

## REPRODUCTIVE ECOLOGY OF BOINE SNAKES WITH EMPHASIS ON BRAZILIAN SPECIES AND A COMPARISON TO PYTHONS

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**ABSTRACT:** Boids occur in North, Central and South America, the West Indies, Africa, including Madagascar, Asia and in some Pacific Islands as well. In Brazil they occur in a wide range of habitats and climatic zones throughout the country. This study presents reproductive and morphometric data for eleven Brazilian boid species and subspecies (*Boa c. constrictor*, *B. c. amarali*, *Corallus caninus*, *Co. hortulanus*, *Co. cropanii*, *Epicrates c. cenchria*, *Ep c. assisi*, *Ep c. crassus*, *Eunectes murinus*, *Eu. deschauenseei* and *Eu. notaeus*) including some morphometric data for Madagascan (*Sanzia madagascariensis* and *Acrantophis dumerili*) and Pacific boas (*Candoia carinata*, *Ca. aspera* and *Ca. bibroni*). These large snakes present a very conservative pattern in terms of seasonality in female reproductive cycles, size at maturity, litter and offspring relative size, and reproductive frequency. The reproductive pattern is similar among the boid species we studied and also similar to pythonids. Females' cycles are non-annual and always seasonal, usually with births occurring mostly in the spring-summer. These snakes show sexual dimorphism occurs in mean body length, head size, spur size and stoutness. In species in which males exhibit combat behavior prior to the mating season, mean body size dimorphism is not present (i.e. *Ep. cenchria* subspecies). Boid males' reproductive cycles are more variable, being continuous or seasonal depending on the species.

**KEYWORDS:** reproduction, fecundity, sexual maturity, sexual dimorphism, body size, reproductive pattern.

### INTRODUCTION

Reproductive data for vertebrates are of great importance for testing hypothesis and elaborating evolutionary models that integrate many ecological attributes of the organism (Shine, 1980a, 1983; Madsen *et al.*, 1992; Krebs, 1999; Olsson *et al.*, 1999). The best studied aspect of snake reproduction is the reproductive cycle. Snakes from temperate areas reproduce seasonally according to the warmer seasons of the year (Seigel and Ford, 1987). However, in tropical and subtropical areas, reproductive cycles vary widely from seasonal to continuous (Janeiro-Cinquini *et al.*, 1993; Fowler *et al.*, 1998; Marques, 1996a; Pizzatto and Marques, 2002; Shine, 2003; Balestrin and Di-Bernardo, 2005; Brown and Shine, 2006).

Reproductive events can be highly correlated with climatic variables (e.g. temperature, rainfall, photoperiod), ecological factors such as resources availability, reproductive mode and/or phylogenetic relationships (*cf.* Seigel and Ford, 1987; Vitt, 1987; Marques, 1996a,b, Madsen and Shine, 1996a,b, 1999; Brown and Shine, 2006). Specifically, studies on Neotropical species have suggested that phylogeny is a strong factor constraining reproduction in snakes (e.g., Marques, 1996a,b; Hartmann *et al.*, 2002; Valdujo

*et al.*, 2002) however its influence can be variable in the different lineages.

The family Boidae is a basal lineage within Macroscotomata represented by the subfamilies Boinae, Erycinae and Ungaliophiinae (Lee and Scanlon, 2002; Slowinski and Lawson, 2002; Vidal and Hedges, 2002; Vidal *et al.*, 2007). Boids are phylogenetically closely related to the Pythonidae, and at least the boines, like pythons, are large size snakes. In Brazil, the boids are represented by eight species and six subspecies belonging to the subfamily Boinae. This work presents reproductive and morphometric information on all the Brazilian boids (except for *Ep c. maurus*) including reproductive cycles of males and females, body sizes, size at sexual maturity, sexual dimorphism, and reproductive output. For comparative purposes, we also present data on size at sexual maturity and sexual dimorphism for Pacific and Madagascan boas. The reproductive patterns are compared among the boids (mostly the boines but including some erycines) and to the pythonids, and we discuss the influence of phylogeny on boid reproduction.

### MATERIAL AND METHODS

A total of 2787 preserved specimens belonging to the taxa *Boa constrictor constrictor* (N = 442),

*B. c. amarali* (N = 201), *Corallus caninus* (N = 87), *Co. cropanii* (N = 4), *Co. hortulanus* (N = 475), *Epicrates cenchria assisi* (N = 108), *Ep c. cenchria* (N = 238), *Ep c. crassus* (N = 127), *Eunectes deschauenseei* (N = 78), *Eu. murinus* (N = 413), *Eu. notaeus* (N = 34), *Candoia carinata* (N = 221), *Ca. aspera* (N = 128), *Ca. bibroni* (N = 186), *Sanzinia madagascariensis* (N = 38) and *Acrantophis dumerili* (N = 7) were examined from herpetological collections. For each snake we recorded the sex and measured the snout-vent length (SVL, nearest 1 cm), tail length (TL, nearest 1 cm), head length (HL, nearest 0.1 mm) and head width (HW, nearest 0.1 mm), mid-body circumference (BC, nearest 0.1 mm), lateral flatness at mid-body (LF – represented by mid-body height/mid-body width, nearest 0.1 mm), the length of the right spur that was visible from outside of the body (SL, nearest 0.1 mm). In some specimens, and especially in females, the spur is too small to be measured *in situ*. As spur size were not significantly related to snake SVL, we compared the absolute size between sexes using Mann-Whitney test (Zar, 1999). Color was recorded in *Co. caninus* as it varied according to size.

Specimens were dissected by a mid-ventral incision. Using a caliper we recorded the length of the largest follicle or embryo diameter; number of follicles in secondary vitellogenesis or embryos; length, width and thickness of both testes and diameter of deferent duct close to the cloaca. Because sometimes the size of the embryo in the embryonic sac does not reflect embryonic development (see data for *Ep c. crassus* in Fig. 1) we classified embryos as follow: stage 1 – just following ovulation (and probably fecundation) when only yolk was visible, stage 2 – a small embryo could be observed but yolk was still very abundant, and stage 3 – a large embryo was present and totally developed, without yolk (*cf.* Pizzatto, 2005).

The Brazilian specimens were collected in different localities within the range of each species/subspecies. As our aim was to understand the general reproductive pattern of the species as a whole we did not consider geographic variation. Additionally, some preliminary analysis did not identify significant differences among populations in species with large sample sizes and broad occurrence areas such as *Co. hortulanus* and *Ep c. cenchria*.

Females with vitellogenic follicles larger than 10 mm (*cf.* Shine, 1978) and/or folded oviducts, which reflect previous ovulation and gestation, were considered mature. Males were mature when testes

were turgid and deferent ducts were opaque and convoluted (*cf.* Shine, 1980b; Slip and Shine, 1988).

Occasional observations of reproductive behavior were recorded from specimens kept in outdoor enclosures or in indoor cages in the Laboratório de Herpetologia of the Instituto Butantan (IB); in both places temperature and humidity were not artificially controlled. Data on birth dates and newborn sizes were obtained from snakes that were pregnant or giving birth when received at IB.

Size at sexual maturity was compared among species by ANCOVA, using SVL of the smallest mature individual as covariable, mean SVL of mature snakes as independent variable and sex as factor (Zar, 1999). For the Australian pythons we used data on mean SVL and smallest mature snakes from Shine and Slip (1990) and Slip and Shine (1988). Mean SVL of snakes was compared between the sexes in co-specifics using t-tests, and by sex among species using ANOVA (Zar, 1999). Sexual size dimorphism (SSD) as calculated as [(mean SVL of the larger sex/mean SVL of the smaller sex) - 1]; when females are larger than males the index is positive and when males are larger it is negative (*cf.* Shine, 1994). We used ANCOVA to compare TL, HL, HW, LF (co-variables) between sexes of co-specifics; SVL was the independent variable and sex the factor (Zar, 1999). Data were log-transformed when necessary to achieve the premises of parametric tests. The relationship between litter size and female SVL was analyzed within each species using linear regressions and Spearman correlation when data could not be normalized (Zar, 1999). Data on clutch size and newborn SVL of pythonid, erycine and *Candoia* spp. were obtained from the literature. We used ANCOVA to compare clutch size and newborn SVL (co-variables) between boine and pythonine, with subfamily as factors and female SVL as independent variable. Data were log-transformed when necessary (Zar, 1999). Because life traits are influenced by phylogeny we used independent analysis (Felsenstein, 1985) to compare these variables among species. We ran the contrast analyses twice, using two alternative phylogenetic hypotheses. In both cases the pythonid phylogeny was the same, and was taken from Kluge (1993). However, this hypothesis did not resolve relationships among *Antaresia* spp., thus, we have used the arrangement *A. maculosa* (*A. stimsoni* (*A. childreni*)) but have run all other possible arrangements also, and all give the same results. For the boids we used two different phylogenies: one based on morphology (primarily osteology, Kluge 1991) and one that used molecular data also (Burbrink 2005). In both scenar-

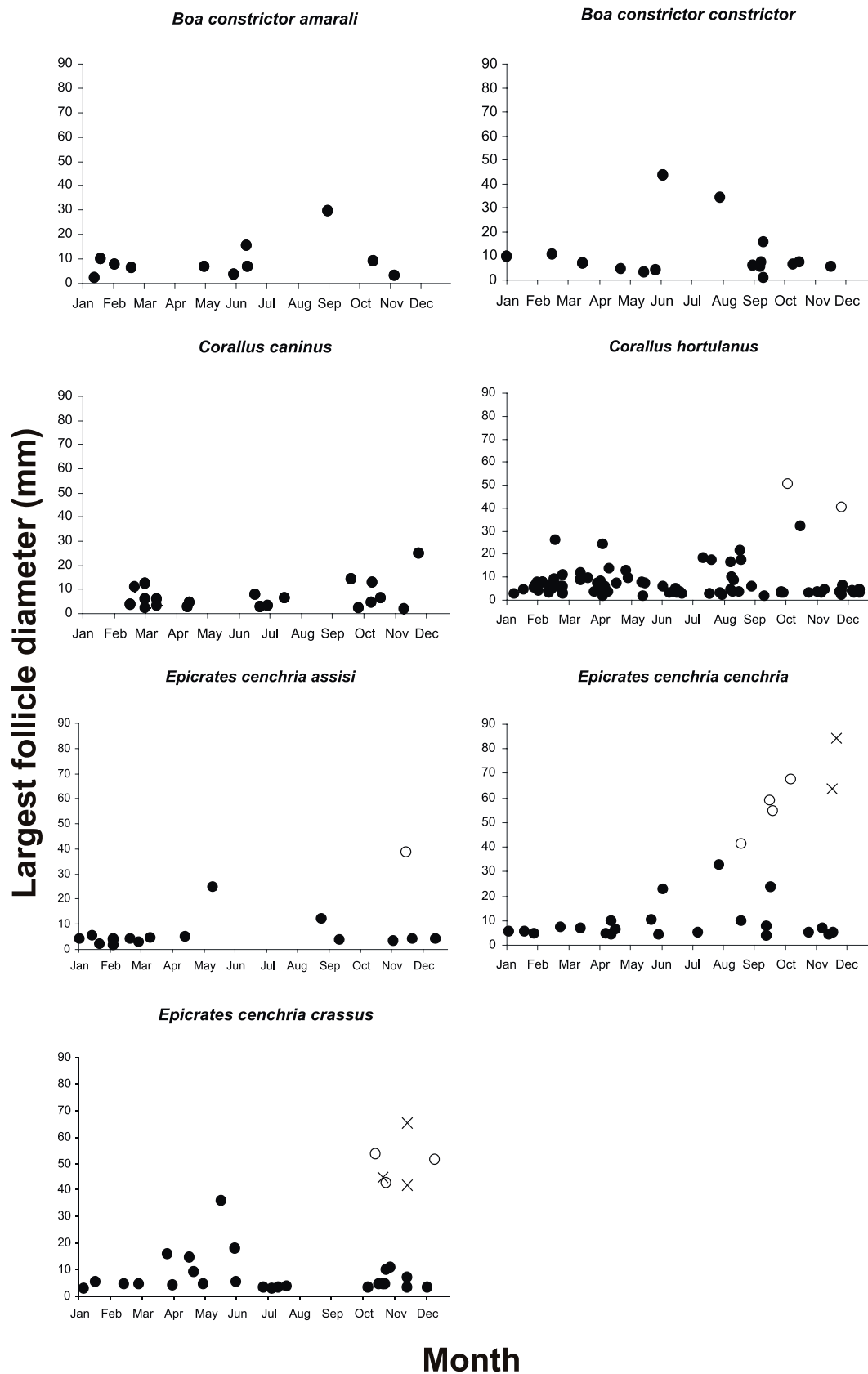


FIGURE 1. Seasonal follicular changes in Brazilian bovine snakes. Closed circles = ovarian follicle, open circles = stage 1 embryo, triangles = stage 2 embryo, crosses = ovarian follicle with corpus luteum.

ios, we considered the two Brazilian *Boa constrictor* subspecies as sister taxa and included relationships among the subspecies of rainbow boas *Ep c. cenchria* (*a(crassus(assisi))*), treating *Ep. cenchria hygrophilus* as a synonym of *Ep c. cenchria* and *Ep c. polylepis* as a synonym of *Ep c. crassus*, according to Passos (2003; see Pizzatto *et al.*, 2007a,b for the phylogenetic trees). Independent contrast analyses were run in Mesquite 1.05 (Maddison and Maddison, 2004) and PDAP package (Midford *et al.*, 2002). All branch lengths were adjusted to 1 and relationships between the contrasts of the variables were analyzed by linear regression forced through the origin (i.e., intercepts adjusted to 0: Martins and Hansen, 1996).

Reproductive frequency was estimated by the proportion of reproductive females in the samples (*cf.* Seigel and Ford, 1987). Volume of testes was calculated by the ellipsoid formula  $4/3\pi abc$ , in which  $a$  = length/2,  $b$  = width/2 and  $c$  = thickness/2. Testes volumes indicate sperm production (Volsøe 1944; Fox, 1952) and diameter of deferent duct can indicate sperm storage (Yokoyama and Yoshida, 1993; Almeida-Santos *et al.*, 2006). Variation in testes volumes and deferent duct diameter in the Brazilian boines was compared among the four seasons (summer: January-March, autumn: April-June, winter: July-September, spring: October-December) using Kruskal-Wallis test (KW) and Dunn method post hoc (Zar, 1999). In some species, testes volume and deferent duct diameter were related to SVL and the KW tests were performed using the proportion of the measures by SVL.

## RESULTS

### Sexual maturity and body size

Most females reached sexual maturity at 80-90% of mean adult SVL (mean  $78 \pm 11$  SD, range 61-95%; Table 1) and males at 60-70% (mean  $70 \pm 10$  SD, range 59-95%; Table 1). However, the mean proportional size at maturity did not differ significantly between the sexes (ANCOVA,  $F(\text{slopes}) = 0.71$ ,  $df = 23$ ,  $p = 0.408$ ,  $F(\text{intercept}) = 2.25$ ,  $df = 24$ ,  $p = 0.147$ ). A re-analyze for the Australian pythons showed the same trend (ANCOVA,  $F(\text{slopes}) = 1.83$ ,  $df = 23$ ,  $p = 0.189$ ,  $F(\text{intercept}) = 1.02$ ,  $df = 24$ ,  $p = 0.322$ ) with males reaching sexual maturity with 51-89% (mean  $71 \pm 12$  SD,  $n = 14$ ) and females with 57-97% ( $76 \pm 13$  SD,  $n = 13$ ; see original data and analysis on Shine and Slip, 1990). Mean body size of adult snakes differed among species (ANOVA:  $F_{(1,1559)} = 133.4$ ,  $p < 0.0001$ , Table 1).

### Sexual dimorphism

Except for *A. dumerili*, females were larger than males in all species, but the differences were significant only for *B. c. amarali*, *Co. caninus*, *C. hortulanus*, *Eu. murinus* and *Candoia* spp. (Tables 1 and 2). Two species of *Eunectes* (*Eu. murinus* and *Eu. notaeus*) were among the boids with higher SSD (0.608 and 0.309, respectively; Table 1). On the other hand *Eu. deschaunseei* showed a low value (0.079). The lowest SSD values were recorded in *A. dumerili* (males larger than females) and the genus *Epicrates* ( $\leq 0.030$  for all species, see Table 1). Relative tail length was larger in males than females, except in arboreal snakes (*Corallus* spp., *S. madagascariensis* and *Ca. bibroni*; Table 2, Appendix I). Some species also showed sexual dimorphism in relative head length, relative head width, lateral flatness of the body and body circumference (Table 2, Appendix I). The small sample sizes for female *Eu. murinus* and *Eu. deschaunseei* did not permit comparison of spur size between the sexes. However, spurs were larger in males than in females for Brazilian boines ( $p = 0.02$  in *Eu. deschaunseei* and  $p < 0.00001$  in all other species). In females of most species spurs were not externally detected. This is also true in newborn snakes of both sexes. In most species in which dimorphisms were recorded, they were not present in newborn snakes. One exception was newborn *Boa c. constrictor* females (mean SVL =  $445.2 \pm \text{SD}34.8$ ;  $N = 67$ ) which were larger than newborn males ( $441.2 \pm 35.8$ ;  $N = 65$ ,  $t = 2.27$ ,  $p = 0.024$ ), and had shorter tails (ANCOVA, slopes:  $F_{(1,119)} = 1.00$ ;  $p = 0.318$  intercept:  $F_{(1,120)} = 34.25$ ;  $p < 0.0001$ ).

### Female reproductive cycles

Vitellogenesis was long, lasting from autumn (April-June) to winter (July-September) in most species. However in both subspecies of *B. constrictor*, it was longer, starting in the summer (January-February), and in *Co. caninus* it lasted until spring (October-December) (Fig. 1 and 2). There were no vitellogenic follicles in the female samples of *Eunectes* spp., but based on distribution of hatchlings (SVL  $< 685$  mm in *Eu. murinus* and 539 mm in *Eu. deschaunseei*) throughout year, we can infer that vitellogenesis occurs from autumn to spring in *Eu. deschaunseei*, late winter to summer in *Eu. murinus* and from winter to early spring in *Eu. notaeus* (Fig. 2). Length of gestation was from four to six months in most species but may last up to nine months in the anacondas (Fig. 2).

TABLE 1. Snout-vent length (SVL, mm), proportional size at maturity, sexual size dimorphism index (SSD) and presence of combat bouts in boinae snakes. In parenthesis: range, N = sample size, bold letters: statistical significant results ( $p < 0.05$ ).

Species	SVL ♀♀ (mean ± SD)	SVL ♂♂ (mean ± SD)	t-student	Body size at maturity	SSD
<i>B. c. amarali</i>	1501.1 ± 162.6 (1270-1800, N = 47)	1418.4 ± 192.4 (1060-2130, N = 70)	t = 2.42 p = 0.017	♂♂: 0.74 ♀♀: 0.85	0.058
<i>B. c. constrictor</i>	2030.9 ± 468.6 (1418-3118, N = 37)	1903.4 ± 522.5 (1162-3713, N = 74)	t = 1.25 p = 0.213	♂♂: 0.61 ♀♀: 0.70	0.062
<i>Co. caninus</i>	1385.5 ± 182.5 (1120-1710, N = 25)	1055.3 ± 202.8 (835-1405, N = 11)	t = 4.83 p < 0.0001	♂♂: 0.65 ♀♀: 0.84	0.252 Combat
<i>Co. hortulanus</i>	1389.2 ± 136.9 (1168-1887, N = 104)	1233.3 ± 161.2 (802-1600, N = 107)	t = 7.56 p < 0.0001	♂♂: 0.79 ♀♀: 0.81	0.126
<i>Co. cropanii</i> *	1510 (N = 1)	1080, 1177, 1348 (n = 3)	—		0.338
<i>Ep. c. assisi</i>	1223.4 ± 107.5 (1085-1446, N = 18)	1204.5 ± 145.3 (988-1480, N = 25)	t = 0.47 p = 0.643	♂♂: 0.82 ♀♀: 0.89	0.016 Combat?
<i>Ep. c. cenchria</i>	1510.5 ± 88.4 (1420-1640, N = 35)	1466.1 ± 216.0 (946-1630, N = 48)	t = 1.15 p = 0.255	♂♂: 0.64 ♀♀: 0.94	0.030 Combat
<i>Ep. c. crassus</i>	1102.6 ± 93.4 (970-1371, N = 27)	1094.6 ± 116.5 (876-1301, N = 36)	t = -0.29 p = 0.771	♂♂: 0.80 ♀♀: 0.88	0.007 Combat
<i>Eu. deschauenseei</i>	1655.3 ± 300.4 (1200-2307, N = 12)	1537.6 ± 266.0 (1300-2107, N = 35)	t = -1.15 p = 0.258	♂♂: 0.84 ♀♀: 0.72	0.076
<i>Eu. murinus</i>	3626.7 ± 720.2 (2963-4480, N = 6)	2256.2 ± 407.1 (1335-3329, N = 35)	t = -6.75 p < 0.0001	♂♂: 0.59 ♀♀: 0.82	0.608
<i>Eu. notaeus</i>	2500, 2255 (N = 2)	1816.5 ± 214.3 (1515-2161, N = 8)	—	♂♂: 0.83	0.309
<i>A. dumerili</i>	1427.0 ± 80.0 (1350-1510, N = 3)	1553.0 ± 86.0 (1470-1708, N = 6)	—	♂♂: 0.95 ♀♀: 0.95	-0.064
<i>S. madagascariensis</i>	1471.0 ± 303.0 (1100-1910, N = 13)	1382.0 ± 222.0 (1106-1850, N = 13)	t = 0.86 p = 0.400	♂♂: 0.80 ♀♀: 0.75	0.883 Combat
<i>Ca. carinata</i> **	602.0 ± 156.0 (405-725, N = 69)	480.0 ± 76.0 (317-720, N = 61)	p < 0.05 see original paper	♂♂: 0.66 ♀♀: 0.67	0.254
<i>Ca. aspera</i> **	588.0 ± 142.0 (345-930, N = 43)	428.0 ± 83.0 (225-584, N = 21)	p < 0.05 see original paper	♂♂: 0.59 ♀♀: 0.63	0.374
<i>Ca. bibroni</i> **	983.0 ± 317.0 (600-1460, N = 13)	720.0 ± 229.0 (460-1190, N = 15)	p < 0.05 see original paper	♂♂: 0.64 ♀♀: 0.61	0.339

\* Probably adults (non dissected or eviscerated). \*\*Data from Harlow and Shine, 1992.

TABLE 2. Summary of sexual dimorphism in boine snakes showing the sex with larger measures. Statistics is showed in Appendix I and Table 1 (except for *Eumetes notaeus* from Argentina – see original paper). *Corallus cropanii*, *Eu. notaeus*, *Eu. murinus* (Brazilian populations) and *Acrantophis dumerilli* are absent due to the small sample size for most traits.

Species	SVL	TL	HL	HW	BC	LF	SL
<i>B. c. amarali</i>	♀♀	♂♂	♀♀	ND	ND	ND	♂♂
<i>B. c. constrictor</i>	Probably ♀♀	♂♂	♀♀	ND	ND	♂♂	♂♂
<i>Co. caninus</i>	♀♀	ND	ND	ND	ND	ND	♂♂
<i>Co. hortulanus</i>	♀♀	ND	♀♀	ND	ND	ND	♂♂
<i>Ep. c. assisi</i>	ND	♂♂	ND	ND	ND	ND	♂♂
<i>Ep. c. cenchria</i>	ND	♂♂	ND	ND	ND	ND	♂♂
<i>Ep. c. crassus</i>	ND	♂♂	ND	ND	ND	ND	♂♂
<i>Eu. deschauenseei</i>	Probably ♀♀	♂♂	ND	ND	ND	ND	♂♂
<i>Eu. notaeus</i> *	♀♀	♂♂	ND	—	—	—	♂♂
<i>S. madagascariensis</i>	ND	ND	ND	ND	ND	ND	♂♂
<i>Ca. carinata</i>	♀♀	♂♂	ND	♀♀	ND	ND	♂♂
<i>Ca. aspera</i>	♀♀	♂♂	ND	ND	ND	ND	♂♂
<i>Ca. bibroni</i>	♀♀	ND	ND	ND	ND	ND	♂♂

ND = no significant difference. SVL = snout-vent length, TL = tail length, HL = head length, HW = head width, BC = body circumference, LF = lateral flatness of the body, SL = spur length. \*Data from Waller *et al.*, 2007.



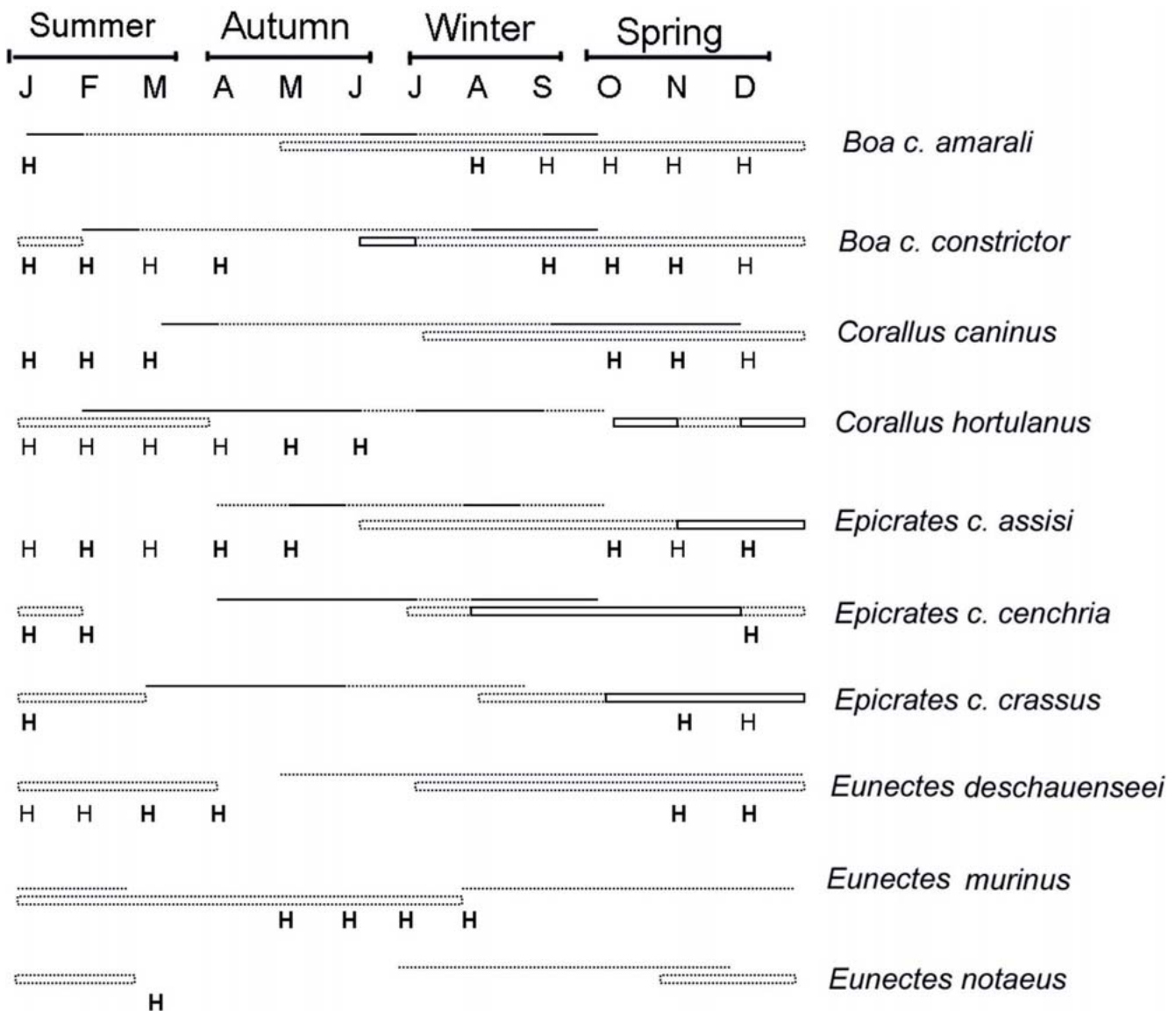


FIGURE 2. Female reproductive cycles in Brazilian boine snakes. Lines: vitellogenesis. Boxes: gestation. Solid lines and boxes: registered data from museum specimens, dotted lines and boxes: inferred data. Bold H = registered hatchlings, non-bold H: inferred hatchlings.

Hatchlings occurred mainly from spring to summer, extending until the autumn in some species (Fig. 2). Different from the other boids, hatchlings of the green anaconda (*Eu. murinus*) were found from autumn to winter (N = 4 litters, Fig. 2).

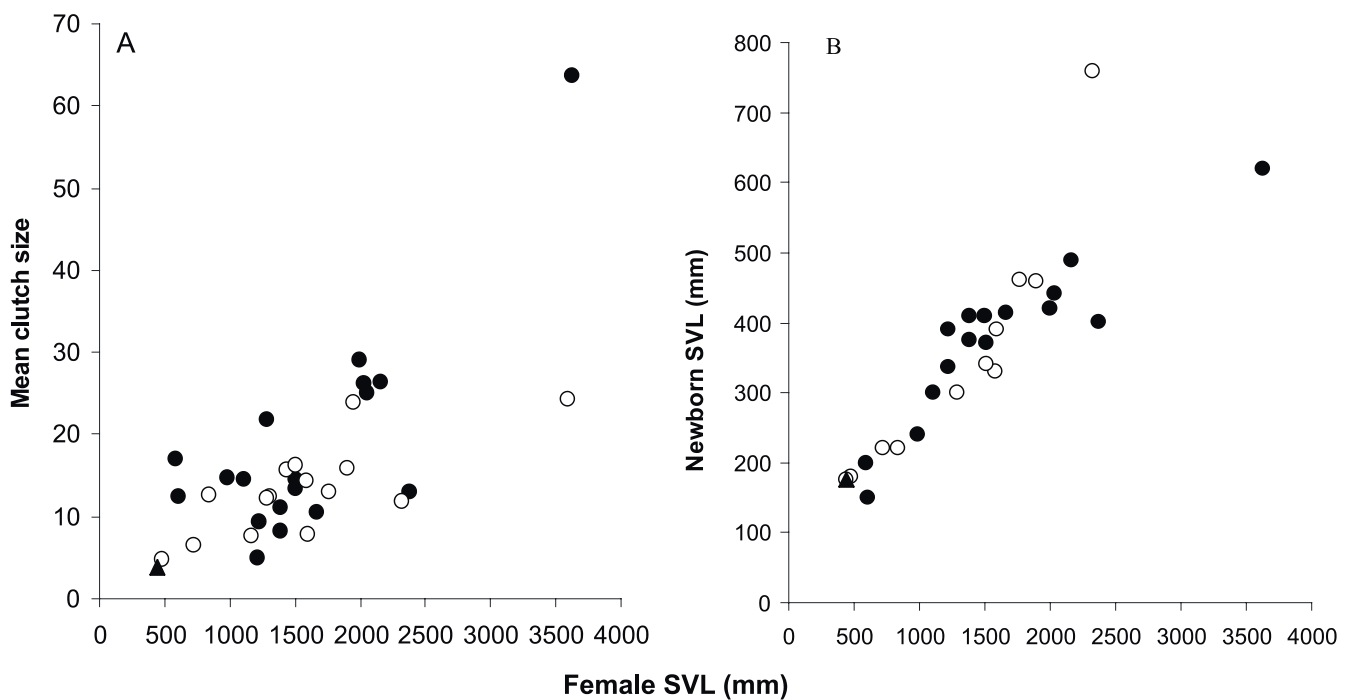
#### Reproductive output and newborn

Litter size varied from three to 82 newborn among the species (Table 3) and was positively related to female SVL in *B. c. amarali*, *B. c. constrictor* and *Co. hortulanus*. The relationship also tended to be positive in *Ep c. cenchria* and *Eu. deschauenseei* although results were not statistically significant (Table 3). Newborn SVL ranged from 285 mm in

*Ep c. assisi* and *E. c. crassus* to 685 mm in *Eu. murinus* (Table 3). After removing phylogenetic effects and considering both phylogenetic hypothesis, mean litter size increased with female SVL among boine and pythonine snakes (results for hypothesis based on Kluge (1991, 1993):  $R^2 = 0.27$ ,  $p = 0.005$ ; and based on Burbrink (2005) and Kluge (1993):  $R^2 = 0.28$ ,  $p = 0.004$ ). Clutch or litter size is similar among boine, erycine and pythonid snakes (ANCOVA between boine and pythonid, data log transformed, slopes:  $F_{(24,1)} = 0.28$ ,  $p = 0.760$ ; intercept:  $F_{(25,1)} = 2.28$ ,  $p = 0.143$ ; Fig. 3a). The relationship between female SVL and newborn SVL also did not differ among groups (ANCOVA between boinae and pythoninae, data log transformed, slopes:  $F_{(19,1)} = 0.60$ ,

TABLE 3. Mean litter size (followed by SD, range and sample size), newborn size and reproductive frequency in Brazilian boine snakes.

Species	Mean litter size	Litter size x mother SVL	Newborn SVL (mm)	Reproductive frequency
<i>B. c. amarali</i>	14.5 ± 6.9 (5-10, N = 9)	Rs = 0.83, p = 0.042	410.0 ± 52.1 (301-466, N = 24)	13.6% (N <sub>total</sub> = 22)
<i>B. c. constrictor</i>	27 ± 8.15 (18-41, N = 11)	Rs = 0.88, p = 0.004	453.0 ± 31.3 (341-495, N = 85)	16.7% (N <sub>total</sub> = 18)
<i>Co. caninus</i>	8.3 ± 3.7 (3-15, N = 10)	Rs = -0.22, p = 0.576	375.0 ± 10.6 (360-390, N = 7)	35.0% (N <sub>total</sub> = 20)
<i>Co. hortulanus</i>	11.1 ± 4.8 (3-24, N = 38)	R <sup>2</sup> = 0.18, p = 0.007	398.2 ± 41.1 (282-455, N = 43)	50.6% (N <sub>total</sub> = 83)
<i>Ep. c. assisi</i>	9.33 ± 2.6 (7-14, N = 60)	Rs = -0.39, p = 0.439	Smallest 285.0	30.3% (N <sub>total</sub> = 18)
<i>Ep. c. cenchria</i>	13.1 ± 4.9 (8-25, N = 10)	Rs = 0.44, p = 0.207	370.8 ± 21.3 (312-400, N = 25)	66.5% (N <sub>total</sub> = 18)
<i>Ep. c. crassus</i>	12.7 ± 4.5 (8-22, N = 10)	Rs = -0.09, p = 0.789	Smallest 285.0	60.2% (N <sub>total</sub> = 27)
<i>Eu. deschauenseei</i>	10.6 ± 9.6 (3-27, N = 5)	—	419.3 ± 50.9 (290-530, N = 53)	33.3% (N <sub>total</sub> = 11)
<i>Eu. murinus</i>	63.7 ± 15.1 (49-82, N = 4)	—	618.0 ± 55.1 (435-685, N = 250)	—
<i>Eu. notaeus</i>	13 (N = 1)	—	400.7 ± 8.5, (390-410, N = 11)	—

FIGURE 3. Relationship between female snout-vent length (SVL) and clutch size (left) and newborn size (right) in boine (closed circles), erycine (triangles) and pythonid (open circles) snakes. Data on *B. c. occidentalis*: Bertona and Chiaraviglio, 2003, *B. c. imperator*: Boback, 2005; Boback and Carpenter, 2007; *Candoia* spp.: Harlow and Shine, 1992; *Eunectes notaeus*: Waller *et al.*, 2007; Erycinae: Hoyer and Stewart, 2000; Pythonidae: Slip and Shine, 1988; Shine and Slip, 1990; Madsen and Shine, 1996; Shine *et al.*, 1998, 1999a,b; Aubret *et al.*, 2003.

p = 0.447; intercept:  $F_{(20,1)} = 0.61$ , p = 0.444; Fig. 3b). Proportion of reproductive females in the samples varied from 13.6% in *B. c. amarali* to 66.5% in *Ep. c. cenchria* (Table 3).

Newborn *Co. caninus* (SVL = 360-390 mm) were orange in color, varying from yellowish to reddish. The largest orange juvenile was 525 mm in SVL and after this size juveniles usually turned to green.

Among 29 juveniles smaller than 525 mm only three (SVLs = 437, 492 and 514 mm) were green.

#### Male reproductive cycles

Male samples sizes were not large enough to perform statistical analysis for the boas or for detecting any pattern for the anacondas and *Co. caninus*. Testes volume and deferent duct diameter seemed to be constant in *B. c. amarali* (Fig. 4a and 5a) but in *B. c. con-*

*strictor* testes were apparently biggest in January and February (summer), and the deferent duct diameter was larger in April and May (autumn) (Fig. 4b and 5b). There were no statistically significant variations in testes volume ( $H_{(3,31)} = 1.35$ ,  $p = 0.72$ , Fig. 4c) or deferent duct diameter ( $H_{(3,34)} = 2.78$ ,  $p = 0.43$ , Fig. 5c) in *Co. hortulanus*, *Ep c. assisi* and *Ep c. cenchria* (Table 4, Fig. 4 and 5). However *Ep c. crassus* showed maximum testes volume in summer-autumn (Jan-June), decreasing during winter-spring (July-

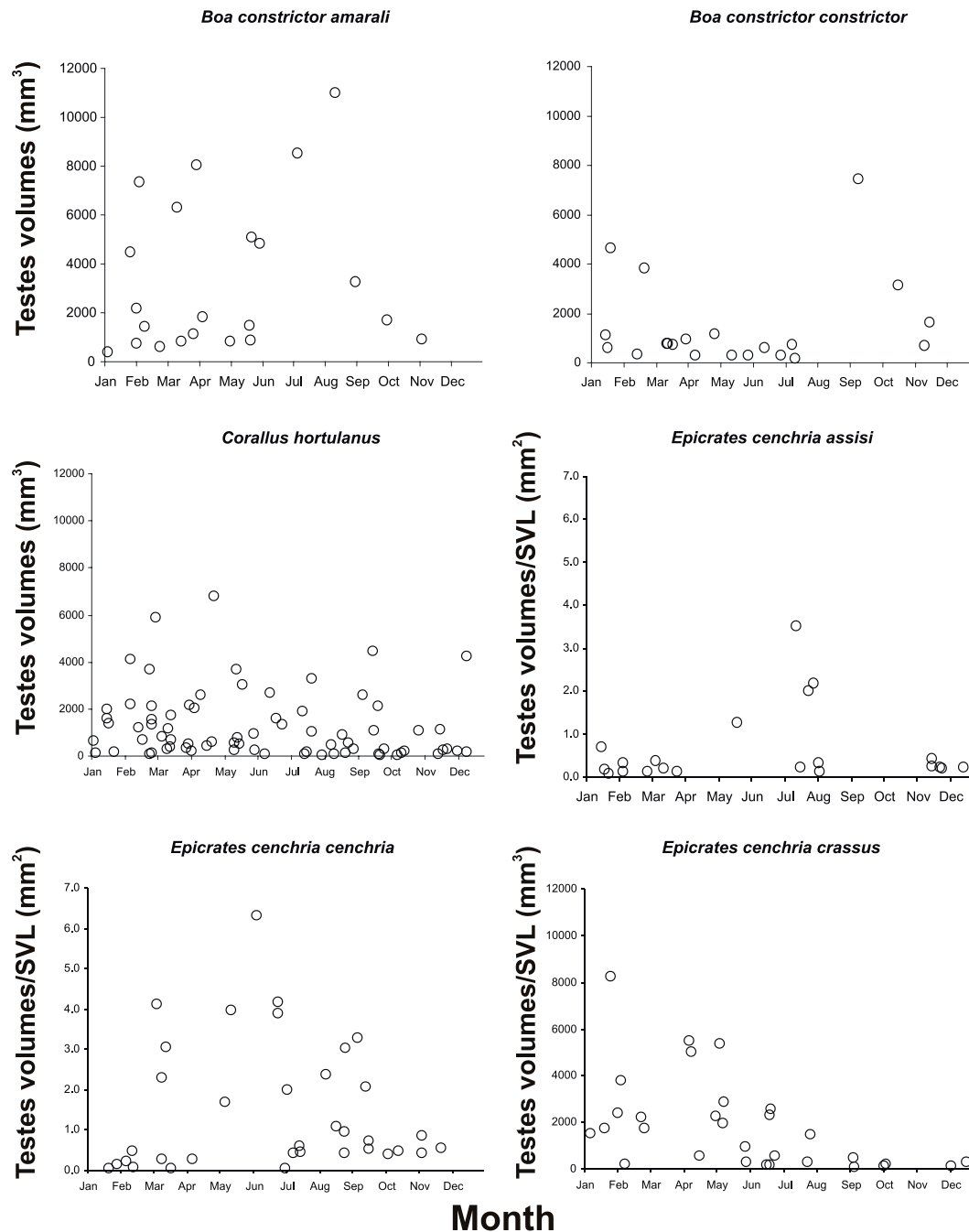


FIGURE 4. Seasonal variation in the volume of testes in Brazilian boine snakes.



TABLE 4. Statistical results of the comparison of testes volume and deferent duct diameter among seasons in Brazilian boine snakes.

Species	Testes volume	Deferent duct diameter
<i>Co. hortullanus</i>	$H_{(3,31)} = 1.35$ , $p = 0.720$	$H_{(3,34)} = 2.78$ , $p = 0.430$
<i>Ep. c. assisi</i>	$H_{(3,17)} = 1.13$ , $p = 0.346$	$H_{(3,16)} = 0.66$ , $p = 0.535$
<i>Ep. c. cenchria</i>	$H_{(3,31)} = 0.52$ , $p = 0.675$	$H_{(3,31)} = 1.45$ , $p = 0.246$
<i>Ep. c. crassus</i>	$H_{(3,30)} = 10.94$ , $p = 0.012^*$	$H_{(3,31)} = 8.12$ , $p = 0.045^*$

December, Table 4, Fig. 4) whereas deferent duct diameter increased during autumn-winter (April-September, Table 4, Fig. 5).

### Courtship and mating

In *B. c. amarali*, two courtship events were recorded, one in the outdoor enclosure of the Instituto Butantan in April 2003 and one in an indoor cage, in June 2004. Mating was observed in the middle of July 2003 in the outdoor enclosure. A courtship event was

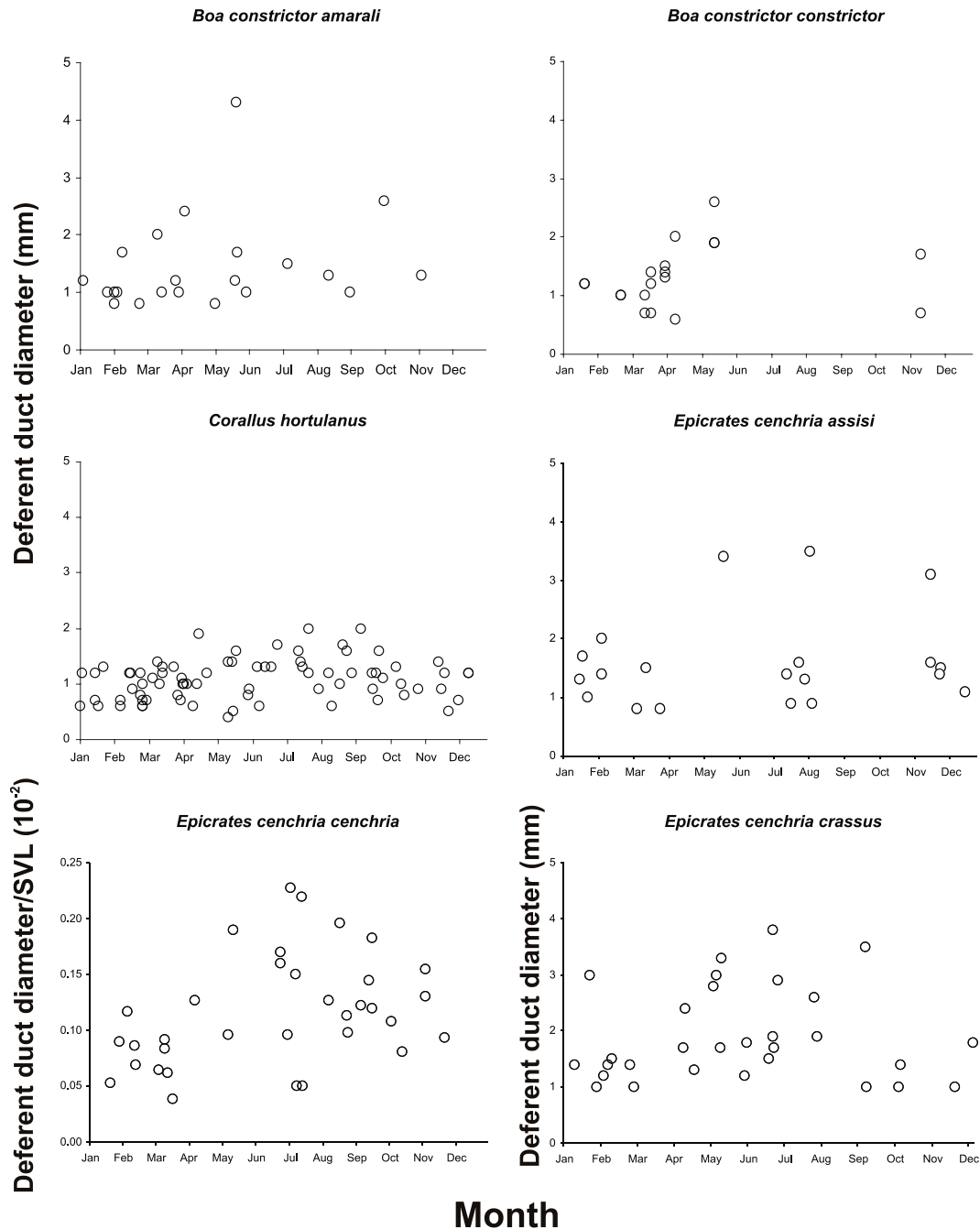


FIGURE 5. Seasonal variation in the diameter of deferent duct in Brazilian boine snakes.

observed between one male *B. c. constrictor* and one female *B. c. amarali* in mid-June 2004, in an indoor cage.

## DISCUSSION

### Size at maturity and sexual dimorphism

Boines are large size snakes, typically larger than 1.0 m in SVL, with the exception of *Candoia* species which rarely exceed this value. In most snakes males attain sexual maturity with smaller body sizes (Parker and Plummer, 1987), but the proportional size at maturity in boids and pythonids do not differ between sexes. Both sexes mature at a large size, that is to say, maturation is late, probably with advanced age, in these snakes.

Sexual dimorphism occurs in a set of morphological characteristics of the studied boids. Similar to pythonids, the predominant pattern among the boid is females are larger than males. Large body size as well as the relative larger mid-body circumference in most of the Brazilian boids may allow for increased reproductive output (clutch size, offspring size or even reproductive frequency) (see Shine, 1994, 2003). On the other hand, in some species of boids and pythonids, males and females do not differ significantly in mean body size (and consequently present a low SSD) and males of these species usually engage in combat bouts (Shine, 1994; Schuett and Schuett, 1995, Tolson 1992; Pizzatto *et al.*, 2006). Tail length is commonly longer in male snakes due to the presence of the hemipenis and retractor muscles (King, 1989), and it is not an exception for the boids. Long tails, however, are very useful in arboreal locomotion (Lillywhite and Henderson, 1993) thus arboreal boids lacked tail dimorphism (see also Pizzatto *et al.*, 2006, 2007b). Surprisingly, tail dimorphism is not present among Australian pythonids, even in the terrestrial species, this probably being a phylogenetic constraint. Female *B. constrictor*, *Co. hortulanus* and *Ca. carinata* presented larger heads than males. This occurs in many different groups of snakes, and it is usually related to sexual divergence in diet, with females exploring larger prey items (see Shine, 2003). Due to the fact that in some cases this dimorphism is present but no diet divergence is detected, other hypotheses were proposed but remain untested (Luiselli *et al.*, 2002). The few data on female and male diet obtained in preserved snakes (LP unpublished) do not permit detection of any sexual divergence in diet, and the meaning of the head size dimorphism in those spe-

cies remains unknown. We recorded larger spurs in males than in females in all Brazilian boines and it is also observed in *Eu. notaeus* from Argentina (Waller *et al.*, 2007) and *Eu. murinus* from Venezuela (Rivas, 1999). In *B. constrictor* the reduced spur in females is accompanied by absence of an ilius (the internal bone joined to spur; Hoge, 1947). This sexual dimorphism is common in most boids and pythonids and males usually use the spurs during combat and courtship (see Gillingham, 1987). However, in some species, such as *Epicrates* spp. and *Corallus* spp. spurs are so small, even in the males, and they are probably not used in any of these situations (see Schuett and Schuett, 1995; Pizzatto *et al.*, 2006).

### Reproductive timing

Despite the fact that Brazilian boids are broadly distributed throughout the country and dwell in different habitats, the reproductive timing is synchronized in most of the species and always seasonal. Vitellogenesis and gestation occurs mainly from autumn to spring (dry season) and parturition in spring-summer (rainy season). This general pattern is similar to boids from other localities in South and Central America, or even species occurring in the Old World. Gametogenesis and gestation occurring from autumn to winter is also recorded in the Argentinean boa *B. c. occidentalis* (Bertona and Chiaraviglio, 2003), in the yellow anaconda in the Argentinean Chacos (Waller *et al.*, 2007), in other species of *Corallus* (*Co. cookii*, *Co. grenadensis*, *Co. hortulanus* and *Co. ruschenbergerii*: Henderson, 2002), *Epicrates* (*Ep. fordii*: Murphy and Guese, 1977, Murphy *et al.* 1978, Tolson 1992, Tolson and Henderson, 1993; *Ep. c. cenchria*, *Ep. g. gracilis*: Murphy *et al.*, 1978; *Ep. c. assisi*: Vitt and Vangilder, 1983; *Ep. inornatus*: Reagan, 1984, Wiley, 2003), and even for captive boines of many species (Hanlon, 1964; Buden, 1975; Murphy *et al.*, 1978; Ross and Marzec, 1990). However, some species of Caribbean *Epicrates* present pregnancy during the summer and birth in autumn (Tolson, 1992, Tolson and Henderson, 1993). The parturition of captive Madagascan boas *Sanzinia madagascariensis* occurs in spring-summer, but births are recorded to *Acrantophis dumerilli* from winter to early spring (Ross and Marzec, 1990). Unfortunately, there are no data available on reproductive timing for Madagascan or Pacific boas (*Candoia*) in natural conditions.

Surprisingly, reproductive pattern in boids is also similar in the pythonids, despite the oviparity in the later. Most Australian pythons of the genera *Aspi-*

*dites*, *Liasis*, *Antaresia*, *Leiopython*, and *Morelia* and the some African-Asian *Python* species lay eggs in spring and hatching occurs in spring-summer, in both captive and natural conditions (Murphy *et al.*, 1978, 1981; Barker *et al.*, 1979; Charles *et al.*, 1985; Ross and Marzec, 1990; Shine and Slip, 1990; Barker and Barker, 1994). In *Python reticulatus* oviposition occurs during the spring (Shine *et al.*, 1998, 1999a), but *Python curtus* and *P. brongersmai* lay eggs during the autumn (Shine *et al.*, 1999b). Otherwise *Liasis fuscus* exhibits some plasticity in the reproductive time and frequency due to environmental conditions but oviposition occurs mostly in the spring and hatchlings in summer (Slip and Shine, 1990; Madsen and Shine, 1996b, 1999; Shine *et al.*, 1997). Timing of reproduction in the green anaconda also differs from the general pattern seen in other boids and pythonids with newborn *Eu. murinus* having been found only from May to August (except for one record in October – see Hero and dos Santos, 1987). The period between May and August correspond to the dry season (autumn-winter) in Brazil and these data agree with those from the Venezuelan llanos (Rivas, 1999), Guiana, Ecuador, Peru and Trinidad and Tobago (Strimple, 1993). Thus, reproductive timing in *Eunectes murinus* seems to be more related to precipitation regime and water level in the rivers (Rivas, 1999).

Both aggregations and combat are present among the boid and pythonid species. Combat is recorded in *Epicrates cenchria* ssp. (Schuett and Schuett, 1995; Pizzatto *et al.*, 2006), *Corallus caninus* (Osborne, 1984), some Caribbean *Epicrates* (*Ep. angulifer*, *Ep. exul*, *Ep. striatus*, *Ep. subflavus*: Tolson, 1992; Henderson and Tolson, 1993), *Candoia* spp. (see Schuett *et al.*, 2001), in the erycine *Eryx colubrinus* (see Schuett *et al.*, 2001), in pythonids such as *Antaresia* spp., *Morelia* spp. (except *M. spilota variegata*), *Liasis* spp. (Shine, 1994) and *Python regius* (see Schuett *et al.*, 2001), whereas aggregations are recorded in *Eunectes murinus* (Rivas, 1999; Rivas *et al.*, 2007), *Boa constrictor occidentalis* (Bertona and Chiaraviglio, 2003), and *Morelia spilota variegata* (Shine and Fitzgerald, 1995). There are no records of aggregation for Brazilian boas; however, in captivity mating only occurs when more than one male is present in the same cage (Ross and Marzec, 1990, Thiago Lima, pers. comm.).

Courtship, mating and related activities (male-male combat or reproductive aggregations) are usually recorded in captivity and occur in autumn-winter (dry season) for many boines and pythonids species (*B. c. amarali*, *B. c. constrictor*: this work; *B. c. oc-*

*cidental*: Bertona and Chiaraviglio; 2003, *Co. caninus*: Osborne, 1984; *Ep. cenchria* group: Schuett and Schuett, 1995; Pizzatto *et al.*, 2006; *Ep. f. fordii*: Murphy and Guese, 1977; Tolson and Henderson, 1993; *Eu. murinus*: Strimple, 1993; Australian pythons: Barker and Barker, 1994; Charles *et al.*, 1985, Shine and Slip, 1990; Barker *et al.*, 1979; Asian and African pythons: Murphy *et al.*, 1978, 1981 Ross and Marzec, 1990). However, spring mating seems to be a more common pattern in Caribbean *Epicrates* (Tolson, 1992; *Ep. angulifer*: Murphy *et al.*, 1978; Ross and Marzec, 1990; Tolson and Henderson, 1993; *Ep. subflavus*: Ross and Marzec, 1990; Tolson and Henderson, 1993; *Ep. striatus*: Hanlon, 1964; *Ep. inornatus*: Grant, 1932 *apud* Reagan, 1984; Peres-Rivera and Velez, 1978 *apud* Reagan, 1984; Tolson and Henderson, 1993), and also occurs in the Australian python *Morelia spilota* ssp. (Shine and Fitzgerald, 1995). *Eunectes murinus* in Venezuelan llanos and *Eu. notaeus* in the Argentinean Chacos mate from late winter to spring, the dry season in both areas (Rivas, 1999; Waller *et al.*, 2007). According to data on captive snakes, courtship, combat and mating season in Madagascan boas can be highly variable. Combat was observed in *Sanzinia madagascariensis* during summer-autumn and mating was recorded in autumn (*cf.* Carpenter *et al.*, 1978; Ross and Marzec, 1990). Courtship and mating in *Acrantophis dumerili* were observed in summer (Murphy *et al.*, 1981), autumn and winter (Ross and Marzec, 1990) and in *A. madagascariensis* in the summer (Murphy *et al.*, 1981) or all year round (Ross and Marzec, 1990). No field data on mating, combat or courtship are available for these species.

Male reproductive cycles are more variable among the boids. Continuous cycles were recorded in some Brazilian boines such as *B. c. amarali*, *Co. hortulanus*, *Ep. c. cenchri* and *Ep. c. assisi* (present study). Seasonal spermatogenesis, occurring in different seasons depending on the species, is also recorded among the boines (*e.g.* *Ep. c. crassus*, *B. c. constrictor*: present study; *B. c. occidentalis*: Bertona and Chiaraviglio, 2003; *Eu. notaeus*: Waller *et al.*, 2007) as well as in pythonids (*Python reticulatus*: Shine *et al.*, 1998, 1999a; *P. curtus* and *P. brongersmai*: Shine *et al.*, 1999b). In *Epicrates c. crassus* and *B. c. constrictor*, female and male gametogenesis are asynchronous with mating season occurring after sperm production and the increase in the deferent duct diameter suggests that males store sperm for a short period (over winter). Short-term sperm storage also occurs in male *Eunectes notaeus* (Waller *et al.*, 2007).

## Reproductive output

Litter size and offspring size are related to female size, as in most snakes and other animals (see Shine, 2003). Arboreal boids and pythonids have relatively smaller clutches/litters (Pizzatto *et al.*, 2007a). Island populations of *Boa constrictor* also have smaller litters and offspring than mainland populations in Belize (Boback, 2005). However, when all boides, erycines and pythonids were compared together the clutch/litter size and offspring size do not differ among the groups, showing a general conservative pattern.

Reproductive frequency as calculated in this work is low for most species. This suggests that boids do not reproduce annually, similar to most pythonids (Shine and Slip, 1990; Shine *et al.*, 1998, 1999a,b). Most snakes including the boids do not eat during reproductive period (Shine, 1980a; LP unpublished data) and due to the extended gestation period females are probably unable to start a new follicular cycle after giving birth. Thus, non-annual female reproductive cycle is probably a general pattern in viviparous snakes. The reproductive frequency was high among the *Ep c. cenchria* and *Ep c. crassus* ssp. when compared to the other boids. This might be due to differences in habitat use and/or behavior of pregnant females in both subspecies which could increase their exposure and probability of being caught.

In summary, boinae snakes show a general conservative pattern in the proportional size at maturity, female reproductive timing and fecundity, even when considering the broad climatic areas where they inhabit. This conservative pattern is also similar to most of the pythonids species. Male reproductive cycles are more variable, as are timing of courtship and mating. Two distinct behaviors associated to mating systems occur: reproductive aggregations and male-male combat, usually reflecting different patterns in sexual size dimorphism.

## RESUMO

Boídeos ocorrem na América do Norte, Central e do Sul, África, incluindo Madagascar, Ásia, bem como em algumas ilhas do Pacífico. No Brasil, ocorrem ao longo de uma ampla variedade de habitats e áreas climáticas. Este estudo apresenta dados reprodutivos e morfométricos para onze espécies e subespécies de boídeos brasileiros (*Boa c. constrictor*, *B. c. amarali*, *Corallus caninus*, *Co. hortulanus*, *Co. cropanii*, *Epi-crates c. cenchria*, *Ep c. assisi*, *Ep c. crassus*, *Eunectes murinus*, *Eu. deschauenseei* and *Eu. notaeus*),

incluindo dados morfométricos para os boídeos de Madagascar (*Sanzinia madagascariensis* e *Acrantophis dumerili*) e ilhas do Pacífico (*Candoia carinata*, *Ca. aspera* e *Ca. bibroni*). Essas serpentes de grande porte apresentam padrão conservativo em termos de sazonalidade do ciclo reprodutivo feminino, tamanho na maturidade, tamanhos relativos da ninhada e dos filhotes, e frequência reprodutiva. O padrão reprodutivo dos Boidae é similar ao de Pythonidae. Os ciclos femininos são não anuais e sempre sazonais, geralmente com os nascimentos ocorrendo principalmente na primavera-verão. Estas serpentes apresentam dimorfismo sexual no comprimento corporal médio, tamanho da cabeça, comprimento do esporão e robustez. Em espécies nas quais os machos realizam combate ritual previamente à época de cópula não ocorre dimorfismo no tamanho corporal médio (i.e. subespécies de *Ep. cenchria*). O ciclo reprodutivo masculino dos boídeos é mais variável, podendo ser sazonal ou contínuo, dependendo da espécie.

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## APPENDIX I

ANCOVA results to sexual size dimorphism in tail length (TL), head length (HL), head width (HW), lateral flatness of the body (LF) and body circumference (BC) among boine snakes. Fs = slopes F value, Fi = intercept F value.

Species	TL	HL	HW	LF	BC
<i>B. c. amarali</i>	Fs(1,105) = 0.0005; p = 0.983; Fi(1,106) = 45.14; p < 0.0001	Fs(1,90) = 1.95; p = 0.166; Fi(1,91) = 8.30; p = 0.005	F <sub>s(1,99)</sub> = 0.59; p = 0.444; F <sub>i(1,100)</sub> = 2.73; p = 0.101	F <sub>s(1,47)</sub> = 2.24; p = 0.141; F <sub>i(1,48)</sub> = 0.09; p = 0.760	F <sub>i(1,105)</sub> = 0.79; p = 0.375; F <sub>i(1,106)</sub> = 0.62; p = 0.432
<i>B. c. constrictor</i>	Fs(1,99) = 0.34; p = 0.558; Fi(1,100) = 16.31; p < 0.0001	Fs(1,101) = 6.52; p = 0.012	Fe(1,94) = 0.07; p = 0.788; Fi(1,95) = 0.39; p = 0.533	Fs(1,40) = 1.22; p = 0.276; Fi(1,41) = 5.15; p = 0.028	Fs(1,106) = 0.001; p = 0.975; Fi(1,107) = 1.23; p = 0.270
<i>Co. caninus</i>	Fs(1,32) = 1.08; p = 0.307; Fi(1,33) = 1.93; p = 0.174	Fs(1,37) = 0.07; p = 0.793; Fi(1,38) = 3.11; p = 0.086	Fs(1,24) = 1.11; p = 0.303; Fi(1,25) = 1.72; p = 0.201	Fs(1,31) = 2.31; p = 0.139; Fi(1,32) = 0.86; p = 0.360	Fs(1,27) = 0.28; p = 0.601; Fi(1,28) = 1.73; p = 0.199
<i>Co. hortulanus</i>	Fs(1,204) = 0.01; p = 0.937; Fi(1,205) = 0.45; p = 0.501	Fs(1,203) = 2.82; p = 0.094; Fi(1,204) = 43.49; p < 0.0001	Fs(1,194) = 0.76; p = 0.385; Fi(1,195) = 0.56; p = 0.456	Fs(1,193) = 0.02; p = 0.896; Fi(1,194) = 2.32; p = 0.129	Fs(1,179) = 0.13; p = 0.721; Fi(1,180) = 9.00; p = 0.0031
<i>Ep. c. assisi</i>	Fs(1,38) = 4.01; p = 0.052; Fi(1,39) = 13.89; p = 0.0006	Fs(1,36) = 0.01; p = 0.926; Fi(1,37) = 0.60; p = 0.444	Fs(1,29) = 0.12; p = 0.730; Fi(1,29) = 0.0001; p = 0.993	Fs(1,32) = 0.76; p = 0.391; Fi(1,33) = 0.0002; p = 0.988	Fs(1,38) = 1.19; p = 0.282; Fi(1,39) = 1.54; p = 0.221
<i>Ep. c. cenchria</i>	Fs(1,72) = 0.58; p = 0.447; Fi(1,73) = 9.11; p = 0.003	Fs(1,77) = 0.04; p = 0.847; Fi(1,78) = 1.97; p = 0.164	Fs(1,67) = 0.004; p = 0.950; Fi(1,68) = 0.01; p = 0.910	Fs(1,65) = 1.45; p = 0.232; Fi(1,66) = 0.66; p = 0.419	Fs(1,77) = 0.02; p = 0.895; Fi(1,78) = 1.72; p = 0.194
<i>Ep. c. crassus</i>	Fs(1,59) = 1.44; p = 0.234; Fi(1,60) = 11.21; p = 0.0014	Fs(1,50) = 3.54; p = 0.066; Fi(1,51) = 0.36; p = 0.549	Fs(1,53) = 3.97; p = 0.051; Fi(1,53) = 0.16; p = 0.688	Fs(1,57) = 0.12; p = 0.725; Fi(1,58) = 0.58; p = 0.147	Fs(1,56) = 0.76; p = 0.386; Fi(1,57) = 15.54; p = 0.0002
<i>Eu. deschauenseei</i>	Fs(1,20) = 0.002; p = 0.968; Fi(1,21) = 5.22; p = 0.033	Fs(1,16) = 0.001; p = 0.970; Fi(1,17) = 1.53; p = 0.233	Fs(1,18) = 0.31; p = 0.586; Fi(1,19) = 0.38; p = 0.544	—	Fs(1,15) = 0.18; p = 0.675; Fi(1,16) = 3.89; p = 0.066
<i>Eu. murinus</i>	Apparently larger in males*	Apparently did not differ*	Apparently did not differ*	Apparently did not differ*	Apparently larger in females*
<i>S. madagascariensis</i>	Fs(1,15) = 0.78; p = 0.783; Fi(1,16) = 2.05; p = 0.171	Fs(1,15) = 0.88; p = 0.363; Fi(1,16) = 2.72; p = 0.118	Fs(1,13) = 0.72; p = 0.412; Fi(1,14) = 0.29; p = 0.505	—	—
<i>Ca. aspera</i>	Fs(1,75) = 1.95; p = 0.617; Fi(1,76) = 4.88; p = 0.030	Fs(1,57) = 0.26; p = 0.609; Fi(1,58) = 3.22; p = 0.080	Fs(1,56) = 0.16; p = 0.692; Fi(1,57) = 0.54; p = 0.467	Fs(1,60) = 2.82; p = 0.098; Fi(1,61) = 0.05; p = 0.824	Fs(1,79) = 1.34; p = 0.295; Fi(1,80) = 12.85; p = 0.0006
<i>Ca. carinata</i>	Fs(1,130) = 0.43; p = 0.512; Fi(1,131) = 15.3; p = 0.0001	Fs(1,131) = 1.56; p = 0.214; Fi(1,132) = 1.46; p = 0.228	Fs(1,130) = 0.80; p = 0.373; Fi(1,131) = 4.04; p = 0.046	Fs(1,129) = 0.03; p = 0.858; Fi(1,130) = 0.02; p = 0.891	Fs(1,130) = 0.47; p = 0.492; Fi(1,131) = 4.62; p = 0.0033
<i>Ca. bibroni</i>	Fs(1,48) = 2.45; p = 0.124; Fi(1,49) = 0.47; p = 0.495	Fs(1,48) = 2.84; p = 0.098; Fi(1,49) = 0.04; p = 0.840	Fs(1,47) = 0.10; p = 0.750; Fi(1,48) = 0.43; p = 0.469	Fs(1,46) = 0.48; p = 0.493; Fi(1,47) = 0.07; p = 0.799	F <sub>s(1,48)</sub> = 0.15; p = 0.700; F <sub>i(1,49)</sub> = 0.21; p = 0.651

\*Sample size not large enough to run statistical tests.