Seasonal activity patterns and diet divergence of three sympatric Afrotropical tortoise species (genus *Kinixys*)

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Abstract

Three species of hinge-back tortoises (*Kinixys belliana nogueyi, Kinixys erosa, Kinixys homeana*) are found in simpatry in the rainforests of the Niger Delta, southern Nigeria (west Africa). The seasonal activity patterns and food habits of these tortoises are studied in the present paper. *K. erosa* and *K. homeana* have similar activity patterns, with peaks occurring during the wet season. *Kinixys belliana* was found only during the wet months. There was no evidence of any specific effect of humidity of the air on their activity intensity, and it seems likely that, more than absolute values of air humidity, the crucial factor to force tortoises into high activity is the sudden change between dry days and very wet days at the onset of the rainy season (end of March – early April). *K. homeana* was significantly more active in the early phase of the wet season. Common items, which were consumed by all three predator species, were: plant matters, fruits and berries, fungi, Oligochaeta, and Gastropoda Pulmonata, whereas Araneidae were also consumed by all species, but much more rarely. Common prey items, which were consumed by *K. homeana* and not by *K. erosa* were: Coleoptera *larvae*, Dermaptera, and termites. *K. homeana* appeared more generalist than *K. erosa,* and the respective diets diverged considerably both in dry and in wet seasons. On the other hand, the diets of *K. erosa* and *K. belliana* were more similar (at least in wet season).

Contents

Introduction

Although some groups of reptiles (notably lizards and snakes) have become very popular subjects for community ecology studies (e.g., Scott and Campbell, 1981; Pianka, 1973, 1975, 1986; Barbault, 1977, 1991; Toft, 1985; Luiselli et al., 1998, 2002), chelonians have been largely overlooked in this respect (Scott and Campbell, 1981). Indeed, relatively few information is available on the organization and the forces structuring the communities of sympatric chelonians, and in most cases the available data concern with freshwater turtles, whereas very few data are available for communities of terrestrial species (Lagler, 1943; Legler, 1976; Vogt, 1981; Williams and Christiansen, 1981; Jackson, 1988; Vogt and Guzman, 1988; Moll, 1990; Stone et al., 1993; Hailey, 1995; Sammartano, 1995; Teran et al., 1995; Kennett and Tory, 1996; Baard, 1997; Allanson and Georges, 1999; Luiselli et al., 2000; Pritchard, 2001).

The forest habitats of west and central Africa house a rich chelonian fauna (Villiers, 1958; Iverson, 1992) which can be an ideal target for studies on community ecology and species' interactions. However, the few papers published up to now on terrestrial hinge-back tortoises (genus *Kinixys*) analysed aspects of their conservation ecology (Lawson, 2000; Luiselli, 2003; Luiselli et al., 2003), morphometrics (Lawson, 2001), or ecological correlates of their local distribution (Luiselli et al., 2000). No specific emphasis was placed on community ecology studies of terrestrial species.

The Niger Delta region (southern Nigeria, West

Africa) is characterized by the presence of three sympatric species of terrestrial hinge-back tortoises (*Kinixys belliana nogueyi, Kinixys erosa,* and *Kinixys homeana,* cf. Luiselli et al., 2000; Luiselli, 2003). It is particularly noteworthy, as it is very unusual to find all these species sympatric in other regions of Africa, due to their different ecological and habitat requirements (Ernst and Barbour, 1992).

My aims in the present study are to investigate the seasonal activity patterns and the food habits of these three tortoise species in sympatric populations, their variations in relation to season, and the potential for inter-specific competition for food which could eventually regulate their coexistence dynamics. In addition, my data are compared to food data for other *Kinixys* species which have been carefully studied during the recent years (Hailey, 1995, 1997, 1998; Hailey et al., 1997, 1998, 2001).

Materials and methods

The study species

Detailed statistical studies, based on logistic regression predictive models, of the habitat requirements and distribution of the three *Kinixys* species in the Niger Delta are presented in Luiselli et al. (2000). Based on this study, it resulted that *K. belliana* is the rarest of the three species, and is found only in a few sites between the upper Orashi and upper Sambreiro River courses, with open forest patches, clearings and bushy edges. *K. homeana* is the most common and widespread of the three species, and its presence is statistically linked to the presence of secondary swamp-forest, secondary dry forest, and mangrove formations along river banks. *K. erosa* is less common than *K. homeana,* and its presence is statistically linked to the presence of secondary swamp-forest. *K. homeana* and *K. erosa* are similar in terms of habitat requirements, and their local distributions widely overlap, although *K. homeana* is more easily found than *K. erosa* in nearly every sites where the two species are sympatric.

Study areas and methods

Data were collected, from September 1996 to January 2002, in the eastern side of the Niger Delta (Bayelsa, Rivers, and Anambra States). A detailed description of the study sites where data were collected is presented in Luiselli et al. (2000).

Tortoises were searched for by means of different surveying procedures: (i) random searching along all forest micro-habitats potentially inhabited by tortoises, (ii) pitfalls with drift fences checked every day, and (iii) examination of specimens captured by local people and generally traded in bush-meat markets (e.g., see Luiselli et al., 1998, 2003b; Lawson, 2000), which are generally found along the main roads and in the riverine villages (Ojonugwa, 1986).

Random searching was done during 711 different days, 338 during the wet season (May to September), and 373 during the dry season (October to April), whereas bush-meat markets were visited on a regular basis (at least twice on each month). All the bush-meat markets situated along the courses of the rivers Sambreiro (= Sombreiro) and Orashi, and those in the vicinities of the urban centres of Yenagoa, Sagbama, Port Harcourt, Peterside, Bonny, Obrikom, Oguta, Ahoada, Abonnema, and Degema, were visited (Luiselli et al., 2003).

Every tortoise, whether free-ranging or traded, was examined to species, sex, plastron length, and body weight. Free-ranging tortoises were permanently individually marked by unique sequences of notches filed into the marginal scutes, and their food habits were determined by faeces analysis. Faeces samples were obtained from animals that defecated on handling, and stored in jars of 10% formalin. Each sample of faeces was placed in a shallow dish of water, and the presence of different food items was noted. The samples were then divided into four parts: those recognisable as vascular plants, fungi, invertebrates, and others. The faecal pellets were then dried and examined as in Hailey et al. (1997). Tortoises, offered for sale, which were already dead at the time of examination, were dissected for any food item in the stomach. Moreover, the sellers (which normally were also the hunters) were interviewed to learn more about the

time of capture and the habitat of capture of the traded specimens (see also Luiselli et al., 2003).

All data were statistically analysed by STATIS-TICA (versions 5.0, for Windows) PC+ package, with all tests being two-tailed and alpha set at 5%. To avoid statistical problems due to "pseudo-replication" of the data (cf. Licht et al., 1966; Mathur and Silver, 1980; Hurlbert, 1984), I took food data only once from each tortoise individual, i.e. the recaptured individuals were never used again for data recording. To avoid problems in mixing data from both stomach contents of dissected specimens (in which it is often possible to count the exact numbers of items eaten by each tortoise) and faecal pellets of living specimens (in which it is often impossible to do it), I always considered for my analyses the total number of specimens containing a given prey type, and not the total number of prey items.
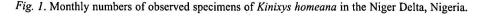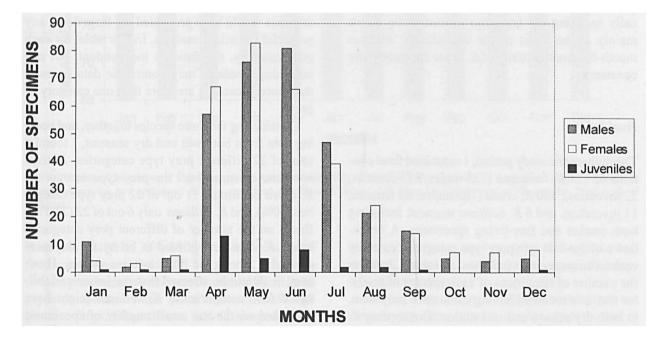
Results

Seasonal activity patterns

The monthly numbers of *Kinixys* specimens observed at the study areas (cumulating data from both markets and the field) are given in Figure 1 (*K. homeana*) and Figure 2 (*K. erosa*). No figure is given for *K. belliana* due to the too small sample examined: only 8 specimens were found, all in wet season (4 in April, 3 in May, 1 in June). There were significant month-by-month variations in the numbers of observed specimens (= above-ground activity intensity) in both *K. homeana* and *K. erosa* (for *K. homeana* – males: $\chi^2 = 349.11$, df = 11, $P < 0.00001$, females: $\chi^2 = 340.10$, df = 11, $P < 0.00001$, juveniles: $\chi^2 = 58.24$, df = 11, $P < 0.00001$; for *K. erosa* – males: $\chi^2 = 72.01$, df = 11, $P < 0.00001$, females: $\chi^2 = 45.12$, df = 11, $P < 0.00001$, for juveniles χ^2 value is not calculated due too the small sample examined), and most of the specimens of both species were found during the wet season months (Figures 1 and 2). However, there was no effect of monthly relative humidity (Figure 3) on the numbers of observed specimens of both *K. homeana* (for males: $F_{8,2} = 0.71$, $P = 0.700$; for females: $F_{8,2} = 0.51$, $P = 0.796$) and *K. erosa* (for males: $F_{8,2} = 0.59$, $P = 0.755$; for females: $F_{8,2} = 0.34$, $P = 0.887$).

In inter-specific comparisons (after having pooled males, females and juveniles), it resulted that, although both species had activity peaks during the wet months, there were significant differences in
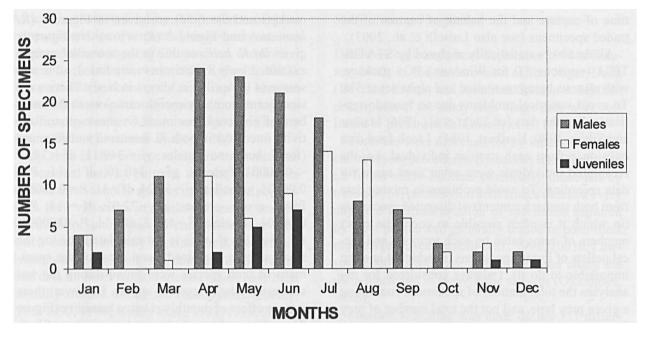

Fig. 1. Monthly numbers of observed specimens of *Kinixys homeana* in the Niger Delta, Nigeria.

Fig. 2. Monthly numbers of observed specimens of *Kinixys erosa* in the Niger Delta, Nigeria.

terms of monthly numbers of observed specimens (observed versus expected $\chi^2 = 89.132$, df = 11, $P < 0.000001$). In this regard, *K. homeana* was found active particularly in the early phase of the wet season (April, May and June), and *K. erosa* in the late phase of the wet season. Therefore, practically speaking, *K. homeana* proved to be active mainly at the onset of the wet season, whereas month-by-month activity of *K. erosa* appeared more constant.

Food habits

Throughout the study period, I examined food contents of 374 *K. homeana* (135 males, 217 females, 22 juveniles), 180 *K. erosa* (103 males, 66 females, 11 juveniles), and 6 *K. belliana nogueyi*, including both market and free-living specimens. A breakdown of the data into prey type categories eaten by each tortoise species is presented in Table 1. It shows the number of specimens of each species of predator that was recorded having eaten each prey item, in both dry season and wet season. Concerning *K. belliana*, samples were collected only during the wet season. Data for both males and females, in *K.*

homeana as well as in *K. erosa*, were cumulated after having tested that the two sexes did not differ significantly in terms of taxonomic dietary composition (in all cases, at least $P > 0.3$ at χ^2 test). Data for both sexes of *K. belliana* are cumulated due to the too small sample examined, which in any case would have prevented me from doing any powerful statistical analysis. In this table, for each prey category, the data are independent, but one individual predator may contribute data to more than once because it ate more than one category of prey.

Considering the three species together, and pooling data from both wet and dry seasons, I found a total of 22 different prey type categories. *Kinixys homeana* consumed all the prey type categories, *K. erosa* consumed 11 out of 22 prey type categories (50%), and *K. belliana* only 6 out of 22 (27.3%). Based on the number of different prey categories eaten, *K. homeana* proved to be by far the most generalist among the three tortoise species. However, it should be stressed that the lesser variability of food categories in *K. belliana* might have depended on the too small number of specimens examined in comparison to the other two species. Indeed, there was an apparent effect of the sample
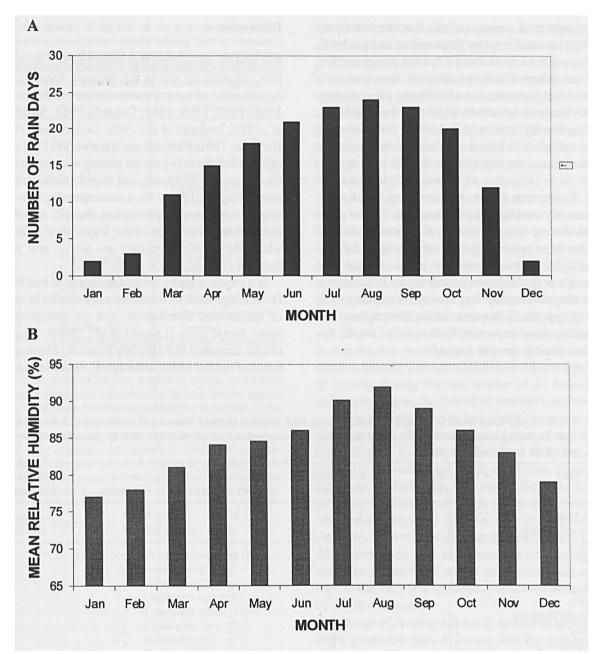
Fig. 3. Number of rain days per month (graphic A) and mean monthly relative humidity (graphic B) at a typical locality of southern Nigeria where the two species of *Kinixys* are found sympatric (Calabar; data from the Department of Geography, University of Calabar).

sizes (respectively, 374, 180, 6) on the number of food categories utilised (22, 11, 6).

Common items, which were consumed by all three predator species, were: plant matters, fruits and berries, fungi, Oligochaeta, and Gastropoda Pulmonata, whereas Araneidae were also consumed by all species, but much more rarely. Common prey

items, which were consumed by *K. homeana* and not by *K. erosa* were: Coleoptera *larvae*, Dermaptera, and termites.

The list of prey type categories which were not eaten by the three tortoise species are presented in Table 2. These data permit to notice easily (i) the much wider choice of prey consumed by *K. homeana*

compared to *K. erosa*, and (ii) that the extra prey categories consumed by *K. homeana* and not by *K. erosa* are not an artefact of the sample examined, i.e. not the result of one aberrant *homeana* individual that just ate a lot of different prey species.

An analysis by season (Table 3) indicated that, during the dry season, *K. erosa* did not feed upon nine categories of food which were consumed by *K. homeana*, and especially it did not feed upon at least three categories of food (i.e. Coleoptera larvae, Coleoptera adults, and termites) which were commonly consumed by *K. homeana*. On the other hand, during the wet season, *K. homeana* did not eat on three prey categories consumed (occasionally) by *K. erosa*, whereas *K. erosa* did not feed upon six prey categories consumed by *K. homeana*. It is also noteworthy that four of these categories, i.e. Miriapoda, Coleoptera larvae, Dermaptera, and termites, were important food sources for *K. homeana* during the wet season.

Discussion

It is widely recognized that inter-specific competition, whether or not is the primary force in the organization of natural communities (cf. Schoener, 1968, 1982, 1983, 1985; Connell, 1983; Strong et al., 1984, Barbault et al., 1985; Underwood, 1986; Barbault, 1991; Barbault and Stearns, 1991), should occur when there is overlap among coexisting species in spatial, temporal, and trophic niche dimensions (Pianka, 1986). As a consequence, to avoid competition, many species are thought to subdivide resources in three major ways: they differ in where they live, when they are active, and what they eat (Pianka, 1973, 1975; 1986).

In a previous study, it was demonstrated that Niger Delta hinge-back tortoises are very similar in terms of habitat and distribution, and are sympatric in many forest areas (Luiselli et al., 2000). Thus, it can be supposed that they are basically identical in terms of spatial niche, although *K. belliana* is more

Table 1. List of prey items found in stomach contents of hinge-back tortoises (*Kinixys homeana, K. erosa,* and *K. belliana*) in the Niger Delta, including both market and free-living specimens. Numbers indicate the numbers of stomachs containing a given food type, and not the numbers of prey items.

Prey Type	*K. homeana* Dry season	*K. homeana* Wet season	*K. erosa* Dry season	*K. erosa* Wet season	*K. belliana* Wet season
Plant Matters	33	27	21	17	4
Fruits and Berries	8	6	3	2	2
Seeds	4	3	3	3	-
Fungi	21	13	12	7	2
Oligochaeta	13	7	4	6	1
Gastropoda	48	7	3	3	1
Bivalvia	-	1	-	-	-
Crustacea Decapoda	1	-	-	1	-
Isopoda	17	7	2	2	-
Chilopoda	11	5	3	1	-
Miriapoda	16	11	1	-	-
Araneidae	3	-	-	1	1
Scorpiones	2	-	-	-	-
Arthropoda ind.	15	9	2	-	-
Coleoptera adults	8	4	-	1	-
Coleoptera larvae	11	6	-	-	-
Lepidoptera larv.	2	-	-	1	-
Orthoptera	1	-	-	-	-
Dermaptera	1	4	-	-	-
Formicidae	-	1	-	1	-
Termites	8	4	-	-	-
Poultry (scavenging)	-	1	-	-	-
EMPTY STOMACHS	42	71	38	21	0

Table 2. Summary of the data on the prey categories which were not consumed by each tortoise species. Numbers in parentheses in columns of the table relative to *Kinixys erosa* indicate how many *Kinixys homeana* individuals were recorded as having eaten each prey item not consumed by the other congener.

K. homeana	K. erosa	K. belliana nogueyi
		Seeds
	Bivalvia (1)	Bivalvia
		Crustacea Decapoda
		Isopoda
		Chilopoda
		Miriapoda
	Scorpiones (2)	Scorpiones
		Arthropoda ind.
		Coleoptera adults
	Coleoptera larvae (17)	Coleoptera larvae
		Lepidoptera larv.
	Orthoptera (1)	Orthoptera
	Dermaptera (5)	Dermaptera
		Formicidae
	Termites (12)	Termites
	Poultry (scavenging) (1)	Poultry (scavenging)

Table 3. Summary of the data, entered by season, on the prey categories which were not consumed by each tortoise species in the Niger Delta. Numbers in parentheses in columns of the table relative to *K. erosa* indicate how many *K. homeana* individuals were recorded as having eaten each prey item not consumed by the other congener, and numbers in columns of the table relative to *K. homeana* indicate how many *K. erosa* individuals were recorded as having eaten each prey item not consumed by the other congener. *Kinixys belliana* is not included in this table.

K. homeana Dry Season	K. erosa Dry Season
	Crustacea Decapoda (1)
	Araneidae (3)
	Scorpiones (2)
	Coleoptera adults (8)
	Coleoptera larvae (11)
	Lepidoptera larv. (2)
	Orthoptera (1)
	Dermaptera (1)
	Termites (8)

K. homeana Wet season	K. erosa Wet season
Crustacea Decapoda (1)	
	Bivalvia (1)
	Miriapoda (11)
Araneidae (1)	
	Coleoptera larvae (6)
Lepidoptera larv. (1)	
	Dermaptera (4)
	Termites (4)
	Poultry (scavenging) (1)

linked to open bush, and so appears extremely rare and marginal in the study region. Lawson (2000, 2001) suggested that, in south-western Cameroon, *K. erosa* is more ubiquitous than *K. homeana,* which appears to be absent from some apparently suitable habitats. In the Niger Delta, the reverse is true (Luiselli et al., 2000), but apart from these locally-determined discrepancies in local distribution patterns, it is evident that both species are linked to the same habitat types.

Considering that daily activity patterns are not really indicative of niche divergence between potential competitors (Jaksic, 1982; Capizzi and Luiselli, 1996), I suggest to use in this case the incidence of seasonal activity rhythms as potential niche parameters. Also under this aspect, both *K. erosa* and *K. homeana* were generally similar, as they exhibited similar activity patterns with peaks during the wet season. *Kinixys belliana* was also found only during the wet months, but the sample size is too small to be sure. Lawson (2000) also reported peaks of activity during the wet season in *K. homeana* and *K. erosa* from the forests of western Cameroon.

Although both species had similar seasonal activity patterns, there was no evidence of any specific effect of humidity of the air on their activity intensity. It seems likely that, more than absolute values of air humidity, the crucial factor to force tortoises into high activity is the sudden change between dry days and very wet days at the onset of the rainy season (end of March – early April), as demonstrated by the high numbers of specimens observed at the onset of the rainy season, in contrast to the very few specimens observed at the end of the dry season.

In terms of feeding habits, *K. homeana* appeared more generalist than *K. erosa,* and the respective diets diverged considerably both in dry and in wet seasons. Although most of the absent food items can be explained by smaller sample sizes for *K. erosa,* it is likely that the most biologically significant differences are the absence of Coleoptera larvae, Dermaptera and termites, which may indicate that *K. homeana* feeds more in leaf litter and rotting wood, or be due to its smaller body size. The diets of *K. erosa* and *K. belliana* were more similar (at least in wet season), but their ecological coexistence is perhaps facilitated by the different micro-habitat characteristics (*belliana* is found only

in drier micro-habitats, whereas *erosa* lives in very wet micro-habitats, cf. Luiselli et al., 2000). Contrasting *K. homeana* with *K. erosa,* it perhaps that their inter-specific competition is reduced not only by prey type selection, but also by prey size selection, as *homeana* is considerably smaller than *erosa* both in Nigeria (Luiselli, 2003) and in Cameroon (Lawson, 2001), and differences in relative body sizes are well known to reduce competition intensity among coexisting species (Pianka, 1986). In this regard, it must be noticed that *K. belliana* has approximately the same average body size as *K. homeana* (Vetter, 2002).

As in my study, all species of *Kinixys* have been reported to be omnivorous that eat on both fungi, plants, and invertebrates (Villiers, 1958; Blackwell, 1968; Bertram, 1979; Broadley, 1989a, 1989b, 1989c), but the only detailed data have been provided for *K. spekii* (Hailey, 1997, 1998; Hailey et al., 1997, 1998, 2001). It is supposed that the consumption of both fungi and arthropods by *Kinixys* species is due to the presence of chitinase in this genus (Hailey et al., 1997). In general, my data on Niger Delta species are fully consistent with those reported by Hailey and colleagues for *K. spekii.* This latter is, however, a species of more arid environment.

In conclusion, my study demonstrates that inter-specific competition is potentially an important force in structuring the coexistence of sympatric hinge-back tortoises in the rainforests of tropical Africa, and that, as a response to it, two potential competitors (*K. homeana* and *K. erosa*) evolved diverging foraging strategies (extreme versus moderate dietary generalist habits) in both wet and dry seasons. Removal experiments, currently in progress, will serve to demonstrate what are the precise mechanisms of it.

Acknowledgements

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