Life–history and ecological distribution of chameleons (Reptilia, Chamaeleonidae) from the rain forests of Nigeria: conservation implications

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Abstract

Life–history and ecological distribution of chameleons (Reptilia, Chamaeleonidae) from the rain forests of Nigeria: conservation implications.— Five species of chameleons were observed in the continuous forest zone of southern Nigeria: *Chamaeleo gracilis gracilis* Hallowell, 1842, *Chamaeleo owenii* Gray, 1831, *Chamaeleo cristatus* Stutchbury, 1837, *Chamaeleo wiedersheimi* Nieden, 1910, and *Rhampholeon spectrum* (Bucholz 1874). Many original locality records are presented for each species. One species is apparently rare and confined to montane habitats (*C. wiedersheimi*), another species is relatively common and its habitat is generalist (*C. gracilis*), and the other three species are vulnerable and limited to specific micro–habitats. Female *R. spectrum* had clutch sizes of two eggs each and exhibited a prolonged reproductive season with oviposition likely occurring during the late phase of the dry season. Females of both *C. cristatus* (clutch sizes: 11–14 eggs) and *C. owenii* (clutch sizes: 15–19 eggs) have a shorter reproductive season with oviposition occurring most probably at the interphase between the end of the wet season and the onset of the dry season, and female *C. gracilis* (clutch sizes: 14–23 eggs) appeared to exhibit two distinct oviposition periods (one at the interphase between the end of the wet season and the onset of the dry season, and one at the peak phase of the dry season). Diets of four sympatric species of chameleons consisted almost exclusively of arthropods. There were significant inter–group differences at either intra–specific level (with the females of the two best studied species, i.e. *R. spectrum* and *C. gracilis,* having a wider food niche breadth than males) or inter–specific level (with a continuum of dietary specialization from the less generalist (*C. cristatus*) to the more generalist (*C. gracilis*). However, "thread–trailing" experiments indicated that activity patterns of Nigerian chameleons were relatively similar among species. The overall abundance of chameleons (as estimated from the number of specimens observed in the time unit of field effort) was relatively similar in three contrasted habitat types, but lizards were more abundant in the mature secondary forest. When greatly altered by massive logging activity, the overall abundance of chameleons in the mature secondary forest habitat declined only slightly, whereas the species diversity declined drastically. This was an effect of (i) the simultaneous extinction of three of the four species originally present in the forest plot, and of (ii) the rapid increase in abundance of a single species (*C. gracilis*) as a response to habitat alteration. The conservation implications of all these data are also discussed.

Key words: Chameleons, Habitat, Feeding habits, Activity, Comparative ecology, Conservation status.

Resumen

Estrategia vital y distribución ecológica de camaleones (Reptilia, Chamaeleonidae) de los bosques húmedos de Nígeria: implicaciones en la conservación.— Se observaron cinco especies de camaleones en la zona de bosque ininterrumpido del sur de Nigeria: *Chamaeleo gracilis gracilis* Hallowell, 1842, *Chamaeleo owenii* Gray, 1831, *Chamaeleo cristatus* Stutchbury, 1837, *Chamaeleo wiedersheimi* Nieden, 1910 y *Rhampholeon spectrum* (Bucholz 1874). Se presentan muchos registros de localidad originales para todas las especies. Una especie es aparentemente rara y está confinada a los hábitats montañosos (*C. wiedersheimi*), otra especie es relativamente común y generalista en cuanto al hábitat (*C. gracilis*), y las otras tres especies son vulnerables y están limitadas a microhábitats específicos. El tamaño de cada puesta de la hembra de *R. spectrum* fue de dos huevos, mostrando una prolongada estación reproductora con oviposición durante la última fase de la estación

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húmeda. Las hembras de *C. cristatus* (tamaño de puesta: 11–14 huevos) y *C. owenii* (tamaño de puesta: 15–19 huevos) tienen una estación reproductora más corta y la oviposición se da con mayor probabilidad en la interfase entre el final de la estación húmeda y el inicio de la estación seca, y la hembra de *C. gracilis* (tamaño de puesta: 14–23 huevos) presenta dos periodos distintos de oviposición (uno en la interfase entre el final de la estación húmeda y el inicio de la estación seca y el otro durante el período más seco de la estación seca). Las dietas de cuatro especies simpátricas de camaleones consistían prácticamente de forma exclusiva en artrópodos. Había diferencias significativas dentro del grupo tanto a nivel intraespecífico (con las hembras de las dos especies mejor estudiadas, es decir *R. spectrum* y *C. gracilis,* con un extenso nicho alimentario más amplio que los machos) o interespecíficas (con una continua especialización alimentaria desde los menos generalistas (*C. cristatus*) a los más generalistas (*C. gracilis*). Sin embargo los experimentos "thread–trailing" indican que los patrones de actividad de los camaleones de Nigeria eran relativamente similares entre especies. La abundancia de camaleones (estimada a partir de el número de especímenes observado en la unidad de tiempo de esfuerzo de campo) era relativamente similar en tres tipos de hábitats contrastados, pero el bosque secundario maduro fue el hábitat donde los lagartos fueron más abundantes. En cuanto al hábitat del bosque secundario, cuando estaba fuertemente alterado por una fuerte explotación forestal, la abundancia de camaleones disminuía sólo ligeramente, mientras que la diversidad de especies disminuía de forma drástica. Esto era debido a: (i) la extinción simultánea de tres de las cuatro especies originalmente presentadas en el bosque, y (ii) el rápido incremento en abundancia de una única especie (*C. gracilis*) como respuesta a una alteración del hábitat. Se discuten las implicaciones de estos datos sobre la conservación.

Palabras clave: Camaleones, Hábitat, Hábitos alimentarios, Actividad, Ecología comparada, Conservación.

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Introduction

Chameleons are certainly among the most conspicuous lizards of Afro–tropical rainforest habitats (De Witte, 1965; Böhme, 1985) and they have undergone a remarkable adaptive radiation in montane habitats of the central–western region of Africa, particularly Cameroon (Böhme & Klaver, 1981; Böhme, 1985; Böhme & Schneider, 1987; Klaver & Böhme, 1992; Lawson, 1993; Wild, 1993, 1994; Necas, 1994). The rainforest zone of southern Nigeria is ecologically connected with the western Cameroon forests, and the whole region is an important hot–spot for conservation because many species of flora and fauna are endemic in the area (Kingdon, 1990).

Although information on chameleons in Nigeria–Cameroon rainforests is scarce (but see Wild, 1993, 1994), many species are known to suffer from the multiple conservation problems in the area (Wild, 1993, 1994), to the extent that the conservation status of a lot of these species herein is unknown (see NARESCON, 1992 for Nigeria). At Niger Delta, the various species of chameleons are nowadays very rare (Politano, 1998; Akani et al., 1999; Akani & Luiselli, 2001) and many populations have recently disappeared from many sites (Ojonugwa, 1973; Akani et al., 1999). In a recent study (Akani & Luiselli, 2001) it was found that over 80% of adult local people interviewed about these species reported never to have seen a chameleon. Information about chameleons in other parts of Nigeria is also very scarce (but see Pasqual, 1937; Dunger, 1967a; Butler, 1986; Reid, 1986).

In order to attain conservation programs for chameleons, this study provides basic information on the ecology and habitat distribution of free–ranging populations of several species inhabiting the rainforest region in Nigeria.

The aims of the study are twofold: to analyse the food niche of sympatric species, their diurnal activity, and changes in the community composition at a forest site before, and after, timbering; and to present records for new sites of these species. Data on their conservation problems are presented and some solutions suggested. No attempt is made to review the distribution range of species (see for instance, Talbot, 1912; Pasqual, 1937; Romer, 1953; Dunger, 1967a, 1967b; Butler, 1986; Reid, 1986; Akani et al., 1999), but only new records data set are presented.

Materials and methods

Study areas

Chameleons were studied at different forest habitats of southern Nigeria as follows: moist lowland forest, deltaic freshwater swamp–forest, and coastal mangrove (see Luiselli et al., 2000 for a detailed description of the area and Luiselli & Angelici, 2000 for the territories used during field surveys). Field work was performed from September 1994 to April 2001. The whole area has a tropical climate, with the wet season from May to September, and dry season from October to April. The rainfall peak is in June–July, and the driest period between late December and February. Annual precipitation averages between 2,000 and over 3,000 mm per year. The air temperature is generally high (average around 27–28°C), and varies little throughout the year. The annual range of the monthly average temperature varies only between 3°C and 3.5°C. The human population density is high, and the landscape is characterised by fragmented patches of rainforest interspersed within a sea of urban centres, industry, farmlands and plantations (Politano, 1998).

Field methods

Observations of free–ranging chameleons were made opportunistically during more general surveys for other forest vertebrates (mainly snakes; for the general survey methods, see Luiselli & Angelici, 2000; Luiselli et al., 1998, 1999, 2000). For this paper, the following variables were recorded each time a chameleon was observed:

Site

A GPS "Garmin 12" was used. Habitat type, time of day, and species of each chameleon sighting were also recorded.

Biometry

Snout–vent length (SVL) with a calliper to the nearest ± 1 mm. Chameleons were individually marked with a number painted in white on the back, a useful method for short–term reptile studies (e.g. see Luiselli et al., 1996), including chameleons (Kauffmann et al., 1997; Cuadrado, 1998). The marked specimens were also sexed. Body mass was not systematically recorded.

Diet

Faeces from free–living specimens of chameleons were examined for this study. To obtain faeces from free–ranging specimens while minimizing handling (which may produce stress and damages to the handled animals), chameleons captured from the wild were kept separately into small terraria until defecation occurred. Faeces were analysed in the laboratory. Prey were sorted, and identified to the lowest taxonomic level possible, and measured (to ± 0.1 mm) under a binocular microscope 10×40 equipped with a micrometer. As in a previous chameleon study (Pleguezuelos et al., 1999), characteristic body parts of arthropods (mandible width for Orthoptera, head width in Coleoptera, Diptera, Hemiptera, Hymenoptera, Mantodea, and Odonata; chelicera length for arachnids) were measured in order to estimate

the size of the prey, but attempts failed in some cases when prey fragments were broken and/or difficult to size. Diet analysis was performed on a species and sexual basis, and summarised by absolute frequency (i.e. numbers of prey belonging to a given prey type) and by frequency of appearance of a given prey type in the pellets (i.e. numbers of faecal pellets where a given prey type was observed). Diet data reported here were recorded from a single study site (Eket, Akwa–Ibom State).

Reproductive data

Clutch sizes of females were determined by palpation in some cases (two cases in *C. gracilis,* two cases in *C. cristatus,* two cases in *C. owenii,* six cases in *R. spectrum*), and by dissection in other cases, when the females were found dead in the field (four cases in *C. gracilis,* and two cases in *C. owenii*).

Daily activity and foraging habits

A continuous monitoring procedure of a few specimens encountered in the field was applied, thus devising a monitoring protocol quite equivalent to the "thread–trailing" strategy developed to study activity of tortoises (BREDER, 1927; HAILEY & COULSON, 1999). Three specimens, from three different species (*C. owenii, C. gracilis, C. cristatus*), were "thread–trailed", for 14 days each, five hours every day (i.e. for a total of 70 hours of trailing for each specimen), by remaining at approximately 10 m distance, so as not to interfere in the chameleon's normal activities. Binoculars (8x40) were also used to facilitate observations.

Population abundance and structure

Population abundance and structure of chameleons were studied at three forest patches situated in the surroundings of Calabar (Cross River State). All these areas were surveyed during the dry seasons of 2000 (area B) and 2001 (area C), and both 1998 and 2001 (area A). Area A (50x30 m) was a mature secondary forest in the first year of study (1998), but was partially affected by industrial timbering activities during the second year of study (2001, when about 40% of the former wooded surface was cut). This allowed us to test for the effects of habitat reduction on animal abundance and species composition. Area B (approximately 120x10 m) was a riparian woodland growing along the banks of the Rhoko River. Area C (40x40 m) was a secondary bush–grassland mosaic, with plants of 50–150 cm height, surrounded by plantations (of cassava and pineapples) and farmlands. All these areas are virtually flat, at elevations of 300 m a.s.l. (area A), 385 m a.s.l. (area B) and 320 m a.s.l. (area C). In order to compare the abundance patterns of chameleons in the three areas, a "time–constrained–searching" protocol was applied. To do this, each area was carefully explored for a total of 45 hours by two researchers, each moving independently, both by day (hrs 07.00–16.30 h) and at night (20.30–00.30 h). A balance was maintained between diurnal and nocturnal samplings at each area (50% of survey time for both diurnal and nocturnal searches). Roosting sites of each individual were noted on a scaled map of the study site.

Niche width and niche overlap

These variables were estimated by using SIMPSON's (1949) diversity index and PIANKA's (1986) symmetric equation index which ranges from 0 (no overlap) to 1 (total overlap). In both cases, the different Orders of–prey types were used as operative taxonomical units to calculate niche widths and overlaps.

Statistical analysis

An SPSS (version for Windows) computer package was used for all statistical analyses. All tests were two tailed, and alpha was set at 5%. Mean values +/- one standard deviation are provided.

Results

Species distribution and types of habitats

Five species of chameleons (*Rhampholeon spectrum, Chamaeleo cristatus, C. owenii, C. gracilis gracilis, C. wiedersheimi*) were found at the following sites:

Rhampholeon spectrum spectrum (Bucholz 1874)

Sites. Akwa–Ibom State: Eket (riverine forest along the River Kwa–Ibo (= Quo–Ibo); 04°50' N, 07°58' E), Stubbs Creek Forest Reserve (04°49' N, 08°00' E); Cross River State: Iko–Esai Forest (along the Rhoko River banks, 70 km N of Calabar; 05°28' N, 08°23' E), Osomba (05°21' N, 08°24' E), Oban (05°18' N, 08°34' E), Itu (05°14' N, 07°59' E), Ikpan Forest (30 km N of Calabar; 05°00'–05°15' N, 08°35'–08°45' E), Akpabouyoh (04°50' N, 08°22' E); Benue State: Ogoja (06°40' N, 08°47' E).

Habitat. The species is very common in wet forests with closed canopy (primary as well as mature secondary forests) either at sea level (e.g., Stubbs Creek Forest Reserve) or on hills (e.g., Oban). During daylight it was always observed on the ground, whereas it was observed on low bushes at night–time.

Rhampholeon sp.

Sites. Rivers State: Bonny Island (04°25' N, 07°15' E).

Habitat. Three undetermined *Rhampholeon* were found in the stomachs of two snakes (the colubrids *Rhamnophis aethiopissa* and *Hapsidophrys lineatus,* cf. LUISELLI et al., 2000, 2001) which were captured at the coastal barrier island forest of

Bonny island. These specimens were most probably *spectrum,* but as digestion was too advanced to positively identify species level, they have been placed separately from ascertained records of *R. spectrum* in this section.

Chamaeleo (Trioceros) cristatus Stutchbury, 1837

Sites. Edo State: Oredo Forest, 18 km SW of Benin City (06°03' N, 05°12' E); Bayelsa State: Sagbama (05°10' N, 06°05' E); Rivers State: Upper Orashi Forest Reserve (04°44' N, 07° 10' E); Akwa–Ibom State: Eket (riverine forest along the River Kwa-Ibo (= Quo–Ibo); 04°50' N, 07°58' E); Cross River State: Oban (05°18′ N, 08°34′ E); Osomba (05°21′ N, 08°24′ E); Ikpan Forest (30 km N of Calabar; 05°00'–05°15' N, 08°35'–08°45' E); Obudu Cattle Ranch (06°37' N, 08°46' E); Iko–Esai Forest (70 km N of Calabar; 05°28′ N, 08°23′ E); Okarara (04°50' N, 08°23' E); Ekang (05°23' N, 08°39' E).

Habitat. Uncommon. This species was seldom observed in mature forests and riparian forests, either at the sea level (e.g. in Niger Delta) or in hilly areas (e.g., Oban and Obudu). It was most frequently observed in low, thick, flowering bushes and, much more rarely, ground–dwelling in the leaf litter of the forest floor.

Chamaeleo (Trioceros) owenii Gray, 1831

Sites. Bayelsa State: Sagbama (05°10' N, 06°05' E), Yenagoa (05°12' N, 06°05' E), Taylor Creek Forest Reserve (05°16' N, 06°11' E); Rivers State: Upper Orashi Forest Reserve (04°44' N, 07°10' E), Otari–Abua (04°53' N, 06°41' E), Ahoada (05°04' N, 06°38' E), Buguma Creek (04°43' N, 06°50' E), Elem–Sangama (04°40' N, 06°39' E), Igbeta–Ewoama (04°34' N, 06°21' E), Degema (04°48' N, 06°48' E); Akwa–Ibom State: Eket (riverine forest along the River Kwa–Ibo (= Quo–Ibo); 04°50' N, 07°58' E); Cross River State: Calabar (04°47' N, 08°21' E), Ikpan Forest (30 km N of Calabar; 05°00'–05°15' N, 08°35'–08°45' E), Itu (05°14' N, 07°59' E).

Habitat. Our original records confirm its presence at several sites east of the River Niger, but we failed to find this species in any locality west of the course of the River Niger. Thus, based on our data, it is possible that *C. owenii* would be much rarer, if occurring at all, in the western forests of Nigeria, which is also in good agreement with the range of this species at the continental level (e.g., SCHMIDT, 1919). It also seems that *C. owenii* is found in lowland forests, along river banks, as well as in forest-plantation mosaics and in mature secondary forests. A specimen from the Upper Orashi Forest Reserve was eaten by the snake *Rhamnophis aethiopissa* (LUISELLI et al., 2000).

Chamaeleo wiedersheimi Nieden, 1910

Sites. Cross River State: Obudu Cattle Ranch (06°37' N, 08°46' E).

Habitat. Our single locality record was relative to two males observed at an open bush sub–montane area, at the border of a forested site.

Chamaeleo (Chamaeleo) gracilis gracilis Hallowell, 1842

Sites. Lagos State: Lekki (06°30' N, 04°08' E); Ondo State: Ashewele (06°48' N, 04°55' E), Ifetedo (07°27' N, 04°35' E); Delta State: Sapele (05°53' N, 05°42' E), Eku (riverine bushland along the River Benin; 05°49' N, 06°00' E); Edo State: Ologbo Game Reserve (05°55' N, 05°27' E), Oluku (05°59' N, 05°41' E); Bayelsa State: Sagbama (05°10' N, 06°05' E), Yenagoa (05°12' N, 06°05' E), Taylor Creek Forest Reserve (05°16' N, 06°11' E), Zarama–Epie (05°15' N, 06°08' E); Rivers State: Upper Orashi Forest Reserve (04°44' N, 07°10' E), Otari–Abua (04°53' N, 06°41' E), Ahoada (05°04' N, 06°38' E), Odiokwu (05°06' N, 06°37' E), Degema (04°48' N, 06°48' E), Bonny Island (04°25' N, 07°15' E), Peterside (04°29' N, 07°10' E); Anambra State: Onitscha (06°08' N, 06°46' E), Oguta (AGIP Oilfield forest; 05°58' N, 06°44' E); Abia State: Blue River banks (20 km N of Aba; 05°14' N, 07°13' E); Akwa–Ibom State: Eket (riverine forest along the River Kwa–Ibo (= Quo–Ibo); 04°50' N, 07°58' E), Ikot–Ekpene (05°12' N, 07°45' E), Uyo (05°09' N, 07°51′ E); Cross River State: Calabar (04°47' N, 08°21' E), Itu (05°14' N, 07°59' E), Akpabouyoh (04°50' N, 08°22' E), Akamkpa (05°20' N, 08°21' E).

Habitats. Our records came not only from mature lowland forests (e.g., Upper Orashi Forest Reserve), but also from altered forests (Abonnema), bushy spots surrounding farmlands and plantations (Uyo), and even derived savannas (Onitscha).

In general, chameleons of genus *Chamaeleo* were observed mainly along paths crossing humid secondary forests, where, usually, three vegetation strata were discernible, and with abundance of lianes and patches of undergrowth as general features. Counts of buttresses of commercially felled trees within five hectares from every spot of capture of chameleons were found to average $3.2 \pm 2.7 \times ha^{-1}$ (n = 46, with a range of 0 to $7 \times ha^{-1}$; e.g. $2 \times ha^{-1}$ at Oredo, $4 \times ha^{-1}$ at Zarama, and $5 \times ha^{-1}$ at Otari). Most forests where chameleons were observed had also been dissected by series of roads created for trucks to cart away the timber. The forest floor of all these sites had damp soils and considerable leaf litters in which eggs or juveniles can be hidden during the reproductive season (e.g., see BRANCH, 1988). Habitat alteration may be locally high: for instance, Oredo forest had a history of fire episodes from neighbouring farmlands. Chameleons were also found at seasonally flooded areas: for instance, Otari forests were subject to seasonal flood from River Nun and Sombreiro River.

Reproductive biology of females

All the species were oviparous. Females with shelled eggs were found in February (n = 1), May

(n = 4), and June (n = 1) in *R. spectrum*; in August (n =1) and September (n = 3) in *C. cristatus*; in July (n = 3), August (n = 1), and September (n = 1) in *C. owenii;* in August (n = 2), September (n = 3), December (n = 1), and January (n = 2) in *C. gracilis*. Thus, based on these preliminary data, it can be suggested that (i) female *R. spectrum* show a prolonged reproductive season with oviposition likely occurring during the late phase of the dry season; (ii) females of both *C. cristatus* and *C. owenii* have a shorter reproductive season with oviposition occurring most probably at the interphase between the end of the wet season and the onset of the dry season; (iii) female *C. gracilis* have at least two distinct oviposition periods, one at the interphase between the end of the wet season and the onset of the dry season, and one at the peak phase of the dry season. For this latter species, it could not be excluded that reproduction may in fact take place all the year round. Clutch size was invariably two eggs in six *R. spectrum*, and was respectively 11 and 14 eggs in two *C. cristatus,* 17, 15, 17, and 19 eggs in four *C. owenii,* and 19, 15, 21, 23, 16, and 14 in six *C. gracilis.*

Diet composition, food niche width and overlap of sympatric chameleons

A total of 116 chameleons were examined for food items in their faeces: 47 were *R. spectrum* (23♂, 24♀), 20 were *C. owenii* (14♂, 6♀), 15 were *C. cristatus* (9♂, 6♀), and 34 *C. gracilis* (16♂, 18♀). Results are shown in table 1. Diet composition of all the four species of chameleons consisted exclusively of invertebrates (arthropods), although a case of frog–eating was recorded in *C. cristatus.* In both *R. spectrum* and *C. gracilis*, females exhibited a wider food niche width than males (*R. spectrum,* ♂ B = 5.181, ♀ B = 7.782; differences significant at $P < 0.01$ at Mantel linear test; *C. gracilis,* ♂ B = 5.397, ♀ B = 10.020; $P < 0.00001$ at Mantel linear test) (fig. 1). Concerning *C. owenii,* the food niche width of males (B = 6.211) and females (B = 6.897) was very similar ($P > 0.7$, Mantel linear test), and the same was true for *C. cristatus* (♂ B = 5.618, ♀ B = 4.310; inter–sexual differences: P = 0.372 at Mantel linear test).

At a inter–specific level, the four species proved to be arranged along a continuum in terms of taxonomical food niche width, from the less generalist (*C. cristatus* B = 4.964, after pooling data for the two sexes) to the more generalist (*C. gracilis* B = 7.708), with the other two species at intermediate places of this continuum (*R. spectrum* B = 6.481, and *C. owenii* B = 6.554). Trophic niche overlap estimates (in terms of taxonomical dietary composition) among species indicated that the highest similarity occurred between *C. owenii* and *C. gracilis,* whereas a general low similarity occurred between *R. spectrum* and each of the three *Chamaeleo* species (table 2).

In terms of prey size, there were significant differences among the four species (fig. 2; Kruskal–Wallis ANOVA $F_{3,74}$ = 14.456, $P < 0.001$), and a Tukey's HSD post–hoc test indicated that *R. spectrum* preyed on significantly smaller preys than the other three species, and *C. cristatus* preyed on significantly larger preys than the other three species.

Daily and foraging patterns

As observed in other agamids from Africa (ANIBALDI et al., 1998), the chameleon's foraging strategy consisted of frequent predatory attempts, also at very short time intervals between two consecutive trials. *C. cristatus* ingested 276 insects of which 53.6% were taken between 09.00 and 11.00 h local time (fig. 3); *C. gracilis* ingested 247 insects with 53.4% at the activity peak of 09.00–11.00 a.m. (fig. 3), and *C. owenii* ingested 232 insects with 50.4% gulped at the same peak period (fig. 3). Daily patterns of foraging activity were not significantly different among individuals (at least $P > 0.572$ in all comparisons at Mann–Whitney U–test). The feeding strategy pattern exhibited by the three chameleon species indicates that, although these lizards begin hunting very early in the morning, fewer insects are caught at this time. As the sun rises, insect hunting is intensified and the highest number is caught between 09.00 and 11.00 h. During this period the lizards assumed their brightest colour as they also basked in the morning sun. By midday, the hunting propensity, and consequently the number of prey ingested, has dropped, probably as a result of the intense heat from the sun. By 15.00–17.00 h however, hunting ressumes, but not at the same rates as in the morning hours. They appear to be least successful towards dusk, and hunt more or less on the lower branches and undergrowth of the forest, as they return from the higher branches. No feeding attempt was recorded during the night hours, which suggests that Nigerian chameleons are strictly diurnal, at least as far as predatory activity is concerned.

Diet of thread–trailed chameleons (fig. 4) was composed of orthopterans, coleopterans and other pterygotes (winged insects), namely Odonata, Hemiptera and Lepidoptera. Green–type insects (grasshoppers, praying mantis and stick insects) are preferred in relation to brown or multicoloured forms (e.g., *Zonocerus variegatus*). Prey items identified included: *Gryllotalpa africana, Locusta migratoria migratorioides, Zonocerus variegatus, Podagrica sjostedti, Empoasca* sp., *Rhyncophorus phoenicis, Lagria villosa, Heteroligus* sp., *Diacrinia (Spilosoma) maculosa, Acraea eponina,* and *A. terpsicore.* Furthermore, all the species exhibit similar basking habits. At night and early morning hours, chameleons tended to rest climbed on the lower branches, approximately at 30–70 cm from

Table 1. Dietary data recorded from faecal pellets of four species of chameleons recorded at a study plot in southern Nigeria (Eket, Akwa–Ibom State). Dietary composition is assessed by: N. Numbers of items; (n). Numbers of pellets containing that prey type. In addition, one frog was eaten by a male *C. cristatus*. (See text for more details.)

Tabla 1. Datos sobre la dieta registrados a partir de bolas fecales de cuatro especies de camaleones registrados en el área de estudio en el sur de Nigeria (Eket, estado de Akwa–Obom). La composición de la dieta se calcula por: N. Número de unidades; (n). Número de bolas fecales conteniendo este tipo de presa. Además, una rana fue devorada por un macho de C. cristatus. *(Ver el texto para más detalles.)*

	R. spectrum		*C. owenii*		*C. crstatus*		*C. gracilis*	
Prey type	♂	♀	♂	♀	♂	♀	♂	♀
Miriapoda	1(1)	3(3)	1(1)	0	1(1)	0	1(1)	1(1)
Chilopoda	0	0	0	1(1)	0	0	1(1)	0
Isopoda	1(1)	4(3)	0	1(1)	0	0	1(1)	0
Scorpiones	0	1 (1)	0	0	0	1(1)	0	0
Araneae	6(6)	15(10)	2(2)	3(2)	1(1)	5(2)	4(4)	5(4)
Opilionidae	1(1)	2(2)	0	1(1)	0	0	1(1)	1(1)
Dermaptera	1(1)	5(4)	1(1)	1(1)	1(1)	0	0	1(1)
Isoptera	23(5)	12(4)	0	0	1(1)	0	0	5(1)
Orthoptera	10(6)	15(8)	21(7)	6(4)	10(5)	8(3)	18(9)	13(8)
Diptera	1(1)	2(2)	8(6)	1(1)	0	0	4(1)	4(2)
Hemiptera	3(2)	3(2)	4(3)	0	8(3)	7(2)	1(1)	8(5)
Lepidoptera								
adults	2(2)	2(2)	4(4)	0	0	0	2 (2)	7(4)
larvae	2(2)	5(5)	1(1)	0	0	0	2 (2)	6(4)
Odonata	0	0	3(2)	1(1)	12(6)	0	6 (4)	2(2)
Coleoptera (indet.)	0	3(2)	2(2)	1(1)	2(2)	0	1 (1)	3(3)
Carabidae	1(1)	0	0	0	0	0	0	0
Tenebrionide	0	1(1)	0	0	0	0	0	0
Formicoidea	7(3)	21(6)	11(1)	0	0	0	0	6(2)
Vespoidea	0	0	1(1)	1(1)	1(1)	0	1 (1)	1(1)
Apoidea	0	0	2(2)	0	1(1)	1 (1)	1 (1)	0
Blattoidea	0	0	3(3)	1(1)	1(1)	1 (1)	1 (1)	2(2)
Mantodea	0	0	2 (2)	4 (3)	3 (3)	2 (1)	3 (3)	3(3)

the ground. As the day advances, especially by midday, they tended to migrate towards the higher branches of the trees. Skin colour begins to change until it becomes fully brightened. After basking for about 15–25 minutes, they often withdraw and hide behind broad leaves, branches of epiphytes, or twigs, to avoid excessive heating. Hiding behind broad leaves is also the typical antipredatory behaviour exhibited by these animals during daylight hours.

Structure of the population and abundance

Densities were very similar at all study sites (table 3), but highest in the area of mature secondary forest (area A) and lowest in the area of bush–grassland mosaic (area C) (fig. 5). The species diversity was different in the three study areas, with four species (i.e. *C. owenii, C. cristatus, C. gracilis* and *R. spectrum*) recorded in the mature secondary forest (area A), two species

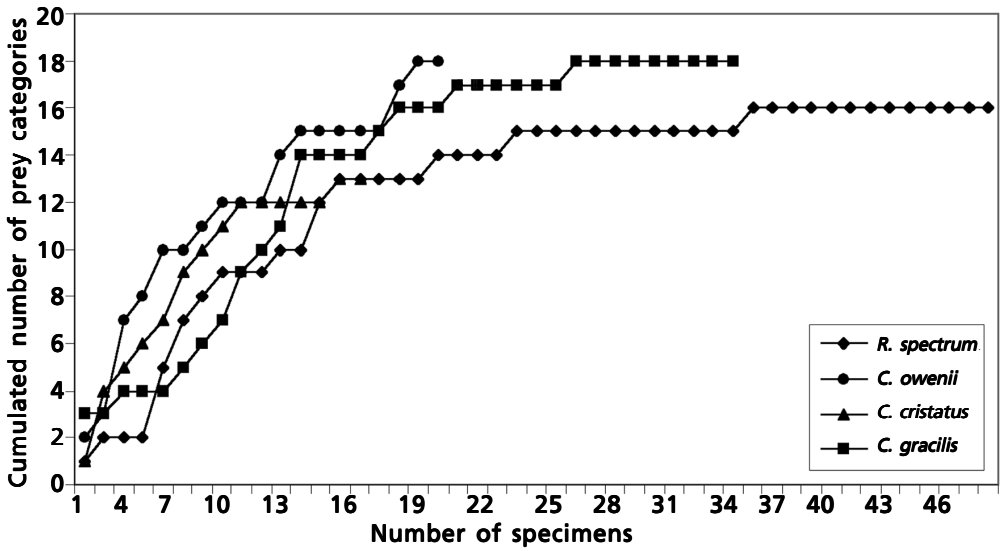

Fig. 1. Plot showing numbers of chameleons from which faeces were examined against cumulative number of prey categories identified from their faeces. Note that an obvious plateau phase was obtained for *Rhampholeon spectrum* and *Chamaeleo gracilis*, whereas the same curve stability was not reached in the other two species.

Fig. 1. Diagrama del número de camaleones cuyas heces se examinaron y según el número acumulado de categorías de presas identificadas a partir de las heces. Nótese que se obtuvo una meseta para Rhampholeon spectrum *y* Chamaeleo gracilis *mientras que la misma estabilidad de la curva no se encontró en las otras dos especies.*

Table 2. Food niche overlap estimates (calculated by PIANKA's (1986) symmetric equation) of taxonomical dietary composition among sympatric species of chameleons from the study area: Rs. *Rhampholeon spectrum*; Co. *Chamaeleo owenii*; Cc. *Chamaeleo cristatus*; Cg. *Chamaeleo gracilis*.

Tabla 2. Estimación del solapamiento del nicho alimentario (calculado mediante la ecuación simétrica de PIANKA (1986) de la composición alimentaria taxonómica entre especies simpátricas de camaleones del área de estudio: Rs. Rhampholeon spectrum; *Co.* Chamaeleo owenii; *Cc.* Chamaeleo cristatus; *Cg.* Chamaeleo gracilis.

	Rs	Co	Cc	Cg
Rs	–	0.513	0.583	0.596
Co	–	–	0.645	0.778
Cc	–	–	–	0.639
Cg	–	–	–	–

(i.e. *C. owenii* and *R. spectrum*) in the riparian woodland (area B), and one species (i.e. *C. gracilis*) in the bush–grassland mosaic (area C).

Concerning area A where logging was undertaken, this manipulation did not substantially reduce the abundance of chameleons (fig. 5), but had dramatic effects on the specific diversity. In fact, three of the four species became extinct after the changes on the initial habitat (i.e. *C. owenii, C. cristatus,* and *R. spectrum*), while one substantially increased its abundance (i.e. *C. gracilis*) (fig. 5).

Discussion

Distribution and habitat

All the species of chameleons found in our study had been already reported for Nigeria (e.g., TALBOT, 1912; PASQUAL, 1937; ROMER, 1953; DUNGER, 1967a, 1967b; BUTLER, 1986; REID, 1986; AKANI et al., 1999), but information was in most cases anecdotal. Other species which are known to occur in western Cameroon and south–eastern Nigeria (cf. BÖHME, 1975; JOGER, 1982; KLAVER & BÖHME, 1997; LEBRETON, 1999; WILD, 1993, 1994) were not observed on any occasion during the present study.

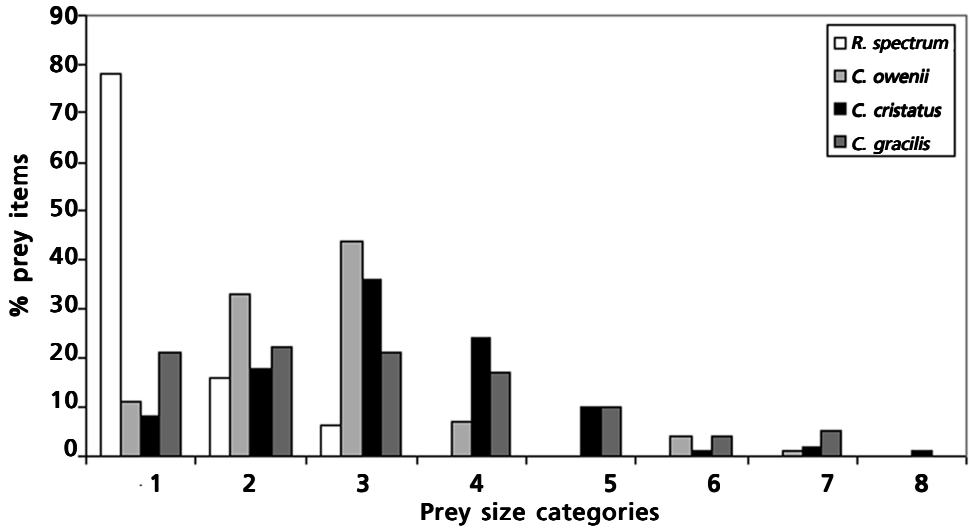

Fig. 2. Prey size distributions for the four species of sympatric chameleons studied in this paper, inferred from faecal pellets. Symbols for prey size categories: 1. 0–3 mm; 2. 3–6 mm; 3. 6–9 mm; 4. 9–12 mm; 5. 12–15 mm; 6. 15–18 mm; 7. 18–21mm; 8. > 21 mm.

Fig. 2. Distribución del tamaño de las presas de cuatro especies simpátricas de camaleones estudiadas en este trabajo, obtenidas a partir de las bolas fecales. Símbolos para cada categoría de presa: 1. 0–3 mm; 2. 3–6 mm; 3. 6–9 mm; 4. 9–12 mm; 5. 12–15 mm; 6. 15–18 mm; 7. 18–21mm; 8. > 21 mm.

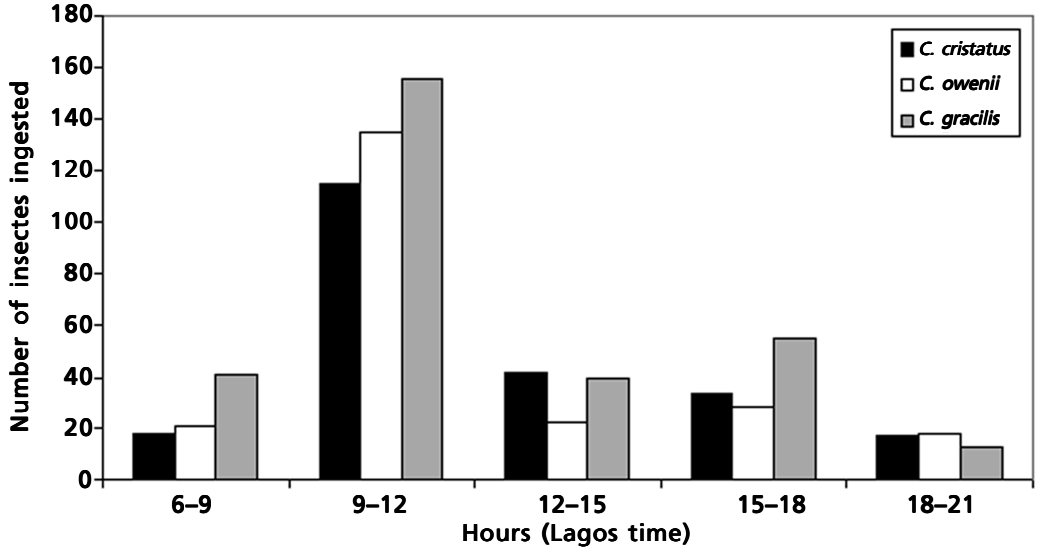

Fig. 3. Diet feeding patterns of three "thread-trailed" chameleons at the Niger Delta (n = 1 for all species).

Fig. 3. Patrones alimentarios de la dieta de tres camaleones "thread–trailed" en el delta del Níger (n = 1 para todas las especies).

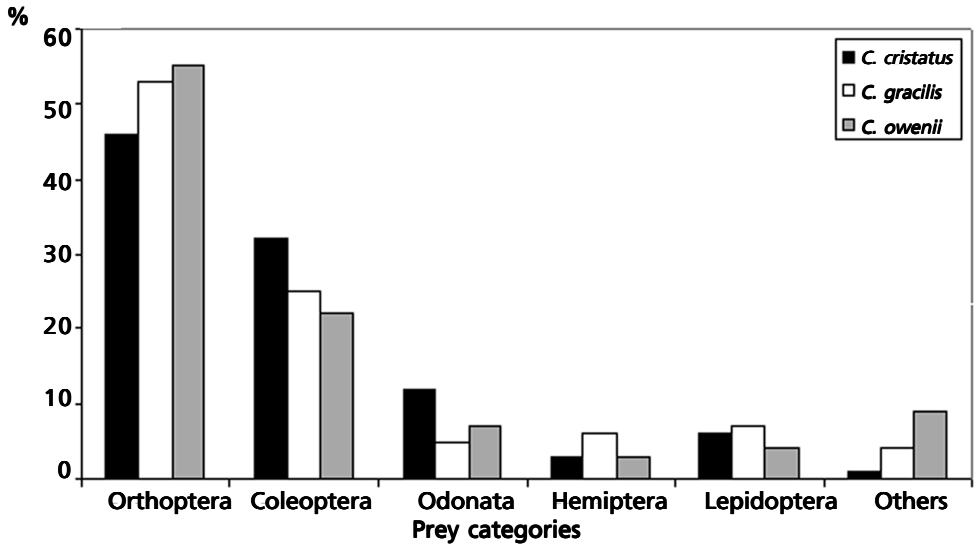

Fig. 4. Dietary spectrum of three specimens of chameleons at the Niger Delta, based on "thread–trailing" continuous monitoring.

Fig. 4. Espectro alimentario de tres especímenes de camaleones en el delta del Níger, basada en controles continuos en "thread–trailing".

Rhampholeon spectrum

The distribution is well known in the extreme south–eastern region of Nigeria (e.g., TALBOT, 1912; REID, 1986), *R. spectrum* is apparently more common in forests east of the Cross River, although the records from Eket and Stubbs Creek Forest Reserve demonstrate it is not a species for which the Cross River course may represent a geographical barrier (as is the case for numerous other small vertebrates, e.g. see KINGDON, 1990). It is described as euryzonal, and abundant in premontane, submontane, and montane forests (500–1,700 m a.s.l.) of western Cameroon, but much more rare in lowland forest (LAWSON, 1993; WILD, 1994). It is unknown whether the same distributional pattern may occur also in Nigeria, but according to several experienced hunters interviewed, this species is very common in the montane forests of the northern Cross River State. Its presence was reportedly influenced by other ecological factors, i.e. co–occurrence of food competitors: WILD (1994) claimed that it may suffer from competition with forest toads (*Bufo camerunensis*), which may have a very similar dietary spectrum.

Chamaeleo cristatus

Well known to occur in south–eastern Nigeria, this species was captured probably around Oban (Cross River State) by TALBOT (1912), and much more recently both east (at Osomba, see REID, 1986), and west (at Eket, see AKANI et al., 1999) of Cross River. Original records of this study also indicate that it is also found in the western portion of the Nigerian forest zone (i.e. at Oredo, western axis of the Niger Delta). Altitude is likely not an important factor in the distribution of *C. cristatus*, which was in fact observed both in lowland moist forests and in hilly–montane sites. However, micro–habitat characteristics seem to be important, as both our observations and those of WILD (1994) indicate a strong preference for specific micro–habitats (low, thick, flowering bushes in our case, and "the shrub layer in primary forest" in Wild's case), and thus a restricted habitat selection.

Chamaeleo owenii

Its presence in the forests of south–eastern Nigeria is well documented (see ROMER, 1953, for Port Harcourt (Rivers State, eastern axis of the Niger Delta, and AKANI et al., 1999, for additional localities of the eastern Niger Delta). Records given here suggest that it is found in lowland moist forests and in forest–plantation mosaics. SCHMIDT (1919) reported similar habitats for conspecifics from the former Belgian Congo.

Chamaeleo wiedersheimi

The less common of the five species of chameleons observed in the present study in

Table 3. Numbers of chameleons observed in three study plots in southern Nigeria.

Tabla 3. Número de camaleones observados en tres áreas estudiadas en el sur de Nigeria.

	Area A			
	Before timbering	After timbering	Area B	Area C
Chamaeleo owenii	4(3♂ 1♀)	0	3♂	0
Chamaeleo cristatus	1♂	0	0	0
Chamaeleo gracilis	1♀	7(3♂ 4♀)	0	4♂
Rhampholeon spectrum	2(1♂ 1♀)	0	4(2♂ 2♀)	0

southern Nigeria. Their distribution is linked specifically to hilly and montane sites, and montane savannas / grasslands in Cameroon (WILD, 1993; JOGER, 1981; DUNGER, 1967b). According to WILD (1994), *C. wiedersheimi* is restricted to the shrub layer in primary forest, the same as *C. cristatus* and *Chamaeleo camerunensis* Müller, 1909.

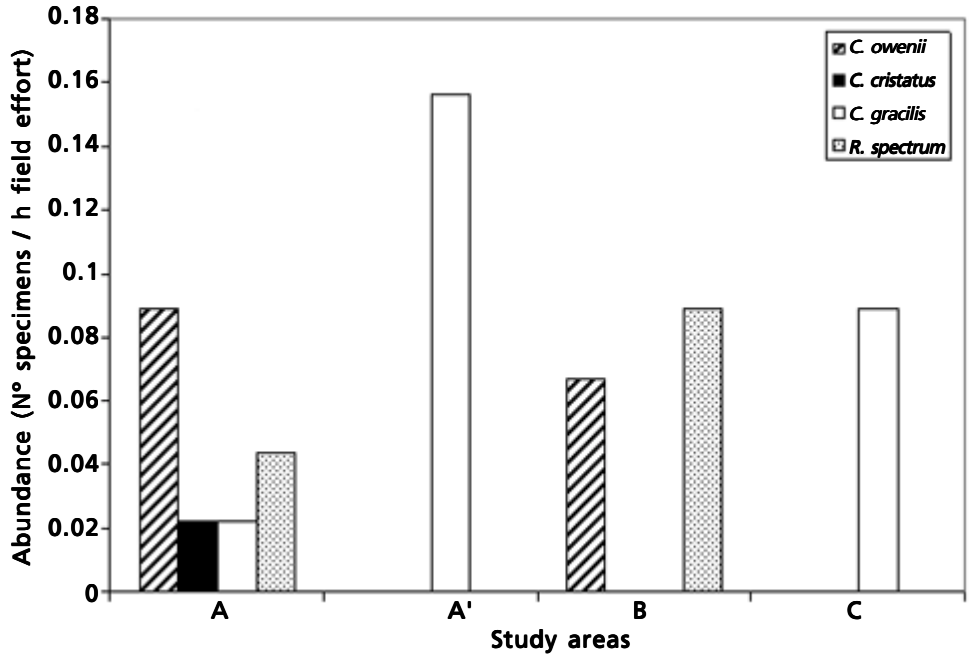

Fig. 5. Abundance of chameleons (number of specimens observed in relation to the number of hours spent in the field) in three study areas of south–easthern Nigeria. Study areas: A. Mature secondary forest before treatment; A'. Mature secondary forest after treatment; B. Riparian woodland; C. Bush–grasland mosaic.

Fig. 5. Abundancia de camaleones (número de especímenes observados con relación al número de horas empleadas en el campo) en tres áreas de estudio del sudeste de Nigeria. Áreas de estudio: A. Bosque secundario maduro antes de ser sometido a explotación; A'. Bosque secundario maduro después de ser sometido a explotación; B. Bosque maduro; C. Mosaico de bosque y pradera.

Table 4. Data on chameleon trade in local markets of the Niger Delta Basin during the year, 2000: N. Number of chameleons on display; P. Unit selling price (in "Nairas"); $. US dollar equivalent (all of them used for traditional medicine).

Tabla 4. Datos sobre el comercio en mercados locales de la cuenca del delta del Níger a lo largo del año 2000: N. Número de camaleones observados; P. Precio por unidad (en "Nairas"); $. Equivalente en dólares americanos (todos ellos utilizados en la medicina tradicional).

Date	Location of market	N	Suppliers	P	($)
17 V 2000	Mile 1, market P. H.	1	Hunter from Bayelsa	2,500	23.0
19 V 2000	Mile 3, market P. H.	3	Hunters from Omoku and Biseni	2,700	25.0
4 VII 2000	Otari	4	Farmers / hunters from Ogbema Abua	3,000	27.0
23 VIII 2000	Yenagoa	2	Farmers / hunters from Zarana Epie	2,800	26.5
27 X 2000	Benin City	6	Hunters from Mosoga, Oredo and Aghara	3,200	29.0
Total		16			

Chamaeleo gracilis

This a typical and common forest species of south–eastern Nigeria (e.g., DUNGER, 1967a; BUTLER, 1986; AKANI et al., 1999), but is certainly found also in the savannas (e.g., see DUNGER, 1967b). As in other countries (e.g., in Cameroon and Liberia, see SCHMIDT, 1919; WITTE, 1965), it is a habitat generalist.

Reproductive biology

Data on reproduction timing of female *R. spectrum* are fully consistent with data from conspecifics at Mt. Kupe (western Cameroon, cf. WILD, 1994), and our data on *C. cristatus* are also in agreement with the single record available on the reproduction of a Nigerian conspecific (REID, 1986). DUNGER (1967b) recorded seven newly–hatched *C. gracilis* on 20th May on a low bush in Jos (09°55' N, 08°53' E), and thus suggested that hatching occurs during the early rains. It is quite consistent with a period of oviposition at the peak of the dry season, as indicated by the original data presented in this study. Concerning *R. spectrum,* an invariable clutch size of two eggs was also detected by WILD (1994) in western Cameroon, which suggests that it is a general pattern for this species (but a clutch size of 2–5 eggs is reported for this species by KAIWI (2000), 1–3 eggs in the closely related *Rhampholeon boulengeri* from the former Belgian Congo [SCHMIDT, 1919], and 3 eggs in a Tanzanian *Rhampholeon uluguruensis* [TILBURY & EMMRICH, 1996]). Clutch sizes of 15 and 17 eggs were reported in two *C. owenii* from the former Belgian Congo (SCHMIDT, 1919), which is very consistent with the original data reported in this study. However, clutch sizes of free–ranging females from Nigeria were considerably smaller than those reported in the layman's literature for either *C. cristatus* (16–37 eggs, see KAIWI, 2000) or *C. gracilis* (20–40 eggs, see KAIWI, 2000), and also a free–ranging female *C. gracilis* from Belgian Congo had 60 eggs (SCHMIDT, 1919).

Feeding ecology

The four studied chameleon species of tropical Nigeria fed almost exclusively upon arthropods. It is consistent with data on *R. spectrum* from south–eastern Nigeria (REID, 1986) and Cameroon (WILD, 1994), with data on *C. owenii* from the former Belgian Congo (SCHMIDT, 1919), and in general with dietary data on chameleons elsewhere (e.g., PLEGUEZUELOS et al., 1999). It is noteworthy however, that a single case of vertebrate–eating (a froglet) by a *C. cristatus* was recorded. Although this predation event appears exceptionally unusual in the wild (at least considering data presented in table 1), Nigerian *C. cristatus* are known to readily eat frogs and newly metamorphosed toads in captivity (REID, 1986), which suggests that they have a natural "attitude" for preying upon small amphibians. In any case, it is certainly premature to stress that amphibian–eating is a trophic niche difference between *C. cristatus* and the other three sympatric species.

In the two better studied species (i.e. *R. spectrum* and *C. gracilis*), there were significant inter–sexual differences in dietary habits, with the females exhibiting a wider food niche width than males. The reasons for this inter–sexual difference are unknown, and are likely not correlated with any sexual size dimorphism (SSD) as SSD is certainly not big enough to justify such an assumption in both

species (WILD, 1994). At the inter–specific level, the apparent continuum of dietary specialisation from the less generalist species (*C. cristatus*) to the more generalist species (*C. gracilis*) may suggest that a true phenomenon of food resource partitioning occurs between sympatric forest chameleons. In this regard, an obvious pattern of resource partitioning among species was also seen with regard to prey size, with *R. spectrum* and *C. cristatus* at the two extremes of the continuum, and *C. gracilis* being the most generalist species. In general terms, *C. gracilis* appears thus not only the most generalist species in terms of habitat, but also in terms of prey type and prey size. The lesser interspecific overlap was observed between *R. spectrum* and *C. owenii.* It is likely that it depended on the combined effect of size and habits (*R. spectrum* is mostly terrestrial–dwelling, whereas *C. owenii* is mainly arboreal).

Despite these interspecific differences found in diet composition, our data should be considered as a "snapshot" of the chameleon diet. A considerably higher variation is likely. Taking into account that the diet composition of thread–trailed specimens and the composition of faeces was very similar, it is concluded that "thread–trailing" is a very good experimental procedure to study chameleon ecology in sites where these lizards are rare or endangered, and when it is particularly difficult to establish an experimental protocol involving the capture of many specimens.

Structure of the population and abundance

Density of chameleons in the forest habitats of southern Nigeria was low and certainly much less than that observed in other African regions (e.g. Madagascar, cf. KAUFFMANN et al., 1997). Moreover, the species diversity at single sites clearly appears much less than that observed in the forests of the adjacent Cameroon (WILD, 1993, 1994). For instance, *R. spectrum* sympatric was observed in this study with up to three *Chamaeleo* species in southern Nigeria, whereas WILD (1994) found up to ten different species in Cameroon forests. However, the diversity of sympatric chameleon species of the Biafran forests is certainly influenced by the the relative elevation: WILD (1994) found seven sympatric species of *Chamaeleo* in montane areas around Mt. Manenguba, but only four species in lowland Cameroon forests.

Despite the differences in the structure of the vegetation among sites, the overall abundance of chameleons was similar, although densities were higher at mature secondary forests. After logging, the overall abundance of chameleons declined only slightly, whereas the species diversity declined drastically. These findings support the hypothesis that the population of free–ranging chameleons declines in rainforest habitats where rapid changes in the environment are occurring.

Implications for conservation

Results of this study provide new insights with important implications for the conservation of chameleons in Nigeria (and probably, West Central Africa). All chameleons in the Niger Delta and in south–eastern Nigeria inhabit very fragile ecosystems such as mature secondary forests and riparian forests. Human alteration of the remnant forest is likely to further destroy this habitat type in the next decades (OLAJIDE & ENIANG, 2000), especially due to the continuing exploration of unaltered biota for oil industry development, which is the main economic income for the country. In addition, hundreds of *C. gracilis* are captured and later desecated every year from the forests around Lagos and Ibadan, and sent to public markets in Calabar, Uyo (and probably other towns) where they are traded for local medicine or juju practices at a low price (Naira 150–400, i.e. approximately 2–4 US dollars, on March 2001) (Akani et al., unpublished). Both factors are likely to have a tremendous influence on species conservation in the near future.

Species diversity changed dramatically in one of our study sites after human impact. Moreover, the only surviving species (*C. gracilis*, i.e. the ecologically most versatile species of the forest region of Nigeria), which was rare before timbering, became much more common (i.e. largely dominant in the chameleon community) after logging. The present results fully agree those of GRAY (1989) who suggested that rare and more specialised species tend to disappear with habitat loss, whereas moderately common species (more habitat generalist) would increase in abundance. Accordingly, *C. owenii, C. cristatus,* and *R. spectrum* may be dramatically affected by habitat loss and forest fragmentation, whereas *C. gracilis* might even benefit from this situation, possibly also because of less inter–specific competition with the other chameleon species.

The broad similarity in activity patterns and feeding habits among two "fragile" species (*C. owenii* and *C. cristatus*) versus one "versatile" species (*C. gracilis*) indicate that these life–history attributes cannot influence differently the species–specific persistence in altered habitats, and so it is likely that prey resource availability does not play an important role in determining the scarcity of some particular species in altered habitats. The rarity of chameleons in the study area is attributed to: 1. Habitat destruction / modification through lumbering and cultivation; 2. Local fires in bush areas, especially at the end of the dry season (March–April), for agricultural purposes; 3. Illegal trade because of the great demand for chameleons following the increasing market values (N 2,500–N3,000; approx. 23–29 US dollar (see table 4); 4. Capture and desiccation for traditional medicinal purposes. The authors wish to encourage State and Local Governments to establish some forest reserves specifically

targeted at chameleon preservation, and enact and adequately enforce laws to persecute the handling or trading of chameleons.

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