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Negative density dependence of sympatric Hinge-back Tortoises (*Kinixys erosa* and *K. homeana*) in West Africa

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Abstract. A series of 59 transect surveys was conducted in selected wet forest habitats, along the coast of West Africa, to estimate the density distribution of African Hinge-back tortoises (*Kinixys homeana* and *K. erosa*). Line transect data were fed into a simple model to derive a detection function. The parameters estimated by the model produced an elaborate characterisation of tortoise distribution, which proved to be useful in the formulation of hypotheses about tortoise densities. Line transect data were analysed by DISTANCE, with a series of key and the series adjustment: the uniform function, the 1-parameter half-normal function, and the 2-parameter hazard-rate function were considered as key functions; the cosine series, simple polynomials, and Hermite polynomials were considered as series expansions. The detection function was estimated separately for *Kinixys homeana* and *K. erosa*, and for transects grouped for each study area by considering all the combinations of the above key functions and series expansions. The Akaike Information Criterion (AIC) was computed for each candidate model and used for model selection. The best model of the detection function, for both the tortoise species was the uniform function with no series expansion. Model results indicated that the density of the two species was inversely related at the local scale, and complementary across the region; such that the density of one species increases from West to East while the other one declines. Overall, the comparison of density estimates between the two tortoises is consistent with a former hypothesis suggesting inter-specific competition and consequent resource partitioning. Other causes may contribute to explain the observed patterns, including the low productivity of rainforest habitats and long-term human perturbation.

Keywords. Conservation, distance sampling, ecology, *Kinixys*, population size, West Africa.

INTRODUCTION

In reptilian guilds of species, resource partitioning may occur along one or more of three niche dimensions: the spatial niche, the trophic niche, and the temporal niche (e.g., Pianka, 1973, 1986; Toft, 1985). Recent reviews highlighted that resource partitioning patterns in consequence of strong interspecific competition is the rule in some groups of reptiles, especially in tropical regions (i.e., snakes, see Luiselli, 2006a; 2008a, 2008b), but not in terrestrial turtles where the potential for interspecific competition seems to be low (Luiselli, 2006b). The niche dimension to be partitioned by sympatric reptiles tends to vary according to the phylogeny of the groups: instead of the majority of snake communities that partition the trophic dimension (e.g., Luiselli, 2006a), lizards and terrestrial turtles generally partition the spatial dimension (e.g., Pianka, 1986 for lizards, and Luiselli, 2006b for turtles).

In the Guinea-Congo rainforests there are two pairs of terrestrial reptiles, one of snakes (the vipers *Bitis gabonica* (Duméril, Bibron and Duméril, 1854) and *Bitis nasicornis* (Shaw, 1802)) and one of turtles (the Hinge-back Tortoises *Kinixys erosa* (Schweigger, 1812) and *Kinixys homeana* (Bell, 1827)) that may represent ecological enigmas because they are ecologically quite similar in many respects and are also morphologically extremely similar, nonetheless they are usually syntopic even at microhabitat scale, and have a wide greatly overlapping distribution across the continent (e.g., Pritchard, 1979; Ernst and Barbour, 1989; Chippaux, 2006). How is possible that these species sharing broad ecological similarities are able to coexist across such a large region despite the predictions of general ecological niche theory, has been a debated question for reptile ecologists since long time (e.g., see Schmidt, 1919 and later studies).

Recent research has demonstrated that the intensity of interspecific competition in both these sets of species increases with rainforest alteration (Luiselli, 2006c), and that the overall response is very similar between coexisting vipers and coexisting tortoises (Luiselli, 2006c). However, modelling analyses also showed that sympatric vipers show an inverse density relationships; i.e. the rainforest productivity does not seem to support abundant populations of these species when sympatric, consequently at least one of the two species is always rare when the other is locally abundant (Luiselli, 2006d). This pattern could also be explained by subtle microhabitat differences that, however, are not easily observable and therefore do not allow a discrimination between the microhabitat types frequented by the two species. Considering that: (i) the Hinge-back tortoises seem to experience similar ecological patterns as the two *Bitis* vipers (i.e. broad coexistence in the Guinea-Congo rainforest region despite their nearly identical habits, ecology and morphology, see Ernst and Barbour, 1989; Lawson, 2000, 2001, 2006); and that (ii) the response to forest habitat alteration is almost identical for the two pairs of species (i.e., increase in potential competition intensity, Luiselli, 2006c), it is likely that the *Kinixys* case study may share other common patterns with the *Bitis* one.

The central question examined in this paper is whether the two tortoise species, which overlap broadly in their niche (Ernst and Barbour, 1989; Luiselli, 2003a; Lawson, 2006) show negative density dependence in their joint occurrence. Negative density dependence, such that when one species is abundant the other is rare, may be caused by a variety of processes including competition, differences in habitat requirements, and asymmetric predation rates (density dependent predation). Our goal here is not to test the competition hypothesis directly but to determine whether the density of the tortoises shows negative density dependence at a large scale in West Africa. The topic of the paper is relevant to community ecology theory and the processes that regulate biodiversity (Schoener, 1982; Simberloff and Dayan, 1991). In addition, one of the tortoise species, *K. homeana*, is on the IUCN Red List (2006) as vulnerable species and information about the processes that influence its density would be valuable to conservationists and natural resource managers in the region.

The density parameters of *K. erosa* and *K. homeana* were collected in wet rainforest habitat sites selected across a wide geographical region including Ghana, Benin, and Nigeria, by means of independent line-transect surveys. Line-transect surveys are a popular field method for assessing the density of free-ranging populations and have been utilised with a wide variety of different species (Eberhardt, 1978, 1979; Gaillard et al., 1993 and references therein). The complete theory of this method – proposed by Leopold in 1933 – was just recently reformulated (Burnham et al., 1980) and revisited in combination with novel statistical approaches (Buckland and Elston, 1993; Buckland et al., 1993, 2001), such as model selection theory (Akaike, 1985) and occupancy modelling analysis (Mackenzie et al., 2002, 2004), to become a statistically sophisticated tool for quantitative assessment (e.g., Katsanevakis, 2006; Luiselli, 2006a). Density profiles generated by line transect surveys are easily standardised in the field and therefore highly valuable for inter-regional comparisons, and therefore used for the present study.

MATERIALS AND METHODS

Study areas

Line-transect surveys were conducted in several areas of Ghana, Benin and Nigeria, by applying exactly the same field and modelling procedures (see below). The selected sites included the tropical forest-grassy vegetation mosaic surrounding Koforidua and Accra in Ghana, the swamps and wet forests of Porto Novo and Cotonou in Benin, and the swamp-forest habitats of Lagos-Lekki, Ibadan, Edo, Bayelsa, Rivers, Akwa-Ibom, and Cross River states in Nigeria. In our analyses, we distinguished 'western Nigeria' including all transects situated West of the Niger River main axis, from 'eastern Nigeria' including transects situated East of the river. This distinction reflects a recognised biogeographical separation, reflected by documented differences in local faunal and floral endemisms (Kingdon, 1990). Detailed description of these forest areas are available respectively in Werre (1991), Politano (1998), and in Luiselli (2005a). In general, we selected study areas that were similar each other in terms of main vegetation characteristics (rainforest), although possibly at different stages of maturity depending on the availability of mature rainforest patches in the various regions. These rainforest patches were generally interspersed among plantations and deforested areas, and/or (especially in southern Nigeria) were characterized by the mosaics of swamps produced by floods from River Niger drainage. Common tree species at most areas were *Lophira alata*, *Pycnanthus angolensis*, *Sacoglottis gabonensis*, *Uapaca* spp., *Hallea ledermannii*, *Albizia adianthifolia*, *Irvingia gabonensis*, *Klainedoxa gabonensis*, *Treculia africana*, *Ficus vogeliana*, and *Elaeis guineensis*, and the understorey is often dominated by rattans. Average tree height (20-25 m) was relatively low for rain forest at all sites, and emergents, which can reach heights of 35-40 m, generally occurred at low densities. The low abundance of emergents was caused by high exploitation of these forest sites by people.

Protocol

Tortoise presence and density were recorded along 59 line transects, each 5,000 m long and 20 m wide, surveyed during different seasons, from 2003 to 2005. The transects were totally independent from each other, however their vegetation structure, species composition, and successional development stage were comparable, and represented the most adequate habitat type for tortoises in each study region. Transects were selected after pilot surveys conducted in the years 2001 and 2002, that were performed to determine the spatial character (uniform, gradient, clustered, etc.) of tortoise abundance in each habitat. This was done to insure that the samples were unbiased, as non-uniform object distributions, particularly loosely clumped distributions, may bias population estimates (Buckland et al., 2001). Thus, we selected only transects where the tortoise distribution appeared relatively uniform and the detectability apparently comparable (Luiselli, 2005a). However, it is not necessary that the animals are randomly or uniformly distributed, whereas it is critical that the line is placed randomly with respect to the distribution of animals. Given the random line placement, it can safely be assumed that animals are uniformly distributed with respect to perpendicular distance from the line (Buckland et al., 2001). During each survey, transects were covered during different hours of the day (see below for details) by walking consistently in the same direction. All the *Kinixys* encountered during transect were captured; the specific site of capture (including the shortest perpendicular distance from the transect), the time, and the habitat type were carefully recorded. The captured tortoises were individually marked by notching a plate of their carapace, and measured while recording plastron length (SVL) and weight.

Modelling density

Density estimates were generated by 'distance sampling analysis'. The data were elaborated with DISTANCE 5.0 (Buckland et al., 2001; Thomas et al., 2007), a dedicated software, utilised with free-ranging animal populations (e.g., see Katsanevakis, 2006). DISTANCE produces a detection function $g(x)$ describing the probability of detecting an object (a tortoise species in our study case) located at distance x from the line transect under survey (see the key and the series adjustment framework described in Buckland et al., 2001).

The relationship between $g(x)$ and p – the proportion of *Kinixys* individuals in area A that was actually detected – can be expressed as:

$$p = w^{-1}\int g(x)dx$$

where $2w$ is the width of the transect, while d represents the density of *Kinixys* tortoises within a surface A;

$$d = N\,(A \times p)^{-1} = \mathrm{N}\,(2wL \times p)^{-1}$$

L: transect length;
N: number of detected individuals.

The detection function $g(x)$ was modelled in the general form:

$$g(x) = \mathrm{key}(x)[1 + \mathrm{series}(x)] \times \{\mathrm{key}(0)[1 + \mathrm{series}(0)]\}^{-1}$$

where key(x) is the key function and series(x) is a series expansion used to adjust the key function. The uniform function, the 1-parameter half-normal function, and the 2-parameter hazard-rate function were considered as key functions; the cosine series, simple polynomials, and Hermite polynomials were considered as series expansions (Buckland et al., 2001). The detection function was estimated separately for *Kinixys homeana* and *K. erosa* and for the transects grouped for each study area (e.g., Koforidua, Accra, Lagos, etc.), by considering all the combinations of the above key functions and series expansions. The Akaike Information Criterion (AIC) was used for model selection (Akaike, 1985) and computed for each candidate model.

The effective strip width (ESW) was estimated for each transect by DISTANCE from the sample data. ESW varied slightly between transects, making the intertransect comparisons feasible. In any cases, values of the effective detection radius (denoted EDR in the following text) are reported where pertinent in the tables included in this article. Given the generally low abundance of tortoises in the field (Luiselli, 2005a, 2006b), in most cases we detected small number of individuals along each transect.

Distance data were not combined with mark-and-recapture data (Alpizar's method, see Alpizar-Jara and Pollock, 1996) as there were too few recapture instances to build a consistent database. All other statistics were computed by means of SPSS (version 11.0) PC package, with all tests being two-tailed and α set at 5%.

In order to correlate density estimates of one species against the other, we used the modelled density values from the better 45 transects, according to AIC scores.

RESULTS

Modelling density

Overall, the two species occurred syntopically in 49 out of 59 transects (83%), while in 10 transects only one of the two species was seen.

In Ghana, we conducted six independent line transects, capturing and marking 8 *K. homeana* and 21 *K. erosa* (Table 1). Because of the small sample of *K. homeana* observed, the statistical power of the estimate relative to this species was less than the one relative to *K. erosa* (see AIC values in Table 1). However, there is no doubt that the small sample size of *K. homeana* genuinely reflected true rarity (hence, reduced density) of the species in this geographic region. In order to increase sample size and improve the power of the analysis, further density estimates were obtained by pooling: (i) the three transects at Koforidua and the three at Accra (Table 1), and (ii) the six Ghana transects (column 'overall' in Table 1). Modelled estimates indicated that: (i) the density of *K. erosa* was higher than that of *K. homeana* at all sites, and (ii) the density of both species was higher at Korofidua than at Accra.

In Benin, six independent transects across two distinct areas inhabited by sympatric *Kinixys* were surveyed with the capture of a total of 16 *K. homeana* and 9 *K. erosa* (Table 2). Model results revealed a considerable degree of variability in tortoise densities between transects, but in general there was a higher density for *K. homeana* than *K. erosa* (Table 2). After pooling the transects relative to the two main areas surveyed (Cotonou and Porto Novo), it emerged that there were no significant differences between species abundances at Porto Novo, whereas at Cotonou limited sample size prevented any reliable density calculation.

In Nigeria (West of the Niger), three line transects were surveyed in the coastal forests of Lagos-Lekki, 3 in the forest around Ibadan, and 3 in the flooded forests of Edo

Table 1. Results of *Kinixys* surveys conducted during six transects in Ghana. Distances from the transect (m) are presented as mean (± SD). 'Overall' refers to estimates generated by pooling all transects in the analysis. Empty cells indicate transects where density parameters could not be reliably calculated (too few data points). Symbols: KOF = Koforidua; ACC = Accra coastal forest surroundings; No. Obs. Ind. = number of observed individuals; K = number of parameters; ESW/EDR = effective strip width/detection radius; D = individuals density per hectare; D (LCL) = lower density confidence limits ; and D (UCL) = upper density confidence limits ; D (CV) = density coefficient of variation.

Species	KOF1	KOF2	KOF3	KOF (POOLED)	ACC1	ACC2	ACC3	ACC (POOLED)	OVERALL
K. homeana									
No. Obs. Ind.	2	1	3	2	1	1	0		8
Distance±SD.	3.7±4.6	0	3.3±4.0	3.6±2.2	0	3		1.5±2.1	--
AIC	9.78		14.48	26.39				6.39	33.22
K	1		1	2				1	2
EDR	7.0		8.0	3.59				3.0	3.31
D	0.286		0.375	0.558				0.222	0.403
D (LCL)			0.024	0.132				0.030	0.133
D (UCL)			5.875	2.349				1.646	1.222
D (CV)			0.711	0.630				0.671	0.535
K. erosa									
No. Obs. Ind.	3	3	4		2	3	6		21
Distance±SD.	0.7±0.6	4.3±3.5	3.8±4.3	3.0±3.4	7.0±5.6	6.0±1.7	4.3±5.2	5.3±4.3	--
AIC	2.0	14.48	20.30	44.24	11.59	13.68	32.49	58.52	104.64
K	1	1	1	2	1	1	1	1	2
EDR	1.0	8.0	8.29	3.82	11.0	7.0	8.88	9.50	5.58
D	3.0	0.375	0.482	0.872	0.182	0.429	0.675	0.386	0.627
D (LCL)	0.221	0.022	0.082	0.374		0.030	0.213	0.136	0.364
D (UCL)	40.76	6.263	2.851	2.036		6.023	2.141	1.100	1.079
D (CV)	0.667	0.731	0.605	0.388		0.677	0.472	0.400	0.265

State, with a total of 23 *K. homeana* and 11 *K. erosa* being captured (Table 3). Results of the modelled densities for both species are given in Table 4. The modelled density of *K. homeana* was constantly higher than that of *K. erosa* at all sites, although the density difference between species was not high. Furthermore, the density of *K. homeana* was much higher at Edo State than at the other transects, whereas there was no significant inter-site difference in the density of *K. erosa*.

In Nigeria (East of the Niger), density estimates were generated for 38 independent transects surveyed in Bayelsa, Rivers, Akwa-Ibom, and Cross River states. Detailed examination of the data transect-by-transect is not given here for brevity; the data pooled for each state surveyed are given in Table 4. In total, 97 *K. homeana* and 60 *K. erosa* were cap-

Table 2. Results of *Kinixys* surveys conducted during six transects in Benin. Distances from the transect (m) are presented as mean (± SD). 'Overall' refers to estimates generated by pooling all transects in the analysis. Empty cells indicate transects where density parameters could not be reliably calculated (too few data points). Symbols: COT = Cotonou; POR = Porto Novo; other symbols are as in Table 1.

Species	COT1	COT2	COT3	COT (POOLED)	POR1	POR2	POR3	POR (POOLED)	OVERALL
K. homeana									
No. Obs. Ind.	4	2	3		1	4	2		16
Distance±S.D.	1.2±1.5	3.5±4.9	1.0±0	1.7±2.2	4	2.3±2.9	3.0±4.2	2.7±2.7	--
AIC	10.79	9.78	2.0	31.32		16.31	9.17	27.08	58.79
K	1	1	1	2		1	1	1	2
EDR	3.0	7.0	1.0	2.32		5.6	6.0	6.0	2.92
D	1.333	0.286	3.0	1.293	0.250	0.720	0.333	0.389	0.914
D (LCL)	0.205		0.237	0.587		0.115		0.117	0.478
D (UCL)	8.672		38.01	2.847		4.522		1.291	1.745
D (CV)	0.643		0.645	0.358		0.629		0.482	0.316
K. erosa									
No. Obs. Ind.	2	1	2		0	3	1		9
Distance±S.D.	3.5±3.5	3	2.5±3.5	3.0±2.5	--	2.7±3.0	1	2.2±2.6	--
AIC	9.17		8.44			12.75		16.22	34.25
K	1		1			1		1	1
EDR	6.0		0.400			6.0		5.02	6.0
D	0.333					0.500		0.266	0.250
D (LCL)						0.031		0.033	0.109
D (UCL)						8.050		2.143	0.573
D (CV)						0.719		0.745	0.395

tured. The highest modelled densities were reached in Bayelsa State for *K. homeana* and in Cross River State for *K. erosa*.

Density relationships between species and among sites

There was a significant negative correlation between the modelled density of *K. homeana* and that of *K. erosa* (r_s = -0.313, n = 45, $P < 0.03$; Fig. 1). The modelled density of *K. homeana* was not significantly related to longitude from West to East (i.e., from Koforidua to Cross River State transects) (r_s = 0.150, n = 11, P = 0.663); the same held also for *K. erosa* (r_s = -0.191, n = 11, P = 0.352). However, the sign of the correlation coefficient was opposite for the two species, suggesting that the density of the two species tended to decrease geographically along a West-to-East gradient in *K. homeana,* the opposite trend being observed in *K. erosa*.

Table 3. Estimated densities of *Kinixys* tortoises along nine line-transects in western Nigeria. Empty cells indicate transects where density parameters could not be reliably calculated (too few data points). Symbols: LAG = Lagos; IBA = Ibadan; EDO = Edo State; other symbols are as in Table 1.

Species	LAG1	LAG2	LAG3	LAG (POOLED)	IBA1	IBA2	IBA3	IBA (POOLED)	EDO1	EDO2	EDO3	EDO (POOLED)	OVERALL
K. homeana													
No. Obs. Ind.	3	0	4	7	2	2	3	7	5	1	3	9	23
Distance±S.D.	0.3±0.6		1.5±1.3	0.8±1.6	0.5±0	0.5±0.7	3.3±3.2	1.4±1.5	0.2±0.4	0	1.3±0.6	0.8±0.5	--
AIC	2.0		10.79	16.60	-0.77	2.00	13.68	24.40	1.58	8.44	6.16	12.69	55.68
K	1		1	1	1	1	1	2	1	1	1	1	2
EDR	1.0		3.0	2.11	0.50	1.00	7.00	2.22	0.74	5.0	2.0	1.3	1.73
D	3.0		1.333	1.102	4.000	2.00	0.429	1.049	6.786	0.400	1.500	2.371	1.480
D (LCL)	0.194		0.199	0.206			0.027	0.310	1.696		0.082	0.683	0.899
D (UCL)	4.6		8.944	5.900			6.888	3.549	27.154		27.300	8.235	2.436
D (CV)	0.707		0.656	0.568			0.719	0.524	0.532		0.759	0.450	0.316
K. erosa													
No. Obs. Ind.	0	1	2	3	1	1	1	3	2	2	1	5	11
Distance±S.D.		1.80	2.0±1.4	1.9±0.8	0	4.2	6.4	3.3±3.6	1.0±1.4	4.5±2.1	5	3.5±2.7	--
AIC	--		6.39	8.59				12.75	4.77	9.17		19.92	41.42
K			1	1				1	1	1		1	1
EDR			3.0	3.0				6.0	2.0	6.0		6.0	6.0
D		0.500	0.667	0.333		0.250	0.143	0.167	1.000	0.333	0.250	0.278	0.204
D (LCL)				0.051				0.027				0.099	0.103
D (UCL)				2.170				1.027				0.783	0.402
D (CV)				0.743				0.442	0.837	0.864		0.435	0.330

Table 4. Results of *Kinixys* surveys conducted during 38 transects in eastern Nigeria. Columns contain estimates generated by pooling all transects conducted in a given state. Symbols: BAY = Bayelsa State (n = 11 transects); RIV = Rivers State (n = 9); AKW = Akwa-Ibom State (n = 8); CRO = Cross River State (n = 10). Distances from the transect (m) are presented as mean (±SD).

Species	AKW	BAY	RIV	CRO
K. homeana				
No. Obs. Ind.	21	39	23	14
Distance±S.D.	2.7±2.0	1.7±1.6	1.5±1.3	1.8±1.6
AIC	80.41	115.29	62.96	47.22
K	1	2	1	1
EDR	5.16	2.20	2.78	3.29
D	0.533	1.611	0.920	0.425
D (LCL)	0.322	1.027	0.543	0.239
D (UCL)	0.884	2.525	1.558	0.756
D (CV)	0.248	0.226	0.256	0.280
K. erosa				
No. Obs. Ind.	10	13	8	29
Distance±S.D.	1.6±0.9	2.0±1.7	3.0±2.7	1.6±1.6
AIC	23.97	40.52	34.46	88.69
K	1	1	1	2
EDR	3.0	3.24	5.73	2.13
D	0.417	0.336	0.155	1.236
D (LCL)	0.165	0.175	0.068	0.707
D (UCL)	1.054	0.646	0.353	2.158
D (CV)	0.460	0.318	0.401	0.274

DISCUSSION

In a recent review of terrestrial turtle communities worldwide, it has been noticed that the potential for interspecific competition should be minor for these reptiles, with much of their species diversity reflecting geographic replacement of one species by another (Luiselli, 2006b). However, the Hinge-back tortoises (*K. erosa* and *K. homeana*) are clearly among the few candidates of their group to show community-organised assemblages because of their nearly identical distribution range at the continental scale (Ernst and Barbour, 1989, Iverson, 1992), and their strong interspecific similarities in: (i) habitat requirements (Ernst and Barbour, 1989; Lawson, 2006), (ii) home range and spacing behaviour (Lawson, 2006), (iii) diet composition (Luiselli, 2003a), (iv) temporal activity (Lawson, 2006, Luiselli, 2003a), and (v) thermal ecology (Luiselli, 2005b); thus indicating very high realised niche overlap (sensu Pianka, 1986). When high overlap in realised niche is found,

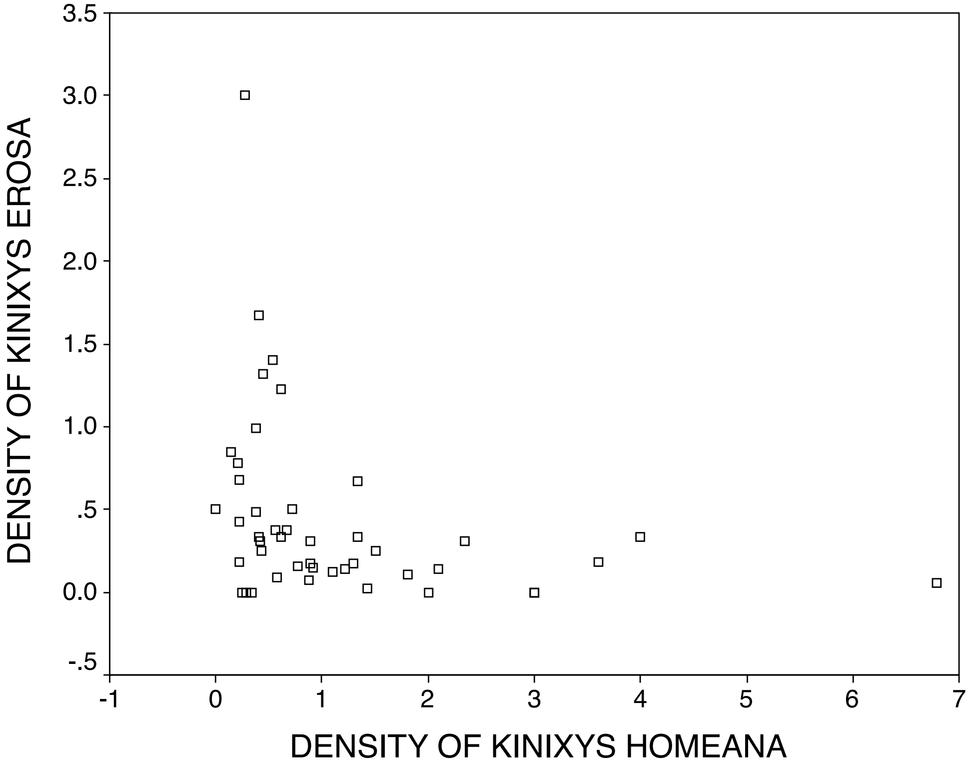

Fig. 1. Relationships between the modelled density of *Kinixys homeana* and *K. erosa*, considering the best 45 independent transects selected by their relative AIC score. For statistical details, see the text.

theory predicts that competition intensity should be strong and one of the potential competitors should begin to decline and eventually even disappear from the site (Schoener, 1974, 1982, 1983). In this paper we did not test directly the competition hypothesis, but we provided the first data on the density of these two species at a large geographical scale. Our data showed that the two species were found coexisting in over 80% of the surveyed transects, suggesting that disappearance of one of the two species does not occur in the wet forest habitats surveyed. On the other hand, there was a negative relationship between the densities of the two species. For instance, in Ghana we observed the lowest modelled density of *K. homeana* and contextually one of the highest modelled densities of *K. erosa;* similarly, in western Nigeria, the highest density of *K. homeana* was observed next to one of the lowest densities for *K. erosa.* However, careful inspection of the results tables for the pooled transects reveals that the confidence intervals of the modelled densities for the two tortoise species overlap considerably, indicating that for most of the sites the populations are in fact not statistically different in abundance. Only in eastern Nigeria do the statistical results suggest that the populations of the two species differ very much in abundance, with *K. homeana* being the dominant species. This pattern may apparently contradict the overall evidence that the density of the two tortoises is negatively related, but it seems clear that the confounding pattern is generated merely by the low abundance exhibited by tortoises at the local scale of the single transects, thus producing problems in the modelling of the estimate confidence intervals. The problem of the low abundance of tortoises is not easily solved in population density studies with these ectotherms, because this low density is indeed a generalized pattern of tortoise populations worldwide (Luiselli, 2006b), with only a minor number of exceptions being known (e.g., Niederberger and Seidel, 1999; Hailey and Willemsen, 2000).

Based on data presented elsewhere (food habits, habitats; Luiselli, 2006b, 2006c), we suggest that the negative density dependence between *Kinixys* populations can be explained by natural community processes, i.e.: (1) interspecific competition and consequent resource partitioning between forest tortoises (see also Luiselli, 2006c); (2) low rain-forest productivity hindering the establishment of abundant populations of the two tortoise species when sympatric; and (3) the two species selecting different microhabitats which are not evenly distributed along transects. Concerning point (2), the same was also supposed for the coexistence of *Bitis gabonica* and *B. nasicornis* in the coastal rainforests of Nigeria (Luiselli, 2006d). Concerning point (3), this is compatible with the opinion expressed by early authors suggesting that *K. erosa* was linked to somewhat wetter microhabitats than *K. homeana* (Ernst and Barbour, 1989), although this suggestion could not be demonstrated during recent field studies (Lawson, 2006; Luiselli et al., 2006).

Overall, this study also indicates that both *Kinixys* tortoises exhibit low population densities throughout the West African range studied, despite our selection of apparently suitable habitats. The methodology used in the present paper has not applied previously with *Kinixys*, and thus our results could not be reliably compared with previous literature data on density patterns of the same genus (e.g., Coulson and Hailey, 2001; Luiselli, 2003b). Nonetheless, it should be remarked that the average densities detected for the two species during the various transects surveyed (ranging in most cases from 0.2 to 2.3 individuals × ha^{-1}, with peaks of around 7 individuals × ha^{-1}) were similar to those recorded by capture-mark-recapture experiments conducted with the Nigerian *K. homeana* (ranging from 0.2 to 2.8), the Nigerian *K. erosa* (from 0.1 to 1.4 individuals × ha^{-1}), the Nigerian *Kinixys belliana nogueyi* (from 0.1 to 2.7 individuals × ha^{-1}) (Luiselli, 2003b, 2006b), and the Zimbabwean *Kinixys spekii* (0.2 individuals × ha^{-1}; Coulson and Hailey, 2001). The low densities we observed, can therefore be considered as the common density values characterising the distribution of these tortoises within their current African range. More in general, this study confirms that land tortoises tend to exhibit low population densities, as already stated by Luiselli (2006b) in a global review of tortoise populations (for a few exceptions, see Hailey et al., 1988; Niederberger and Seidel, 1999; Hailey and Willemsen, 2000).

However, it is also necessary to point out the limits of the method used. Indeed, DISTANCE sampling is very good for getting density data from several areas within a short time-span (as done in this paper), but not really very precise for density estimations when the number of transect replicates and the density of the animals is not high. In our study case, density estimates, particularly of *Kinixys homeana* in Ghana and Benin, are therefore not particularly accurate, as the method would have required more observations and lines to correctly asses the precision of parameters and sampling variance (Buckland et al., 2001). In general, it is recommended to use more than 20 lines to correctly estimate variance in sample size, while the minimum number of observations should be related to the number of parameters of the chosen model and to the needs for stabilizing error estimate (Buckland et al., 2001). As a general rule, we suggest to use usual capture-mark-recapture procedures to estimate population sizes and density of tortoise species rather than DISTANCE estimations, also because it is somewhat difficult to evaluate the independence of the various observations.

In conclusion, this survey established that the two hinge-back tortoises, although effectively coexisting also at a local scale in most forest transects along the coast of West Africa, tend to have a complementary distribution, with the population density of the one species roughly increasing from West to East and the reverse being true for the other species, and exhibit an inverse relationship in terms of population density at the local scale. We infer that the observed effects can be explained by interspecific competition with density regulation at each site being maintained by resource availability and, possibly at the local scale, by historical effects which could be implicated in the dominance of the one species on the other. For instance, in sites where both species are actively hunted by people (for instance in the Niger Delta in southern Nigeria; see Luiselli, 2003b), small-sized individuals tend to achieve a higher life expectancy, whereas large ones are removed (Lawson, 2000). This process could favour the dominance of the smaller sized *K. homeana* over the larger *K. erosa*, despite and beyond natural competition.

A clear understanding of the community dynamics of these sympatric species still requires much research (for instance, by applying removal experiments, etc.); the data presented here provides an encouraging basis for further research addressing the population biology of these tortoises.

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