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# Site occupancy and density of sympatric Gaboon viper (*Bitis gabonica*) and nose-horned viper (*Bitis nasicornis*)

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**Abstract:** The presence and density of two sympatric, large-sized vipers (the Gaboon viper, *Bitis gabonica* and the nose-horned viper, *Bitis nasicornis*) were studied along several transects, during both dry and wet seasons, and at different times of day, in southern Nigeria (West Africa). Three habitat types were found along the various transects (mature rain forest (MF), secondary rain forest (SF), swamp forest (SW)). The detection probabilities for these vipers were modelled with a set of competing models, and the various models were ordered by Akaike Information Criterion procedures. Two classes of models were used: the single-season model, and the multi-species model. The best models (single-season model) suggested that: for the Gaboon viper, habitat types SF and SW were particularly important in detecting this species, especially during the rainy season at 08h00–16h00. For nose-horned vipers, the best models had SW and MF as site-covariates. Application of the multi-species model revealed that there were different detection functions if both species are present at a site, with a 'negative' interaction of occupancy between the species. Females and males were similarly detectable in a logistic regression model, but feeding status and pregnancy slightly increased detection probability in a logistic regression model. Viper density was modelled by a DISTANCE sampling procedure. The density of one species tended to be inversely correlated to the density of the other, suggesting that (1) the rain-forest environment does not support abundant populations of both vipers when sympatric, and (2) the two *Bitis* species subtly partition the habitat resources.

**Key Words:** Africa, Akaike Information Criterion, *Bitis gabonica*, *Bitis nasicornis*, detection probability, ecology, snake, spatial density, site occupancy

## INTRODUCTION

The tropical regions of Africa house a species-rich snake fauna which is often organized into complicated communities where interspecific competition, resource partitioning and species-specific ecological constraints are crucial in determining the assembly rules and the number of coexisting species (Luiselli 2006a). Some of these species have evolved extreme morphological and behavioural adaptations (Luiselli 2006a), and are thus particularly interesting to study in terms of their ecological and life-history traits. The Gaboon viper (*Bitis gabonica* Duméril, Bibron & Duméril, 1854) and the nose-horned or rhinoceros viper (*Bitis nasicornis* Shaw, 1802), with a wide distribution in the African rain forests (Chippaux 1999), are among these 'extreme' species because of their giant size (up to 2 m long), high philopatry and small home-range (Angelici *et al.* 2000, Bodbijl 1994, Linn *et al.* 2006, Perrin & Bodbijl 2001a, 2001b), and their specialization for ambush predation of rodents (Luiselli & Akani 2003, Luiselli *et al.* 1998, Perrin & Bodbijl 2001a). These two giant vipers may have important ecological roles as they are locally very abundant, thus causing local depletion of their prey resource (Bodbijl 1994, Linn *et al.* 2006, Luiselli & Akani 2003). These species are found sympatric in several African regions (Chippaux 1999), and when sympatric it seems that they compete for food (Luiselli 2006a). However, a general pattern highlighted in viperids is that the sympatric species which are under competition for food tend to partition the habitats or micro-habitats available (e.g. Luiselli 2006a for a review of several study cases), and thus the eventual occurrence of this pattern may be found also in the two *Bitis* species although never detected up to now (Luiselli 2006a). However, eventual patterns of micro-habitat partitioning and habitat-related density variations between these species cannot be studied

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accurately if not taking into account that, because of their cryptic coloration and elusive behaviour, the eventual non-detection of a given species at a site does not imply that the species is truly absent (MacKenzie *et al.* 2002). Therefore, for studying effectively the density and occupancy of these vipers there is a need to apply sophisticated procedures of analysis for modelling site occupancy of species as a function of their detectability and phenology.

The main objectives of this paper are: (1) modelling the *Bitis* detection probability at different study transects as functions of habitat type, time of day, season, and eventual presence of the other species; (2) exploring whether sex and feeding status may influence viper detectability; and (3) investigating their density at each transect.

## MATERIALS AND METHODS

### Study areas

The field study was conducted in some forest areas in the Port Harcourt area of the Niger Delta, Rivers State, south-eastern Nigeria. The climate is characterized by a long rainy season from March–April to October. Mean annual rainfall averages around 4000 mm, making it one of the wettest areas in Africa. The wet season peaks in July, and the dry season peaks in January and February. However, even during this dry period an average monthly mean of 150 mm rainfall is recorded in the delta. Relative humidity rarely dips below 60% and fluctuates between 90% and 100% for most of the year. During most of the rainy season cloud cover is nearly continuous resulting in 1500 mean annual sunshine hours and an average annual temperature of approximately 28 °C (Barbour *et al.* 1982). Diagrams of monthly rainfall and temperatures for the study area are given in Luiselli (2005, 2006b).

Overall, this area is characterized by forest fragments interspersed within a matrix of deforested territory unsuitable for vipers. Hence, vipers are forced to live in ‘closed’ systems with little or no possibility for immigration/emigration (Eniang *et al.* 2005). Three habitat types for vipers were found at the study areas: MF = mature rain forest; SF = secondary rain forest; SW = swamp-forest and margin of mangrove swamps. MF and SF are similar, but with different density and size of the trees (average density of big trees being much higher in MF).

MF consists mainly of small fragments of sacred forest, whereas SF is often used for tree-cutting, small plantations (e.g. bush-mangoes, banana, plantains), and is therefore characterized by a more open canopy than MF. The sacred forest formation can be seen sparingly within and outside the villages. These remnant forest patches are used for traditional religious practices. They are characterized by some emergent trees (several hundreds in the largest patches), with dense shrubs surrounding the core of the relict forest. In many parts, however, the shade of the dominant tree species keeps the forest floor open and free of shrubs. The most common tree species of this formation are *Protomegabaria macrophylla* Hutchinson, *Anthonota fragrans* (Baker f.) Exell & Hillc., *Erythrophleum ivorense* A. Chev., *Xylopia aethiopica* A. Rich, *Elaeis guineensis* Jacq. and *Combretum* sp. The forest floor is covered by a number of small palms (*Eremospatha* and *Podococcus* spp.) and by members of the Marantaceae and Zingiberaceae (Werre 1991).

SW is formed by the mosaics of swamps produced by the Bonny and Great Kwa River floodplains. Some of the more common tree species here are: *Lophira alata* Banks ex Gaertn. f., *Pycnanthus angolensis* (Welw.) Warb., *Ricinodendron heudelotii* (Baill.) Pierre ex Heckel, *Uapaca* spp., *Hallea ledermannii* (DC.) Leroy, *Albizia adianthifolia* W.F. Wight, *Irvingia gabonensis* Baill., *Treculia* spp., *Ficus vogeliana* Miq., and *Elaeis guineensis*, and the understorey is often dominated by rattans (e.g. *Calamus deerratus* Mann. & H. Wendl). Other tree species include Euphorbiaceae (*Uapaca* spp., *Klaineanthus* spp., *Anthostema* spp., *Macaranga* spp.), Annonaceae (*Xylopia* spp., *Hexalobus* spp.), Guttiferae (*Symphonia* spp., *Pentadesma* spp.), Rubiaceae (*Hallea* spp., *Rothmannia* spp.), Myristicaceae (*Coelocaryon preussii* Warb., *Pycnanthus* spp.) and Ctenolophonaceae (*Ctenolophon* spp.). In drier sections the most common emergents were *Lophira alata*, *Sacoglottis* spp., *Irvingia gabonensis* and *Klainedoxa* spp., while in the wetter sections the most common were *Alstonia boonei* De Wild and *Ctenolophon* spp. The shrub layer is dominated by *Diospyros preussii* Hiern, *Ouratea* spp., *Massularia acuminata* (G. Don) Bullock ex Hoyle, *Monodora* spp., *Homalium* spp. and *Alchornea cordifolia* Müll. Arg. This habitat is the least disturbed of all as a result of poor accessibility. Descriptions of these habitat types are available in Werre (1991) and Politano (1998).

### Protocol

This study was part of a series of transect surveys which were planned to assess density of forest snakes, chameleons and tortoises by using distance estimate models. Viper presence and density were studied along 11 independent line transects, each 5000 m long and 20 m wide, which were surveyed at different periods of the year in the years 2003, 2004 and 2005. Seven surveys for each transect were done during the dry season (November to April) and seven during the wet season (May to October). During each survey, the whole transect was walked at different hours of the day in only one direction, and all the vipers encountered were captured and their site of capture, time and habitat type were recorded. For each snake, the perpendicular

**Table 1.** Summary of the site covariates (= habitat variables) associated with each line-transect surveyed during the present study. Symbols: 1 = presence; 0 = absence; MF = mature rain forest; SF = secondary rain forest; SW = swamps.

| Transect | MF | SF | SW |
|---|---|---|---|
| A | 1 | 0 | 0 |
| B | 1 | 1 | 0 |
| C | 1 | 0 | 0 |
| D | 1 | 1 | 1 |
| E | 0 | 1 | 0 |
| F | 1 | 0 | 0 |
| G | 0 | 1 | 1 |
| H | 1 | 0 | 1 |
| I | 1 | 0 | 1 |
| J | 0 | 1 | 0 |
| K | 0 | 1 | 1 |

distance from the transect was recorded. The snakes were also individually marked by scale-clipping and measured for snout–vent length (SVL) and weight. The captured vipers were considered juveniles when their SVL was shorter than 600 mm (Luiselli & Akani 2003). Pregnancy condition was eventually assessed in adult females by abdominal palpation, and the same as for feeding status (i.e. fed versus unfed, see Luiselli & Akani 2003).

## Statistical analyses, modelling and simulations

*Modelling detection/non-detection data and occupancy estimates.* Detection/non-detection data were analysed by PRESENCE software (MacKenzie *et al.* 2002). Detection/non-detection models were applied after redefining the sample unit, given that with only 11 'sites' (= transects) it is difficult to say much about occupancy. In order to assess the a priori hypothesis that habitat type affects occupancy probability of either species, independent sections of transect were treated as sites. For example, transect D contains all three habitat types (Table 1), hence the 5 km × 20-m transect was split into three different 'transects' corresponding to the different habitat types. Obviously, the transect length in each habitat type may vary, but this was included in the model as a covariate.

Two classes of model were used: the single-season model (MacKenzie *et al.* 2002), and the multi-species model (MacKenzie *et al.* 2004). The single-season model was applied because data were regularly collected, i.e. without long phases of interruption in the sampling effort, and because the average climate conditions (rainfall, number of rainy days per year, and monthly temperatures) were remarkably similar in the 3 years (data from the Department of Geography, University of Port Harcourt). The multi-species model, which is also a single-season model but for multiple species, was applied because these two species are potential competitors (see Luiselli 2006a, Luiselli & Akani 2003), and so the possible interaction among species may be important in this case.

The single-season model assumes that the sites are closed to change in the state of occupancy for the duration of sampling; a condition clearly fulfilled by the various study areas. In other words, since the habitat did not change during the survey period in any transect, and since there was no evident difference between years in the impact of humans, the assumptions were made that (1) no viper species became locally extinct during the 3 years of study, and (2) the vipers did not abandon the study area due to the lack of disturbance and their usual maintenance of small home ranges (Angelici *et al.* 2000, Bodbijl 1994). A major assumption of the MacKenzie *et al.* (2002) model is that the occupancy state of the sites does not change for the duration of the survey. This may be violated in some situations, for instance, species with large home ranges where the species may temporarily be absent from the site during the surveying. This is not the case for the two *Bitis* species, which are highly site-specific, sedentary, and with small home ranges (Angelici *et al.* 2000, Bodbijl 1994).

To be consistent with literature on these methods, readers are introduced here to some basic notation. MacKenzie *et al.* (2002) present a model for estimating the site occupancy probability (or PAO) for a target species in situations where the species is not guaranteed to be detected even when present at a site. The model framework of MacKenzie *et al.* (2002) is flexible enough to allow for missing observations, e.g. occasions when sites were not surveyed (for instance, because it was not logistically possible to always sample all sites). In effect, a missing observation supplies no information about the detection or non-detection of the species, which is exactly how the model treats such values. The model also enables parameters to be functions of covariates. For example, occupancy probability may be a function of habitat, while detection probability is a function of environmental conditions (e.g. rainfall). The model therefore allows relationships between occupancy state and site characteristics to be investigated. Covariates are entered into the model by way of a logit link function (MacKenzie *et al.* 2002).

Let $\psi$ be the probability that a site is occupied and $p[j]$ be the probability of detecting the species in the $j$th survey, given it is present at the site. MacKenzie *et al.* (2002) use a probabilistic argument to describe the observed detection history for a site over a series of surveys. For example the probability of observing the history 1 0 0 1 (denoting the species was detected in the first and fourth surveys of the site) is:

$$\psi \times p[1](1 - p[2])(1 - p[3])p[4].$$

The probability of never detecting the species at a site (0 0 0 0) would therefore be,

$$\psi \times (1 - p[1])(1 - p[2])(1 - p[3])(1 - p[4]) + (1 - \psi),$$

**Table 2.** Summary of the sampling covariates (time-of-day). Lagos standard time is used. Three sampling covariates were used: 1 = 16h00–00h00; 2 = 00h01–08h00; 3 = 08h01–15h59. Symbols: DS1 = first dry season survey; WS2 = second wet season survey.

| Transect | DS1 | DS2 | DS3 | DS4 | DS5 | DS6 | DS7 | WS1 | WS2 | WS3 | WS4 | WS5 | WS6 | WS7 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | 1 | 1 | 2 | 1 | 1 | 3 | 3 | 1 | 2 | 2 | 1 | 3 | 1 | 1 |
| B | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 2 | 1 | 3 | 3 | 1 | 1 |
| C | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 3 | 1 | 1 | 3 | 2 | 1 | 1 |
| D | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 1 | 3 | 2 | 1 | 1 |
| E | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 3 | 2 | 1 | 1 |
| F | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 1 | 3 | 3 | 3 | 1 |
| G | 1 | 1 | 1 | 3 | 3 | 1 | 1 | 1 | 2 | 2 | 2 | 3 | 3 | 1 |
| H | 2 | 1 | 1 | 1 | 1 | 1 | 3 | 2 | 2 | 2 | 3 | 2 | 3 | 3 |
| I | 3 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 2 |
| J | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 1 | 3 | 3 | 3 | 2 | 2 | 1 |
| K | 1 | 1 | 1 | 1 | 3 | 2 | 3 | 3 | 2 | 2 | 2 | 1 | 1 | 1 |

which represents the fact that either the species was there, but was never detected, or the species was genuinely absent from the site $(1-\psi)$. By combining these probabilistic statements for all $N$ sites, maximum likelihood estimates of the model parameters can be obtained.

Standard error of $\psi$ (SE) was estimated using a non-parametric bootstrap method (Buckland & Garthwaite 1991): a random bootstrap sample of 11 sites was taken from all the surveyed transects, and the histories of the sites in the bootstrap sample were used to obtain a bootstrap estimate of $\psi$. The bootstrap procedure was repeated 1000 times, and the estimated standard error is the sample standard deviation of the bootstrap estimates (MacKenzie *et al.* 2002, Manly 1997). The number of parameters in each model was denoted $K$. Site-specific covariates (habitat types) did not change across sampling occasions, and these may influence either occupancy or detection probabilities. Sampling covariates (hour of day) often change for each sampling occasion and may influence detection probability only. A goodness-of-fit test (GOF) was performed on the most parameterized model in the candidate model set (MacKenzie & Bailey 2004). Model selection was based on information-theoretic methods (Akaike Information criterion, AIC), and more precisely on the small-sample-size correction (AICc), but if overdispersion was detected in the most-parameterized model ($\hat{c} \gg 1.0$), then the small-sized quasi-AIC (QAICc) was used (Burnham & Anderson 2002). The formulae for these AICc and QAICc are as follows:

$$\begin{aligned}\text{AICc} = {} & -2 \log \text{Likelihood} \\ & + 2K + 2K(K+1)/(n\text{-}ess - K - 1)\end{aligned}$$

and the QAICc:

$$\begin{aligned}\text{QAICc} = {} & -2 \log \text{Likelihood}/\hat{c} + 2K \\ & + 2K(K+1)/(n\text{-}ess - K - 1)\end{aligned}$$

In the above formulae, *n-ess* is the sample size. The best model was that with lowest AICc or QAICc (Burnham & Anderson 2002). AIC is a term that measures the fit of the model to the data (based on the likelihood) and a penalty term for the number of parameters in the model (Burnham & Anderson 2002), and $\Delta$AIC$j$ is the difference in AIC between the minimum value and the value for model $j$ (Burnham & Anderson 2002). In the text, naïve estimates indicate the percentage of the sites where a given species was detected by direct sighting (MacKenzie *et al.* 2002).

In my model, site-specific covariates were three habitat types: MF = mature rain forest; SF = secondary rain forest; SW = swamps. The distribution of these covariates across transects is given in Table 1. Three groups of sampling covariates were used: 1 = 16h00–00h00; 2 = 00h01–08h00; 3 = 08h01–15h59 (all cases, Lagos standard time) (Table 2). Night sampling was done because many snakes can be more easily detected and captured at night, as they avoid hot temperatures during daylight hours by resting inside their burrows (Angelici *et al.* 2000). The multi-species model is an extension of the single-season model, and it is fully explained in MacKenzie *et al.* (2004). For brevity, details are not explained here, but readers can refer to the original source. As co-occurrence options, occupancy detection of the one species was assumed to be independent of detection of the other ($\delta = 1$). The multi-species model (MacKenzie *et al.* 2004) estimates species-specific occupancy probabilities and a species interaction factor (SIF, denoted $\gamma$ in the following text). This term indicates an estimation of the magnitude of the interaction between species: $\gamma < 1$ would suggest species avoidance, i.e. the two species co-occur less frequently than if they were distributed independently, and $\gamma > 1$ would suggest contagion, i.e. a tendency to co-occur more frequently than expected under independence.

*Modelling population density.* Estimates were generated by the program DISTANCE 5.0 (Buckland *et al.* 2001). In this program, a detection function ($g(x)$) described the probability of detecting an object (for instance, a snake in our study case) given that it is at distance $x$ from the line transect under survey. The detection function was the uniform model (see the key and the series adjustment framework described in Buckland *et al.* 2001). Distance data were not combined with mark-and-recapture data (Alpizar's method, see Alpizar-Jara & Pollock 1996) because there were too few recapture instances to make the data solid.

I used the logistic regression to test the influence of sex (males versus females), reproductive status (pregnant versus non-pregnant) and feeding condition (fed versus unfed) on presence/absence of each species, in each transect, and in each survey date. Logistic regression analyses were run after having run separate sex-specific occupancy analysis to determine whether the assumption of equal detection among the sexes, within each species, holds (data not shown for brevity). These statistics were computed by SPSS (version 10.0) PC package, with all tests being two-tailed and $\alpha$ set at 5%.

## RESULTS

### Modelling detection/non-detection data and occupancy estimates

Overall, 81 Gaboon vipers and 92 nose-horned vipers were captured in the 11 study transects (see Appendix 1). Gaboon vipers were not encountered in 2 out of 11 transects (F and J), and nose-horned vipers were not found in three transects (D, I and K). Naïve estimates of presence were 0.818 (i.e. 81.8% of the transects; *B. gabonica*) and 0.727 (*B. nasicornis*). After splitting the transects in habitat-dependent sections to improve sample size and hence power of the models, naïve estimates of presence were 0.778 for *B. gabonica* and 0.555 for *B. nasicornis*.

*Single-season model.* Modelled occupancy estimates for transect sections (divided by habitat type) were much higher than naïve estimates in *B. gabonica* (0.787 ± 0.09 (SE), versus the estimate of 1.00 ± 0.0 if the complete transects were considered for the analyses), and slightly higher than naïve estimates in *B. nasicornis* (i.e. 0.556 ± 0.117, versus 0.732 ± 0.136 if the complete transects were considered for the analyses). The 'best' models with covariates that were fitted to the data, ranked according to AIC, are given in Table 3 for both viper species. The fact that there are covariates included in the best models suggests that there are differences in occupancy among habitat types and detection probabilities among time-of-day or even dates for both species. Indeed, for the Gaboon viper, most of the best models included SF and SW among the site covariates and, particularly, sampling covariate 1

**Table 3.** Set of competing models (using the single-season model) with selection and fit statistics for the two viper species at the 11 study transects and their habitat-sensitive sections, during the 14 study surveys. The 'best' models are ranked top of the list, and the first six are in boldface. Detection probability was modelled as constant across all sites and sample occasions (denoted p(.)) or varied according to sampling covariates or dates (denoted p(sampl cov or dates)). When the proportional length of each habitat type within transects is taken into account, the symbol denoting it is SF%, or SW%, or MF% depending on the type of habitat. Model selection was based on AICc or QAICc if overdispersion was detected ($\hat{c} \gg 1.0$). The models with the lowest ΔAICc are considered 'best'. Symbols: AICc = small-sample size Akaike Information Criterion; 1 = 16h00–00h00; 2 = 00h01–08h00; 3 = 08h01–15h59; MF = mature rain forest; SF = secondary rain forest; SW = swamps.

| Model | AICc or QAICc | ΔAICc | K | −2log(likelihood) |
|---|---|---|---|---|
| *Bitis gabonica* | | | | |
| **ψ (habitat) p (season+time of day)** | **193** | **0** | **6** | **181** |
| **ψ (habitat) p (samp cov 1)** | **201** | **8** | **2** | **197** |
| **ψ (.) p (survey effect)** | **201** | **8** | **14** | **173** |
| **ψ (SF%) p (sampl cov 1)** | **201** | **8** | **2** | **197** |
| **ψ (SF) p (sampl cov 1)** | **203** | **10** | **2** | **200** |
| **ψ (SF) p (survey effect)** | **204** | **11** | **14** | **176** |
| ψ (SW) p (sampl cov 1) | 205 | 12 | 2 | 201 |
| ψ (SW) p (survey effect) | 205 | 12 | 14 | 177 |
| ψ (SW%) p (survey effect) | 205 | 12 | 14 | 177 |
| ψ (MF) p (sampl cov 1) | 205 | 12 | 2 | 201 |
| $\hat{c}$ of ψ (*habitat*) *p* (*season+time of day*) = 2.41, GOF test P = 0.005 | | | | |
| *Bitis nasicornis* | | | | |
| **ψ (habitat) p (season+time of day)** | **199** | **0** | **6** | **187** |
| **ψ (SW) p (survey effect)** | **214** | **15** | **14** | **204** |
| **ψ (MF) p (.)** | **214** | **15** | **2** | **210** |
| **ψ (.) p (.)** | **215** | **16** | **2** | **211** |
| **ψ (SW) p (.)** | **215** | **16** | **2** | **211** |
| **ψ (SF) p (.)** | **216** | **17** | **2** | **212** |
| ψ (MF%) p (sampl cov 1) | 216 | 17 | 2 | 212 |
| ψ (SW%) p (sampl cov 1) | 216 | 17 | 2 | 212 |
| ψ (MF) p (sampl cov 1) | 216 | 17 | 2 | 212 |
| ψ (habitat) p (sampl cov 1) | 217 | 18 | 2 | 213 |
| $\hat{c}$ of ψ (*habitat*) *p* (*season+time of day*) < 1.0, GOF test P = 0.407 | | | | |

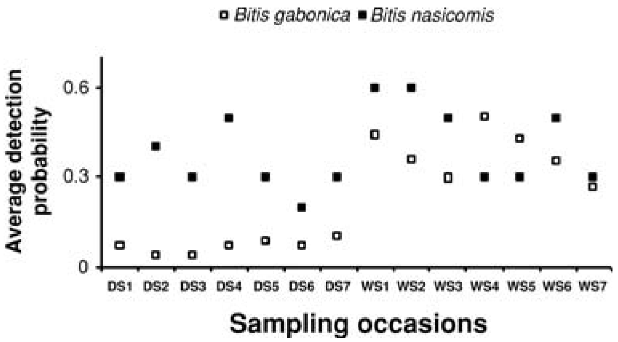

**Figure 1.** Relationships between detection probabilities (average calculated between-habitats on each survey date) and sampling date in Gaboon vipers and nose-horned vipers. Note that, in overall, the detection probability was higher in nose-horned vipers than in Gaboon vipers, and that the interspecific difference was much higher during the dry season dates. Symbols: DS = dry season; WS = wet season.

among the three sampling covariates. Therefore, these are the most important parameters when modelling viper occupancy (Table 3). Based on the sign of the site and sampling effect, it indicated that Gaboon vipers were: (1) clearly more common in SF (occupancy estimate for this habitat type: 0.817± 0.183) and SW (0.840± 0.153) than in MF (0.719± 0.172); (2) with the lowest probability of detection in dry season during 16h00–00h00 (occupancy estimate = 0.039± 0.017); (3) most likely to be found during the wet season (0.858± 0.056); and (4) with a positive, logit-linear effect of time of day on detection probability, with the most likely probabilities of detection in the wet season between 08h00–16h00 (0.723± 0.050). Nose-horned vipers were: (1) more common in MF and SW than in SF, and (2) most likely to be detected during the wet season + sampling covariate 1 (see also Table 3 for the pertinent models).

Overall, the detection probability was higher for nose-horned vipers than Gaboon vipers, and the interspecific difference was much higher during the dry season, when the probability of detection of the Gaboon viper was not only much less than in the wet season but also much less than that of the nose-horned viper during the same dry season (Figure 1). This fact indicates that, under the same conditions, *B. nasicornis* is more readily observed than *B. gabonica*, and presence pattern more closely resembles the true presence pattern than that of *B. gabonica.*

*Multi-species model.* The most parsimonious model fitted to the data (Table 4) suggests that the detection probability for each species is different if the other species is also present and that there is very strong evidence that the two species avoid each other: $\gamma = 0.72 \pm 0.13$ (± SE). Other good models had the sampling covariates as factors (Table 4), thus indicating that the estimated probability of occupancy as a function of habitat type tended to be divergent between species (i.e. better in SF and SW for Gaboon vipers, and better in MF and SW for nose-horned vipers). Overall, these patterns are consistent with evidence from the single-season model, and in general suggest that (1) there are different detection functions if both species are present at a site, and (2) there is evidence of a 'negative' interaction between the species in terms of occupancy probabilities.

**Table 4.** Summary of model fit and selection statistics for multi-species models where AICc is small-sample size Akaike Information Criterion, and ΔAICc is the absolute difference in AICc values relative to the model with the smallest AICc. Only the 'best' models are ranked in this table. The terms in parentheses represent the factors in the model for the respective parameter, with 'S' denoting that species has been used as factor, 'SAC' denoting that site covariate has been used as a factor, 'SIC' denoting that site covariates has been used as a factor, and '.' indicating a parameter set equal across species and survey dates. $\psi$ (S) denotes that the occupancy probability has been estimated separately for both species; absence of parameter $\gamma$ in the model notation implies $\gamma(.)$.

| Model | K | AICc | ΔAICc |
|---|---|---|---|
| $\psi$ (S)$\gamma$(.)p(S)r(S) | 7 | 438 | 0 |
| $\psi$ (SxSAC)p(SxSAC)r(S) | 14 | 453 | 15 |
| $\psi$ (SxSIC)p(SxSIC)r(S) | 14 | 455 | 17 |
| $\psi$ (S) $\gamma$(.)p(SxSAC)r(S) | 11 | 462 | 24 |
| $\psi$ (S)p(S)r(S) | 6 | 464 | 26 |
| $\psi$ (S)p(S) | 4 | 466 | 28 |

## Influence of sex, pregnancy and feeding status on detection probability

Overall, the adult sex ratio did not depart from equality in any study transect (males being from about 45% to about 56% of the total in *B. gabonica*, and from 43% to 52% in *B. nasicornis*). The logistic regression of P(detection) on sex was not significant for either species (*B. gabonica:* Wald's $\chi^2 = 2.11$, $P = 0.126$; *B. nasicornis:* Wald's $\chi^2 = 1.98$, $P = 0.141$). Adding reproductive condition (gravid versus non-gravid) as a factor improved the model in both species (*B. gabonica:* AIC = 164 versus 150 for sex alone; *B. nasicornis:* AIC = 152 vs. 145 for sex alone), showing that there was a slightly higher probability of being detected if a gravid female than if a male or a non-reproductive female. Adding feeding status (fed versus unfed) as a factor conspicuously improved the model in both species (*B. gabonica:* AIC = 174 versus 150 for sex alone; *B. nasicornis:* AIC = 169 versus 145 for sex alone), showing that there was a higher probability of being detected if a fed individual, independent of sex. As females of both species avoid feeding during pregnancy (Luiselli & Akani 2003), it was impossible to test for the interaction term 'reproductive condition × feeding status' on detection probability.

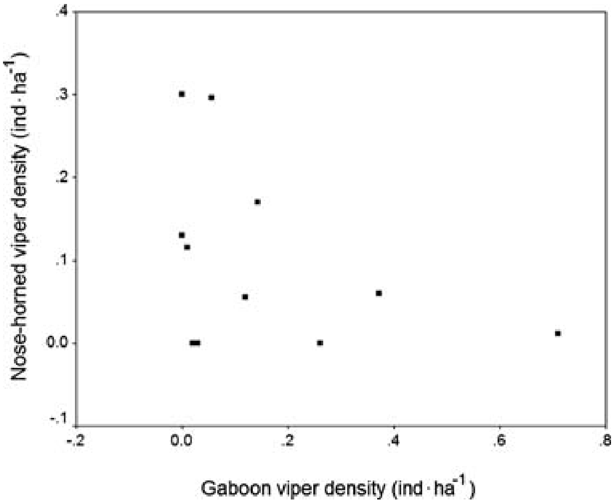

**Figure 2.** Relationships between the density (number of individuals ha$^{-1}$) of Gaboon vipers and that of nose-horned vipers at each study transect. Note that the density increases of a species are accomplished with density decreases of the other species ($\beta = -0.406$, n = 11, $P < 0.01$).

### Modelling population density

Considering the whole transects (n = 11), estimated density was slightly higher in Gaboon vipers ($x = 0.157 \pm 0.22$ individuals ha$^{-1}$; n = 11) than in nose-horned vipers ($x = 0.103 \pm 0.11$ indiv. ha$^{-1}$; n = 11), but the interspecific difference was not statistically significant (one-way ANOVA, $F_{1,20} = 0.531$, $P = 0.474$). The estimated density in each transect varied between 0.014 and 0.372 indiv. ha$^{-1}$ in *B. gabonica* (coefficient of variation between 0.419 and 1.112) and between 0.011 and 0.299 indiv. ha$^{-1}$ in *B. nasicornis* (coefficient of variation between 0.346 and 0.837). The estimated density of the one species was inversely related to that of the other species ($\beta = -0.406$, n = 11, $P < 0.01$) (Figure 2). Apparently this result may depend on the point situated on the bottom right of Figure 2, but once this data point is deleted from analysis the densities of the two viper species were still negatively correlated at a statistically significant level ($r_s = -0.64$, n = 10, $P < 0.045$). Repeating the same DISTANCE analyses with the resized (by habitat type) sample (n = 18), the results were reinforced with the densities of the two vipers being strongly negatively correlated ($r_s = -0.73$, n = 18, $P < 0.02$).

## DISCUSSION

### Modelling detection/non-detection data and occupancy estimates

The two *Bitis* species have a scattered distribution in the Guinea–Congo rain-forest belt, being locally abundant in a few regions (Luiselli & Akani 2003). This study reveals that the true occupancy of the Gaboon vipers may be likely higher than the observed, given their elusive habits. The Gaboon viper was predicted to be present in all transects by the models, but was not actually observed in some of the transects during the surveys. This was however in part an effect of the small sample sizes, as indicated by the fact that when sample size is redefined (i.e. the transects were subdivided into independent sections), the modelled occupancy was < 1. Comparison of the various competing models by AIC procedure demonstrated that a habitat type was included in all of the top models for both the species (the 'preferred' habitats were however different between species). For models with $\psi$ constant among habitats, $\psi$ (intpt) was clearly not favoured, but it is difficult to assess whether these latter models are actually giving good estimates given the high number of parameters (K = 15, in some cases) compared to the number of sample sites (n = 18). SF and SW were clearly the 'best' habitats for Gaboon vipers, and SW and MF for nose-horned vipers. Sampling covariates and rainy season were also important for increasing detection probability of both the viper species, but the influence of these variables was modelled somewhat less clearly in nose-horned vipers than in the Gaboon viper. Indeed, there was a much stronger inter-seasonal (wet season versus dry season dates) difference in the detection probability of Gaboon vipers than in nose-horned vipers (Figure 1). For nose-horned vipers, all models provided an estimate of the overall occupancy rate that was only slightly greater than the number of sites where these vipers were detected at least once; this suggests that detection probabilities were large enough that nose-horned vipers probably would be detected during the monitoring if present.

In general, it is strongly suggested that scientists should perform this kind of modelling analyses on all species of African rain-forest reptiles, so that we can be aware of the potential reliability of the various surveys when assessing the biodiversity value of a given forest and hence when ranking the conservation priorities of that forest site. Obviously, complex analyses do not offer a panacea against a lack of information, and hence the importance of collecting large datasets by marking and recapturing hundreds of individuals in long-term studies is still to be emphasized.

### Influence of sex, pregnancy and feeding status on detection probability

Morphological or physiological characteristics of the snakes (e.g. body size, sex, reproductive status, moulting status, presence of prey in the stomach) are well known to play crucial roles in their catchability (Bonnet & Naulleau 1996, Brown 1991). My analyses revealed that detection probabilities of the two vipers were influenced in a similar way by reproductive condition of females (pregnant vipers were easier to detect), and by feeding status (fed individuals were easier to detect), but not by sex alone. These results are not surprising if the snakes were from temperate climates, because both pregnancy and fed status are well known to influence positively the catchability of snakes (see Bonnet & Naulleau 1996 and references therein). However, it is generally assumed that these differences in catchability are related to increased thermal needs of pregnant and fed snakes, hence to their need to rest in thermoregulation (and consequently visible in open spots) for more time than non-gravid or unfed individuals. Thus, this pattern should be expected particularly in temperate and cool climates, but much less in tropical climates where snakes are not active thermoregulators (Akani *et al.* 2002, Shine & Madsen 1996). However, evidence provided in this study indirectly suggests that the two *Bitis* species are active thermoregulators in at least some specific phases of their life (e.g. when pregnant and when fed), exactly as observed in four species of water snake from tropical Nigeria (Luiselli & Akani 2002). By applying the same transect methodology and statistical procedures as done in this paper on a greater variety of African tropical snakes it will be possible indirectly to explore some aspects of their thermal ecology, and ultimately to conclude whether it is true that thermoregulation is not important for the great majority of tropical snakes as predicted by Shine & Madsen (1996). However, it is obvious that the collection of field data on body, operative and external temperatures will remain an indispensable tool to explore the thermal ecology of African tropical snakes.

### Modelling population density

In terms of density, overall the two species appeared relatively similar, although their density varied remarkably from one site to another. Distance sampling data are not available from any tropical rain-forest snake, and hence our data could not be validly compared with literature data. However, the fact that the density of the one species tended to be inversely correlated to the density of the other species suggests that (1) the productivity of the rain-forest environment does not support abundant populations of these two vipers when sympatric and (2) the two species select different microhabitats and these microhabitats are not evenly distributed along transects. Indeed, their ecological distribution was modelled as non-random, as already seen in other tropical and non-tropical snakes (Luiselli 2006c, Pringle *et al.* 2003, Reinert 1993, Shine *et al.* 2003a, b). The different selection of microhabitats may in turn be dependent on species-specific ecophysiological reasons/constraints or, alternatively, on possible interspecific competition between these two species (for instance for food, Luiselli & Akani 2003) forcing the two species to partition the spatial niche axis to facilitate coexistence (Luiselli 2006a). These hypotheses should clearly be tested with field experiments.

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**Appendix 1.** Summary of the results of *Bitis* surveys conducted during 14 periods, along 11 independent study transects (each 5 km long). Numbers indicate the number of different viper individuals captured. Main transects are in bold. Symbols: DS1 = first dry season survey; WS2 = second wet season survey; etc; concerning transects: for instance, D1 = section of the transect D characterized by the occurrence of habitat type MF; D2 = section of the transect D characterized by the occurrence of habitat type SF; D3 = section of the transect D characterized by the occurrence of habitat SW, etc.

| Transect | DS1 | DS2 | DS3 | DS4 | DS5 | DS6 | DS7 | WS1 | WS2 | WS3 | WS4 | WS5 | WS6 | WS7 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *B. gabonica* | | | | | | | | | | | | | | |
| **A** | **0** | **0** | **0** | **2** | **1** | **0** | **0** | **0** | **3** | **0** | **3** | **2** | **0** | **2** |
| A1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 3 | 2 | 0 | 2 |
| **B** | **4** | **0** | **0** | **0** | **0** | **1** | **0** | **3** | **6** | **0** | **1** | **3** | **0** | **0** |
| B1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 |
| B2 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 4 | 0 | 1 | 2 | 0 | 0 |
| **C** | **0** | **0** | **0** | **0** | **0** | **2** | **0** | **1** | **0** | **1** | **3** | **2** | **0** | **0** |
| C1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 3 | 2 | 0 | 0 |
| **D** | **0** | **0** | **0** | **4** | **0** | **0** | **0** | **4** | **6** | **2** | **5** | **2** | **0** | **0** |
| D1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 0 | 0 |
| D2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 3 | 2 | 3 | 1 | 0 | 0 |
| D3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 |
| **E** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **5** | **2** | **0** | **2** | **2** | **0** | **0** |
| E2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 2 | 0 | 2 | 2 | 0 | 0 |
| **F** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** |
| F1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **G** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **1** | **1** | **0** | **0** | **0** | **0** | **0** |
| G2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| G3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| **H** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **1** | **1** | **0** | **0** |
| H1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| H3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| **I** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **2** | **0** | **0** | **0** | **0** | **0** | **0** |
| I1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| I3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| **J** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** |
| J2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **K** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **1** | **0** | **0** | **0** |
| K2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| K3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *B. nasicornis* | | | | | | | | | | | | | | |
| **A** | **0** | **1** | **0** | **2** | **1** | **1** | **0** | **0** | **3** | **1** | **3** | **1** | **1** | **1** |
| A1 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 3 | 1 | 3 | 1 | 1 | 1 |
| **B** | **0** | **0** | **0** | **0** | **2** | **2** | **0** | **0** | **0** | **4** | **3** | **2** | **0** | **0** |
| B1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 3 | 2 | 0 | 0 |
| B2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| **C** | **1** | **0** | **0** | **0** | **0** | **3** | **1** | **0** | **0** | **2** | **2** | **4** | **1** | **1** |
| C1 | 1 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 2 | 2 | 4 | 1 | 1 |
| **D** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** |
| D1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| D2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| D3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **E** | **0** | **1** | **2** | **1** | **0** | **0** | **0** | **1** | **0** | **0** | **0** | **0** | **0** | **0** |
| E2 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| **F** | **0** | **1** | **1** | **1** | **2** | **0** | **1** | **0** | **0** | **4** | **5** | **0** | **1** | **0** |
| F1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 | 0 | 0 | 4 | 5 | 0 | 1 | 0 |
| **G** | **0** | **0** | **0** | **1** | **0** | **0** | **0** | **0** | **1** | **0** | **0** | **0** | **0** | **0** |
| G2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| G3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| **H** | **1** | **1** | **1** | **0** | **0** | **1** | **0** | **1** | **0** | **0** | **1** | **2** | **0** | **0** |
| H1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| H3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 |
| **I** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** |
| I1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| I3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **J** | **1** | **0** | **0** | **1** | **0** | **0** | **3** | **0** | **1** | **2** | **4** | **4** | **0** | **2** |
| J2 | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 1 | 2 | 4 | 4 | 0 | 2 |
| **K** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** |
| K2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| K3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |