Reproductive Biology, Mating Aggregations, and Sexual Dimorphism of the Argentine Boa Constrictor (*Boa constrictor occidentalis*)

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ABSTRACT.—We provide data on sexual dimorphism, reproductive biology, and mating aggregations of the Argentine Boa Constrictor (*Boa constrictor occidentalis*), a poorly known, threatened species. Snakes were examined by ultrasound scanning between 1998 and 2001. Adult females were 14% longer and 51% more massive than adult males. Litter size averaged 25.05 and increased significantly with maternal body size. Reproductive activity was seasonal and associated, with vitellogenesis and spermatogenesis occurring during the dry season (April to September). The ratio of reproductive to nonreproductive females was 1:1, suggesting females do not reproduce annually in this population. Reproductive females were in better body condition (mass relative to body length) than nonreproductive females, indicating that a female's initial "decision" to reproduce in any given year may be driven by her body condition (storing enough energy for a long period before expending it on reproduction: "capital breeder"). Aggregated boas were found only during the dry season. The high proportion of solitary reproductive males and the operational sex ratio (male:female, 1.53:1) suggests a system of "prolonged mate-searching polygyny."

Linkages between reproductive ecology and life history represent trade-offs between size and number of offspring, costs of producing offspring, seasonal production of offspring, and local environmental variation. Interactions among these factors determine energy investment in reproduction, both in the short term for the individual's survival by balancing reproductive energy expenditure with daily maintenance energy requirements, and in the long term by determining an individual's success transferring its genes into the next generation (Zug et al., 2001). Although many organisms gather energy used for breeding during the reproductive season, most animals rely to some extent on "capital" (stored energy) to support reproductive expenditure. This "capital-breeding" tactic is particularly common in ectotherms, especially long-lived species (Doughty and Shine 1998).

In most snakes, fecundity is dependent on body mass or size, with larger females producing more offspring than smaller ones (Slip and Shine, 1988a; Whittier and Crews, 1990). As reptiles continue to grow throughout life, older individuals tend to be larger and have more offspring. However, once a given size or age is passed and sexual maturity is attained, reproduction may not occur annually and is modulated by factors other than size. A factor that has received much attention is the nutritional condition of females as represented by relative body mass and stored fat

reserves (Whittier and Crews, 1990). The rate at which a female is able to replace the mass lost at parturition may be a key factor influencing her frequency of reproduction (Farrel et al., 1995). When costs of reproduction are relatively high, as in snakes with viviparity, two mechanisms may counterbalance these costs: producing larger broods and lowering the frequency of reproduction (Brown, 1991).

Most species of snakes are solitary; perhaps the most widely reported form of "sociality" in reptiles involves the tendency for individuals of many species to form aggregations. Unlike social species, access to a male during critical periods in the reproductive cycle is not necessarily guaranteed (DeNardo and Autumn, 2001). In the reproductive season, it is critical that reproduction is synchronized at the individual level to assure that a mate is available. For reproduction to occur, snakes must encounter, persuade, discriminate among, and synchronize behavior with potential mates (Greene, 1997).

Considering that the Neotropical boine fauna includes several of the most "famous" snake species in the world and that some of them are commercially exploited, it is remarkable how little is known about the most fundamental aspects of their natural history (Henderson et al., 1995). The Argentine territory supports the world's largest and southernmost population of *Boa constrictor occidentalis*, a threatened subspecies. In spite of this, its basic biology remains virtually unknown. The aim of the present study is to provide basic data on sexual dimorphism and reproductive biology of the Argentine Boa

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Constrictor. In addition, we discuss the importance and possible role of aggregations.

MATERIALS AND METHODS

Study Species and Area.—The Argentine Boa Constrictor (*B. c. occidentalis*) is a viviparous, large (up to 4 m), heavy-bodied, nonvenomous, constricting snake. It is one of the four species of the Boidae found in the subtropical temperate west and center-west of Argentina (Cei, 1993). In Córdoba province, it is found in the north and west (Di Fonzo de Ábalos and Bucher, 1981, 1983; Chiaraviglio et al., 1998a). Argentine Boa Constrictors are active throughout the year (unpubl. data). They are associated with burrows of vizcachas (*Lagostomus maximus*), for both prey and refuge (Cei, 1993; Sironi et al., 2000). Males and females reach sexual maturity at an average snout–vent length (SVL) of 149 cm and 164 cm, respectively (Chiaraviglio et al., 2001). The species is subject to strong hunting and capture pressures for skin and pet trade (Gruss, 1991; Ávila and Acosta, 1996), and its habitat is being severely modified by intense farming and cattle raising in the area. As a consequence, it is considered a threatened species (Scrocchi et al., 2000) and has been included in appendix 1 of CITES (1997).

The study area (approximately 240 km^2) is located in the District of Pocho (31°50′S; 64°20′W) in the west plain of Córdoba province, Argentina. Cabrera (1976) described the site as the driest territory of Occidental Chaco. It is characterized by a xerophytic forest of *Aspidosperma quebracho-blanco* and *Prosopis nigra* and shrublands of *Larrea divaricatta* and *Mimozyganthus carinatus* (Cabido and Zak, 1999). Annual average temperatures range from 18° to 23°C and rainfall, from 300 to 550 mm with distinct dry (April to September) and wet (October to March) seasons (Capitanelli, 1979).

Survey Methods.—Snakes were captured by hand each month between 1998 and 2001. At each capture, we recorded date, location (with a GPS Garmin III), aggregation status (aggregated or solitary) and group size. For the purpose of this study, an "aggregation" was defined as the occurrence of two or more individuals in association with the same refuge. Animals were sexed, measured (SVL and mass), and individually marked by ventral scale clipping. In the laboratory, reproductive structures were observed by ultrasound scanning (Toshiba Sonolayer SSA-270, linear 7.5 Mhz transducer; Chiaraviglio et al., 1998b). The diameters of testes and follicles were measured using the caliper measurement function for distances on the screen. Testicular volume was calculated using the equation for volume of an ellipsoid (Méndez and Villagrán, 1998). The reproductive

status of females was determined by the ultrasound appearance of follicles that were assigned to one of three categories. Ovaries in early follicular growth were identified as round hipoechogenic masses (< 10 mm diameter, nonvitellogenic follicles). Vitellogenesis was determined by the presence of hiperechogenic follicles with two exterior zones, iso- and hipoechogenic (10–28 mm diameter, vitellogenic follicles). After ovulation, females had follicles (> 28 mm; oviductal follicles) aligned in a row. The hiperechogenic interior of oviductal follicles has a heterogeneous appearance. Females were considered in breeding condition if they had vitellogenic and/or oviductal follicles. Males were scored as "reproductive" if they had turgid testes (Slip and Shine, 1988a). Litter size was estimated based on the number of vittellogenic and/or oviductal follicles.

A hundred thirty individuals (72 males and 58 females) were captured. Ultrasound images were obtained from 109 specimens: 12 juveniles, 49 adult males, and 48 adult females. Snakes were released at their capture site.

Data Analysis.—A variety of statistical tests were applied after checking data for normality and equality of variances. We used analysis of variance (ANOVA) to compare traits of interest between sexes, reproductive status, months and seasons. Analysis of covariance (ANCOVA) was used to examine patterns for variables that were significantly influenced by some other trait, such as body mass. Additionally, we used Mann-Whitney U-tests to test sexual dimorphism.

To obtain a measure of a snake's body condition (mass relative to length), we calculated residual scores from the general linear regression of ln-transformed body mass to SVL (Madsen and Shine, 1999a,b; 2001). Snakes with lower mass than expected for their SVL were represented by negative residual scores, whereas more massive snakes generated positive residuals. Because body shape differs between the sexes, these regressions were performed separately for males and females. The relationship between litter size and female body size (SVL) was examined using a Pearson's correlation analysis. Contingency table analyses were used to test interaction between sexes, reproductive status and aggregation status. All statistics were performed with InfoStat (vers. 1.1, Grupo InfoStat, Universadad Nacional de Córdoba, Argentina, 2002) at $\alpha = 0.05$. All mean values are presented ± standard error (SE).

RESULTS

Morphometrics and Sexual Dimorphism.—We captured 130 specimens, 106 were considered adults (56 males and 50 females; no recaptures). There was clear sexual dimorphism in body size.
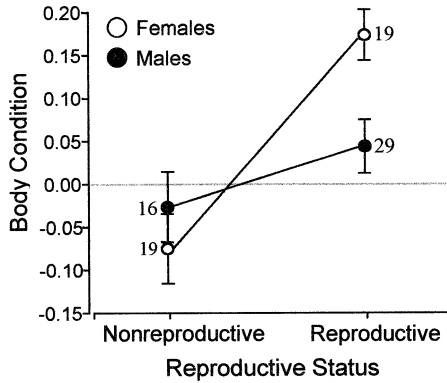
Adult males averaged 180 ± 3 cm SVL ($N = 56$; range 149–223) and adult females averaged 205 ± 4 cm SVL ($N = 50$; range 169–285; $U = 3476.50$, $P < 0.0001$). Females were 14% longer than males. Sexual dimorphism was also marked in the body mass, which was significantly higher in adult females (51% more massive; 6128 ± 316 g; $N = 50$; range 2500–11600) than in adult males (4056 ± 141 g; $N = 56$; range 2250–6300; $U = 3503$, $P < 0.0001$).

To compute the difference in male versus female size, we used the sexual size dimorphism index (SSD = [larger sex/smaller sex] − 1) proposed by Gibbons and Lovich (1990). This index is arbitrarily expressed as positive if females are the largest sex and negative if males are the largest sex. The SSD index of *B. c. occidentalis* for the present study was +0.142.

Reproductive Biology.—Reproduction was strongly seasonal in both sexes. Reproductive females were found during the dry season (April to August), with a significantly increased diameter of the follicles throughout this season (one-factor ANCOVA with month as the factor, body weight as the covariate, and follicular diameter as the dependent variable: $F_{4,13} = 3.14$; $P = 0.05$; slope $F_{1,13} = 6.10$; $P = 0.03$; Contrasting Test for First Order Lineal Tendencies: $F = 11.76$; 1 df; $P = 0.004$; Fig. 1). Reproductive males were found from March to August. Their testicular volume was significantly lower from March to May (11.49 ± 7.25 cm³; $N = 13$) than from June to August (15.83 ± 5.97 cm³; $N = 16$; one-factor ANOVA with ln testicular volume as the dependent variable; $F_{1,27} = 5.78$; $P = 0.02$).

Many adult-size males and females did not appear to reproduce each year. During the dry season, 50% of adult females (19 of 38) and 64% of adult males (29 of 45) were reproductive. Four of the 29 reproductive males were caught toward the end of the wet season (end of March). The operational sex ratio (OSR; reproductive males: females) was 1.53:1. Proportion of reproductive females (50%) to nonreproductive females did not differ significantly from parity ($\chi^2 = 0.00$; 1 df; $P > 0.99$). Reproductive females were in better body condition than those that were nonreproductive. This tendency was not observed in males (two-factor ANOVA with sex and reproductive status as the factors, and body condition as dependent variable; sex effect $F_{1,79} = 1.24$, $P = 0.27$; reproductive status effect $F_{1,79} = 19.35$, $P < 0.001$; significant interaction effect $F_{1,79} = 6.11$, $P = 0.02$; Fig. 2). The proportion of reproductive females was significantly lower in the 164–205 cm SVL category (36%; eight of 22), compared to females that were more than 205 cm in SVL (69%; 11 of 16; $\chi^2 = 3.96$, 1 df, $P = 0.046$). Litter size averaged 25.05 ± 1.25 ($N =$

FIG. 1. Seasonal variation in the diameter of the nonvitellogenic (open squares), vitellogenic (shared squares) and oviductal follicles (solid squares) of adult females of *Boa constrictor occidentalis*.

19; range 15–33) and increased strongly with maternal body size ($r = 0.72$; $P < 0.001$; Fig. 3).

Mating Aggregations.—Boa aggregations were found only during the dry season. The first aggregations of the year were detected in April and the last in August. These aggregations consisted of one adult female and one to three adult males.

There was a strong link between reproductive condition and aggregation status. Forty-three boas (51%) of the 84 captured during the dry season were found in aggregations and of these, 33 (78%) were reproductive. In contrast, 41 boas (49%) were observed alone and, of these, only 15 (37%) were reproductive ($\chi^2 = 14.24$; 1 df; $P < 0.001$). During the last three months of the dry season (July to September), when gonads of males and females reach the maximum values, the association between reproductive condition and aggregation status was more evident: 29 (94%) of 31 reproductive boas caught during this period were found aggregated. In contrast, only four (24%) of the 17 reproductive boas captured from April to June were aggregated ($\chi^2 = 26.24$; 1 df; $P < 0.0001$). Aggregated nonreproductive snakes (10 of 36) were found in July and August (end of the dry season) associated with reproductive snakes. Sixteen of 19 reproductive females (84%) were found in aggregations, whereas only 17 of the 29 reproductive males (59%) were found in aggregations ($\chi^2 = 3.71$; 1 df; $P = 0.05$).

DISCUSSION

There was clear sexual dimorphism in body size. Our results demonstrate that adult females

FIG. 2. Variation (mean ± SE) in the body condition (mass relative to body length) by sex and reproductive status of *Boa constrictor occidentalis*. Numbers aside the symbols indicate sample size.
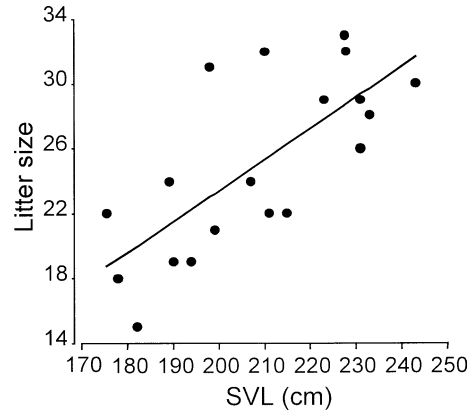

FIG. 3. The relationship between maternal snout–vent length (SVL) and litter size (number of vitellogenic and/or oviductal follicles) in females of *Boa constrictor occidentalis* (linear regression: litter size = $0.19 \cdot SVL - 14.71$).

were 14% longer and 51% more massive than adult males. The sexual size dimorphism (SSD) index of *B. c. occidentalis* for the present study (+0.142) supports the link between SSD skewed toward females and the lack of male-male combat behavior (Shine, 1994). Male-male combat behavior has not been observed in our field or laboratory studies (unpubl. data). The larger size of female Argentine Boa Constrictors may be relation to an increase in fecundity: maternal SVL described 52% of the variation in litter size. The tendency for larger females to produce larger clutches is widespread in snakes, perhaps ubiquitous, but species differ in the relationship between maternal size and offspring number (Seigel and Ford, 1987). Litter size, as in other large and prolific boids like *B. c. constrictor* (Fitch, 1985) and *Eunectes murinus* (Muñoz and Rivas, 1994), is much influenced by the size and age of the female. The advantages of larger clutch size for female reproductive success should impose selection for larger female size in most or all snakes, but the intensity of such selection may vary among species. Overall, size dimorphism is more common in medium to large species than in small ones; greater length is associated with females of those species that produce large clutches or litters (Greene, 1997).

When gonadal and hormonal events coincide, the cycle is "associated" (Whittier and Crews, 1987). Associated reproduction is common in temperate reptiles (Zug et al., 2001). Our data suggest that reproductive activity in *B. c. occidentalis* is seasonal and associated. Toward the end of the wet season (March), the first males with turgid testicles are observed, whereas the first females with vitellogenic follicles are detected early in the dry season (April). *Boa constrictor occidentalis* shows prenuptial spermatogenesis with testicular enlargement occur-

ring in the dry season. Although we did not observe copulation in the field, ovulation (and possible fertilization) was detected toward the end of the dry season (July to August). This coincides with the greatest number of aggregated reproductive specimens, before regression of testes occurs (September) and mating groups disperse (see below). We did not find gravid females, which were likely inside vizcacha burrows for prolonged periods (unpubl. data). Pregnancy probably occurred during the wet season. Shine (1977) proposed that spring ovulation is adaptive in snakes of temperate localities, ensuring that females will be gravid during a season when high body temperatures are easier to obtain, and soil temperatures and insolation are only high enough to allow rapid embryonic development (Shine, 1985). Monguillot (1988) recorded parturition in March in a captive gravid female captured in the field. Newborns at parturition averaged 47.2 cm total length and 78.5 g. The shortest snakes found were a 59.6 cm SVL (66 cm total length) newborn in April and a 51.6 cm SVL (58 cm total length) newborn in May, which indicates that parturition takes place at the end of the wet season (February to March).

The ratio of gravid to nongravid females in a population is commonly used to determine the reproductive frequency of snakes. However, because of the lack of gravid females found during our study, we calculated the ratio of reproductive (R) females to nonreproductive (NR) ones (Aldridge et al., 1995; Tsai and Tu, 2001). The R:NR ratio of *B. c. occidentalis* was 1:1, which has typically been interpreted as a biennial reproductive cycle (Blem, 1982; Seigel and Ford, 1987; Macartney and Gregory, 1988; Holycross and Goldberg, 2001; Tsai and Tu, 2001). However,

inferring frequency of reproduction from pro-portion of adult breeding females is contro-versial, as is the notion of rigidly biennial reproductive cycles (Blem, 1982; Seigel and Ford, 1987). Brown (1991) observed that in *Crotalus viridis* about half of mature females captured were gravid which suggested biennial cycles. However, by palpation of recaptured females over a succession of years, Brown did not find data to fit the mean expectation of 50% gravid females. As pointed out by Seigel and Ford (1987), accurately determining reproductive fre-quency in many squamates requires recapturing marked females.

Many researchers have questioned the exis-tence of a genetically determined biennial reproductive cycle and have suggested that a female's attempt to produce a litter is a function of available fat stores (Aldridge, 1979; Blem, 1982; Macartney and Gregory, 1988; Whittier and Crews, 1990; Brown, 1991). Frequency of reproduction in neartic vipers appears to be facultative and determined primarily by a com-bination of food availability, fat reserves, length of the active season, and population structure (Blem, 1982; Seigel and Ford, 1987). Female *Liasis fuscus* reproduce, on average, once every second year, but with substantial variation based on body size, body condition, local food availability, and nest-site location (Shine and Madsen 1997; Madsen and Shine 1999a,b). Bonnet et al. (1992) have demonstrated that reproduction in *Vipera aspis* is dependent on females reaching a mini-mum threshold in body condition, and only females that reach this threshold mate (Naulleau et al., 1999). This species is a typical "capital breeder" in terms of its reliance on stored reserves for maternal "decisions" concerning reproductive frequency (Bonnet et al. 2001). *Crotalus viridis* (Macartney and Gregory, 1988), *Crotalus horridus* (Brown, 1991), *Crotalus willardi* (Holycross and Goldberg, 2001), and *Trimeresu-rus stejnegeri stejnegeri* (Tsai and Tu, 2001) require energy from fat stored during the previous year to vitellogenesis. It is our claim that nonrepro-ductive females of *B. c. occidentalis* that store enough energy during one year become repro-ductive in the next dry season. For boas, the decision to reproduce in a given year depends primarily upon the magnitude of stored reserves. Like many other kinds of organisms that depend upon stored reserves for reproduction (capital breeders), boas dot not reproduce unless they have attained a threshold level of body condi-tion (and, thus, energy reserves). Our data show that the largest females (greater SVL or better body condition) reproduced more frequently and contained more follicles than smaller females. The increased energy used for growth in younger snakes may be responsible for their less frequent reproduction (Macartney and Gregory, 1988; Shine, 1993).

Our study shows that Argentine Boa Con-strictors aggregate during the breeding (dry) season. The highest frequency of aggregations during the last three months of the dry season coincides with the highest gonadal development observed in both sexes. Individuals may aggre-gate as a result of direct attraction between con-specifics. The ability of individuals to orient based on pheromonal cues in the environment can have significant consequences to their re-productive success (LeMaster et al., 2001). In-traspecific attraction plays a significant role in the formation of aggregations. Chiaraviglio and Briguera (2001) found that male *B. c. occidentalis* showed a stronger response to the stimulus of female skin than to male skin. The same response was observed in the rainbow boa *Epicrates cenchria alvarezi* (Briguera et al., 1994, 1997). Observations of accurate trail-following by males of *Morelia spilota spilota* (Slip and Shine, 1988a) suggest that this may be the mechanism by which females are located. These findings sug-gest that chemical signals from females' skin send important messages to con-specific males in a reproductive context.

Duvall et al. (1992) described the mating system of *Crotalus viridis viridis* as Prolonged Mate Searching Polygyny (PMSP). In this mating system, males search for widely distributed and scarce receptive females. The larger proportion of solitary reproductive males compared to that of females (41% vs. 16%), and the OSR (1.53:1) observed in *B. c. occidentalis* is consistent with PSMP. This mating strategy appears to occur in several species of snakes that differ in some aspects of their life history (SSD, male-male combat, mating season) but, like *B. c. occidentalis*, are similar in that receptive female are scarce and scattered in the environment (Duvall et al. 1992; Aldridge 1979, 2001; Slip and Shine 1988a,b). Duvall et al. (1992) stressed that, because females are widely distributed in species with PSMP, sexual selection should act on mate searching ability and not male-male combat ability.

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