Potential effects of climate change on high- and low-abundance populations of the Gaboon viper (*Bitis gabonica*) and the nose-horned viper (*B. nasicornis*) in southern Nigeria

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During the last 15 years, intensive field research has been conducted on the ecology and population abundance of the Gaboon viper (*Bitis gabonica*) and the nose-horned viper (*Bitis nasicornis*) in southern Nigeria. During these studies, we determined the occurrence of several high-abundance and low-abundance populations for these two species. In the present study, we analysed the potential effects of climate change by modelling the current dataset on viper abundance (both high and low) using generalized additive models. We used climatic surfaces of current conditions as spatially explicit predictors, and projected viper abundance into a future climatic scenario. The future climatic conditions seemed appropriate for a wide extension of the climatic niche for high-abundance Gaboon viper populations across our study area. On the contrary, the future climatic niche for high-abundance nose-horned viper populations is predicted to become narrower than at present. In future scenarios, the two species are predicted to have a larger overlap in their climatic niche, which is likely to increase interspecific competition.

Key words: climate change, GAM, modelling, Viperidae, West Africa

INTRODUCTION

Global warming is thought to be one of the most profound and far-reaching threats to biodiversity (Thomas et al., 2004), with strong negative effects predicted for insects (Singer & Thomas, 1996), birds (Root, 1999), mammals (Taulman & Robbins, 1996), amphibians (Pounds, 2001; Galloy & Denoel, 2010) and reptiles (Janzen, 1994), both in tropical and temperate regions (Pounds et al., 1999; D'Amen & Bombi, 2009). Adverse effects of global warming include changes in the distribution of species, altered reproductive phenology and negative population trends that may lead to extinction (Parmesan et al., 2000).

The Gaboon viper (*Bitis gabonica*) and the nose-horned viper (*B. nasicornis*) are characterized by large body size, disruptive markings and coloration, and powerful venom. The two species have been subject to detailed field ecology studies in southern Africa (Berry, 1963; Ionides & Pitman, 1965; Haagner, 1986; Bodbijil, 1994; Linn et al., 2006; Warner, 2009). During our long-term research efforts in Nigeria, we have collated a considerable dataset on food habits (Luiselli & Akani, 2003), occupancy and density (Luiselli, 2006a), habitat (Luiselli, 2006a), reproductive strategies (Luiselli et al., 1998a), home range (Angelici et al., 2000) and interspecific competition (Luiselli et al., 1998b; Luiselli, 2006b). From these studies it appears that the two species 1) coexist in a good number of forest sites (especially in Delta, Rivers, Bayelsa, Akwa-Ibom and Cross River States in Nigeria), 2) are active mainly by the onset of the wet season and in the early night hours, 3) feed mainly on rodents and 4) have low reproductive potential. *Bitis gabonica* and *B. nasicornis* are the *Bitis* species that are most tightly linked to rainforest habitats, although they may also inhabit swamplands, farmed areas, grasslands and forest-derived habitats (Phelps, 1989; Mallow et al., 2003). Global warming effects are predicted to be especially relevant to rainforest ecosystems and forest-linked species, and Africa is thought likely to be particularly affected (Hulme, 1996; IPCC, 2001); some studies predict an average temperature increase of 2.8 °C throughout tropical Africa, and an associated precipitation increase of 4.2 mm/month by 2100 (IPCC, 2007). Hence, these two viper species, and especially the rainforest-linked *B. nasicornis*, appear potentially susceptible to profound alterations in their distribution or population abundance due to global warming. Long-term monitoring has indeed revealed a strong decline in recent years, even in apparently well-preserved areas (Reading et al., 2010).

Since these vipers are forest species with a wide distribution across the Guinea–Congo rainforest belt (Spawls & Branch, 1995) and appear to compete interspecifically more strongly in forest habitats that have been altered by humans, via a higher dietary overlap (Luiselli, 2006b), they provide good opportunities for exploring the potential effects of climate change on rainforest reptiles. The eventual changes in mature forest habitats due to climate change may also profoundly alter interspecific relationships.

Our aims in this paper are to 1) clarify the relationships between climatic parameters and population abundance

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of *B. gabonica* and *B. nasicornis* in southern Nigeria, and 2) predict, in a spatially explicit manner, the consequences that climate change may have for their abundance. We hypothesize that future climate conditions will affect the width of the suitable thermal niche, given that the two species are differentially linked to mature forest habitats (Spawls & Branch, 1995). We adopted an ecological modelling technique (generalized additive models) aimed at analysing species–environment interactions for current and future climatic conditions. We chose southern Nigeria as a study case because this is the only region where long-term ecological studies have been performed for the species under study, and because this is a rapidly developing region (De Montclos, 1984).

MATERIALS AND METHODS

Both Gaboon and nose-horned vipers are sit-and-wait predators that inhabit forests and have an elusive lifestyle. Both species feed primarily on rodents, and nose-horned vipers also on frogs (Luiselli & Akani, 2003). They are live-bearing, and widespread in south-eastern Nigeria (Luiselli, 2006a). Gaboon vipers are found especially in secondary forests, whereas nose-horned vipers are more common in swamp and mature forests (Luiselli, 2006a).

Study area and field protocol

During long term field studies (1994–2009) in the forest zone of southern Nigeria, we regularly surveyed 96 sites for the two *Bitis* species. The study sites are situated in the Niger Delta region (Delta State, Bayelsa State, Rivers State), in Akwa-Ibom State and in Cross River State. All sites range from 20 to 75 ha in size, and are characterized by secondary or mature lowland rainforest and swamp forest. The forest sites are generally owned by the nearby village, separated from each other by a matrix of plantations and/or suburbs. Snakes cannot move from one site to another.

For the present paper, we divided the study sites into two categories for each species: sites with high abundance, and sites with low abundance. We determined whether a site was high abundance or low abundance for each species by a suite of empirical methods. Firstly, we retained only those sites in our analysis that met two different criteria: 1) they were explored by at least two field researchers for at least 100 field hours during the activity peak of the vipers (early night hours, at the onset of the rainy season, both these criteria being developed after modelling analysis of the field data as explained in Luiselli, 2006a; average field effort by site: 143 hours; range 103–162); and 2) they were subjected to periodical collection of the snake fauna by local people for the purpose of our studies. The main activities of local people at the study sites were hunting and, especially, cultivation. Although periodical collection of snakes by local people was not standardized, we have no reason to believe that survey effort differed between high- and low-abundance sites. However, since habitat and other conditions would have been different at each site, detection probability is likely to have varied among sites and observers (Luiselli, 2006a). High-abundance sites were sites where 1) we found at least 20 individuals during field searches (i.e. at least two individuals for every 10 hours in the field); and 2) the study species represented at least 20% of the total snakes collected by the locals. We previously observed that an average encounter rate of one viper every five hours of field research is possible only in populations with high numbers of individuals (Luiselli et al., unpublished data). When only one or none of the two criteria was met, the site was considered low abundance for the target species. All snakes were individually marked by ventral scale clipping, so that identical individuals would not be counted several times. Based on considerable research conducted all over the study region in 1994–2009, we conclude that no large absence areas occur for either species.

Statistical modelling

In order to clarify the relationships between abundance of vipers and climate, we utilized environmental predictors derived from the WorldClim databank (version 1.4; www.worldclim.org) (Hijmans et al., 2004). WorldClim provides climate surfaces with global coverage for 19 climatic variables for the period 1950–2000 (see Table 1 for the list of the climatic variables). We utilized climatic surfaces with a spatial resolution of 2.5 minutes of geographic degree (approximately 5 km). This spatial resolution was also maintained in the output models. A geographical information system (GIS)-based procedure (ArcGIS 9.2 software) was used to assign the corresponding climatic values to each site.

Because viper population density (low/high abundance) was spatially autocorrelated, we introduced a distance weighted function of neighbouring response values (autocovariate) for estimating the degree to which the response variable at any one site was affected by the response values at surrounding sites (Dormann et al., 2007). For each site (i), the autocovariate (A) was calculated as:

$$A_i = \sum w_j\, y_j$$

where w_{ij} is the geographic weight of the other sites (j) and y_j represents the response value at site j. The weight given to site j is $w_{ij} = 1/h_{ij}$, where h_{ij} is the Euclidean distance between sites i and j. The factor (y) assumes values –1/1 in site j according to its abundance (low/high, respectively) (Smith, 1994; Augustin et al., 1996; Dormann et al., 2007). We calculated the residuals of the population abundance by using a linear regression with the autocovariate as predictor, and we used these residuals as response variable in the following analyses.

For each species, we fitted generalized additive models (GAM) with a Gaussian link, using the residuals of population abundance as dependent variable and climatic parameters as predictors. GAMs are semi-parametric extensions of GLMs (generalized linear models), where some predictors can be modelled non-parametrically in addition to linear and polynomial terms for other predictors. The only underlying assumptions made were that 1) the functions are additive and 2) the components are smooth. The strength of GAMs is their ability to deal with highly non-linear and non-monotonic relationships between the response and the set of explanatory variables.

Table 1. List of the climatic variables used to model current and future distribution of the two viper species studied in this paper. AIC scores of the five best variables for each species are indicated in italics.

	Bitis gabonica	*Bitis nasicornis*
Annual mean temperature	*103.55*	52.43
Temperature seasonality	106.49	67.02
Maximum temperature of warmest month	105.22	*51.85*
Minimum temperature of coldest month	114.10	65.31
Annual temperature range	111.62	*47.95*
Mean temperature of wettest quarter	108.01	64.01
Mean temperature of driest quarter	*103.77*	58.94
Mean temperature of warmest quarter	*96.28*	*51.30*
Mean temperature of coldest quarter	108.01	64.67
Annual precipitation	109.86	51.89
Precipitation of wettest month	107.07	*35.24*
Precipitation of driest month	*91.67*	70.26
Precipitation seasonality	112.18	55.01
Precipitation of wettest quarter	110.25	60.14
Precipitation of driest quarter	*96.44*	61.91
Precipitation of warmest quarter	105.01	*24.43*
Precipitation of coldest quarter	110.25	54.39

GAMs were elaborated in R 2.8.1 (R Development Core Team, 2008) utilizing one variable at a time. We then used an AIC-based approach for selecting the five best, non-correlated (R^2<0.7) variables in the final models (Table 1). Finally, the models obtained were cross-validated by calculating the AUC score (Fieldings and Bell, 1997; Guisan & Zimmerman, 2000).

Forecasts were obtained by projecting viper abundance into the climatic scenario for 2100 from the CCM3 model by the National Center for Atmospheric Research (www.cgd.ucar.edu) assuming an increase of twice current (1990–1999) levels of CO_2 (Govindasamy et al., 2003). We utilized the CCM3 model because a twofold increase in GHG (greenhouse gas) emissions by the end of the century represents approximately the average projections from the IPCC–SRES scenarios (Nakićenović et al., 2000). The predictions of these scenarios range from a slight reduction (B1 scenario) up to a large increase (approximately four times more than current levels) of GHG emissions by 2100 (IPCC, 2007). The IPCC–SRES scenarios do not include additional climate policies above current ones, but assume different socio-economic, demographic and technological changes (IPCC, 2007). For southern Nigeria, the CCM3 scenario predicts a general increase in the annual mean temperature and a clear change in the geographic pattern of rainfall.

RESULTS

High-abundance sites for Gaboon vipers were mainly located in the Niger Delta area (Fig. 1A), whereas those for the nose-horned vipers were mostly in Cross River State, close to the border with Cameroon (Fig. 1B).

Bitis gabonica

For this species, the five most significant variables which were retained in the final model were annual mean temperature, mean temperature of driest quarter, mean temperature of warmest quarter, precipitation of driest month and precipitation of driest quarter (Table 1). The final model had good predictive performance (AUC = 0.82). The areas of southern Nigeria climatically most suitable for harbouring high-abundance populations of Gaboon vipers were situated in Delta, Rivers and Akwa Ibom States (Fig. 1C). The climatic niche for high-abundance Gaboon viper populations is expected to expand across the study area in the future, with the entire southern portion of Nigeria and the neighbouring areas of Cameroon becoming suitable (with the exception of Mount Cameroon, Fig. 1E).

Bitis nasicornis

Univariate GAMs showed that maximum temperature of warmest month, temperature annual range, mean temperature of warmest quarter, precipitation of wettest month and precipitation of warmest quarter were the five most important climatic variables influencing population abundance (Table 1). The spatially explicit prediction based on this model (AUC = 0.81) evidenced that current climatic conditions supported high population densities of nose-horned vipers mainly in Delta, Edo and Akwa Ibom States and along the Cross River basin, as well as in adjacent Cameroon (Fig. 1D). The future climatic niche for high-abundance populations of the nose-horned viper is expected to remain in western Nigeria, and in the extreme south-east of Nigeria (Cross River State) and adjacent Cameroon (Fig. 1F).

DISCUSSION

Our modelling approach revealed that high-abundance populations of *B. gabonica* and *B. nasicornis* were separated in space (Fig. 1A,B). This pattern can be interpreted either as negative density-dependence of these sympatric vipers (Luiselli, 2006b), or of different ecological requirement optima for the two species. For example, the preferred habitat of nose-horned vipers is dense rainforest and swamp forest, often in the vicinity of water basins, both in southern Nigeria (Luiselli, 2006 a) and in the rest of Africa (Mallow et al., 2003). To date, there is no reliable data that can support either of these alternatives.

The main result of our model was a clear increase in overlap of the suitable climatic niches of the two species,

Fig. 1. Study sites (high abundance = black dots; low abundance = white dots) used for predicting the distribution of high-density populations of the Gaboon viper (A) and nose-horned viper (B); predicted distribution of high-abundance populations of Gaboon vipers (C) and nose-horned vipers (D) under current time; predicted distribution of high-abundance populations of Gaboon vipers (E) and nose-horned vipers (F) under a climate change scenario. For more details, see text.

especially due to the more favourable conditions for the Gaboon viper. Assuming that this scenario is sufficiently reliable, and considering the fact that habitat alteration produces an intensification of the interspecific competition for food between *B. gabonica* and *B. nasicornis* (Luiselli, 2006b), it seems likely that interspecific competition between these two vipers would increase further at a wide spatial scale, with possible negative consequences for the demography and population density of *B. nasicornis*. Climate change could also mediate the competition between these two species (see also Costa et al., 2008). Given that both species (and especially the nose-horned viper) are mainly forest species, the predicted expansion of the suitable climatic niche for high-density populations will probably be hindered by the capacity of the forest vegetation to expand (at least in the heavily deforested western part of Nigeria), which is unlikely given the current human population density (De Montclos, 1984). The region where the climatic niche for high-abundance populations of the nose-horned vipers was predicted to be particularly suitable is very densely populated, highly fragmented and degraded. As such, the likelihood of effective shifts in high-abundance populations by *B. nasicornis* is uncertain, although the species is known to occasionally inhabit plantations and even suburban areas (Mallow et al., 2003).

Several variables other than climate may influence the population density of animal species, and prey availability, competitive interactions and epidemic diseases may alter their distribution. Due to ongoing deforestation, predicting the abundance of vipers as a function of climatic variables is rather simplistic. Our model has nevertheless produced the first evidence that climate change may have profound and divergent consequences for Africa's giant vipers. Although the present study has highlighted the increased spatial overlap of high-density populations of *Bitis* species across southern Nigeria due to climate change, and consequently the increased strength of interspecific competition process, further studies are required to improve our understanding of the effects of climate change on the biology of Afrotropical vipers, such as interspecific interactions under changing external conditions and sensitivity to disease.

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REFERENCES

Angelici, F.M., Effah, C., Inyang, M.A. & Luiselli, L. (2000). A preliminary radiotracking study of movements, activity patterns and habitat use of free-ranging Gaboon vipers, *Bitis gabonica*. *Revue d'Ecologie (Terre et Vie)* 55, 45–55.

Augustin, N.H., Mugglestone, M.A. & Buckland, S.T. (1996). An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology* 33, 339–347.

Berry, P.S.M. (1963). The Gaboon viper of the plateau forests of northern Rhodesia. *Puku* 1, 71–74.

Bodbijl, T. (1994). *The Autecology of the Gaboon Adder,* Bitis gabonica gabonica. MSc thesis. Pietermaritzburg, South Africa: University of Natal.

Costa, G.C., Wolfe, C., Shepard, D.B., Caldwell, J.P. & Vitt, L.J. (2008). Detecting the influence of climatic variables on species distributions: a test using GIS niche-based models along a steep longitudinal environmental gradient. *Journal of Biogeography* 35, 637–646.

D'Amen, M. & Bombi, P. (2009). Global warming and biodiversity: evidence of climate-linked amphibian declines in Italy. *Biological Conservation* 142, 3060–3067.

De Montclos, M.-A. (1984). *Le Nigéria*. Paris: Kurthala.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609–628.

Fieldings, A.H. & Bell, J.F. (1997). A review of methods for the assessment of prediction errors in conservation presence: absence models. *Environmental Conservation* 24, 38–49.

Galloy, V. & Denoel, M. (2010). Effect of temperature increase on the fitness of an amphibian. *Acta Oecologica* 36, 179–183.

Govindasamy, B., Duffy, P.B. & Coquard, J. (2003). High-resolution simulations of global climate, part 2: effects of increased greenhouse cases. *Climate Dynamics* 21, 391–404.

Guisan, A. & Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling* 135, 147–186.

Haagner, G. (1986). Notes on the diet of the Gaboon viper. *Lammergeyer* 37, 56.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2004). *The WorldClim Interpolated Global Terrestrial Climate Surfaces*, *Version 1.3.* http://biogeo.berkeley.edu

Hulme, M. (ed.) (1996). *Climate Change and Southern Africa: An Exploration of Some Potential Impacts and Implications in the SADC region*. WWF report. Norwich, UK: Climate Change Group, UEA.

Ionides, C.J.P. & Pitman, C.R.S. (1965). Notes on three east African venomous snake populations. *Puku* 3, 87–95.

IPCC (Intergovernmental Panel on Climate Change) (2001). *Climate Change 2001: Impacts, Adaptation and Vulnerability*. Cambridge: Cambridge University Press.

IPCC (Intergovernmental Panel on Climate Change) (2007). *IV Assessment Report: Climate Change 2007*. New York: IPCC.

Janzen, F.J. (1994). Climate change and temperature-dependent sex determination in reptiles. *Proceedings of the National Academy of Sciences of the USA* 91, 7487–7490.

Linn, I.J., Perrin, M.R. & Bodbijl, T. (2006). Movements and home range of the Gaboon adder, *Bitis gabonica gabonica*, in Zululand, South Africa. *African Zoology* 41, 252–265.

Luiselli, L. (2006a). Site occupancy and density of sympatric Gaboon viper (*Bitis gabonica*) and nose-horned viper (*Bitis nasicornis*). *Journal of Tropical Ecology* 22, 555–564.

Luiselli, L. (2006b). Food niche overlap between sympatric potential competitors increases with habitat alteration at different trophic levels in rain-forest reptiles (omnivorous tortoises and carnivorous vipers). *Journal of Tropical Ecology* 22, 695–704.

Luiselli, L. & Akani, G.C. (2003). Diet of sympatric Gaboon vipers (*Bitis gabonica*) and nose-horned vipers (*Bitis nasicornis*) in southern Nigeria. *African Journal of Herpetology* 52, 101–106.

Luiselli, L., Akani, G.C., Angelici, F.M. & Barieenee, I.F. (1998a). Reproductive strategies of sympatric *Bitis gabonica* and *Bitis nasicornis* (Viperidae) in the Niger Delta (Port Harcourt, Nigeria): preliminary data. *Amphibia–Reptilia* 19, 223–229.

Luiselli, L., Akani, G.C. & Capizzi, D. (1998b). Food resource partitioning of a community of snakes in a swamp-rainforest of south-eastern Nigeria. *Journal of Zoology* 246, 125–133.

Mallow, D., Ludwig, D. & Nilson, G. (2003). *True Vipers: Natural History and Toxinology of Old World Vipers*. Malabar: Krieger Publishing Company.

Nakićenović, N., Davidson, O., Davis, G., Grubler, A., Kram, T., La Rovere, E.L., Metz, B., Morita, T., Pepper, W., Pitcher, H., Price, L., Riahi, K., Roehrl, A., Rogner, H.-H., Sankovski, A., Schlesinger, M., Shukla, P., Smith, S.J., Swart, R., Van Rooijen, S., Victor, N. & Dadi, Z. (2000). *Special Report on Emissions Scenarios: A Special Report of Working Group III of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.

Parmesan, C., Root, T.L. & Willig, R. (2000). Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society* 81, 443–450.

Phelps, T. (1989). *Poisonous Snakes*. London: Blandford Press.

Pounds, J.A. (2001). Climate and amphibian declines. *Nature* 410, 639–640.

Pounds, J.A., Fogden, M.P.L. & Campbell, H. (1999). Biological response to climate change on a tropical mountain. *Nature* 398, 611–615.

R Development Core Team (2008). *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. http://www.Rproject.org (downloaded January 2009).

Reading, C.J., Luiselli, L., Akani, G.C., Bonnet, X., Amori, G., Ballouard, J.M., Filippi, E., Naulleau, G. , Pearson, D. & Rugiero, L. (2010). Are snake populations in widespread decline? *Biology Letters* 6, 777–780.

Root, T.L. (1999). *Earth Systems: Processes and Issues*. Cambridge: Cambridge University Press.

Singer, M.C. & Thomas, C.D. (1996). Evolutionary responses of a butterfly metapopulation to human and climate-caused environmental variation. *American Naturalist* 148, 9–39.

Smith, P.A. (1994). Autocorrelation in logistic regression modeling of species' distributions. *Global Ecology and Biogeography Letters* 4, 47–61.

Spawls, S. & Branch, B. (1995). *The Dangerous Snakes of Africa*. Dubai: Oriental Press.

Taulman, J.F. & Robbins, L.W. (1996). Recent range expansion and distributional limits of the nine-banded armadillo (*Dasypus novemcinctus*) in the United States. *Journal of Biogeography* 23, 635–648.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Townsend Peterson, A., Phillips, O.L. & Williams, S.E. (2004). Extinction risk from climate change. *Nature* 427, 145–148.

Warner, J.K. (2009). *Conservation Biology of the Gaboon Adder (*Bitis gabonica*) in South Africa.* MSc thesis. Johannesburg: University of the Witwatersrand.

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