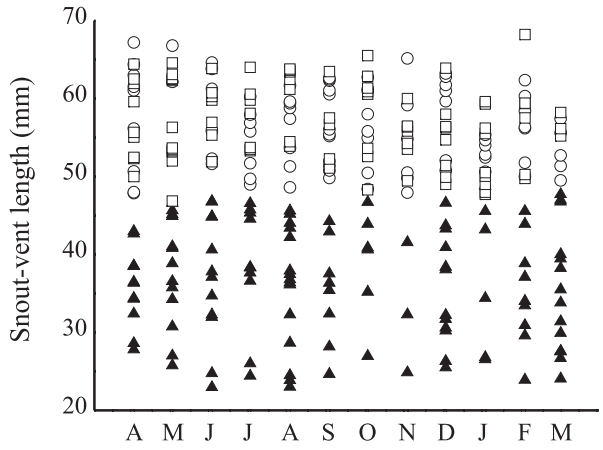

Fig. 6. Snout-vent length (mm) of *Hemidactylus mabouia* Moreau de Jonnés, 1818 from Valinhos. Are represented 119 juveniles (▲), 88 adult females (□) and 88 adult males (○).

males (TRIVERS, 1972, 1976). Because *H. mabouia* has a fixed clutch size there are no evolutionary pressures to increasing female body size relative to male body size which could contribute for the lack of sexual body size differences in the species.

In lizard species with "fixed" clutch size the maximization of reproductive effort may result from two mechanisms: investment in egg size, or in clutch frequency (ANDREWS & RAND, 1974; VITT, 1986; SELCER, 1990; DOUGHTY, 1997). Additionally, in a tropical seasonal environment, rainfall may influence clutch frequency of gekkonid lizards (SEXTON & TURNER, 1971). As expected for this invader species, this population living in a tropical environment with rainy season presented a year-round reproduction (VITT, 1986; BUTTERFIELD *et al*., 1993; MESHAKA *et al*., 1994), although there is some evidence of a non-continuous reproduction in a population from southern Brazil (see BONFIGLIO *et al*., 2005). But, differently from what was pointed out by MESHAKA *et al*. (1994), the high reproductive frequency doesn't occur throughout the year. There was a positive correlation between female body size and egg volume in this population, unlike the results reported by VITT (1986) for a northeastern Brazilian population.

The females of the studied population do not differ in their investment in egg size and egg number between dry (April to September) and wet (October to March) season. Nevertheless, on December 2002 (middle of the wet season) all females collected (n=3) had both oviductal eggs and enlarged yolked follicles, suggesting multiple clutches by each female and that during the peak of the wet season some females could be increasing clutch frequency.

Based on the number of follicles with diameters larger than 1.0mm, MESHAKA *et al*. (1994) assumed that *H. mabouia* could produce more than seven clutches per year. However, without information about juveniles' recruitment pattern, growth and development of ovarian follicles of this year-round reproducing gekkonid species, any assertion about the number of reproductive events become speculative. *Hemidactylus brooki* Gray, 1845 is a species with seasonal reproduction and in each ovarian cycle four ovarian follicles are produced, but only one attains a size large enough for ovulation (SHANBHAG *et al*., 1998). The other three follicles degenerate and the ovarian cycle starts again with the production of new follicles (SHANBHAG *et al*., 1998). Thus, even though *H. mabouia* might produce some follicles with diameter larger than 1.0mm (MESHAKA *et al*., 1994), or oviductal eggs and enlarged yolked follicles (this report), the follicles can become atretic, and new follicles may be recruited from the ovarian germinal bed. Our data do not support the MESHAKA *et al*. (1994) high fertility theory for this invader gekkonid species. Nevertheless a *H. mabouia* population living in a temperate weather region from south of Brazil presented a seasonal reproductive period with females showing both oviductal eggs and vitellogenic follicles (BONFIGLIO *et al*., 2005). This study indicate a plasticity in reproductive strategy of this invader species living in an unfavourable environment since that closer of equatorial region the populations tend to present a year-round reproduction cicle (FITCH, 1970; VITT, 1986).

As in females, the males also presented a seasonal reproductive investment; during a period of year (between August 2002 and December 2002) we registered enlarged testis. The increase in testis volume, or size, does not necessarily denote sperm production, and this could be induced by an increase in the number of germinal bed cells (SHANBHAG *et al*., 1998) or may indicate the overall effect of environment water availability on hydration of tissues (VITT, 1986). In tropical regions where temperature changes are less extreme than in temperate regions, rainfall and/or moisture may serve as an important environmental cue for gonadal recrudescence and breeding in reptiles (LOFTS, 1987; WHITTIER & CREWS, 1987). In Valinhos the rainfall is markedly seasonal and the increase of testis volume seems to precede the increase in rainfall, thus the increase on testis volume can represents the increase on germinal beds number or even sperm production.

The mean size of hatchlings was 23.1 ± 1.0mm, and the smallest newborn hatched in captivity measured 22.2mm. Field data showed that juveniles with body size close to that of newborns hatched at the laboratory occured in all months throughout the year, and this reinforces the idea of a continuous reproduction of the studied population.

Although this *H. mabouia* population studied presents a year-round reproduction, the climatic conditions during winter (dry season) in Valinhos could represent a limiting factor for newborns. Thus, the presence of both oviductal eggs and secondary vitellogenic follicles during a favorable season, summer (wet season), represent an efficient strategy of maternal investment to this "fixed" clutch sized lizard. Other important cue of maternal investment detected from this population was the larger and presumably older females producing larger eggs, which suggest that they are investing relatively more energy in reproduction than in body growth. Although there is some suggestion that the local environment of *H. mabouia* may affect the way the species will reproduce continuously or non-continuously, it is possible that the seasonal increase on testis volume coupled with females clutches frequency increase (by both oviductal eggs and secondary vitellogenic follicles) during a favorable season may have favored the colonization and establishment of this exotic and invader gekkonid in Valinhos.

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