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DIET OF *THELOTORNIS KIRTLANDII* (SERPENTES: COLUBRIDAE: DISPHOLIDINI) FROM SOUTHERN NIGERIA

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Thelotornis kirtlandii is an arboreal, venomous colubrid snake with a wide distribution ranging from the islands of the Bijagos Archipelago, Guinea Bissau; east through forested areas of west Africa and the Congo basin to Uganda and southern Sudan; south to northern Angola, north-western Zambia and south-central Tanzania (for review, see Broadley, 2001). It is typically a forest species (Broadley, 2001), and in southern Nigeria may attain high population densities in mangrove habitats (Luiselli & Akani, 2002).

Although the diet of its savanna congener, *Thelotornis capensis*, is well known (Shine *et al.*, 1996), few data are available on the food habits of *T. kirtlandii,* possibly due to its elusive habits and relatively inaccessible rainforest and mangrove habitats. Apart for general comments in books (e.g., "this snake feeds on lizards, birds, etc.", e.g. see Phelps, 1981), there are very few precise dietary records in the literature: this snake was found to prey upon nestling birds (*Spermophaga ruficapilla*), agamids (*Acanthocercus atricollis*), and scincids (*Mabuya maculilabris*) in the Democratic Republic of Congo (Loveridge, 1942); upon lacertids (*Ichnotropis capensis*) in Zambia (Broadley, 1991); and upon colubrid snakes (*Philothamnus carinatus)* in Zaire DCR (Bogert, 1940). From a swamp-rainforest of south-eastern Nigeria, Luiselli *et al.* (1998) recorded eight food items: one small bird (*Cisticola galactotes*) and seven geckos (*Hemidactylus fasciatus*). Here we present a detailed account of the diet of free-ranging *T. kirtlandii* from a region situated within the continuous Guinea-Congo rainforest belt (i.e. southern Nigeria, West Africa), with an analysis of prey-size predator-size relationships.

Our field study was carried out from September 1996 to May 2002 (with additional data recorded in 1994 and 1995), in some localities of south-eastern Nigeria (for the territories surveyed cf. Luiselli & Angelici, 2000), situated in the eastern axis of the Niger Delta (Bayelsa and Rivers States), in Anambra, Akwa-Ibom, Abia and Cross River States. The study region is tropical, with a wet season from May to September and a dry season from October to April. The wettest period of the year is June-July, and the driest period between late December and February.

Methods used to survey the study area, capture snakes and analyse their food items, are detailed elsewhere (e.g. Luiselli *et al.*, 1998, 2002). Fieldwork was conducted under all climatic conditions, but with a bias toward diurnal hours (from 0800-1800 hrs) due to security constraints related to the prevailing unstable political situation. Field effort was almost identical in the wet (421 field days) and dry (418 field days) seasons.

We searched for snakes along standardized routes in the various microhabitats frequented by snakes at the study areas. We captured snakes by hand, but additional free-ranging specimens were captured by pitfall traps with drift fences and by traps used by locals to capture terrestrial animals. We always recorded the site of capture and the habitat at each capture site. Each snake was measured for snout-vent length (SVL, to the nearest 0.1 cm), weighed with an electronic balance, and individually marked by ventral scale clipping for future identification. Then, the snakes were palpated in the abdomen until regurgitation of ingested food or defecation occurred. In addition, specimens found already dead during our surveys (e.g. snakes killed by farmers, or by cars, etc) were dissected to determine if prey were present. We identified prey items to the lowest taxonomic level possible. We estimated mass of prey items at the time of its ingestion, when possible, by comparing the item to intact conspecifics of various sizes from our own personal collection, or measuring the fresh biomass in perfectly preserved items. This was not possible in faecal samples, which generally consisted of scales of reptiles. Although in this article we used data collected from both stomachs and faeces, specimens for which stomach contents were used were not generally used for faecal pellets, to avoid multiple counts of the same food items. However, the food contents from both faeces and stomachs of a same snake specimen were considered in the cases in which, for instance, faecal samples contained mammal hair and the stomach a gecko).

Vouchers (of both prey and predators) were deposited in the herpetological collections of the Rivers State University of Science and Technology (Port Harcourt, Nigeria), of the Department of Agricultural Sciences of Uyo University (Uyo, Nigeria), of the Faculty of Sciences of the University of Calabar (Calabar, Nigeria), of the Ecology Lab at F.I.Z.V. (Rome, Italy), and of the Cross River National Park (collections in both Akamkpa and Butatong, Nigeria).

All statistical tests were two-tailed, with alpha set at 0.05. Means are followed by ±1 SD.

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A total of 133 specimens (44 smaller than 50 cm total length – assumed to be subadults in this study – and 89 larger than 50 cm total length) were examined for the present study (see Appendix 1 for a list of the localities of capture). Maximum size was 122.5 cm for males, and 131.4 cm for females. When only specimens >50 cm in length are considered, males and females were similar in terms of mean length (males: 89.8±17.4 cm, n=39; females: 91.2±18.3 cm, n=41; differences between two samples: one-way ANOVA $F_{1,77}$=2.384, P>0.3).

A list of prey items is presented in Table 1. Based on this table, it is evident that 100% of the dietary spectrum of specimens >50 cm in length consisted of vertebrates, whereas a very few arthropod items were found in juveniles. It is not known whether these arthropod remains were primary feeding records, or secondary ingestion following the complete digestion of the original predator, e.g. a gecko or amphibian. It is likely that the second option would be more likely, as (1) specimens of *Thelotornis kirtlandii* kept in captivity never fed upon invertebrates; (2) these prey items were almost completely digested; and (3) there are no records supporting primary arthropod feeding by *Thelotornis* (e.g. see Shine *et al.*, 1996). Amongst vertebrates, nearly all the prey items were reptiles, with a single case of avian prey (the same record was presented in Luiselli *et al.*, 1998) and a single case of amphibian prey. Amongst reptiles, snakes were rarely eaten, whereas lizards – and particularly gekkonids – formed the main prey.

Female body size significantly positively influenced the size of the prey eaten (Spearman's r^2=0.312, ANOVA: $F_{1,18}$=6.882, P=0.0189), whereas the same relationship was not found in males (r^2 =0.103, ANOVA: $F_{1,14}$= 0.108, P=0.594). The slopes of these two regressions differed significantly (heterogeneity of slopes test: $F_{1,30}$=4.139, P=0.026).

To the best of our knowledge, there are no other scientific reports on the diet of a large number of free-ranging specimens of *T. kirtlandii* from a single geographic region (although Shine *et al.*, 1996, presented a very detailed dietary study on the savannah congener *T. capensis*). Thus, it may be assumed that the present study, being the largest of its type available for *T. kirtlandii*, may have permitted finer (and perhaps different) conclusions from those already available in the literature. Nonetheless, at least in general terms, this study confirms previous literature suggesting that lizards account for a remarkable portion of the diet of free-ranging *T. kirtlandii*. It is interesting, however, that no chameleons were eaten by these snakes, although they were regularly found in congeners from elsewhere (e.g. *T. capensis*, see Shine *et al.*, 1996; *T. mossambicanus*, D. Broadley, *pers. comm.*). It perhaps reflects a global scarcity of these potential prey in the rainforest habitats of southern Nigeria (Akani *et al.*, 2002). On the contrary, gekkonids (and to a lesser extent also Scincidae) obviously represented the primary prey sources for both adult and subadult snakes. Our data also demonstrate that rainforest *T. kirtlandii* do not have as wide a dietary spectrum as their savannah congeners (Shine *et al.*, 1996), which are known to forage frequently also on amphibians (especially *Breviceps*, but including *Chiromantis xerampelina*) and on large lizards like *Acanthocercus atricollis* and *Gerrhosaurus* spp., in addition to snakes and mammals) (D. Broadley, *pers. comm.*). Amphibian and snake prey were extremely rare in forest *T. kirtlandii* from Nigeria. However, it is noteworthy that Lawson (1993) recorded

TABLE 1. Compilation of the original data available on food items of *Thelotornis kirtlandii* from south-eastern Nigeria.

Prey	Numbers of prey items in specimens <50 cm length	Numbers of prey items in specimens >50 cm length	Cumulative number of prey items
Invertebrates			
Mantodea	2	0	2
Birds			
Cisticola galactotes	0	1	1
Reptiles			
Gastropyxis smaragdina	0	1	1
Philothamnus sp.	0	2	2
Mabuya sp.	7	11	18
Panaspis sp.	1	0	1
Agama agama	4	7	11
Hemidactylus fasciatus	2	8	10
Lygodactylus sp.	2	6	8
Undetermined Gekkonidae	3	4	7
Amphibians			
Phrynobatrachus sp.	0	1	1
TOTAL	21	41	62

a case of predation by *T. kirtlandii* on *Phrynobatrachus auritus* in Korup National Park (western Cameroon, close to the border with Nigeria). According to Don Broadley's unpublished data (*pers. comm.*), geckos represented in the diet of savanna species were mostly *Lygodactylus*, but there was one *Hemidactylus platycephalus*. In our case, both *Hemidactylus* and *Lygodactylus* spp. were frequently preyed upon. It is noteworthy that there was an apparent conflict in our data of a diurnal snake feeding on a nocturnal gecko – e.g. *Hemidactylus fasciatus*. However, these geckos are often found during the daytime at the mouths of tree holes inside the shady forest, and we suppose that *T. kirtlandii* may ambush them in these situations, or – alternatively – they may have a specific hunting strategy that allows them to locate nocturnal geckos in their retreats.

In general, it is likely that these differences between *T. kirtlandii* and *T. capensis* may reflect local variations in prey resource availability (due to different habitat structure and geographic regions) rather than species-specific, genetically-encoded, divergence in foraging habits.

As for the prey-size/predator-size relationships, it is noteworthy (but as yet inexplicable) that the two sexes exhibited very different patterns, with the females tending to prey on larger organisms in relation to increases in their own body size, whereas the males which did not. It is possible that these diverging patterns may be linked to the different energy requirements of the two sexes for reproduction to take place, but supporting data are needed before this hypothesis can be tested.

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APPENDIX 1

Gazetteer of the localities of capture of *Thelotornis kirtlandii*. When possible, geographic coordinates taken by GPS "Garmin 12" are reported. When geographic coordinates were not taken, the site of capture is made available to further readers by citing its Local Government Area, or the main town close to it.

ABIA STATE: Aba; AKWA-IBOM STATE: Eket (04°50'N, 07°59'E); Stubbs Creek Reserve; Ifon (Etinang Local Government Area); BAYELSA STATE: Nembe (Nelga Local Government Area); Dagbabiri (Sagbama Local Government Area); Toru-Ebeni (Mein/Oakiri Local Government Area); Sangana (Brass Local Government Area); Otukpoti (Ogbia Local Government Area); CROSS RIVER STATE: Ikpan Forest (08°38'N, 05°11'E); Okwangwo village; Obubra (06°08'11"N, 05°40'12"E); DELTA STATE: Abraka (banks of Ethiope River); Okuovu (Sapele Local Government Area); Patani; Ughelli (Isoko North Local Government Area); ONDO STATE: Osse River (06°58'13"N, 05°40'08"E); RIVERS STATE: Otari (04°53'N, 06°41'E); Tombia mangrove (04°46'51"N, 06°51'54"E); Orashi River (04°44'43"N, 06°38'10"E); Peterside (04°29'N, 07°10'E); Bonny Island (04°25'N, 07°15'E); Abonnema (Akulga Local Government Area); Ke (Degema Local Government Area); Kula (Degema Local Government Area); Ngo (Andoni Local Government Area); Okrika (Walga Local Government Area); Odiokwu (05°06'N, 06°37'E); Bikkiri (04°46'N, 06°36'E); Egita (05°15'N, 06°41'E); Awarra (05°21'14"N, 06°49'02"E).