

## Modelling the distribution of the Boid snakes, *Epicrates cenchria alvarezi* and *Boa constrictor occidentalis* in the Gran Chaco (South America)

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**Abstract.** The viviparous snake species *Epicrates cenchria alvarezi* and *Boa constrictor occidentalis* inhabit the Gran Chaco region of South America. Ecological factors determining their distribution are poorly known. GIS-based modelling of a species' environmental requirements using occurrence records provides essential information of the species' distribution. We modelled the geographical distribution of *E. c. alvarezi* and *B. c. occidentalis* in the Gran Chaco and analyzed the degree to which their distribution is associated with different environmental variables (precipitation, normalized difference vegetation index (NDVI), land surface temperature and altitude) using Logistic Regression Analysis. We found that *E. c. alvarezi* and *B. c. occidentalis* would be more frequent in areas with high levels of NDVI (positive relationship with NDVI), with low levels of precipitation (negative relationship with PRE1) and with lower altitude (negative relationship with ALT). However, the analysis also revealed specific differences in the environmental requirements of the snakes, showing that *B. c. occidentalis* is more frequent than *E. c. alvarezi* at sites with higher levels of NDVI. Additionally, *E. c. alvarezi* is more frequent at sites with lower temperatures in the dry season. The maps obtained show that both are highly likely to be present in the Dry subregion of the Gran Chaco. The results of the present study can be an important contribution to a better understanding of the ecological requirements of the species and of the impact of global environmental change on its distribution.

**Keywords:** Boidae, conservation, GIS analysis, logistic regression analysis, modelling distribution.

### Introduction

The geographic distribution of species is affected by many factors and varies in space and time usually with the readiness of the environmental components necessary for life (MacArthur, 1972; Litvaitis et al., 1996; Anderson et al., 2002). There have been many attempts to explain how climate, along with other environmental factors, determine the spatial preferences of organisms and, thus, define their distribution (Gertseva et al., 2006). Global patterns of reptile distribution indicate that the physical environment restricts the spatial distribution of species (Zug et al., 2001).

Snakes' ecological processes are susceptible to variables such as temperature, precipitation, seasonality, and habitat structure (Saint Girons, 1982; Zug et al., 2001; Guisan and Hofer, 2003; Santos et al., 2006; Cardozo et al., 2007). Broad patterns of distribution have been described for boines (Henderson et al., 1995), but many details remain to be elucidated. In Argentina, two phylogenetically related subspecies of boid snakes occur sympatrically in the Gran Chaco domain: *Boa constrictor occidentalis* and *Epicrates cenchria alvarezi* (Henderson et al., 1995; Burbrink, 2005). Both subspecies occur in the semiarid plains of the phytogeographic province of Gran Chaco, from south of Bolivia and west of Paraguay, to the south, across the flat areas and semi-arid submountains of the Argentinean northwest, down to approximately 33-36°S (Henderson et al., 1995; Waller et al., 1995). Although these areas have been characterized in terms of vegetation and climate, the factors determining the distrib-

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ution of *E. c. alvarezi* and *B. c. occidentalis* are still not clear; and a detailed ecological analysis of distribution is necessary (Henderson et al., 1995).

Some snakes are highly vulnerable to extinction due to several life history traits and certain morphological characteristics, such as low levels of genetic variability, long generation time, low reproductive frequency, large size, conspicuousness, and specially distribution (the latter being generated from the interaction between natural ecological characteristics and human impact on the natural habitat) (Filippi and Luiselli, 2000; Webb et al., 2002; Santos et al., 2006; Santos et al., 2007). It has been demonstrated that *B. c. occidentalis* has specialized habitat use because reproductive females prefer sites with less substratum and greater arboreal cover (Chiaraviglio, 2006; Chiaraviglio and Bertona, 2007). Likewise, Rivera et al. (2005) reported low levels of polymorphism in two populations of *B. c. occidentalis*. However, up to the present, no studies on life history or habitat use of *E. c. alvarezi* have been conducted in Argentina.

Over the last decade, the enhancement of ecological modelling techniques and their inclusion and inter-changeability with Geographical Information Systems (GIS) have prompted conservation biology studies with new and more robust methods (Guisan and Zimmermann, 2000; Brito and Crespo, 2002; Anderson et al., 2003; Elith et al., 2006; Santos et al., 2006). These tools rely on the identification of relevant habitat cues for the occurrence of species, quantification of the factors restricting their distribution, and geographical prediction of habitat-suitable areas for the species (Reutter et al., 2003). Models of species distribution attempt to provide detailed predictions of distributions by relating presence or abundance of species to environmental predictors. Indeed, distribution models have provided researchers with an innovative tool to explore diverse questions in ecology, evolution, and conservation, including ecological and geographical differentiation of

the distributions of closely-related species (Elith et al., 2006). Ecological modelling techniques may also contribute to the evaluation of the conservation status of secretive species (Santos et al., 2006) and may offer insights to explain sympatry (Brito and Crespo, 2002).

In this study, we model the geographical distribution of *E. c. alvarezi* and *B. c. occidentalis* in the Gran Chaco and analyze the degree to which their distribution is associated to different abiotic and/or biotic features. Such relations are of interest not only because both snakes are considered sympatric, but also because the associations can explain the current distribution of both subspecies.

## Materials and methods

### Study species

*Boa c. occidentalis* and *E. c. alvarezi* are viviparous snakes of different body size, the former being longer (up to 3 m) (Chiaraviglio et al., 2003) and heavier than the latter (1.5 m) (Ceï, 1986). *B. c. occidentalis* presents low levels of genetic variability (Rivera et al., 2005) and is heavily hunted and captured for skin and pet trade (Gruss, 1991; Ávila and Acosta, 1996). The habitat of both snakes is being severely modified by intense farming and cattle breeding in the area (Zak et al., 2004; Cardozo et al., 2007). *B. c. occidentalis* is considered a threatened subspecies (Scrocchi et al., 2000) and has been included in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 1997) whereas *E. c. alvarezi* has been included in Appendix II.

### Study area

The Gran Chaco covers more than 1 000 000 km<sup>2</sup> across the plains and low ranges of northern Argentina, western Paraguay, south-eastern Bolivia, and a small portion in Brazil (Prado, 1993; Pennington et al., 2000; The Nature Conservancy et al., 2005). The Gran Chaco is the largest dry forest in South America and its vegetation comprises a mosaic of xerophytic forests, woodlands, scrubs, savannas, and grasslands (Bucher and Saravia Toledo, 2001). The vegetation in the Gran Chaco is composed of typical species from dry environments, such as *Schinopsis quebracho colorado*, *Aspidosperma quebracho blanco*, *Prosopis* sp., *Larrea divaricata*, and *Opuntia glomerata*. The forest is being lost at an annual rate of 2.2%, the highest deforestation rate estimated for South America (Zak et al., 2004). In Argentina, the Gran Chaco extends from 22°S to subtropical zones at 31°S. Annual average temperatures range from 18 to 23°C; annual rainfall ranges between 300 and 550 mm with distinct dry (April to September) and wet (October to March) seasons (Capitanelli, 1979).

### Species and environmental data

A total of 90 records of the presence of *Epicrates cenchria alvarezii* and 93 records of *Boa constrictor occidentalis* in Argentina were gathered from authors' field data and supplemented with records from the literature (fig. 1). Thus, presence sites were composed of the pixel with the exact geographical coordinates of the locality and its closest eight neighbour pixels (we assume similar values in those pixels due to the fact that they are environmental variables). To characterize the "absence" of the snakes, we decided to add random points throughout South America, excluding the area where presence of each subspecies was confirmed, according to reliable literature (Cei, 1986; Chiaraviglio et al., 1998; Giraud and Scrocchi, 2002). Since the random points needed to be confirmed as true absence, we denominated them "pseudo absence", as suggested by Anderson et al. (2003).

Modelling was performed using the following biogeophysical variables: monthly average series of precipitation; normalized difference vegetation index (NDVI), which is a derivative of the photosynthetically active biomass and represents greenness; land surface temperature (LST); and altitude (ALT).

Precipitation data corresponded to a 1950-2000 monthly total precipitation series with a pixel size of 1 km × 1 km obtained from WorldClim (Hijmans et al., 2004). NDVI and LST were derived from the Advanced Very High Resolution Radiometer (AVHRR) on-board the National Oceanic and Atmospheric Administration's (NOAA) polar-orbiting meteorological satellites, having a post-processing pixel size of 8 km × 8 km. NDVI and LST data are monthly averaged products derived from satellite images from the 1982-2000 period. Finally, a 1 km × 1 km spatial resolution South America ALT of spatial resolution data obtained from WorldClim (Hijmans et al., 2004) was included in our analysis. The biogeophysical variables mentioned were selected because they have been reported as meaningful to the ecology and distribution of other snake species (Real et al., 1997; Brito et al., 1999; Guisan and Hofer, 2003; Fitzgerald et al., 2005; Santos et al., 2006).

Environmental data were georeferenced to a latitude-longitude coordinate system and were resampled to adjust the pixel size to 8 km × 8 km. ENVI 4.1 software (System Research) was used in all data analyses. Resulting data layers had 714 × 1063 pixels and covered South America between 13° and 56°S and between 33° and 82°W.

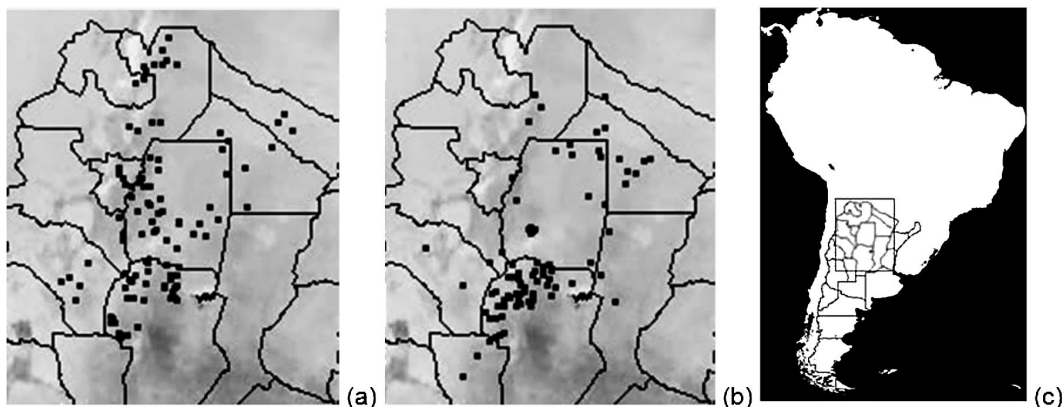
We summarized the NDVI, LST and precipitation time series using PCA analysis to determine the predominant patterns of variance in such datasets, according to Eastman and Fulk (1993). PCA is an attractive statistical technique to summarize information from time series images because it decomposes the series into a sequence of spatial and temporal components. Typically, the first component indicates the characteristic value of the variable, whereas subsequent components represent change elements of decreasing magnitude. Applied to an image series, coarse spatial variation is typically gathered by the first PCA component. Finer-scale spatial patterns and temporal changes are captured by the second and higher order components of the PCA. To generate the environmental dataset, we built a composite image with the PCA components that accounted for greatest variability plus a single ALT layer.

### Ecological modelling technique

A logistic regression analysis was performed to predict the presence or absence of a subspecies at a set of survey sites in relation to biogeophysical variables, thereby enabling the probability of occurrence of the snake to be predicted at unsurveyed sites (Pearce and Ferrier, 2000). The analysis was conducted using SPSS 8.0 for Windows (SPSS Inc. Chicago, Illinois).

The model building strategy followed the procedures used by Brito et al. (1999) and Brito and Crespo (2002): a forward stepwise elimination process was performed and the variables were ranked according to the resulting statistics of this step. The variables with  $P > 0.05$ , which were not significant at each step of the variable selection procedure, were eliminated.

We constructed two models using the absence and presence data (0/1; dependent variable) of the subspecies (*B. c.*



**Figure 1.** Map of the study area indicating the localities where *E. c. alvarezii* (a) and *B. c. occidentalis* (b) were recorded as present in Argentina, (a) and (b) are enlargements of the area shown in (c).

**Table 1.** Classification Table describing the occupied and unoccupied sites from the habitat models (cut-off point 0.6) of *E. c. alvarezii* and *B. c. occidentalis* applied to the original data.

		Recorded	
		Present	Absent
<i>E. c. alvarezii</i>	Predicted Present	734	77
	Predicted Absent	77	734
<i>B. c. occidentalis</i>	Predicted Present	622	64
	Predicted Absent	57	615

*occidentalis*, *E. c. alvarezii*) recorded on the environmental dataset (independent variables) (table 2). Then, to find differences in the coefficients of each variable between both models, we examined the confidence intervals of each variable (Sokal and Rohlf, 1990).

We evaluated the predictive capability following Fielding and Bell (1997), Pearce and Ferrier (2000), Brito and Crespo (2002) and Luck (2002). Hence, we used correct classification rates (1) and assessed the discrimination performance (2) using the Presence/Absence data from a Classification Table, shown in table 1. Then we obtained diagnostic measures of Sensitivity, Specificity and Kappa ( $\kappa$ ) statistic. We plotted pair-wise sensitivity values and their equivalent (1-specificity) in a ROC (Receiver Operator Characteristic) plot for each model, to obtain the area under the ROC function (AUC) (Fielding and Bell, 1997).

## Results

The PCA analysis performed for NDVI, LST, and precipitation time series indicates that the first two components of each environmental variable accounted for about 99% of the total variance of each series (table 2).

In table 3, we present the final models for *E. c. alvarezii* and *B. c. occidentalis*, which show that the biogeophysical variables used (precipitation, NDVI, temperature, and altitude), have a significant effect on the distribution of the snakes. We observed coefficients explaining the distribution of both species that are similar in value and sign. The environmental variables that appear to have a determinant role were entered into the forward selection models differently for both species (table 3). The analysis of the influence of habitat variables on the species' distributions revealed that *E. c. alvarezii* and *B. c. occidentalis* would be more frequent in areas with high levels of NDVI (positive relationship with

NDVI1), hence, with low levels of precipitation (negative relationship with PRE1) and with lower altitude (negative relationship with ALT).

To have a better understanding of the finer-scale spatial patterns and temporal changes captured by the second principal component of precipitation, NDVI and temperature, we correlated each component with each image of the monthly average series. Specifically, we observed for PRE2 a negative correlation with the wet season months. In contrast, for NDVI2 and TEMP2, we found a positive correlation with the dry season months. Therefore, *E. c. alvarezii* and *B. c. occidentalis* would be more frequent in areas with decreasing levels of NDVI in the dry season (negative relationship with NDVI2), where precipitation is high in the wet season (negative relationship with PRE2) and temperature is low in the dry season (negative relationship with TEMP2).

However, when examining the confidence intervals of each variable for both models, we found specific differences in the environmental requirements of *E. c. alvarezii* and *B. c. occidentalis*, which show that *B. c. occidentalis* is more frequent than *E. c. alvarezii* at sites with higher levels of NDVI. Additionally, *E. c. alvarezii* is more frequent at sites with lower temperatures in the dry season.

For each model, we also obtained correct classification rates for the presence, absence and a combination of both. The cut-off point that produces the most correct classification rate of the presences is 0.6 and the correct classification is above 90%. Therefore, because the absence may not correspond to a real absence, and since it is better to have higher rates in correct presence classification; we decided to use a cut-off point of 0.6 to generate the probability maps.

We obtained evaluation indices of the models for a cut-off point of 0.6. For the *E. c. alvarezii* model, the specificity was 0.9051, the sensitivity was 0.9051, and the Kappa statistic was 0.8101, and for the *B. c. occidentalis* model, the specificity was 0.9057, the sensitivity was 0.9161, and the Kappa statistic was 0.8218. The

**Table 2.** Predictor variables, their abbreviations and the eigenvalues of the PCA analysis for all the variables used in the LR models.

Abbreviation	Predictor variable	Eigenvalue
PRE1	Component axis 1 of a PCA on 12 monthly mean precipitation maps	305 638 868.1477
PRE2	Component axis 2 of a PCA on 12 monthly mean precipitation maps	19 272.5249
NDVI1	Component axis 1 of a PCA on 12 monthly mean NDVI maps	112 662.2841
NDVI2	Component axis 2 of a PCA on 12 monthly mean NDVI maps	505.5431
TEMP1	Component axis 1 of a PCA on 12 monthly mean temperature maps	257 729.9237
TEMP2	Component axis 1 of a PCA on 12 monthly mean temperature maps	64.1274
ALT	Altitude	–

**Table 3.** Variables included in the regression equations of the models for *E. c. alvarezi* and *B. c. occidentalis*. Forward selection of variables was employed in the model building, using a criterion ( $P < 0.05$ ) for their inclusion. (Explanations: PRE1, first principal component of precipitation; PRE2, second principal component of precipitation; NDVI1, first principal component of normalized difference vegetation index; NDVI2, second principal component of normalized difference vegetation index; TEMP2, second principal component of land surface temperature; ALT, a single altitude layer.)

Variable	B	S.E.	R	P	Exp(B)
<i>E. c. alvarezi</i> model					
PRE1	–2007.07	123.1611	–0.3424	0.0000	0.0000
PRE2	–87.403	6.2498	–0.2934	0.0000	0.0000
NDVI1	22.973	1.6528	0.2916	0.0000	9.485E+09
TEMP2	–9.401	1.2488	–0.1497	0.0000	0.0001
ALT	–36.3712	5.8717	–0.1272	0.0000	0.0000
NDVI2	–10.6011	1.6518	–0.1320	0.0000	0.0000
Constant	1900.058	117.0695		0.0000	
<i>B. c. occidentalis</i> model					
PRE1	–2234.59	154.8956	–0.3309	0.0000	0.0000
NDVI1	29.5504	2.0778	0.3262	0.0000	6.82E+12
PRE2	–83.4442	7.2557	–0.2630	0.0000	0.0000
ALT	–24.9508	5.1217	–0.1074	0.0000	0.0000
NDVI2	–10.8178	1.6204	–0.1504	0.0000	0.0000
TEM2	–3.4121	1.5609	–0.0384	0.0288	0.033
Constant	2094.204	146.5031		0.0000	

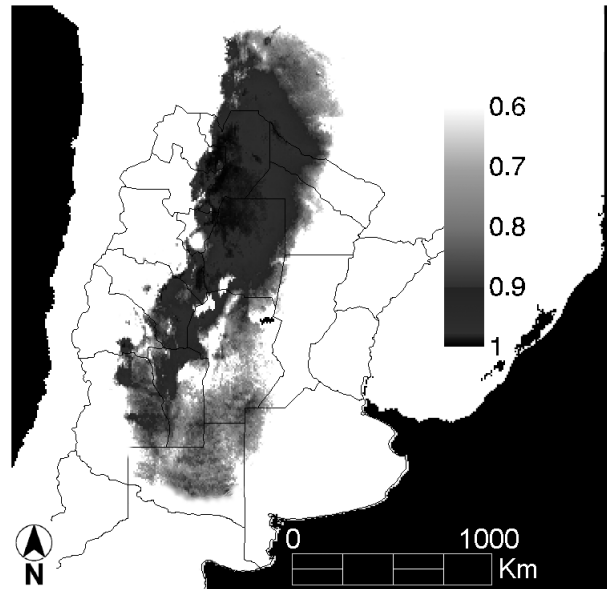
values of the model for these measures are high. The assessment of the model accuracy by AUC indicates high performance, with values of 0.92 for the *E. c. alvarezi* model and 0.95 for the *B. c. occidentalis* model.

Figures 2 and 3 show the occurrence probability maps for *E. c. alvarezi* and *B. c. occidentalis*, determined by their respective models. The most noticeable result observed in the maps is that potential areas of occurrence are the same for both species, but the areas with the highest probability of occurrence are different. The probable distribution of *E. c. alvarezi* is found between 18°39' and 37°50'S, and extends from 60°1' to 65°45'W. The probable distribution of *B. c. occidentalis* is found between 15°55' and

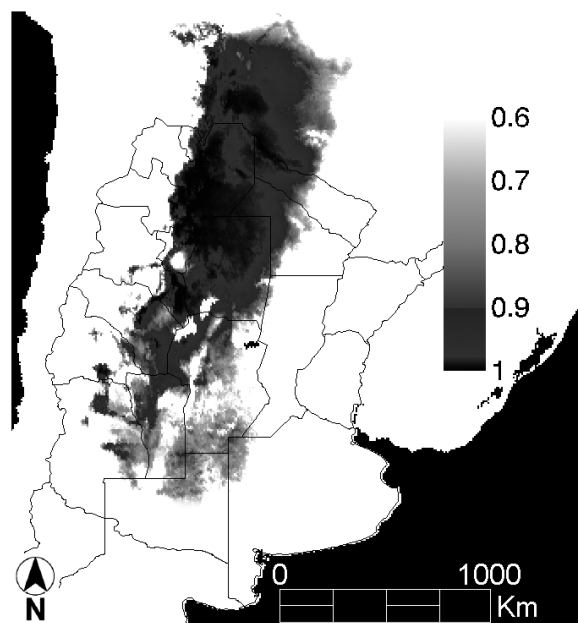
36°42'S, and extends from 60°2' to 65°47'W. The altitude in areas of predicted presence for *E. c. alvarezi* ranges from 100 m to 1300 m, whereas *B. c. occidentalis* can be found at an altitude of 1500 m.

## Discussion

In this study, we provide evidence for the role of environmental variables (precipitation, NDVI, temperature, and altitude) as significant and highly accurate predictors of the distribution of *E. c. alvarezi* and *B. c. occidentalis* (table 3). The models obtained reveal that the variables as a whole model the distribution of the species studied. The present results are in ac-



**Figure 2.** Probability area for the occurrence of *E. c. alvarezii* according to the logistic regression model (cut-off point 0.6).



**Figure 3.** Probability area for the occurrence of *B. c. occidentalis* according to the logistic regression model (cut-off point 0.6).

cordance with the effect of biogeophysical factors, such as climate, topography and vegetation, which have been previously reported by Guisan and Hofer (2003) to be of great importance for reptile distribution and more specifically for the distribution of species such as *Lacerta schreieri* (Brito et al., 1999), Vipers (Brito and Crespo, 2002) and Elapids (Fitzgerald et al., 2005). Although studies that evaluate the influence of environmental factors on reptile features are not necessarily recent, this is the first study that identifies these factors objectively from an assemblage of predictor variables in large-scale distribution models of boid species in Argentina.

According to our results the distribution of *E. c. alvarezi* would be influenced firstly by precipitation (PRE1 and PRE2), secondly by vegetation (NDVI1) and thirdly by temperature (TEM2). Likewise, the variables that have a determinant role in *B. c. occidentalis* presence are the same; however, there are some variations, since the importance of each variable appears in a different order (table 3).

For *E. c. alvarezi* and *B. c. occidentalis*, precipitation component 1 was the most important predictor (table 3). This variable is an evenly weighted average of the monthly precipitation values and therefore represents the overall precipitation. Both species decreased in occurrence as precipitation increased (negative coefficients of PRE1), which leads us to infer that *E. c. alvarezi* and *B. c. occidentalis* prefer dry areas. Therefore when matching the probability area of occurrence of both snakes with the mean precipitation of the area, it coincides with the rainfall range of 400-800 mm year<sup>-1</sup> (National Weather Service – Climatological Normal Statistics 1961-1990, unpublished data), and also is in accordance with the rainfall pattern described for the Gran Chaco by Zak et al. (2004), where precipitation concentrates mainly in summer (November to March) and decreases from >700 mm year<sup>-1</sup> in SE to <550 mm year<sup>-1</sup> in NW. This leads to a higher water deficit in the western portion of the region, explaining the

occurrence of *B. c. occidentalis* in areas with only 100-200 mm of annual precipitation, and of *E. c. alvarezi* in areas that receive 300-400 mm annually (Henderson et al., 1995). In addition, our results support the allopatric distribution known for the Argentine subspecies of *E. cenchria*: *E. c. alvarezi* inhabits the Dry portion of the Gran Chaco in central and northern Argentina, whereas *E. c. crassus* is characteristic of the Paranaense Forest (Giraudó, 2001).

Since the value of NDVI represents an overall index of 'greenness' (Suarez-Seoane et al., 2002), we are then able to associate this variable with vegetation cover. Both species had a positive relationship with vegetation (NDVI1), indicating that vegetation might be a key factor in species' biology. Indeed, tree cover was reported by Attademo et al. (2004), Chiaraviglio (2006) and Chiaraviglio and Bertona (2007) to be associated with differences in thermal preferences in the thermoregulatory behaviour of *B. c. occidentalis* that depend on boas' reproductive condition. The thermoregulatory process is important for gravid females because phenotype and fitness of their offspring depend upon the body temperatures offspring experience during development (Shine, 2004).

The fact that species presences are associated with the second principal components (table 3) might be indicating that the biology of the species is responding to the seasonality of the Gran Chaco region. Each second principal component showed that other important sources of variation for each variable were the annual cycle of green biomass, temperature, and precipitation, with a strong difference between winter and summer. It has also been reported that some ecological processes of boids, like reproductive activity, change throughout the year, following a seasonal pattern (Waller et al., 1995; Chiaraviglio et al., 2003). Organisms with 'slow' life histories, like *B. c. occidentalis*, could be reacting to proximate as well as evolutionary responses to the limited and seasonal resources availability in forest habitats (Cardozo et al., 2007).

Previous studies suggest that snake population dynamics is driven by prey availability, which varies considerably throughout the year due to annual variation in rainfall patterns (Madsen and Shine, 2000; Madsen and Shine, 2002). Indeed, snakes' seasonal reproductive cycles occur so that neonates are present in synchrony with an increased availability of potential prey (Andrade et al., 1996; Martins and Oliveira, 1998).

The obtained models also show that the species would be more frequent in areas with lower levels of NDVI in the dry season (negative relationship with NDVI2 that shows the variation of the annual cycle in green biomass). Previous studies have shown that *B. c. occidentalis* is active during the winter (Chiaraviglio et al., 2003) and furthermore reproductive activity is carried out during the cold months (Bertona and Chiaraviglio, 2003). Hence, because thermoregulation is a precise temporal behaviour for reproductive females, we assume that *E. c. alvarezi* and *B. c. occidentalis* show a preference for low vegetation cover during the dry season, probably because such cover provides the species with horizontal vegetation heterogeneity to perform the thermoregulatory process during winter. This is especially important when considering the findings of Chiaraviglio (2006), who reported that reproductive females of *B. c. occidentalis* prefer sites with access to open sunny habitats to increase their body temperature, and shaded forest to decrease it and hence facilitate thermoregulation.

Temperature would be an important factor that determines the boundaries of a latitudinally wide ranging species like *B. constrictor*, since winter temperature appears to constrain the geographical limits of the species (Henderson et al., 1995). The two species studied are associated with areas with low temperature in the dry season (TEMP2), which could favour behavioural and physiological processes, possibly related to reproduction. Both species seem to prefer sites that allow them to begin the reproductive process during periods of low tempera-

tures and give birth during the warm season. In viper species that inhabit temperate regions, it is known that reproduction starts in autumn with courtship and vitellogenesis, followed by sperm storage in winter, and finishing with fertilization and embryogenesis during spring (Macartney and Gregory, 1988; Almeida-Santos and Salomao, 2002).

We found that the occurrence of *E. c. alvarezi* and *B. c. occidentalis* is negatively correlated with altitude, since the species apparently select habitats at low altitudes. Indeed, their distribution pattern exhibits a continuous presence across the plains of the Gran Chaco region. Henderson et al. (1995) described that in general mainland boine fauna occurs at elevations of <1000 m a.s.l. In particular, he described that the altitudinal range for *B. constrictor* is between 0 and 1500 m and for *E. cenchria*, between 0 and 1000 m. However, our results show that our subspecies *B. c. occidentalis* may be present at altitudes between 60 and 1600 m, and *E. c. alvarezi* between 70 and 1300 m.

In both models, we noticed that the same variables are important, although when analyzing the confidence intervals of each variable, we observed differences in the coefficient values for NDVI1 (being 22.973 for *E. c. alvarezi* and 29.5504 for *B. c. occidentalis*) and TEMP2 (being -9.401 for *E. c. alvarezi* and -3.4121 for *B. c. occidentalis*). This indicates variations in the environmental requirements of the subspecies. The probability of occurrence of both snakes increased as overall greenness increased, but when we considered the NDVI1 coefficient, *B. c. occidentalis* was more frequent than *E. c. alvarezi* at sites with higher levels of NDVI. This could be interpreted as a higher dependence of *B. c. occidentalis* on vegetation cover, which could be related to thermoregulation needs. Previous studies have shown that reproductive individuals choose woody sites that allow them to thermoregulate (Attademo et al., 2004; Chiaraviglio and Bertona, 2007). Furthermore, on a local scale, Cardozo et al. (unpublished) in Cardozo et al. (2007), found that populations as-



sociated with forest patches show a higher reproductive frequency than those associated with shrublands. Consequently, forest loss could affect populations.

The TEMP2 coefficient indicates that *E. c. alvarezii* can be present in areas with lower temperatures in the dry season, which seems to show that *E. c. alvarezii* is less dependent on temperature. This climate condition might be indicating that the smaller-sized snake is more tolerant than *B. c. occidentalis* in the selection of potential habitats. The differences in body size could explain the variation found for both subspecies in the models.

For ectotherm species, it is known that the length of the growing season is related to the physiological time available for development and also that small species require fewer resources than larger ones. Hence, in seasonal environments, where resources are available for a shorter time and animals have less time to grow, small species will be able to persist at higher latitudes (Mousseau, 1997; Olalla-Tárraga et al., 2006).

The maps we obtained (figs 2 and 3) support the endemism of *E. c. alvarezii* and *B. c. occidentalis* in the Gran Chaco (Di Fonzo de Ábalos and Bucher, 1981; Henderson et al., 1995; Waller et al., 1995; Giraudo and Scrocchi, 2002) and indicate that the highest probability of occurrence of the subspecies is restricted to the Dry subregion of the Gran Chaco. However, the predicted distribution of both snakes is slightly extended to the phytogeographic provinces of Monte, Espinal and Pampa.

The maps cover southern and western regions of the Gran Chaco that do not completely correspond to the actual presence of both subspecies. This is a feature of many prediction maps: organisms do not always occupy habitats that are suitable for them or are not always found even when they do occur (Rogers et al., 1996). This may be related to historical and ecological factors (e.g. barriers to dispersal, inter-specific competition, predation pressure (Peter-

son, 2001; Luiselli, 2006b)) that were not taken into account in our approach.

Based on the contributions of Filippi and Luiselli (2000) and Santos et al. (2007) and taking into account the highly associated distribution to forest habitats and the life history traits of our snakes, there are obvious threats to many of their natural populations. We support the fact that conservation measures are important to preserve natural areas where rare snake species are present, such as *B. c. occidentalis* and *E. c. alvarezii* in the Gran Chaco region of South America.

The approach we used to map the distribution of the subspecies proved to be a useful modelling technique to predict the distribution and ecological requirements of these snakes, enabling us to identify the variables that best predict areas of apparent suitability. The distributional modelling technique used in this study provides an improvement and indicates where the subspecies can be expected, unlike the broad-stroke maps typical of field guides, based on dot and shaded outline maps, which only indicate where a taxon has been found and are often of limited value due to spatial generalization or subjective judgment (Skov, 2000; Anderson and Martínez-Meyer, 2004).

This procedure can be widely used in ecological studies of poorly known species and in peripheral populations occurring in marginal areas of the distribution range (Álvarez and Brito, 2006). It also contributes to the evaluation of the conservation status of secretive species, since research on any threatened species of wildlife poses significant logistical problems (Fitzgerald et al., 2005).

An accurate knowledge of the variables considered in relation to the distribution of the snakes studied here is necessary for a better understanding of the ecological requirements of the species in the future. This might enhance our ability to predict how the distribution of snake species might be affected in light of the current environmental changes in the region.

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