

REPRODUCTIVE TRAITS OF TWO SYMPATRIC VIVIPAROUS SKINKS (*MABUYA MACRORHYNCHA* AND *MABUYA AGILIS*) IN A BRAZILIAN RESTINGA HABITAT

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The reproductive cycles, fat body cycles and some life-history traits of the sympatric viviparous skinks *Mabuya macrorhyncha* and *M. agilis* were compared in a seasonal "restinga" habitat of south-eastern Brazil. Both male and female reproductive and fat body cycles are very similar between species, with gestation lasting 9-12 months and parturition occurring during the early wet season. Clutch size of *M. macrorhyncha* was smaller than that of *M. agilis*. Females mature at a larger size in *M. macrorhyncha* than in *M. agilis*, but males of both species appear to mature at similar sizes. In both species, females are larger than males, but the latter have proportionately larger heads. Reproductive traits of *M. agilis* are typical of Neotropical *Mabuya*, but those of *M. macrorhyncha* have some peculiarities, one of which (small clutch size) is believed to result from constraints imposed by its morphological adaptation (i.e. relatively flattened body plan) to bromeliculous habits.

Key words: Reproduction, life history, *Mabuya*, Brazilian skink

INTRODUCTION

The genus *Mabuya* is one of the most speciose and widely distributed genera of the Scincidae, with about 90 species found over most of tropical Africa, Asia, and America (Shine, 1985; Nussbaum & Raxworthy, 1994). Not surprisingly, this genus is also extremely diverse ecologically, with species utilizing a wide variety of habitats and microhabitats (e.g. Huey & Pianka, 1977; Castanzo & Bauer, 1993; Nussbaum & Raxworthy, 1994, 1995; Ávila-Pires, 1995; Vrcibradic & Rocha, 1996). Concomitant with such geographical and ecological radiation, lizards within this genus have developed a considerable diversity of reproductive characteristics in different reproductive modes that includes both oviparity and viviparity (Fitch, 1970, 1985; Vitt & Blackburn, 1983; Shine 1985; Blackburn & Vitt, 1992). Although both viviparous and oviparous *Mabuya* species occur in the Old World, only viviparous forms are found in the New World (Fitch, 1985; Shine, 1985; Vitt & Blackburn, 1983, 1991; Blackburn & Vitt, 1992). Actually, New World *Mabuya* seem to constitute a monophyletic group derived from an African lineage (Greer, 1970; Shine, 1985; Bauer, 1993) and, apparently, all of its species possess a peculiar type of viviparity characterized by an extreme degree of placental nutrient transfer that is unique among squamates (Shine, 1985; Blackburn & Vitt, 1992). The great diversity of reproductive features among *Mabuya* species makes the study of reproduction in lizards of this genus very informative, as many questions about ecological and evolutionary reproductive responses may be addressed. Special interest should be paid to the analysis of reproductive patterns of sympatric *Mabuya*, from

which present differences may highlight those historical forces that may select for certain reproductive characteristics. Indeed, differences in reproductive characteristics among sympatric and allopatric populations of congeners have been reported for this genus in Africa (Huey and Pianka, 1977; Pianka, 1986).

At many localities along the coastal sand plains of south-eastern Brazil, which are characterized by sand-dune habitats (restinga), two species of *Mabuya* usually occur sympatrically: *Mabuya macrorhyncha* and *M. agilis* (Araújo, 1991, 1994; Rocha & Vrcibradic, 1996; Vrcibradic & Rocha, 1996). Some information on reproductive traits exists for the former species (Vanzolini & Rebouças-Spieker, 1976; Rebouças-Spieker & Vanzolini, 1978; Zanotti, Sant'Anna & Latuf, 1997) and virtually none for the latter. Although living sympatrically in these habitats and being similar in body size, these species differ markedly in morphology and microhabitat use, with *M. macrorhyncha* showing some tendency to scansoriality and living mainly on and among ground bromeliads. On the other hand, *M. agilis* is a ground-dweller which basks and forages on leaf litter (Rocha & Vrcibradic, 1996; Vrcibradic & Rocha, 1996). The comparatively more flattened body and head, and longer fingers in *M. macrorhyncha* have been suggested to be adaptive traits related to its habit of living among bromeliads (Vrcibradic & Rocha, 1996). Flattening of the body plan to suit ecological specializations (such as life in rock crevices) may impose some reproductive constraints to females of some lizard species (Broadley, 1974; Vitt, 1981).

We analysed the reproductive ecology and sexual dimorphism of *Mabuya macrorhyncha* and *M. agilis*, specifically addressing the following questions: (1) Do the two sympatric species differ in their reproductive and fat body cycles at Barra de Maricá? (2) Does litter size differ between species and is it correlated with fe-

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male body size within species? (3) At what size do males and females attain sexual maturity in each species? (4) Within species, is monthly variation in fat body mass more conspicuous in females than in males, considering the low energetic demands of sperm production (see Blem, 1976) compared to gestation? (5) Are the species sexually dimorphic?

MATERIALS AND METHODS

STUDY AREA AND CLIMATE

Field work was carried out at the Barra de Maricá restinga (22° 57' S, 43° 50' W), 38 km east of Rio de Janeiro city in the Rio de Janeiro State, SE Brazil. Restingas are Quaternary sand-dune habitats covered with herbaceous and shrubby vegetation, common along the Brazilian coast (Suguio & Tessler, 1984; Eiten, 1992). The area has marked tropical seasonality (Fig. 1), with a wet season between October and March and a dry season between April and September (Franco *et al.*, 1984; Rocha, 1992). The mean annual temperature varies between 22 and 24°C and the mean annual rainfall ranges from 1000 to 1350 mm (Nimer, 1979).

COLLECTING METHODS AND ANALYSIS

Lizards were collected monthly from May 1989 to April 1992 with an air rifle. Shots were always directed to the head and neck of the lizards, in order to kill them immediately. Each lizard was then immediately transferred to a plastic sac containing cotton soaked in ether. This was done in order to quickly anaesthetize lizards that may not have been killed instantaneously and to ensure a painless death. Shooting was by far the most efficient method we found to collect *Mabuya* in a restinga area characterized by large patches of vegetation. Catching them by hand or with elastic bands when they are basking is very difficult (*M. macrorhyncha* usually basks on the spiny-edged leaves of ground

bromeliads) and noosing them is practically impossible (the lizards are very skittish and usually retreat to the interior of thickets of vegetation or bromeliad patches when they sense any disturbance). The characteristics of the study area also make the use of pitfall and drift fence traps not feasible, since the patches of vegetation are too dense compared to another restinga areas where we have successfully used such technique to catch skinks (see Vrcibradic & Rocha, 1995 for more details).

To ensure sufficient data were collected for statistical analyses, the number of skins collected per month usually ranged from one to ten (September 1991 was an exception). We believe the impact caused on the skink population was negligible, since we sampled only a small portion of the available habitat during the study. Also, on subsequent visits to the area, after the monthly collections had ceased, we did not note any visible decrease in the frequency of skins sighted per day (both species are fairly abundant in the area).

Each collected lizard was weighed (to the nearest 0.01 g) with a Pesola balance, prior to fixation in 10 % formalin. The snout-vent length (SVL), head length (HL), head width (HW), mouth length (ML) and head height (HH) of each lizard was measured using vernier calipers (to the nearest 0.1 mm). Specimens were then dissected for sex determination and excision of reproductive organs (including embryos) and fat bodies (the few lizards whose organs were damaged by the shot were not considered).

We counted and measured ovarian follicles, oviductal ova and embryos of each female, for both species. The reproductive state of each female was assessed according to the following categories (modified from Patterson, 1990). *Stage 1*: no yolking follicles; no ova established in oviducts; *Stage 2*: yolking follicles; no ova established in oviducts; *Stage 3*: ova or embryo sacs (less than 4 mm in diameter) in oviducts; *Stage 4*: embryo sacs more than 4 mm, chorioallantois established, embryos undeveloped; *Stage 5*: embryos occupying $\geq 50\%$ of embryo sac; eyes and limb buds (or limbs) evident (Stages 30 - 36 of Dufaure & Hubert, 1961); *Stage 6*: well formed (near-term or term) foetuses (Stages 37 - 40 of Dufaure & Hubert, 1961)

Females were considered reproductively active if they contained ova or embryos in the oviducts (stages 3 to 6). Mean brood size was estimated for each species using data from all females containing oviductal ova or embryos. To evaluate the extent to which female body size affects brood size, we performed a linear regression of brood size on female SVL.

For each male, we recorded the longest and shortest axes of each testis and estimated testis volume using the formula for an ellipsoid (Mayhew, 1963). To assess reproductive condition of males, paraffin sections were taken from the middle of the left testis (including the epididymes) and stained with haematoxylin and eosin. Males were considered reproductively active if spermatozoa were present either in testes or in the epididymes.

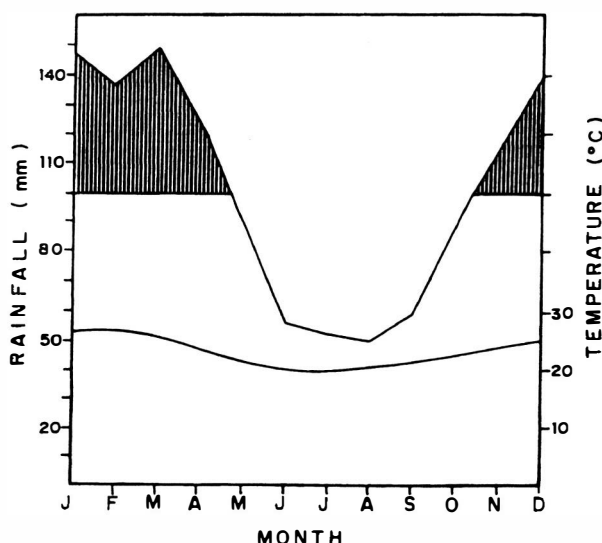


FIG. 1. Average monthly long-term rainfall and mean temperature of Barra de Maricá, Rio de Janeiro, Brazil. Extracted from Rocha (1992).

All linear measurements of gonads and embryos were taken with digital calipers (to the nearest 0.1 mm). The combined mass of both fat bodies (for each sex, in both species) was recorded using a Mettler electronic balance (to the nearest 0.001 g).

To assess the monthly variation in male testis volume (expressed as the averaged volume of the two testes in each male) and in fat body mass for both sexes, we calculated the residuals of the regressions of testis volume on SVL (both log-transformed) and of fat body mass on SVL (*idem*), respectively, and took the mean value (plus 1 SD) of the residuals for each month (only sexually mature lizards were included for this purpose). Residuals of fat body mass of adults were correlated with residuals of mean testis volume (in males) and with mean embryo sac diameter (in females) using regression analysis, to evaluate the degree of usage of fat reserves throughout the reproductive cycle. For *M. macrorhyncha* (the monthly sample sizes of *M. agilis* are too small), the effect of three environmental variables (total monthly rainfall, mean monthly temperature and photoperiod) on mean monthly testis volume (expressed as mean value of residuals; see above) was analysed by regression analyses. Due to the lack of published data on the temporal gap between environmental changes and changes in lizard testicular activity, we assumed a time-lag of two months because such physiological responses to environmental variation are unlikely to be immediate. Data on average monthly rainfall and mean monthly temperatures for a 38-year period (1931-1968) were obtained from the Departamento Nacional de Meteorologia station of Niterói, located ca. 19 km west of the study area.

We tested for intersexual differences in lizard SVL within each species using one-way analysis of variance (ANOVA). HL, ML, HW and HH were compared between sexes in each species through analysis of covariance (ANCOVA), using SVL as the covariate.

To increase our sample sizes for analyses involving clutch sizes and morphometric variables (including SVL), for both species, we included data from lizards collected sporadically in Barra de Maricá both before (in 1986) and after (in 1995 and 1996) the study period.

Descriptive statistics are expressed throughout the text as mean \pm standard deviation. Nomenclature of other *Mabuia* species mentioned in this paper follow Ávila-Pires (1995).

RESULTS

FEMALE REPRODUCTIVE CYCLE

Brood size of *M. macrorhyncha* averaged 2.66 ± 0.63 (range 2-4; $n = 38$; Fig. 2a) and was significantly correlated with female SVL ($r^2 = 0.258$; $F_{1,35} = 12.16$; $P = 0.001$).

The smallest female *M. macrorhyncha* containing oviductal ova measured 59.9 mm in SVL. Another female of the same size (collected on 25 November 1996) had undeveloped oviducts and contained no vitellogenic follicles in its ovaries, which suggests that

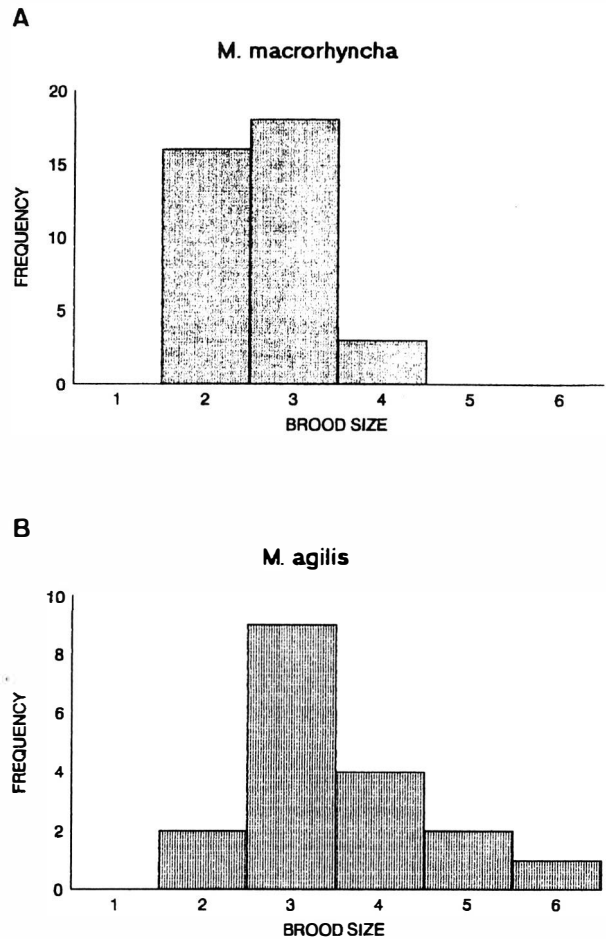


FIG. 2. Frequency of brood sizes (expressed as number of broods for each brood size) among *M. macrorhyncha* (a) and *M. agilis* (b) at Barra de Maricá, Rio de Janeiro, Brazil.

it was not sexually mature. Three females contained embryos/ova in different development stages simultaneously (respectively, in stages 3 and 4, 3 and 5, and 3, 4 and 5). Two females (SVLs = 68.0 and 72.8 mm) containing well-formed foetuses were collected in late October 1991 (Fig. 3a); another female collected on 5 December 1996 contained three well-formed foetuses. The smallest individual in our sample, a male (36.3 mm SVL; umbilical scar present), was collected on 13 December 1991. Yolking ovarian follicles of *M. macrorhyncha* ranged in diameter from 0.9 mm to 2.2 mm; the smallest oviductal ova were 2.3 mm in diameter. Three well-formed foetuses from a female collected in October 1991 ranged from 24.9 to 25.7 mm in SVL. Ovulation apparently occurs from December to March and implanted ova undergo little increase in size until about June, when embryos begin their rapid development phase until they are ready to be born, about October-November (Fig. 4a).

Brood size of *M. agilis* averaged 3.50 ± 1.04 (range 2-6; $n = 18$; Fig. 2b) and was not significantly correlated with female SVL ($r^2 = 0.131$; $F_{1,16} = 2.41$; $P = 0.14$).

The smallest female *M. agilis* with oviductal ova had a SVL of 49.2 mm. Females with well-formed embryos were collected in mid-September 1989, early and late

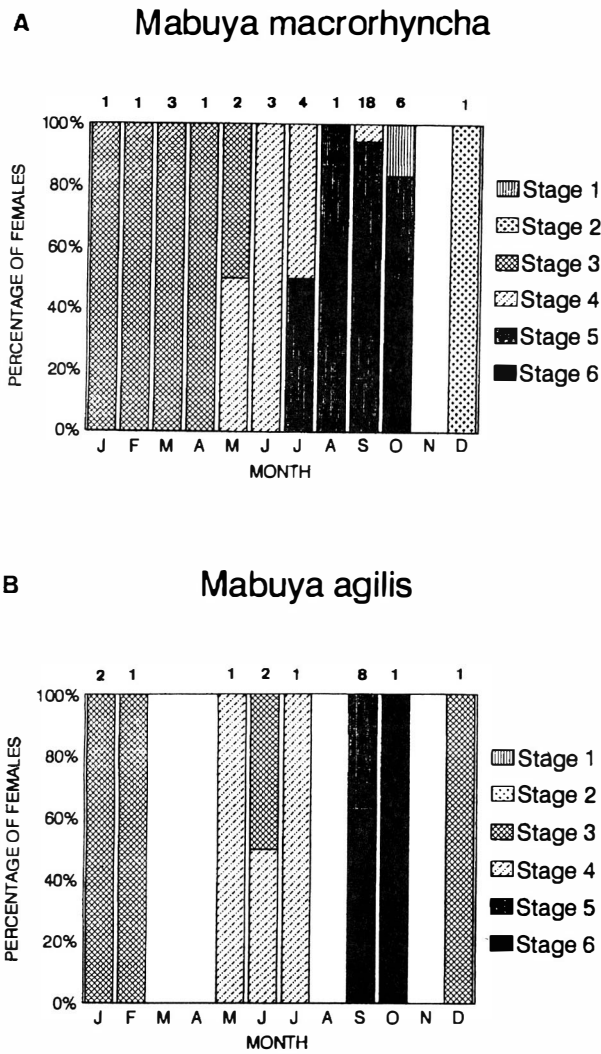


FIG. 3. Percentages of sexually mature female *M. macrorhyncha* (a) and *M. agilis* (b) in each reproductive stage (see text) for each month during the study period (May 1989-April 1992) at Barra de Maricá, Rio de Janeiro, Brazil. Monthly sample sizes are expressed by numbers above bars and represent pooled data from different years.

September 1991, and late October 1991 (Table 2), and were all larger than 70 mm in SVL. The three females in reproductive stage 5, from September 1991 (see Fig. 3b) ranged from 63 to 68 mm in SVL. The smallest individual in the sample, a female (SVL = 47.6 mm) was collected on 13 May 1991 and very young individuals (SVL ≤ 45 mm) were seen in the field on 30 December 1991. One female containing enlarged follicles (about

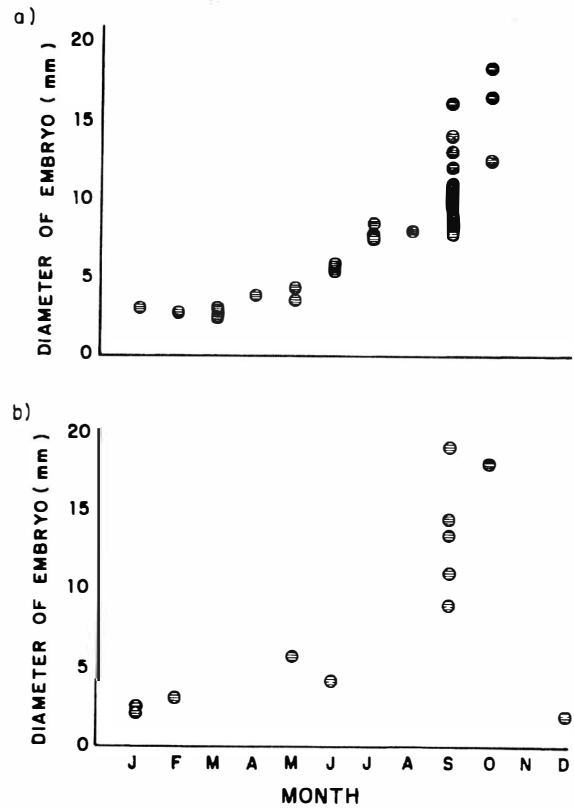


FIG. 4. Monthly distributions of embryo size (expressed as maximum diameter of the largest oviductal ova or embryo sac for each female) for *M. macrorhyncha* (a) and *M. agilis* (b) at Barra de Maricá, Rio de Janeiro, Brazil.

to be ovulated) and no implanted ova was collected on 28 November 1995. Yolking follicles ranged from 1.1 to 2.2 mm in diameter and the smallest oviductal ova measured 1.5 mm. Four well-formed fetuses from a female collected in October 1991 ranged in SVL from 24.7 to 26.7 mm. Ovulation in *M. agilis* appears to begin in November and ova apparently stay relatively small until May-June, when rapid embryonic growth begins (Figs. 3b and 4b). Embryos are well developed by September-October and parturition apparently occurs mainly during October-November. Brood size of *M. agilis* was significantly greater than that of *M. macrorhyncha* (ANOVA: $F_{1,54} = 14.15$; $P < 0.001$). Most (ca. 90 %) of the females containing oviductal ova or embryos, in both species, also had vitellogenic follicles in their ovaries.

TABLE 1. Values of morphological characters of *Mabuya macrorhyncha* at Barra de Maricá, Rio de Janeiro, Brazil. *F*-ratios test for differences between the sexes using ANCOVA, with SVL as the covariate. *** $P < 0.001$.

	Head Width		Mouth Length		Head Height		Head Length	
	males	females	males	females	males	females	males	females
<i>n</i>	45	49	52	55	42	42	51	54
Mean	8.31	8.46	10.15	10.07	5.42	5.44	14.03	13.93
SD	0.93	0.74	0.92	0.80	0.79	0.61	1.28	1.03
Range	5.2-9.4	6.7-9.5	6.8-11.5	6.9-11.2	3.2-6.9	3.4-6.4	9.3-15.8	9.8-15.6
<i>F</i> -ratio	28.71***		63.36***		17.77***		78.87***	

TABLE 2. Values of morphological characters of *Mabuya agilis* at Barra de Maricá, Rio de Janeiro, Brazil. *F*-ratios test for differences between the sexes using ANCOVA, with SVL as the covariate. ****P*<0.001.

	Head Width		Mouth Length		Head Height		Head Length	
	males	females	males	females	males	females	males	females
<i>n</i>	20	18	21	19	20	18	21	18
Mean	8.35	7.91	9.45	9.12	6.45	6.00	13.75	12.93
SD	0.48	0.68	0.53	0.66	0.39	0.62	0.72	0.94
Range	7.4-9.5	6.4-8.6	8.6-10.8	7.2-9.8	5.8-7.0	4.4-6.8	12.4-15.6	10.6-13.9
<i>F</i> -ratio	35.72***		25.48***		37.72***		66.98***	

MALE REPRODUCTIVE CYCLES

The smallest male *M. macrorhyncha* containing spermatozoa in the lumina of seminiferous tubules and/or epididymes (from 28 October 1991) had a SVL of 55.9 mm. However, both this individual, and a slightly larger one (58.4 mm SVL; collected 29 September 1991) contained very few mature spermatozoa. The monthly distribution of residuals of the testis-volume - SVL regressions (Fig. 5a) showed that testes are at their largest from November through January, decrease in size from February onwards, remaining small until August or September, when they begin to enlarge again.

The smallest male *M. agilis* (collected on August 1986) measured 55.5 mm in SVL and had its testes and epididymes filled with spermatozoa, indicating that it was sexually mature. The monthly testicular cycle in

Fig. 5b suggests that testes are in a regressed state during mid-dry season months (May-July), start the size increase in August and remain enlarged from September through March, shrinking thereafter.

The relationships between mean monthly testis volume of *M. macrorhyncha* and the three environmental variables tested were positive in all cases. The regressions of testis volume on temperature ($r = 0.93$, $P < 0.001$) and on rainfall ($r = 0.94$, $P < 0.001$) were both significant, whereas the regression of testis volume on fotoperiod ($r = 0.01$, $P = 0.76$) was not.

FAT BODY CYCLES

Monthly variation in fat body mass was somewhat similar between sexes in both species (Fig. 6). A pattern is more evidently seen in female *M. macrorhyncha*, whose fat reserves appear to reach a peak during the middle of the dry season and decrease after August-September (Fig. 6a).

In male *M. macrorhyncha*, the variation in fat body mass was not significantly correlated to the variation in testis volume ($r = 0.03$, $F_{1,29} = 0.02$, $P = 0.88$). In females, fat body mass was negatively and significantly related to embryo sac diameter ($r = -0.42$, $F_{1,27} = 5.67$, $P < 0.05$).

In *M. agilis*, the variation in fat body mass was not significantly correlated with either testis volume (in males; $r = -0.38$, $F_{1,10} = 1.67$, $P = 0.226$) or mean embryo sac diameter (in females; $r = -0.4$, $F_{1,10} = 1.90$, $P = 0.198$), though the relationship was negative in both cases.

SIZE AND SEXUAL DIMORPHISM

Mean adult SVL of *M. macrorhyncha* (66.8 ± 4.52 mm; $n = 98$) was not statistically different from that of *M. agilis* (66.8 ± 7.28 mm; $n = 41$) (ANOVA: $F_{1,137} = 0.0$, $P = 0.997$). The monthly distribution of sizes for each species is shown in Fig. 7.

Male and female *M. macrorhyncha* ranged in SVL from 36.3 to 72.2 ($n = 54$) and from 41.7 to 77.0 mm ($n = 59$), respectively. Adult males (i.e. ≥ 55.9 mm) averaged 65.1 ± 3.77 mm ($n = 43$) in SVL, whereas adult females (i.e. ≥ 59.9 mm) averaged 68.7 ± 4.04 mm ($n = 50$). For lizards with SVLs of 55.9 mm (i.e. the size of the smallest adult male) or larger, sexes differed significantly in mean SVL (ANOVA: $F_{1,94} = 10.92$, $P =$

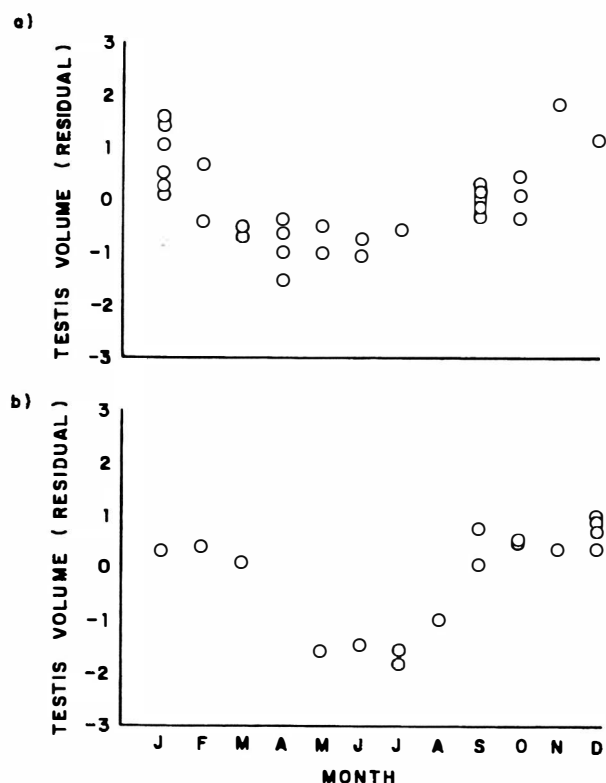


FIG. 5. Monthly distributions of testis volume (expressed as the residuals of the log testis volume-log SVL regression) for *M. macrorhyncha* (a) and *M. agilis* (b) at Barra de Maricá, Rio de Janeiro, Brazil.

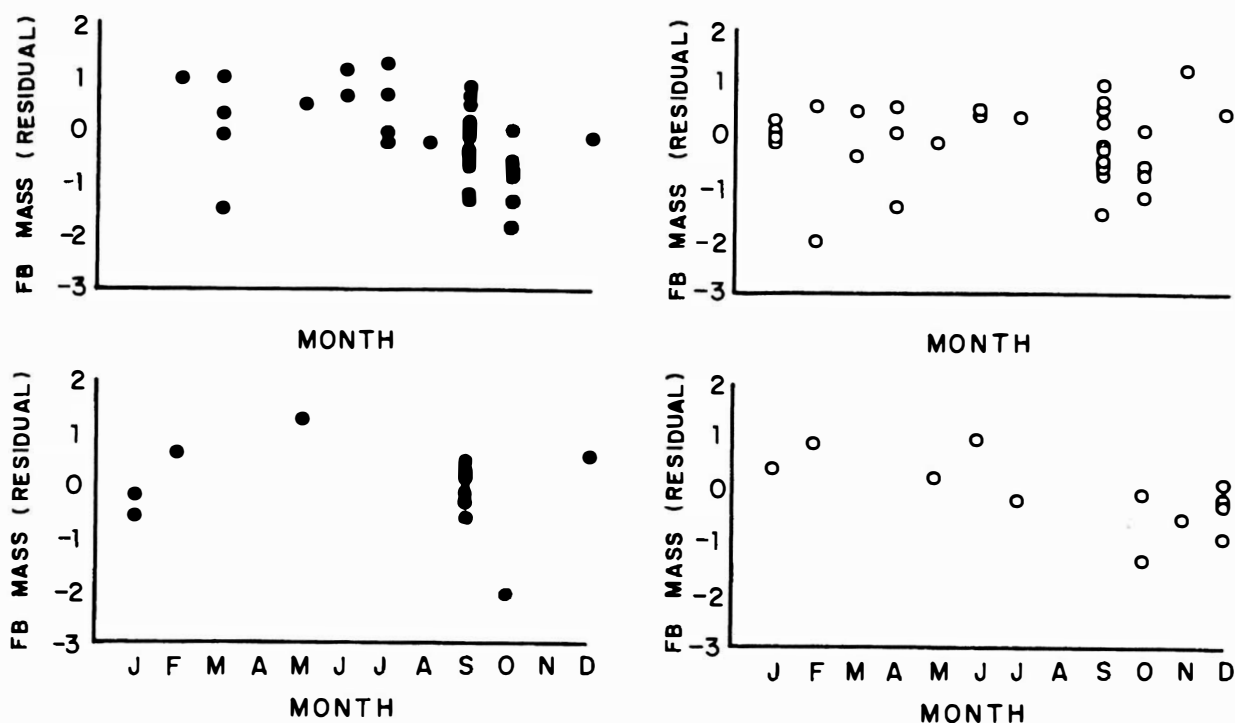


FIG. 6. Monthly distributions of fat body mass (expressed as the residuals of the log fat body mass-log SVL regression) for *M. macrorhyncha* (females - upper left; males - upper right) and *M. agilis* (females - lower left; males - lower right) at Barra de Maricá, Rio de Janeiro, Brazil.

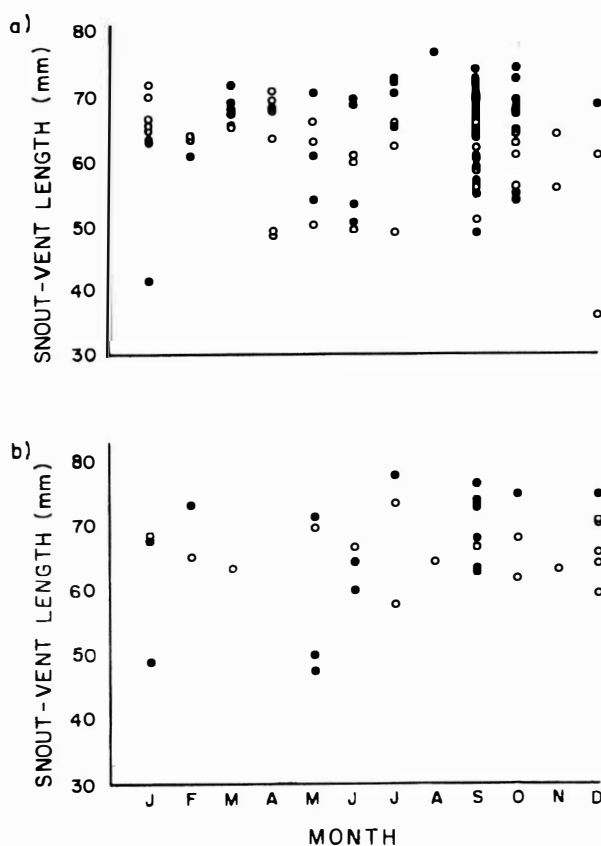


FIG. 7. Monthly distribution of SVL (in mm) of male (open circles) and female (closed circles) *M. macrorhyncha* (a) and *M. agilis* (b) at Barra de Maricá, Rio de Janeiro, Brazil.

0.001), with females reaching larger sizes than males. Sexes differed in the relative values of HL, ML, HW and HH, with higher values for males (Table 1).

Male *M. agilis* examined in this study averaged 66.1 ± 4.74 mm (range 55.5 - 73.8 mm; $n = 21$) in SVL and were all adult-sized. Females ranged from 47.6 to 77.9 mm in SVL ($n = 19$), with only two individuals smaller than 60 mm. Excluding these juvenile-sized individuals, average SVL of female *M. agilis* was 70.7 ± 5.29 mm ($n = 17$) and was significantly larger than that of males (ANOVA: $F_{1,36} = 7.87$, $P < 0.005$). Sexes differed in the relative values of all head dimensions tested, with males attaining higher values (Table 2).

DISCUSSION

Brood sizes of both species at Barra de Maricá (especially *M. macrorhyncha*) were relatively small compared to other Neotropical *Mabuya* species (see Table 3) and to various Old World congeners, both viviparous and oviparous (e.g. Fitch, 1970; Barbault, 1976; Huey & Pianka, 1977; Simbotwe, 1980; Patterson, 1990; Flemming, 1994; Huang, 1994). Brood size of *M. agilis* was comparable to that reported by Somma & Brooks (1976) for *M. mabouia* in the Caribbean island of Dominica, but their data are from only seven gravid females. *Mabuya macrorhyncha* had an even smaller and less variable brood size (usually two or three, rarely four) than its sympatric congener, though it equalled that of a closely related (and yet undescribed) species from north-east Brazil (Stevaux,

1993) (see Table 3). Similarly low values have been observed for allopatric populations of *M. macrorhyncha* in a number of areas (both on the continent and on islands) along the coast of São Paulo state, south-east Brazil, by Vanzolini & Rebouças-Spieker (1976) (Table 3). It appears that, in general, *M. macrorhyncha* gives birth to fewer offspring than its other New World congeners (except for the aforementioned undescribed species), a fact that may have ecological implications. This species is strongly associated with ground bromeliads, which they use as basking and foraging sites and as refugia from predators (Rebouças-Spieker, 1974; Rocha & Vrcibradic, 1996; Vrcibradic & Rocha, 1996), and has a relatively flattened body plan (compared to the ground-dwelling *M. agilis*), which presumably facilitates its movement amidst bromeliad leaves (Vrcibradic & Rocha, 1996). A reduction in the number of offspring and, consequently, in the burden of the brood carried by females (whose body height obviously increases during pregnancy), may be advantageous in a lizard with such characteristics. Indeed, in the caatinga of north-east Brazil, the rock-crevice specialist tropidurid lizard *Tropidurus* (= *Platynotus*) *semitaeniatus* (which has a flattened morphology to suit its microhabitat requirements) has a reduced clutch size (usually two) compared to the sympatric round-bodied tropidurid *Tropidurus hispidus* (referred to as *T. torquatus*), an extreme habitat-generalist, whose clutch ranges from 3 to 14 eggs (Vitt, 1981).

It is interesting to note that three female *M. macrorhyncha* contained embryos/ova in more than one developmental stage (including simultaneous occurrence of stage 3 ova and stage 5 embryos), which may suggest that asynchronous embryo development within a female may occasionally occur in that species (it is also possible, however, that the oviductal ova in those particular females had, for some reason, failed to develop further and remained small; in any case, those ova looked normal, with no signs of degeneration). Asynchronous development among embryos within females is previously unreported for South American *Mabuya*, and may be another peculiarity of *M. macrorhyncha*. It is also probable, however, that egg reabsorption may have taken place, as it has been reported for the closely related *Mabuya* sp. of north-east Brazil (Stevaux, 1993).

We found brood size to be significantly related to female SVL in *M. macrorhyncha* at Barra de Maricá, which did not occur among the populations of this species studied by Vanzolini & Rebouças-Spieker (1976) at the São Paulo coast. We cannot say, however, if this represents actual differences between southern and northern populations of *M. macrorhyncha*, or if other factors such as sample size may be taken into account. In the case of *M. agilis*, on the other hand, we believe that the absence of a relationship may be a result of the small sample size (the presence of juvenile-sized females with implanted ova is unlikely to have affected

TABLE 3. Reproductive characteristics of some Neotropical *Mabuya* species. The letter (I) designates insular populations. *, pooled data from two or more localities; a, mean, range in parentheses; b, time at which parturition occurs; c, calculated from Table 4 of the referenced paper; d, as *M. mabouia*; e, as *M. bistrriata*.

Species	n	Brood Size ^a	Reproductive season ^b	Locality	Source
<i>M. agilis</i>	18	3.5 (2-6)	Oct-Nov	Maricá, SE Brazil	Present study
<i>M. bistrriata</i>	5	- (4-8)*	?	Amazonian Brazil	Ávila-Pires (1995)
<i>M. caissara</i>	17	5.0 (2-8) ^c	Nov-Dec	Ubatuba, SE Brazil	Vanzolini & Rebouças-Spieker (1976)
<i>M. caissara</i>	14	5.6 (3-9) ^c	Nov-Dec	Caraguatatuba, SE Brazil	<i>Ibid.</i>
<i>M. caissara</i>	10	4.0 (2-6) ^c	Nov-Dec	São Sebastião, SE Brazil	<i>Ibid.</i>
<i>M. caissara</i>	12	4.8 (3-6) ^c	Nov-Dec	Bertioga, SE Brazil	<i>Ibid.</i>
<i>M. frenata</i>	12	4.0 (1-8)	?	Araguaia, Cent. Brazil	Vitt (1991)
<i>M. frenata</i>	113	4.9 (2-8)	Aug-Nov	Valinhos, SE Brazil	Vrcibradic & Rocha (1998)
<i>M. heathi</i>	131	5.0 (2-9)	Sept-Nov	Exu, NE Brazil	Vitt & Blackburn (1983)
<i>M. mabouia</i> (I)	7	3.3 (3-5)	?	Dominica, West Indies	Somma & Brooks (1976)
<i>M. macrorhyncha</i>	11	2.4 (2-5) ^c	Dec-Feb	Enseada, SE Brazil	Vanzolini & Rebouças-Spieker (1976)
<i>M. macrorhyncha</i>	12	3.2 (1-6) ^c	Dec-Feb	Peruíbe, SE Brazil	<i>Ibid.</i>
<i>M. macrorhyncha</i> (I)	35	3.3 (2-4) ^c	?	Buzios, SE Brazil	<i>Ibid.</i>
<i>M. macrorhyncha</i> (I)	51	2.2 (1-4) ^c	?	Qu. Grande, SE Brazil	<i>Ibid.</i>
<i>M. macrorhyncha</i>	38	2.7 (2-4)	Nov-Dec	Maricá, SE Brazil	Present study
<i>M. nigropunctata</i> ^d	-	- (3-7)	Aug-Nov	Iquitos, Peru	Dixon & Soini (1975)
<i>M. nigropunctata</i> ^d	10	5.2 (4-6)	?Mar-Aug	Santa Cecilia, Ecuador	Duellman (1978)
<i>M. nigropunctata</i> ^c	94	4.7 (2-9)*	Aug-Sept	Amazonian Brazil	Vitt & Blackburn (1991)
<i>M. unimarginata</i>	7	5.2 (2-7)	?	Costa Rica (Pacific slope)	Fitch (1985)
<i>M. sp.</i>	76	2.6 (1-4)	Jan-Feb	Cabaceiras, NE Brazil	Stevaux (1993)

the correlation, since only one female smaller than 60 mm was present in our sample of "gravids", and it had only three ova). Brood size is significantly affected by female body size in other Brazilian *Mabuya* species (Vanzolini & Rebouças-Spieker, 1976; Vitt, 1991; Vitt & Blackburn, 1983, 1991; Stevaux, 1993; Vrcibradic & Rocha, 1998), and it is quite surprising that, in our study, *M. agilis* did not show such a relationship, whereas *M. macrorhyncha*, with their smaller and less variable broods, did.

Like other Brazilian *Mabuya* species whose reproduction has been reasonably well-studied (Vitt & Blackburn, 1983, 1991; Vrcibradic & Rocha, 1998), *M. agilis* attains reproductive maturity at small body sizes (i.e. about 49 mm SVL), presumably when only a few months old (see Blackburn & Vitt, 1992). *Mabuya macrorhyncha*, on the other hand, apparently does not reproduce in its first year, as suggested by our data and by Vanzolini & Rebouças-Spieker (1976). The latter authors also mentioned that the smallest reproductive females in their samples were about 60 mm in SVL, which agrees with our data. Similar patterns have been reported by Stevaux (1993) for the closely related *Mabuya* sp. This relatively delayed reproduction of the *M. macrorhyncha* lineage relative to other congeners (including the sympatric *M. agilis*) is difficult to interpret in the light of our data and deserves further study. Nevertheless, the gestation periods of both *M. macrorhyncha* and *M. agilis* are apparently identical, spanning between nine and twelve months. The pattern of embryonic growth is also apparently similar between the two species, with little increase in ovum diameter during the first five or six months, followed by rapid embryonic growth thereafter, as in other Brazilian *Mabuya* species (Blackburn & Vitt, 1992; Stevaux, 1993; Vrcibradic & Rocha, 1998). The reproductive cycle of *M. macrorhyncha* appears to lag about one month behind that of *M. agilis*: of the 17 gravid females of the former species collected in September, all were in stage 5, whereas five of the eight gravid *M. agilis* from the same month were in stage 6 (i.e. bore well-formed embryos). Thus, *M. macrorhyncha* breeds somewhat later than *M. agilis*, with parturition probably beginning in late October or early November and apparently extending into December, when that of *M. agilis* may have already ceased. Unfortunately, we have very few adult females of both species from the period November-February, so that it is not possible to determine when parturition actually ceases in each of them. It is also interesting to note that the three smallest gravid *M. agilis* from September were in stage 5, while the five largest were in stage 6, suggesting that first-year females of this species may breed somewhat later than older females, as reported by Blackburn, Vitt & Beuchat (1984) for *M. heathi*.

Although late-stage embryos were found in six *M. agilis* and two *M. macrorhyncha*, none of these appeared large enough to be full-term. Among São Paulo populations, neonate *M. macrorhyncha* are apparently

born at a SVL of 32-34 mm (Vanzolini & Rebouças-Spieker, 1976; Zanotti *et al.*, 1997). Three term embryos taken from a female *M. agilis* from the restinga of Grumari, located about 160 km west of Barra de Maricá, averaged 30.6 ± 0.38 mm in SVL (Vrcibradic, unpubl. data), which suggests that the young of this species are born at a SVL of at least 31 mm. The lack of neonate-sized individuals of both species in our sample further obscures our understanding of when parturition actually occurs.

The breeding periods of *M. agilis* and *M. macrorhyncha* are short and well defined, like those of other Neotropical *Mabuya* (see table 3), which would supposedly place them into the category of "non-continuous" breeders, according to the classification of Sherbrooke (1975). Indeed, based on that work, Rocha (1994) referred to *M. heathi* and *M. nigropunctata* (= *M. bistrata*) as having non-continuous reproduction. Although testis cycles in males of the Barra de Maricá species are clearly seasonal and non-continuous, application of such terms to female cycles may not be appropriate: the simultaneous presence of vitellogenic follicles and implanted ova or embryos in the species studied by us indicate that reproduction may actually be continuous, with ovulation occurring shortly or immediately after parturition (almost all sexually mature females of both species were reproductively active). The production of tiny, yolk-poor follicles by female neotropical *Mabuya* is energetically unexpensive, and may occur simultaneously with gestation, which is very long and accounts for those lizards having annual reproduction.

Males of the two *Mabuya* species, unlike females, apparently attain sexual maturity at similar SVLs (55-56 mm), although the minimum reproductive size of male *M. agilis* may be overestimated, since it represented the smallest male in the whole sample. Testis cycles overlap considerably between the two species, with maximum gonadal activity during the wet season, coincident with the period of parturition and ovulation in females. It appears that, for some reason, testes of *M. agilis* suffer a greater reduction in size during the dry season compared to *M. macrorhyncha*. Reproductive cycles (both of males and females) of the two species overlap almost completely, which suggests that they may be regulated by the same factors, such as environmental cues and/or food availability (see Rocha, 1992 and Stevaux, 1993). Environmental variables such as rainfall, temperature and photoperiod seem to strongly influence the testis cycle of *M. macrorhyncha*, whose response to the variation of the first two apparently takes about two months (it is quite puzzling that the response to photoperiod was different). Males of another Brazilian species, *M. frenata*, also respond significantly to the above variables with a time-lag of two months, but the relationship is negative in this inland form (Vrcibradic & Rocha, 1998). Similarly, testis size of male *M. heathi* from north-east Brazil increases as the dry season progresses and decreases when conditions

get wetter (Vitt & Blackburn, 1983), showing a trend opposite to that of *M. macrorhyncha* (and of its close relative, *Mabuya* sp.; see Stevaux, 1993). Maybe the male cycles of neotropical *Mabuya* are more strongly tied to the female cycles than to direct external influences (male peak spermiogenesis always coincides with female late parturition-early ovulation periods), but a better understanding of the effects of environmental cues on male cycles of tropical lizards is needed before any conclusions can be drawn.

Monthly variation in fat body mass does not seem to be too important for male reproductive activity in either species, although a comparison of Figs. 5b and 6 (lower right) suggest an inverse relationship between testis and fat body cycles in *M. agilis* that could, perhaps, be clearer if the sample sizes were larger. A comparison of Figs. 4b and 6 (lower left) is even more suggestive and, again, we believe that the small sample size of *M. agilis* was responsible for the lack of a significant correlation between fat body mass and embryo size. This was not the case for *M. macrorhyncha*, for which the correlation was significant and showed that fat reserves undergo a decrease in mass during the rapid growth phase of the embryos, as in other Brazilian *Mabuya* (see Blackburn & Vitt, 1992; Stevaux, 1993; Vrcibradic & Rocha, 1998). The considerable increase in size of the conceptus of *M. macrorhyncha*, which is similar to that of other New World congeners (Vitt & Blackburn, 1983, 1991; Blackburn & Vitt, 1992; Stevaux, 1993; Vrcibradic & Rocha, 1998), indicates that reproduction is more expensive energetically for females than for males, which may explain the differential importance of fat reserves among sexes (e.g. Gaffney & Fitzpatrick, 1973; Jameson, 1974; Ortega, 1986; Ramirez-Pinilla, 1991; Huang, 1997).

The pattern of sexual dimorphism in size and shape observed for the two species at Barra de Maricá, with females reaching larger body sizes, but having relatively smaller head dimensions than males, agrees with that of other South American *Mabuya* species (Rebouças-Spieker, 1974; Vitt & Blackburn, 1983, 1991; Stevaux, 1993; Vrcibradic & Rocha, 1998). Sexual dimorphism in *M. macrorhyncha* is also clear from Tables 6 to 11 of Rebouças-Spieker (1974), concerning populations from the São Paulo coast. Large female body size among neotropical *Mabuya* may be the product of evolutionary pressures acting to increase the number and volume of offspring carried by the females (e.g. Fitch, 1981; Vitt & Blackburn, 1983, 1991). Such a pressure would not be expected to be strong in *M. macrorhyncha*, whose broods are usually of only two or three (see Vitt (1981) for data on the small-brooded Tropicidurid *Tropidurus semitaeniatus*), but even so, females of this species have SVLs larger than those of males and positively correlated to brood size. It is possible that small brood size in *M. macrorhyncha* is a derived character, acquired after its ancestors adapted to a bromelicolous mode of life (see above), a view opposed to that of Rebouças-Spieker (1974), who proposed that this species is an ancestral form, based on

biogeographical analyses. Naturally, biochemical and genetic comparisons with other New World species are needed before any conclusions can be drawn. Among male neotropical *Mabuya*, attainment of relatively large heads has been suggested to be related to aggressive male-male interactions (Vitt & Blackburn, 1983; 1991). This seems a plausible explanation, though we have never witnessed such behavior in either species at Barra de Maricá (see also Stevaux, 1993 for a discussion of this topic).

We conclude that *M. macrorhyncha* and *M. agilis* have reproductive characteristics and patterns of sexual dimorphism that are typical of New World *Mabuya* in general, e.g. ovulation of minute and yolk-poor ova, gestation lasting about one year (with most of the mass increase of the embryos occurring within the four months prior to parturition), large female body size and relatively large head dimensions in males. *Mabuya macrorhyncha* has, however, some peculiar characteristics that differ from *M. agilis* and its other Neotropical congeners (except a very close relative in north-east Brazil): it does not breed in its first year (delaying first reproduction until attaining a SVL of ca. 60 mm), produces relatively small broods, and females may present asynchronous breeding (or engage in egg reabsorption). These characteristics should not be attributed to possible effects of the sympatry with *M. agilis*, since they are present in allopatric populations in São Paulo State (Vanzolini & Rebouças-Spieker, 1976), nor to the female size-brood size relationship, since the two species do not differ in adult body size. Such unique features of the *M. macrorhyncha* lineage should be better studied in order to investigate if they represent primitive traits or secondary adaptations, possibly related to the species' bromelicolous habits.

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