

Intrapopulation variation in life history traits of *Boa constrictor occidentalis* in Argentina

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Abstract. We provide data on intrapopulation variation of life history traits of *Boa constrictor occidentalis* in the District of Pocho, Córdoba, Argentina. A total of 153 individuals were captured. The distribution of individuals among four size classes differed significantly among the five years of study. The proportion of mature individuals did not differ between sexes but it showed variation among years. Females were longer and heavier than males. The mean litter size of the species was 24 and there was a linear relationship between litter size and maternal snout-vent length. Most boas were captured during the dry season. There were no significant sex differences in the time of capture and air temperature in either the wet or the dry seasons. However, we found significant differences in the time of capture and air temperature between the seasons. The long-term monitoring of wild populations should be a priority for the development of conservation and management plans for this boid.

Introduction

The Argentine boa constrictor or “lampalagua”, *Boa constrictor occidentalis*, is a subspecies found in Argentina in the semiarid plains of the phytogeographic provinces of Chaco, Monte and Espinal (Di Fonzo de Ábalos and Bucher, 1981, 1983; Chiaraviglio et al., 1998a) where its populations are declining (Anónimo, 1994). Due to intense farming, cattle raising and illegal hunting for skin trade and as pets (Gruss, 1991; Avila and Acosta, 1996), the species is endangered and has been included in Appendix I of CITES (1997). In Argentina, this boid has been protected at the national (National Law 22421, 1981, Decree 24/86, SAGP) and provincial (Provincial Decree 4056/58, Córdoba) levels (Anónimo, 1994). Despite this legal protection, hunting pressure still exists. Thus, studies to increase our understanding about its biology in its natural habitat are essential for recovering and preserving wild populations.

Detailed information on the frequency and magnitude of intrapopulation variations in life history traits can be useful in determining whether the observed variations result from proximate or evolutionary sources. For example, high variation in reproductive traits such as clutch size or clutch frequency may be correlated with resource availability or environmental condition, suggesting a proximate basis. Conversely, low variation among years for such traits may suggest a significant adaptive component (Seigel and Fitch, 1985).

Age structure and sex ratio are essential parameters to understand the life history and dynamics of threatened species. The age structure of a population can reveal trends in growth and maturation and may be used to describe other demographic processes (Waye, 1999). Snout-vent length can be used to estimate the age and the reproductive condition in snakes. Changes in the proportions for each age class can be related to changes in the age structure (Bertona et al., 1999). Age structure of the adult population (and its mean size) changes from year to year, depending especially on the youngest cohort, and whether or not it has been unusually successful as a group in numbers, growth and survival. In snake populations, newly-mature individuals may make up as much as half of the total of adult females, but with many changes from year to year (Seigel and Fitch, 1985).

Sex ratio is also a critical demographic feature because it directly affects the growth potential of a population. For bisexual diploid species, the primary sex ratio is 1 : 1 (number of males : females at fertilization), because the heterogametic parents produce equal numbers of male and female gametes (Zug et al., 2001). The operational sex ratio can be used to predict the intensity of mating competition and which sex is more likely to show this behavior. Mating competition increases when the operational sex ratio deviates from 50% (Kvarnemo and Ahnesjö, 1996).

Sexual dimorphism in snakes appears to result from a complex interplay of intrasexual selection, fecundity selection, and natural selection on morphology, color and behavior. Fecundity selection, together with higher fecundity-independent costs of reproduction in females, is thought to be responsible for the fact that female snakes are generally larger than conspecific males (Shine, 1993). Fecundity advantages of larger body sizes in females may also influence sexual size dimorphism because the degree of the latter correlates with the rate at which litter sizes increase with body size. The evolution of viviparity is associated with a consistent shift toward larger female size relative to male size (Shine, 1994). Intrasexual selection, operating mainly through the advantages of larger body size in male-male combat, has resulted in the evolution of large male size in some taxa (Shine, 1993).

Although many snake species are characterized as being diurnal or nocturnal, the cues that initiate or terminate daily activity are rarely known, and our knowledge of why a particular species is active when it is, is usually speculative (Henderson and Winstel, 1997).

In this study we provide data on intrapopulation variation of life history traits of *Boa constrictor occidentalis* in the District of Pocho, Córdoba, Argentina. We studied the age structure of a wild population based on body size and reproductive condition, as well as sex

ratio and sexual dimorphism. We also describe some aspects of the overall daily activity of the species in our study site.

Materials and methods

The study area (approximately 240 km²) is located in the District of Pocho (31°50'S; 64°20'W) in Northwestern Córdoba Province, Argentina. It is characterized by a xerophytic forest of *Aspidosperma quebracho-blanco* and *Prosopis flexuosa*, and shrublands of *Larrea divaricata* and *Mimozyanthus carinatus* (Cabido and Zak, 1999). Annual average temperatures range from 18 to 23°C and rainfall from 300 to 550 mm with distinct wet (October to March) and dry (April to September) seasons (Capitanelli, 1979).

Snakes were captured by hand, monthly, between 1996 and 2000. Sampling effort was constant between the seasons and during the five years of the study, and was concentrated in the vicinity of vizcacha (*Lagostomus maximus*) burrows, where snakes take refuge and prey on these rodents (Sironi et al., 2000). No captures were made during the night.

Date, time and temperature were recorded for each capture, and location was determined with a GPS (Garmin III). Animals were sexed and total length (TL) and caudal length (CL) were measured with a metal tape measure, marked in mm, to obtain the snout-vent length (SVL). Boas were weighed with a commercial balance (limit of reading 50 g). During the course of the project, we routinely recorded time of day and air temperature at each encounter of a snake.

In the laboratory, the 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. Male boas were scored as adult if they had large, turgid testes, and/or opaque, thickened efferent ducts. Females were considered sexually mature if they had oviductal eggs, vitellogenic ovarian follicles (>10 mm diameter), and/or thickened, muscular oviduct. Before releasing the individuals at their capture site, they were marked by ventral scale clipping or by subcutaneous implantation of microchips (Passive Transponder System, ID-100, Trovan).

After observing body coloration, SVL and reproductive condition, males and females were classified into the following life stages (size class): Class I = newborns; Class II = juveniles; Class III = adults; and Class IV = major adults.

All statistics were performed with InfoStat 1.1 (InfoStat, 2002) at $\alpha = 0.05$. All mean values are presented \pm standard deviation (s).

Results

A total of 153 individuals were captured, including 71 females and 82 males. Boas were never recaptured, despite frequent searching.

Size classes

Seventy females and 78 males were measured and classified into the following four size classes:

- Class I: smallest individuals (<101 cm SVL), with a pinkish coloration that is different of that of juvenile and adult boas;
- Class II: immature snakes with the typical adult coloration; females: 101-163 cm SVL, males: 101-148 cm SVL;
- Class III: this class was determined after the SVL of the smallest mature individual found, and it includes adult boas; females: 164-223 cm, males: 149-223 cm;
- Class IV: largest females only (>223 cm SVL).

Significant differences in the distribution of individuals among the four classes were found during the five years of the study ($n = 148$; $\chi^2 = 56.98$; $df = 12$; $P < 0.0001$). The proportion of mature individuals did not differ between sexes (0.81 for males and 0.83 for females; $n = 148$; $\chi^2 = 0.11$; $df = 1$; $P = 0.74$), but it showed differences among years ($n = 148$; $\chi^2 = 14.64$; $df = 4$; $P = 0.01$). However, in the last three years of the study (1998 to 2000) this proportion remained constant (mature: 0.84, immature: 0.16; $n = 112$, $\chi^2 = 0.30$, $df = 2$, $P = 0.86$) (fig. 1).

Sex ratio

The observed male:female sex ratio (1.15:1) did not differ significantly from 1:1 (82 males and 71 females; $\chi^2 = 0.79$; $df = 1$; $P = 0.37$). This ratio did not vary significantly during the course of this study ($n = 153$; $\chi^2 = 6.99$; $df = 4$; $P = 0.14$), but the proportion of males was highest in 1998 (table 1). The operational sex ratio (1.08:1), based on mature individuals (potential breeders), was not significantly different from the expected 1:1 (63 males and 58 females; $n = 121$; $\chi^2 = 0.21$; $df = 1$; $P = 0.65$).

Sexual dimorphism

Females ($n = 70$) were significantly longer (mean $\pm s = 193 \pm 41$ cm SVL, range 58-252 cm) and heavier (mean $\pm s = 5598 \pm 2753$ g, range 150-12400 g) than males ($n = 78$; mean $\pm s = 166 \pm 35$ cm SVL, range 52-223 cm; mean $\pm s = 3618 \pm 1504$ g, range 200-7450 g) (Mann-Whitney *U*-test: SVL $W = 6458.0$, $P < 0.0001$; Weight $W = 6477.5$, $P < 0.0001$). However, males had relatively longer tails (mean $\pm SD = 0.11 \pm 0.01$ CL/SVL, range 0.07-0.14) than females (mean $\pm s = 0.08 \pm 0.01$ CL/SVL, range 0.05-0.10) ($W = 2775.0$, $P < 0.0001$).

Litter size

Based on counts of oviductal eggs and/or vitellogenic ovarian follicles (diameter > 10 mm), the mean litter size was 24 ($n = 19$; litter size range 11-33; SVL range 173-243 cm). Although the sample size was small, there was a linear relationship between litter size and maternal SVL ($n = 19$, Pearson $r = 0.76$, $P < 0.001$; fig. 2).

Activity patterns

Although the sampling effort was constant and equal during the two seasons, most boas ($n = 125$; 82%) were captured during the dry season ($n = 153$; $\chi^2 = 61.50$; $df = 1$; $P < 0.0001$). There were no significant sex differences in the time of capture in either the wet ($n = 26$; $\chi^2 = 15.44$; $df = 11$; $P = 0.16$) and the dry seasons ($n = 123$; $\chi^2 = 10.14$; $df = 9$; $P = 0.34$). However, we found significant differences in the time of capture between the seasons when both sexes are considered together ($n = 149$; $\chi^2 = 51.77$; $df = 13$; $P < 0.0001$). In the dry season, most individuals (56%) were

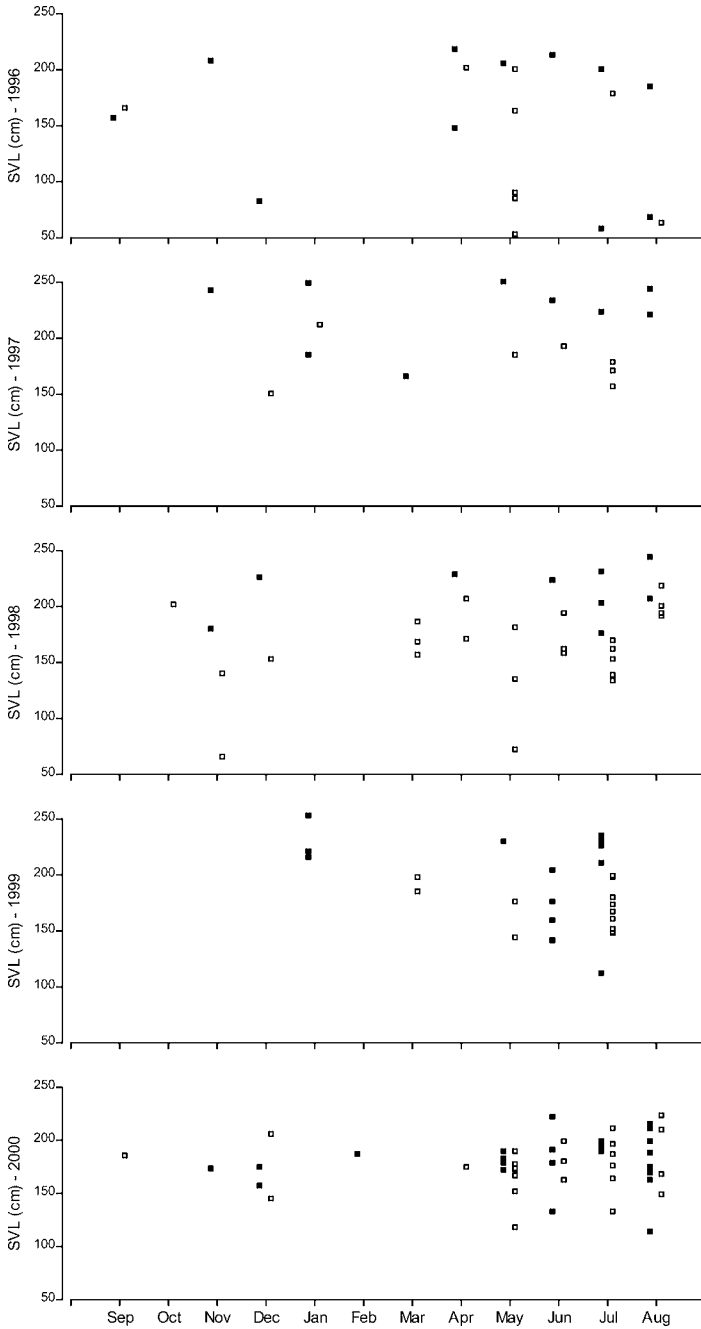
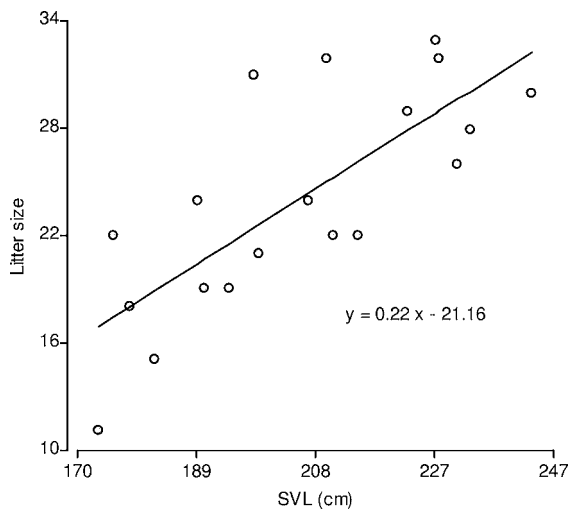


Figure 1. Size (SVL) distributions of male (open squares) and female (solid squares) *Boa constrictor occidentalis* collected during the five years of the study.

Table 1. Sex ratio of *Boa constrictor occidentalis* by year. Relative frequencies (and number of individuals) are shown.

Year	Males	Females	Sex Ratio
1996	0.45 (9)	0.55 (11)	1 : 1.22
1997	0.44 (7)	0.56 (9)	1 : 1.29
1998	0.73 (24)	0.27 (9)	2.67 : 1
1999	0.45 (13)	0.55 (16)	1 : 1.23
2000	0.53 (29)	0.47 (26)	1.12 : 1
Total	0.54 (82)	0.46 (71)	1.15 : 1

**Figure 2.** The relationship between maternal SVL and litter size (based in vitellogenic ovarian follicles >10 mm) in females of *Boa constrictor occidentalis*.

captured between 1300 and 1500 h ($n = 123$; $\chi^2 = 118.91$; $df = 9$; $P < 0.0001$). During the wet season, captures were distributed more evenly during the day ($n = 26$; $\chi^2 = 6.25$; $df = 11$; $P = 0.86$). We also detected strong seasonal differences in the average air temperature during captures (wet season: mean $\pm s = 28.64 \pm 5.02^\circ\text{C}$, range 20-39°C, $n = 25$; dry season: mean $\pm s = 22.39 \pm 4.66^\circ\text{C}$, range 10-36°C, $n = 122$). However, these differences were not significant between the sexes, both in wet and dry seasons (two-factor ANCOVA with season and sex as the factors, SVL as the covariate, and air temperature as the dependent variable: season effect $F_{1,137} = 33.68$, $P < 0.0001$; sex effect $F_{1,137} = 0.08$, $P = 0.78$; interaction non-significant $F_{1,137} = 0.01$, $P = 0.93$; slope $F_{1,137} = 0.02$, $P = 0.90$) (fig. 3).

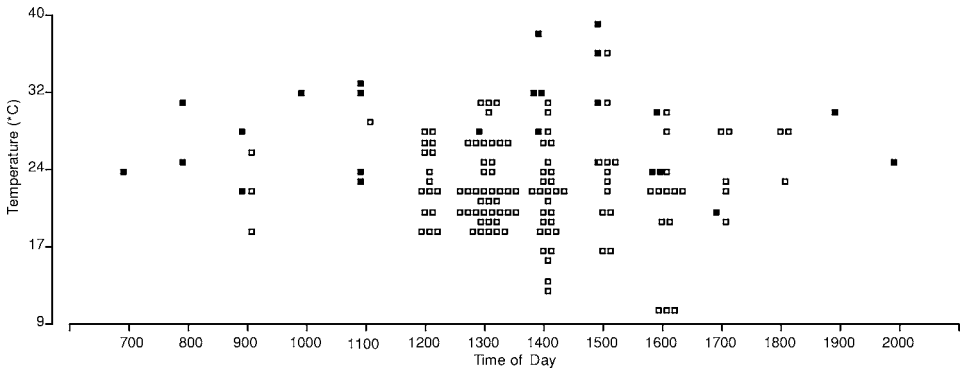


Figure 3. Relationship between time of day and air temperature during captures in *Boa constrictor occidentalis* in the dry (open squares) and wet (solid squares) seasons. Observations made between 700 and 800 h appear at 700 h on the graph; those made between 800 and 900 h appear at 800 h on the graph, etc.

Discussion

Size classes

The observed intrapopulation variation in size structure during the five years of this project emphasizes the need to carry out comparative long-term studies in order to understand tendencies in demographic parameters of wild populations. The low proportion of Class I individuals could be due to factors such as higher predation pressure during early life stages, lower capture success due to differential microhabitat use by young boas, or variability in reproductive events during previous years. Growth in snakes during the first few weeks of life depends largely on the supply of abdominal yolk (Greene, 1997).

We did not find Class IV individuals in 1996 and 2000. In reticulated pythons, females attain larger size than males, but very large females are rarely captured (Shine et al., 1999). In the past, the largest Argentine boa constrictors were longer than 400 cm (Ceí, 1993). However, the longest animals found since 1995 in Córdoba province were a female of 285 cm SVL and a male of 223 cm SVL (Bertona, 1995). This could indicate that the largest animals are suffering a higher hunting pressure than smaller boas.

During this study, we observed a tendency toward an increase in the frequency of Class III individuals. This abundance of potentially reproductive animals could have a favorable long-term effect on wild populations.

Male boas were mature at smaller sizes than females, a pattern also observed among *Morelia spilota* males that can reproduce at shorter SVLs (and presumably younger ages) than females (Slip and Shine, 1988).

Sex ratio

The observed sex ratio is close to the expected 1 : 1. This could indicate that both males and females have similar activity patterns of surface use (May et al., 1996). Interestingly, the

operational sex ratio, based on mature individuals (potential breeders), is also close to 1 : 1, which could reflect that there is no reproductive competition in this species (Kvarnemo and Ahnesjö, 1996). Despite this, we found mating groups with one female and several males that could be competing in some way (Chiaraviglio et al., 2000). In most species, males compete for females. Determination of the limited sex, and hence the structure of the mating system, cannot be made by examining the sex ratio of the potential breeders. Not all mature individuals are ready to mate at any given time. For this reason, the operational sex ratio must be taken as the ratio of fertilizable females to breeding males during the mating season (Zug et al., 2001).

Sexual dimorphism

The observed larger size of female Argentine boa constrictors compared to males could have arisen because of selection for female fecundity. 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). The litter size of Argentine boa constrictors, as in other large and prolific boids like *Boa constrictor constrictor*, is much influenced by the size and age of the female. Newly matured individuals produce relatively small litters compared to large old adults (Fitch, 1985). In *Morelia spilota* (Slip and Shine, 1988), and *Liasis fuscus* (Shine and Madsen, 1997) clutch size was also found to increase with maternal SVL. 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. The evolution of viviparity results in a shift in sexual size dimorphism toward relatively larger size in females; and geographic distribution (and hence, by inference, reproductive frequency) is correlated with sexual size dimorphism, but this correlation may be due to phylogenetic conservatism rather than to a causal relationship. Male-male combat favors the evolution of large body size in male snakes (Shine, 1994). Although male boas in our study population form groups during the mating season, we did not record aggressive behavior among them. This same pattern has also been observed in *Candoia carinata* and *Morelia spilota*, two species that also show sexual size dimorphism with larger females than males (Slip and Shine, 1988; Shine, 1994).

Activity patterns

We observed active boas all year round. This could be due to climate factors, such as a moderate winter with an average annual temperature of 19.5°C. However, the highest capture rate occurred during the dry season, when mating groups formed. Reproductive males and females are probably easier to find and catch in the dry season, when females are basking and males are guarding them (Bertona et al., 1999; Chiaraviglio et al., 2000). On the other hand, the lowest capture rate during the wet and hottest season could be related to movements of the snakes towards more shady and covered areas, making them

more difficult to find. Furthermore, many species of snakes change their daily patterns of activity in response to seasonal differences in environmental temperatures. Activity in some snakes is typically diurnal during the cool season, but becomes nocturnal during the hottest time of the year (Moore, 1978).

These population traits and others vary temporally within population as well as among populations of the same species in response to local environmental conditions (Zug et al., 2001). The Argentine territory supports the largest distribution of this subspecies in the world (Anónimo, 1994), and the natural habitat in its geographic range is rapidly and severely deteriorating (Cabido and Zak, 1999). The long-term monitoring of wild populations should be a priority for the development of conservation and management plans on behalf of this boid.

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