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Landscape changes influence the reproductive behaviour of a key ‘capital breeder’ snake (*Boa constrictor occidentalis*) in the Gran Chaco region, Argentina

Gabriela Cardozo*, Margarita Chiaraviglio

Animal Behaviour Laboratory. School of Exact, Physical and Natural Sciences. National University of Córdoba. Vélez Sársfield 299, Córdoba, CP: 5000, Argentina

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ABSTRACT

Many wild reptile species are threatened by habitat loss. However, the way in which changes in landscape patterns influence intraspecific ecological processes is not completely understood. *Boa constrictor occidentalis* is an endangered species and has a special conservation value since it is endemic of dry forests in the Gran Chaco region. Because the Gran Chaco is largely threatened due to habitat loss it is necessary to know how landscape changes influence this species. Therefore, we evaluated the effects of forest loss and landscape composition on the reproductive life-history parameters. Landscape changes were assessed by analyzing satellite imagery and reproductive parameters were determined by ultrasound images of the reproductive structures. The obtained results indicate that habitat loss may affect body condition, clutch size and testicular volume of the Argentine boa constrictor. We also found that the spatial pattern of vegetation influences the distribution of females and males in the landscape. Matting aggregations are scarce in shrublands. Therefore, our study shows that forest loss could enhance vulnerability to extirpation through constraints placed on reproduction. We encourage resource managers to evaluate sensitive reproductive life-history parameters as well as habitat deterioration to assess the conservation status of the populations of the Argentine boa constrictor. Since the Gran Chaco forest, a key habitat to the species' reproduction, is largely threatened, strong conservation action is needed to halt and reverse forest loss in this region.

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1. Introduction

Recent literature has addressed the need for a better understanding of the ecological mechanisms that underlie herpetofauna population decline associated to structural habitat changes (Cushman, 2006; Neckel-Olivera and Gascon, 2006; Gardner et al., 2007; Cagle, 2008). Although, many species are threatened by habitat loss (Luiselli and Capizzi, 1997; Mac Nally and Brown, 2001; Ishwar et al., 2003), the way in

which changes in spatial patterns influence intraspecific ecological processes is not completely understood. Landscape-scale snake-habitat investigations may provide essential knowledge to elaborate snake conservation measures (Filippi and Luiselli, 2006).

Considering that habitat loss is a serious environmental problem in many ecosystems it is necessary to know the effects of landscape changes on snakes populations. Specifically, as snakes adjust reproductive tactics in response to

* Corresponding author. Address: Laboratorio de Biología del Comportamiento, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Vélez Sársfield 299, Córdoba, CP: 5000, Argentina. Tel.: +54 351 4332100x247; fax: +54 351 4852739.

E-mail addresses: gabicardozo@yahoo.com.ar (G. Cardozo), mchiara@eco.unc.edu.ar (M. Chiaraviglio).

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the energetic constraints imposed by local conditions (Lourdais et al., 2002b; Shine, 2003), traits such as clutch size or reproductive frequency could be depressed. Moreover, as capital breeder snakes do not reproduce unless they have accumulated sufficient energy reserves, the energetic threshold for reproduction constitutes another key feature to evaluate the effects of habitat loss (Madsen and Shine, 1999a; Bertona and Chiaraviglio, 2003; Shine, 2003). Reproductive potential of males is also variable because sperm production and reproductive behaviors have significant costs (Olsson et al., 1997; Shine and Mason, 2005; Schulte-Hostedde and Montgomerie, 2006). Besides, environmental factors influence the spatial distribution of reproductive individuals leading to geographic variations in mating systems (Shine and Fitzgerald, 1995; Shetty and Shine, 2002). Intraspecific variation provides an ideal opportunity to understand the influence of environment on life history characters (Pearson et al., 2002). Thus, the understanding of the effects of landscape changes on the reproductive performance of snakes could be useful to determine population status and design conservation plans.

Our study species is the Argentine boa constrictor (*Boa constrictor occidentalis*) which is the largest ectotherm predator inhabiting dry forests of the Gran Chaco region in South America. The Gran Chaco is a largely threatened wooded region, strongly affected by extensive livestock raising, extractive forestry and poorly planned agricultural expansion (The Nature Conservancy et al., 2005). The woodland in the Chaco region is being lost at an annual rate of 2.2%; one of the highest world rates of deforestation and, in some cases, even higher than those recorded for some tropical rain forest. A massive contraction of forest occurred at the southern edge of the Chaco forest, where this study was carried out: 85% of the original subtropical dry forests (ca. 1.2 million ha), was cleared in only 30 years (Steininger et al., 2001; Zak et al., 2004).

Among the environmental factors that might influence reproductive behaviors in viviparous snakes, vegetation structure would be of great importance (Blouin-Demers and Weatherhead, 2001; Row and Blouin-Demers, 2006; Chiaraviglio and Bertona, 2007). At regional scale, the habitat requirements of *Boa constrictor occidentalis* show that its distribution is associated with dry forests (Di Cola et al., 2008). Besides, although *Boa constrictor* could be a habitat generalist in some tropical regions (Romero-Nájera et al., 2006), studies in temperate regions at microhabitat scale suggest that arboreal sites would facilitate the maintenance of high and constant body temperature in reproductive females (Chiaraviglio, 2006; Chiaraviglio and Bertona, 2007). An effective maternal thermoregulation would be important because the phenotype of the offspring is dependant upon body temperatures during development (Blouin-Demers et al., 2000). In addition, Cardozo et al. (2007) found that the loss of forest connectivity, and its replacement by shrubs, decreased the levels of gene flow in the populations of the Argentine boa constrictor. Since habitat loss could shape distribution of snake species, conservation efforts should emphasize the landscape-scale (Cagle, 2008).

Apart from being considered an endangered species (CITES I, 2007; Scrocchi et al., 2000), *Boa constrictor occidentalis* has a special conservation value since it is endemic of the Gran Chaco. This species has been identified by The Nature Conser-

vancy et al. (2005) as a 'conservation target' with the intention of focusing regional conservation plans. Keystone species may allow conservation managers to focus on a single-species emphasizing ecological mechanisms (Simberloff, 1998; Payton et al., 2002).

To get a better understanding of the consequences of landscape changes on ecological mechanisms of reptiles, we evaluated the effects of forest loss and landscape composition on reproductive life-history parameters of *Boa constrictor occidentalis*. We hypothesized that habitat loss would have adverse effects on reproductive parameters such as reproductive frequency, body condition, clutch size, testicular volume, and mating aggregation establishment. The understanding of snake reproduction-habitat relationships will be useful to plan conservation actions.

2. Materials and methods

2.1. Study species

The Argentine boa constrictor is a large viviparous snake with seasonal reproductive activity. It is considered a capital breeder snake. Larger females reproduce more frequently and contain more embryos than smaller females. Its mating system has been described as prolonged mate-searching polygyny (PMSP) (Bertona and Chiaraviglio, 2003). During the reproductive season, the maximum total distance moved was about 1.5 km for reproductive males and non-reproductive females, and about 0.09 km for reproductive females which would remain associated to natural holes (Chiaraviglio and Bertona, 2007).

2.2. Study area

The study area covers about 250 km² and is located in the District of Pocho (31°50'S; 64°20'W – Province of Córdoba) in the southern portion of the Gran Chaco, in Argentina. Agriculturally, it is considered a marginal land where the main activity is the extraction of trees, which results in the replacement of the forest by shrubs. The subspecies' natural habitat is characterized by a xerophytic forest of *Aspidosperma quebracho-blanco* and *Prosopis nigra* (Cabido and Zak, 1999). Deforested lands have been covered by shrublands of *Larrea divaricata* and *Mimozyanthus carinatus* (Zak et al., 2004).

2.3. Survey methods

Snakes were captured by hand between 1996 and 2003. A total of 173 mature individuals (91 males and 82 females) were captured and then released at their capture site. At each encounter, date and geographic coordinates were recorded. Animals were sexed and individually marked by ventral scale clipping (Brown and Parker, 1976) to confirm that the snake populations of each site were independent from one another. In each specimen, snout-vent length (SVL) and mass were recorded. We did not obtain recaptures. Reproductive structures were observed and measured by ultrasound scanning (Toshiba Sonolayer SSA-270, linear 7.5 Mhz transducer) (Chiaraviglio et al., 1998). Testicular volume was calculated using the

equation for the volume of an ellipsoid (Méndez and Villagrán, 1998) and males were scored as reproductive if they had turgid testes (Slip and Shine, 1988). Testicular volume was considered a measure of the reproductive potential of males because a positive relationship between relatively large testes and production of high-quality ejaculates has been reported in several species (Zenuto et al., 2003). Females were considered reproductive if they had vitellogenic and/or oviductal follicles bigger than 10 mm in diameter. Litter size was estimated based on the number of vitellogenic and/or oviductal follicles. Location and size of mating aggregations were also recorded (Bertona and Chiaraviglio, 2003).

2.4. Landscape analysis

During the field trips, we recorded the types of vegetation structures that occurred at the study area determining two major classes: forest and shrublands. We analyzed the available S10 or 10-day synthesis of the Normalized Digital Vegetation Index (NDVI) provided by The Spot Vegetation Program in order to assess forest loss. Remote sensing imagery had a spatial resolution of 1 km. We calculated the average NDVI of the study area for each year and quantified changes in NDVI during the study period. NDVI fluctuation may contain potential sources of error including rainfall events; however, this index has been used to detect changes of the vegetation cover and to discriminate zones of dry forest ecosystems (Bagour et al., 2006; Dedios, 2006). In our study, we also corroborated that NDVI variation is related to tree cover changes by quantifying forest loss using satellite images Landsat 5 TM from 1997 and 2003 and by comparing NDVI values between forest and shrublands.

To characterize landscape vegetation composition, we analyzed satellite images Landsat 7 ETM + employing ENVI 4.1 program (Research System Inc.). A total of 120 points were characterized at the field and geocoded using a GPS Garmin III Plus. These field sampling waypoints were then used to perform a supervised classification through a Maximum Likelihood algorithm (Chuvieco, 2002). To simplify the image classification and obtain fragmentation metrics, we clumped adjacent similarly classified pixels by applying a moving window using the majority analysis (Baldi et al., 2006). We assessed the forest landscape configuration using the following metrics: Percentage of Forest Landscape (PLAND), Mean Patch Area (AREA_MN) and Mean Euclidean Nearest Neighbor Distance (ENN_MN) using FragStats 3.3 (McGarigal and Marks, 1995; Rutledge, 2003).

2.5. Data analysis

In order to obtain a measure of snakes' body condition (mass relative to length), we calculated residual scores from the general linear regression of ln-transformed body mass to SVL. Because body shape differs between the sexes, these regressions were performed separately for males and females (Madsen and Shine, 1999a, b, 2000; Bertona and Chiaraviglio, 2003). Depending on the features of the data set, we used Pearson or Spearman's correlation to examine the relationship between body condition and reproductive parameters. Linear regression was used to test temporal variations in body

condition, clutch size, and testicular volume. Wilcoxon and Kruskal–Wallis tests were used to compare reproductive parameters of snakes, to examine their variations among different landscape covers and to evaluate changes of environment's features. Contingency table analyses were used to evaluate interaction between reproductive status, frequency of mating aggregations and vegetation structure types. All statistics were performed with InfoStat (2004) 1.1 at $\alpha = 0.05$. All mean values are presented \pm standard error (SE).

3. Results

3.1. Effects of habitat loss on reproductive parameters

We documented forest loss by detecting NDVI diminution throughout the study period (Kruskal–Wallis test with NDVI as dependent variable and year as independent variable; $H = 32.41$; $P < 0.01$) (Fig. 1). Satellite image classification supported this result since forest area decreased from 24.6% to 18.3% between 1997 and 2003. Besides, forest NDVI is higher than shrubland NDVI (Wilcoxon test; $W = 731496.00$; $P = 0.01$) showing that changes in NDVI are mainly due to forest diminution.

Reproductive features of the population also varied among years. Body condition threshold of reproductive snakes and clutch size decreased with forest decline (body condition: $n = 32$, $R^2 = 0.21$, $P = 0.01$; clutch size: $n = 32$, $R^2 = 0.24$, $P < 0.01$) (Fig. 2). Clutch size was correlated with body condition (Pearson's correlation; $R = 0.40$, $P = 0.03$). However, body condition of non-reproductive females did not change ($n = 29$, $R^2 = 0.01$, $P = 0.57$). Reproductive snakes exhibited higher condition indices than non-reproductive ones in every year of our study (Fig. 3). Reproductive frequency of females in the population did not change ($X^2 = 10.84$; 8 df; $P = 0.21$), the mean value was 0.61.

In males, there was an association between body condition and testicular volume index (Spearman's correlation; $R = 0.44$, $P < 0.01$), and both parameters decreased throughout the study period (testicular volume index: $n = 50$, $R^2 = 0.22$, $P < 0.01$; body condition: $n = 50$, $R^2 = 0.18$, $P < 0.01$) (Fig. 4).

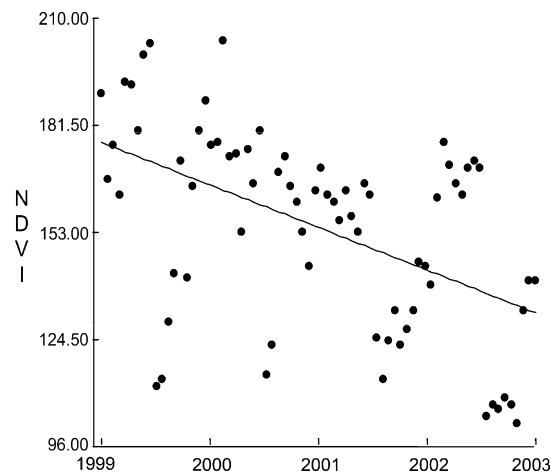


Fig. 1 – Normalized digital vegetation index diminution in the study area.

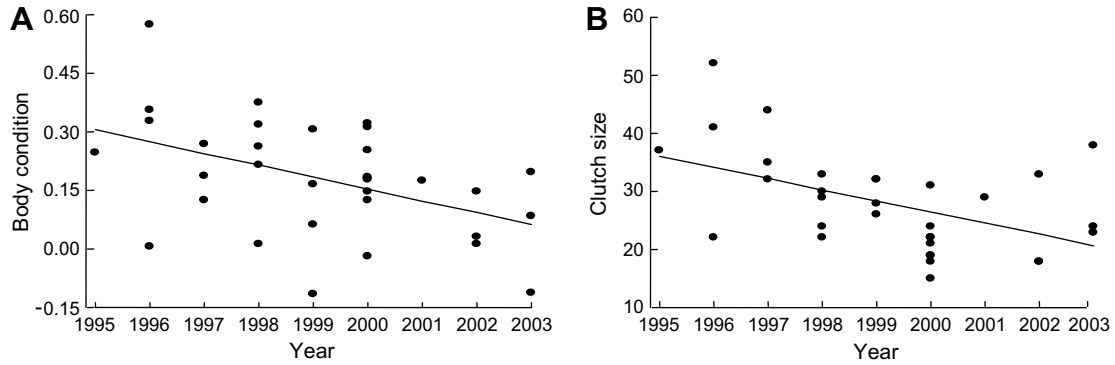


Fig. 2 – Diminution of body condition (A) and clutch size (B) of reproductive females of *Boa constrictor occidentalis* between 1995 and 2003.

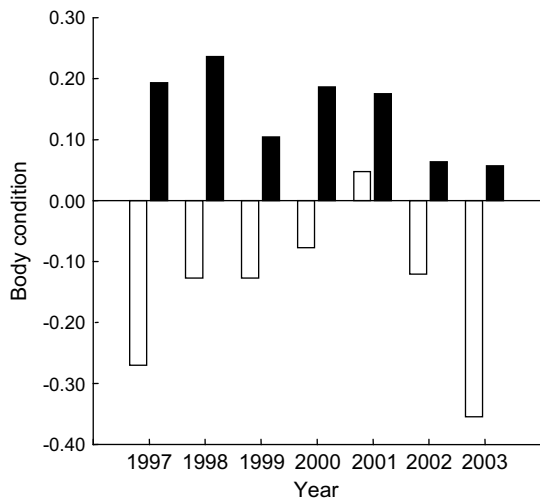


Fig. 3 – Mean body condition of *Boa constrictor occidentalis* reproductive females (solid bars) and non-reproductive females (open bars) from 1997 to 2003.

Reproductive frequency of males in the population does not seem to change ($X^2 = 10.84$; 8 gl; $P = 0.05$) with a mean value of 0.68.

3.2. Influence of landscape composition on reproductive behaviour

The landscape analysis showed that the remnant forest is characterized by a fragmentation pattern. The area covered by forest was 21% whereas shrublands cover peaked 76%. In many sites, shrublands were so low and open that the soil was virtually uncovered. The forest was fragmented in small and isolated patches. The mean patch area was 422.12 ha and the mean Euclidean nearest neighbor distance was 909 m (Fig. 5).

Considering the landscape heterogeneity described, we tested if the reproductive behaviour of the population differed between forest and shrublands areas (Table 1). We found that reproductive frequency was higher in the forest than in the shrublands ($X^2 = 4.65$; 1 df; $P = 0.03$). This trend was also manifested in each sex although there were not statistical

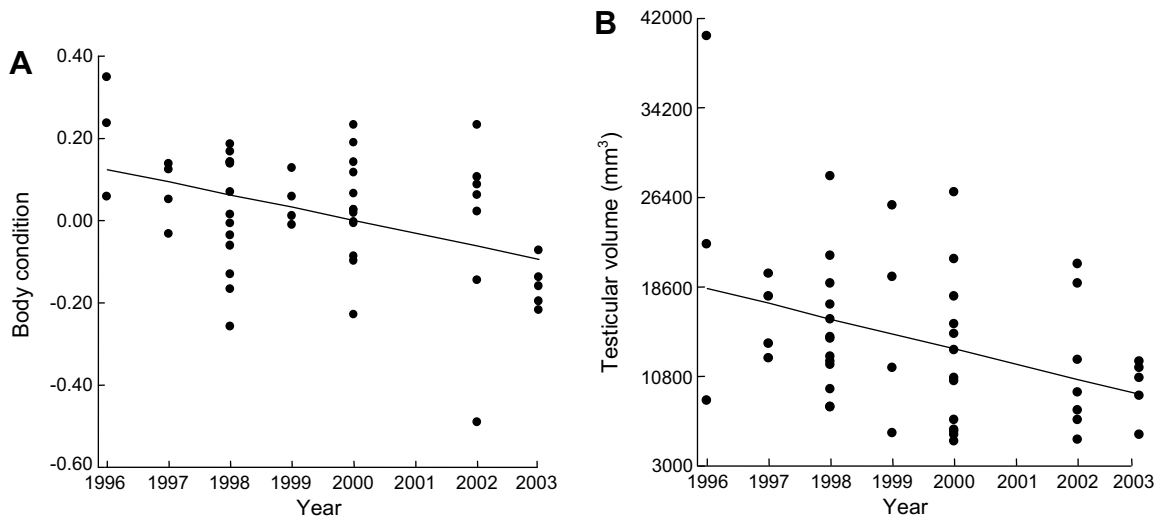


Fig. 4 – Diminution of body condition (A) and testicular volume (B) of reproductive males of *Boa constrictor occidentalis* between 1996 and 2003.

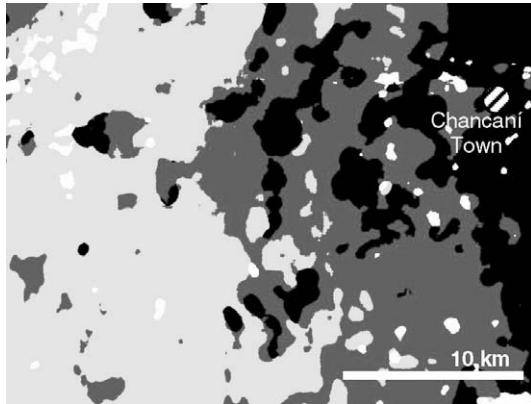


Fig. 5 – Landscape composition of the study area. Supervised classification indicates: black (forest), dark grey (high shrubland), light grey (low shrubland), white (uncovered soil).

Table 1 – Reproductive parameters of *Boa constrictor occidentalis* in two landscape structures

Reproductive parameters	Forest	Shrubland
Reproductive frequency R:NR(*)	0.65:0.35	0.42:0.58
Mating groups frequency(*)	0.92	0.08
Operational sex ratio M:F(*)	1.70:1	1.5:1
Male body condition	0.01 ± 0.02	0.07 ± 0.05
Testicular volume (mm ³)	14 054.64 ± 1 094.57	19 398.49 ± 7 672.34
Reproductive female proportion(*)	0.87	0.13
Female body condition(*)	0.19 ± 0.03	0.12 ± 0.08
Clutch size	27.60 ± 1.7	34.75 ± 3.82

R: reproductive, NR: non-reproductive, M: male, F: female.
*Indicates significant differences.

differences (females: $X^2 = 2.27$; 1 df; $P = 0.13$; males: $X^2 = 2.02$; 1 df; $P = 0.16$).

The establishment of reproductive groups depended on habitat cover, since mating groups frequency was markedly higher in forest areas ($X^2 = 17.64$; 1 df; $P < 0.01$). Furthermore, composition of mating groups could be considered different, since mating groups in shrublands were composed of couples whereas in the forest they were made up of a female and one to three males. Accordingly, the operational sex ratio in forest areas was biased towards males ($X^2 = 4.63$; 1 df; $P = 0.03$) whereas in shrublands the male:female proportion did not differ significantly from 1:1 ($X^2 = 0.40$; 1 df; $P = 0.53$). Regarding males, neither testicular volume index nor body condition seemed to display variations between individuals from the forest and those from the shrubland (testicular volume index: $W = 158.5$, $P = 0.87$; body condition: $W = 181$, $P = 0.40$) (Table 1).

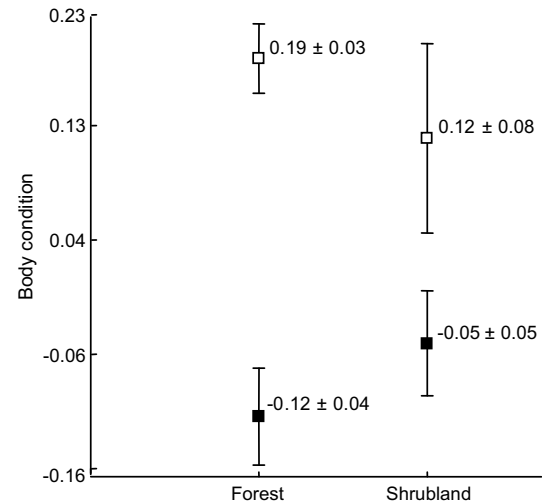


Fig. 6 – Body condition of reproductive (open rectangles) and non-reproductive females (solid rectangles) of *Boa constrictor occidentalis* in the landscape structures of the study area.

However, 33% of the males from the forest showed a greater testicular volume than the greatest value found for males from the shrublands. Those males that could develop bigger testes were also in a considerably better body condition than the other males from the forest ($W = 370$, $P < 0.01$).

Abundance of reproductive females varied between environments ($X^2 = 16.13$; 1 df; $P < 0.01$) (Table 1) and reproductive females settled in the forest were more heavy-bodied than those from the shrublands ($W = 58$; $P < 0.01$). However, contrary to what might be expected, clutch size did not vary between environments ($H = 2.29$; $P = 0.1294$).

The threshold of the reproductive body condition was lower for females from the shrublands than for those from the forest. (forest: mean body condition of reproductive females = 0.19 ± 0.03 ; mean body condition of non-reproductive females = -0.12 ± 0.04 , $W = 249$, $P < 0.01$; shrublands: mean body condition of reproductive females = 0.12 ± 0.08 ; mean body condition of non-reproductive females = -0.05 ± 0.05 , $W = 36$, $P = 0.11$) (Fig. 6). As we have seen above, clutch size did not differ between vegetation types, even though females in the shrublands were longer than females breeding in the forest ($W = 110.5$, $P < 0.01$, mean LHC in the forest = 2102.12 ± 32.47 mm, mean LHC in the shrubland = 2362.50 ± 100.86 mm).

4. Discussion

Some effects of habitat fragmentation on reptiles (Mac Nally and Brown, 2001; Driscoll, 2004; Marchand and Litvaitis, 2004; Stow and Sunnucks, 2004) and, in particular, on snakes (Luiselli and Capizzi, 1997; Blouin-Demers and Weatherhead, 2001; Cardozo et al., 2007) have been reported. However, the novelty of our approach relies on the proximate ecological mechanisms that lead reptiles to decline as consequence of habitat change. Our results show that the loss of native forest over time may affect reproduction of the Argentine boa constrictor by reducing body condition, clutch size and testicular volume. Besides, we detected differences in the plasticity of

reproductive characters and found that spatial patterns of vegetation cover may affect the spatial distribution of females and males, operational sex ratio and mating aggregation processes.

4.1. Effects of habitat loss on reproductive parameters

Identifying the variables that affect the ecological processes of reptiles is imperative in order to determine threats for the species (Urbina-Cardona et al., 2006). Distribution-related factors could be prevailing threats for snake-fauna (Filippi and Luiselli, 2000). Predictive distribution models (Di Cola et al., 2008) indicated that vegetation might be a key factor for *B. c. occidentalis*. The lack of suitable thermal environments to thermoregulate may affect the reproductive processes of the Argentine boa constrictor (Chiaraviglio, 2006). Accordingly, we found that forest reduction may affect the reproductive threshold of females, clutch size, and reproductive potential of males (see Figs. 2 and 4).

Capital breeder snakes can assess resource availability and buffer fluctuations, modifying reproductive output to secure reproductive efficiency (Madsen and Shine, 1999a; Lourdais et al., 2002b). Accordingly, we have evidenced that reproductive frequency and body condition of non-reproductive females remain stable with progressive forest loss but clutch size diminishes, threatening species persistence. Long-lived reptiles may respond to habitat disturbance with high phenotypic plasticity, but this rebound could have negative effects in the long-term (Hoare et al., 2007; Moore et al., 2007). Besides, the continuous depression of the reproductive threshold could be indicating a low probability of survival and/or a small growth rate (Shine and Schwarzkopf, 1992). Other snakes, such as *Liasis fuscus*, respond to habitat variations with a reduction in maternal condition (Ford and Seigel, 1989; Madsen and Shine, 1999a). However, viviparous species which experience prolonged anorexia during pregnancy (Lourdais et al., 2002a) could reduce clutch size instead of body mass as a strategy to minimize post-partum emaciation. Boback and Carpenter (2007) have proposed that clutch size is a plastic character in *Boa constrictor* and, Waller et al. (2007) suggested that body condition of post-reproductive females would be a more stable character in *Eunectes notaeus*. Thus, to preserve body mass could be a way to secure future lifetime production of offspring in *B. c. occidentalis*.

4.2. Influence of landscape composition on reproductive behaviour

We show that landscape patterns affected the reproductive behaviour of the population as reproductive female abundance was greater in the forest than in the shrubland. Because female distribution affects mate searching and sexual selection (Brown and Weatherhead, 1999) we could predict changes in the PMSM mating system (Bertona and Chiaraviglio, 2003). In shrublands the operational sex ratio was similar to 1:1 suggesting that males could improve their reproductive success by remaining with the female instead of dispersing (Abell, 2000). For instance, males of *Morelia spilota* remain with females for long periods when females are in low density (Pearson et al., 2005). Habitat alterations in the landscape

could increase energetic cost for the dispersal of snakes (Roe et al., 2004). Accordingly, Cardozo et al. (2007) have detected a lower dispersal of the Argentine boa constrictor in regions where forest connectivity has been lost. On the contrary, in the forest the operational sex ratio was biased towards males. This produces a much more intense male–male competition (Kvarnemo and Ahnesjo, 2002). Our results indicate that only those males with better body condition would be able to develop bigger testes and could be better competitors (Holt and Van Look, 2004). However, we did not find significant difference in the testicular volume between environments (Bertona and Chiaraviglio, 2003). The apparent contradiction between this pattern and the temporal co-variation of forest and testicular volume could be explained by the reproductive behaviour of males. Since the PMSM mating system implies higher male dispersion, male Argentine boa constrictor could be affected by the general habitat quality as well as by local conditions.

Geographic variation in life-histories independent of habitat loss could occur. Nevertheless, the documented temporal shift in life-history traits associated to forest loss, as well as the spatial patterning reported, allow us to interpret variation in reproductive traits as a response to anthropogenic habitat degradation.

4.3. Implications for conservation

Among the weaknesses of the regional conservation plans, the poor information regarding ecology behaviour constitutes one of the fundamental issues (The Nature Conservancy et al., 2005). Our study provides useful knowledge showing that forest loss may enhance the vulnerability to extinction in the Argentine boa constrictor, through constraints on reproduction. It demonstrates the need for caution in the analysis of the conservation status of this species. Therefore, we encourage resource managers to consider that the mere presence of the species is not a good indicator of its conservation status. We remark the need to evaluate reproductive life-history parameters and single out those that should be taken into account for assessing population status and designing conservation plans. Body condition, clutch size and testicular volume are good indicators of the effect of progressive landscape changes on Argentine boa constrictor populations. Mean reproductive frequency could be a more constant population parameter along the time. However, since this parameter would vary spatially with the quality of landscape resources, it could be suitable to identify higher quality patches. Low frequency of mating aggregations and presence of couples instead of multi-male groups could indicate scarce habitat resources. On the contrary, body condition of males and testicular volume could be somewhat unreliable parameters to evaluate local habitat conditions, considering that males disperse greatly (Rivera et al., 2006; Chiaraviglio and Bertona, 2007).

Since snake communities vary along environmental gradients (Urbina-Cardona et al., 2006; Cagle, 2008), conservationists should also consider species-specific conservation strategies or, at least, take into account the diversity of responses of keystone species. For instance, because some ecological features make snakes more vulnerable to extinction

than others (Webb et al., 2002), we could predict that species with similar ecological traits to the Argentine boa constrictor, such as slow life history, late maturation, high reproductive costs, large corporal size and habitat-specific requirements, would be more vulnerable to habitat loss than others.

To know whether a species is threatened by habitat change it is necessary to determine the nature and severity of the environmental process experienced (Fitzgerald et al., 2004). It is our belief that the Argentine boa constrictor should continue to be considered a species endangered since its reproductive habitat is largely threatened (CITES I, 2007). Considering that only 9% of the Gran Chaco is located in protected areas and that, in Argentina, where the major section of the Gran Chaco is located, the conservation units represent 3.25% of the Argentinean Chaco (The Nature Conservancy et al., 2005), we underline the necessity of efficient control of deforestation, protection of forest remnants and establishment of corridors. This issue is fundamental to this species conservation since female reproductive frequency and body condition diminish in shrublands, whereas the mating groups settle in the forest.

Policy makers must take into account that landscape modifications would affect species' ecological processes at different temporal scales. Endogamy has still not been detected, probably because of the active dispersal behaviour of males searching for females to reproduce (Rivera et al., 2005, 2006). However, it has already been demonstrated that the declination of gene flow (Cardozo et al., 2007) and reproductive parameters could be short-term indicators of the conservation status of long-lived animal species. Nevertheless, potentially costly management decisions for long-lived species should be taken based on long-term monitoring (Moore et al., 2007; Cagle, 2008).

Because of the fragility of the Gran Chaco's natural resources and the difficult reversibility of many of the region's alterations, urgent measures are needed to reach a sustainable development of the region. The protection of the *B. c. occidentalis* will also contribute to the protection of Gran Chaco and consequently to the conservation of its environmental services. The Gran Chaco is a wooded region of exceptional biodiversity with unique ecological processes. Conserving its biodiversity also means maintaining and guaranteeing its cultural identity.

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REFERENCES

- Abell, A.J., 2000. Costs of reproduction in male lizards, *Sceloporus virgatus*. *Oikos* 88, 630–640.
- Bagour, M.H., Al-Mahlafe, S., Jacob, A., Fahsi, A., 2006. Change detection of the vegetation cover based upon advanced very high resolution radiometer (AVHRR) data. *Res. J. Agr. Biol. Sci.* 2, 341–348.
- Baldi, G., Guerschman, J.P., Paruelo, J.M., 2006. Characterizing fragmentation in temperate South America grasslands. *Agr. Ecosyst. Environ.* 116, 197–208.
- Bertona, M., Chiaraviglio, M., 2003. Reproductive biology, mating aggregations and sexual dimorphism of the Argentine Boa Constrictor (*Boa constrictor occidentalis*). *J. Herpetol.* 37, 510–516.
- Blouin-Demers, G., Kissner, K.J., Weatherhead, P.J., 2000. Plasticity in preferred body temperature of young snakes in response to temperature during development. *Copeia* 2000, 841–845.
- Blouin-Demers, G., Weatherhead, P.J., 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* 82, 2882–2896.
- Boback, S.M., Carpenter, M., 2007. Body size and head shape of island *Boa constrictor* in Belize: environmental versus genetic contributions. In: Henderson, R., Powell, R. (Eds.), *Biology of the Boa and Phytons*. Eagle Mountain Publishing, Utah, pp. 102–117.
- Brown, G.P., Weatherhead, P.J., 1999. Female distribution affects mate searching and sexual selection in male northern water snakes (*Nerodia sipedon*). *Behav. Ecol. Sociobiol.* 47, 9–16.
- Brown, W.S., Parker, W.S., 1976. A ventral scale clipping system for permanently marking snakes (Reptilia, Serpentes). *J. Herpetol.* 10, 247–249.
- Cabido, M., Zak, M., 1999. *Vegetación del norte*, first ed. Secretaría de Agricultura, Ganadería y Recursos Renovables de Córdoba. Universidad Nacional de Córdoba, Córdoba.
- Cagle, N., 2008. Snake species distributions and temperate grasslands: a case study from the American tallgrass prairie. *Biol. Conserv.* 141, 744–755.
- Cardozo, G., Rivera, P.C., Lamfri, M., Scavuzzo, M., Gardenal, C., Chiaraviglio, M., 2007. Effects of habitat loss on the genetic structure of the Argentine Boa Constrictor (*Boa constrictor occidentalis*) populations. In: Henderson, R., Powell, R. (Eds.), *Biology of the Boa and Phytons*. Eagle Mountain Publishing, Utah, pp. 329–338.
- Chiaraviglio, M., 2006. The effects of reproductive condition on thermoregulation in the Argentine boa constrictor (*Boa constrictor occidentalis*) (Boidae). *Herpetol. Monogr.* 20, 172–177.
- Chiaraviglio, M., Bertona, M., 2007. Reproductive ecology of the Argentine Boa Constrictor and implication for conservation. In: Henderson, R., Powell, R. (Eds.), *Biology of the Boa and Phytons*. Eagle Mountain Publishing, Utah, pp. 77–86.
- Chiaraviglio, M., Sironi, M., Cervantes, R., Bertona, M., Lucino, S., 1998. Ultrasound imaging of the reproductive structures in *Boa constrictor occidentalis* (Serpentes: Boidae). *Gayana Zoología* 62, 91–95.
- Chuvioco, E., 2002. *Teledetección Ambiental: la observación de la Tierra desde el Espacio*, first ed. Ariel, Barcelona.
- CITES I, 2007. *Convención sobre el Comercio Internacional de Especies Amenazadas de Fauna y Flora Silvestres (CITES)*. Apéndice I. Secretaría de Recursos Naturales y Desarrollo

- Sustentable, Dirección de Fauna y Flora Silvestres, Buenos Aires, Argentina.
- Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biol. Conserv.* 128, 231–240.
- Dedios, M.N., 2006. Management and conservation of dry forest ecosystems. *Lyonia* 9, 21–27. Ecological Park Kurt-Beer, Piura, Peru.
- Di Cola, V., Cardozo, G., Lanfri, M., Scavuzzo, C.M., Chiaraviglio, M., 2008. Modelling the distribution of the vulnerable snake species *Epicrates cenchria alvarezii* and *Boa constrictor occidentalis* (Boidae) in the South American Gran Chaco. *Amphibia – Reptilia* 29, 299–310.
- Driscoll, D.A., 2004. Extinction and outbreaks accompany fragmentation of a reptile community. *Ecol. Appl.* 14, 220–240.
- Filippi, E., Luiselli, L., 2000. Status of the Italian snake fauna and assessment of conservation threats. *Biol. Conserv.* 93, 219–225.
- Filippi, E., Luiselli, L., 2006. Changes in community composition, habitats and abundance of snakes over 10 + years in a protected area in Italy: conservation implications. *Herpetol. J.* 16, 29–36.
- Fitzgerald, M., Shine, R., Lemckert, F., 2004. Life history attributes of a threatened Australian snake (Stephen's Banded Snake, *Hoplocephalus stephensii*, Elapidae). *Biol. Conserv.* 119, 121–128.
- Ford, N.B., Seigel, R.A., 1989. Phenotypic plasticity in reproductive traits: evidence from a viviparous snake. *Ecology* 70, 1768–1774.
- Gardner, T.A., Barlow, J., Peres, C.A., 2007. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. *Biol. Conserv.* 138, 166–179.
- Hoare, J.M., Pledger, S., Nelson, N.J., Daugherty, C.H., 2007. Avoiding aliens: behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. *Biol. Conserv.* 136, 510–519.
- Holt, W.V., Van Look, K.J.W., 2004. Concepts in sperm heterogeneity, sperm selection and sperm competition as biological foundations for laboratory tests of semen quality. *Reproduction* 127, 527–535.
- Infostat, 2004. InfoStat versión 1.1. Facultad de Ciencias Agropecuarias. Universidad Nacional de Córdoba, Argentina.
- Ishwar, N.M., Chellam, R., Kumar, A., Noo, B.R., 2003. The response of agamid lizards to rainforest fragmentation in the Southern Western Ghats, India. *Conserv. Soc.* 1, 79–86.
- Kvarnemo, C., Ahnesjö, I., 2002. Operational sex ratios and mating competition. In: Hardy, I.C.W. (Ed.), *Sex Ratios: Concepts and Research Methods*. Cambridge University Press, Cambridge, pp. 366–382.
- Lourdais, O., Bonnet, X., Doughty, P., 2002a. Costs of anorexia during pregnancy in a viviparous snake (*Vipera aspis*). *J. Exp. Zool.* 292, 487–493.
- Lourdais, O., Bonnet, X., Shine, R., Denardo, D., Naulleau, G., Guillon, M., 2002b. Capital-breeding and reproductive effort in a variable environment: a longitudinal study of a viviparous snake. *J. Anim. Ecol.* 71, 470–479.
- Luiselli, L., Capizzi, D., 1997. Influences of area, isolation and habitat features on distribution of snakes in mediterranean fragmented woodlands. *Biodivers. Conserv.* 6, 1339–1351.
- Mac Nally, R., Brown, G.W., 2001. Reptiles and habitat fragmentation in the box-ironbark forests of central Victoria, Australia: predictions, compositional change and faunal nestedness. *Oecologia* 128, 116–125.
- McGarigal, K., Marks, B., 1995. FRAGSTATS: spatial analysis program for quantifying landscape structure. USDA Forest Service General Technical Report PNW-GTR-351.
- Madsen, T., Shine, R., 1999a. The adjustment of reproductive threshold to prey abundance in a capital breeder. *J. Anim. Ecol.* 68, 571–580.
- Madsen, T., Shine, R., 1999b. Life-history consequences of nest-site variation in tropical pythons (*Liasis fuscus*). *Ecology* 80, 989–997.
- Madsen, T., Shine, R., 2000. Energy versus risk: costs of reproduction in free-ranging pythons in tropical Australia. *Austral Ecol.* 25, 670–675.
- Marchand, M.N., Litvaitis, J.A., 2004. Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. *Conserv. Biol.* 18, 758–767.
- Méndez, F.R., Villagrán, M., 1998. Reproducción asincrónica de *Sceloporus palaciosi* (Sauria: Phrynosomatidae) en México, con comentarios sobre sus ventajas y regulación. *Rev. Biol. Trop.* 46, 1159–1161.
- Moore, J.A., Hoare, J.M., Daugherty, C.H., Nelson, N.J., 2007. Waiting reveals waning weight: Monitoring over 54 years shows a decline in body condition of a long-lived reptile (tuatara, *Sphenodon punctatus*). *Biol. Conserv.* 135, 181–188.
- Neckel-Olivera, S., Gascon, C., 2006. Abundance, body size and movements patterns of a tropical treefrog in continuous and fragmented forests in the Brazilian Amazonian. *Biol. Conserv.* 128, 308–315.
- Olsson, M., Madsen, T., Shine, R., 1997. Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. *Proc. Roy. Soc. Ser. B* 264, 455–459.
- Payton, I.J., Fenner, M., Lee, W.G., 2002. Keystone species: the concept and its relevance for conservation management in New Zealand. *Science for Conservation* 203. Department of Conservation, Wellington. pp. 29.
- Pearson, D.J., Shine, R., Williams, A., 2002. Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia* 131, 418–426.
- Pearson, D.J., Shine, R., Williams, A., 2005. The spatial ecology of a threatened python (*Morelia spilota imbricata*) and the effects of anthropogenic habitat change. *Austral Ecol.* 30, 261–274.
- Rivera, P.C., Chiaraviglio, M., Pérez, G., Gardenal, C.N., 2005. Protein polymorphism in populations of *Boa constrictor occidentalis* (Boidae) from Córdoba Province, Argentina. *Amphibia – Reptilia* 26, 175–181.
- Rivera, P.C., Gardenal, C.N., Chiaraviglio, M., 2006. Sex-biased dispersal and high levels of gene flow among local populations in the Argentine boa constrictor, *Boa constrictor occidentalis*. *Austral Ecol.* 31, 948–955.
- Roe, J.H., Kingsbury, B.A., Herbert, N.R., 2004. Comparative water snake ecology: conservation of mobile animals that use temporally dynamic resources. *Biol. Conserv.* 118, 79–89.
- Romero-Nájera, I., Cuarón, A.D., González-Baca, C., 2006. Distribution, abundance, and habitat use of introduced *Boa constrictor* threatening the native biota of Cozumel Island, Mexico. *Biodivers. Conserv.* 16, 1183–1195.
- Row, J.R., Blouin-Demers, G., 2006. Thermal quality influences effectiveness of thermoregulation, habitat use, and behaviour in milk snakes. *Oecologia* 148, 1–11.
- Rutledge, D., 2003. *Landscape Indices as Measures of the Effects of Fragmentation: can Pattern Reflect Process?* DOC Science International Series 98. Department of Conservation, Wellington. p. 27.
- Schulte-Hostedde, A.I., Montgomerie, R., 2006. Intraspecific variation in ejaculate traits of northern watersnakes (*Nerodia sipedon*). *J. Zool.* 270, 147–152.
- Scrocchi, G., Agüero, I., Arzamendia, V., Cacivio, P., Carcacha, H., Chiaraviglio, M., Giraud, A., Kretzschmar, S., Leynaud, G., López, M., Rey, I., Waller, T., Williams, J., 2000. Categorización de las serpientes de Argentina. In: Lavilla, E., Richard, E., Scrocchi, G. (Eds.), *Categorización de Anfibios y Reptiles de Argentina*. Asociación Herpetológica Argentina, Tucumán, pp. 75–97.

- Shetty, S., Shine, R., 2002. The mating system of yellow-lipped sea kraits (*Laticauda colubrina*, Laticaudinae). *Herpetologica* 58, 170–180.
- Shine, R., 2003. Reproductive strategies in snakes. *Proc. Roy. Soc. London Ser. B* 270, 995–1004.
- Shine, R., Fitzgerald, M., 1995. Variation in mating systems and sexual size dimorphism between populations of the Australian python *Morelia spilota* (Serpentes: Pythonidae). *Oecologia* 103, 490–498.
- Shine, R., Mason, R.T., 2005. Do a male snake's energy stores limit his reproductive effort? *Can. J. Zool.* 83, 1265–1270.
- Shine, R., Schwarzkopf, L., 1992. The evolution of reproductive effort in lizards and snakes. *Evolution* 46, 62–75.
- Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single species management passé in the landscape era? *Biol. Conserv.* 83, 247–257.
- Slip, D.J., Shine, R., 1988. The reproductive biology and mating system of diamond pythons, *Morelia spilota* (Serpentes: Boidae). *Herpetologica* 44, 396–404.
- Steininger, M.K., Tucker, C.J., Ersts, P., Killen, T.J., Villegas, Z., Hetch, S.B., 2001. Clearance and fragmentation of tropical deciduous forest in the Tierras Bajas, Santa Cruz, Bolivia. *Conserv. Biol.* 15, 856–866.
- Stow, A.J., Sunnucks, P., 2004. Inbreeding avoidance in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. *Mol. Ecol.* 13, 443–447.
- The Nature Conservancy (TNC), Fundación Vida Silvestre Argentina (FVSA), Fundación para el Desarrollo Sustentable del Chaco (DeSdel Chaco) y Wildlife Conservation Society Bolivia (WCS), 2005. Evaluación Ecorregional del Gran Chaco Americano/Gran Chaco Americano Ecoregional Assessment. Buenos Aires. Fundación Vida Silvestre Argentina.
- Urbina-Cardona, J.N., Olivares-Pérez, M., Reynoso, V.H., 2006. Herpetofauna diversity and microenvironment correlates across a pasture–edge–interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. *Biol. Conserv.* 132, 61–75.
- Waller, T., Micucci, P.A., Alvarenga, E., 2007. Conservation biology of the Yellow Anaconda (*Eunectes notaeus*) in northeastern Argentina. In: Henderson, R., Powell, R. (Eds.), *Biology of the Boa and Phytons*. Eagle Mountain Publishing, Utah, pp. 341–362.
- Webb, J., Brook, B.W., Shine, R., 2002. What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. *Ecol. Res.* 17, 59–67.
- Zak, M.R., Cabido, M., Hodgson, J., 2004. Do subtropical seasonal forests in the Gran Chaco, Argentina, have a future? *Biol. Conserv.* 120, 589–598.
- Zenuto, R., Vitullo, A., Busch, C., 2003. Sperm characteristics in two populations of the subterranean rodent *Ctenomys talarum* (Rodentia: Octodontidae). *J. Mammal.* 84, 877–885.