# Notes on the natural history of the eublepharid Gecko *Hemitheconyx* caudicinctus in northwestern Ghana

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HEMITHECONYX is an African genus of relatively large terrestrial eublepharid geckoes. Two species are known. Hemitheconyx taylori (Fig. 1) has a small range in northern Somalia and eastern Ethiopia (Largen & Spawls, 2006). Hemitheconyx caudicinctus, the African Fat-tailed Gecko, occurs in the West African savanna. Loveridge (1947) gives its range as 'Nigeria west to Senegal' but it also occurs further east, in Cameroon. There is a specimen in the British Museum from the Adamoua massif in west-central Cameroon and Ineich (1993) lists a specimen from Garoua in the north of that country (shown as a single locality in Chirio & LeBreton [2007]).

These two clearly defined and morphologically similar species must have a recent common ancestor. So it is of zoogeographical interest that they are apparently separated by a gap of over 3000 km and a mountain range (the north-western Ethiopian plateau) largely over 2000 m high and 50-75 million years old (Mohr, 1971). *H. caudicinctus* is a large, attractive and docile lizard that is popular in the pet trade (Bartlett & Bartlett, 1999). Although it is sometimes bred in captivity, significantly large numbers are also taken from the wild. The impact of such collecting is not assessed and there are no CITES quotas (CITES, 2008).

Most of the literature on *H. caudicinctus* consists of descriptions of specimens collected and capture localities (e.g. Papenfuss, 1969; Böhme, 1975, 1978; Miles *et al.*, 1978; Bauer *et al.*, 2006; Leache *et al.*, 2006). Dunger (1968) provides some natural history notes and there are a number of studies of captive specimens, (Werner, 1972; Rösler, 1981; 1983; 1984; Kugler & Kugler, 1984).

The following natural history notes arise from a study I made of the herpetology of the 'Wa' area, northwest Ghana, between September 1979 and September 1981.

# **CLIMATE & STUDY SITES**

Wa town is the regional capital of northwest Ghana, at longitude 02° 30' W, latitude 10° 03' N. I lived at Wa Secondary School, a government school 1.5 km southeast of the town. The vegetation of the Wa area is wooded savanna, usually described as Guinea Savanna Woodland (Survey of Ghana, 1969). White (1983) refers to it as Sudano-Zambezian savanna. Canopy cover in undisturbed Guinea Savanna is around 100% (Baker, 1962) but in the study area (see Fig. 2) the canopy was extensively reduced by exploitative agriculture to less than 2%, although a few undisturbed patches remained. The area is subjected to periodic burning in the dry season.

The only natural permanent water is the Black Volta River, 20 km west of Wa town. The topography of northwestern Ghana is a generally subdued pediplain. In the study area the altitude ranged from 320 to 370 m. About 1% of the land surface is covered with sheet outcrops or low, heavily eroded inselbergs of granodiorite, manifestation of an ancient Precambrian crystalline basement.

There is a single rainy season, with about 1000 mm of rain falling mostly between April and September. January and February are the driest months; at this time the Harmattan (a cold wind from the Sahara) blows. Daily temperatures range from 22 to 39 °C in the rainy season and 16 to 40 °C in the dry season (Wills, 1962).

# MATERIALS AND METHODS

Twenty-four specimens of *H. caudicinctus* were collected during the two years of the study. Twenty-one were found by driving roads at night using a motorcycle, two were found by walking at night and one was dug out of a burrow by day. An average of twelve hours per month were spent night hunting by motorcycle and at least four



Figure 1. Hemitheconyx taylori from Dagah Bur, Ethiopia.

Figure 2. Guinea Savanna woodland, Wa.

hours per month were spent collecting on foot with a torch. The only exception were in August and September 1980 when I was absent from the area. Time and distance covered was recorded after every hunt. When specimens were captured the air temperature at one metre above the ground was usually recorded. In some cases the lizard's body temperature and the ground temperature at 1 cm depth were also recorded using a cloacal thermometer. Relative humidity was also recorded using either a whirling or a hair hygrometer. Snout-vent length (SVL), total length (TL) and mass (g) were also recorded for most specimens within a day of capture. Several specimens were maintained alive in captivity for periods up to eight months. Of the 24 captures, eight were preserved; four specimens were donated to the California Academy of Sciences, three to the Natural History Museum (London) and one to the Natural History Museum of Zimbabwe at Bulawayo. Four specimens died in captivity and were not preserved; twelve specimens were released after having a toe clipped. No recaptures were made.

# RESULTS

# **Activty Patterns**

*H. caudicinctus* is nocturnal. Twenty-three captures were made in 379 hrs of night hunting; this is 16.5 hrs per specimen, (0.061 specimens per hour). The data indicate that *H. caudicinctus* becomes active about an hour after sunset; sunset times in Wa

varied from 17.34 hrs in November to 18.30 hrs in June. The earliest night capture was at 19.05 hrs on the 12th February 1981, fifty-five minutes after sundown. Activity continues to midnight at least. No captures were made after 23.55 hrs, although 27 hours were spent hunting after midnight. No specimens were observed above ground during daylight hours, although another species of African eublepharid, *Holodactylus africanus*, is known to show diurnal activity (Drewes, 1971).

There is some evidence that *H. caudicinctus* is more active during the rainy season than during the dry. Taking the rainy season to be those months when the median rainfall is over 50 mm, the rainy season in Wa is from April to October inclusive, dry season from November to March (Wills, 1962). While I was in Wa the only exceptions to this were a dry October 1979 (46 mm rain) and a wet March 1981, (91 mm rain).

Capture rates for the dry season months during this study were 0.6 per month (6 specimens, 10 months); for the wet season months 1.5 per month (18 specimens, 12 months) (Table 1). Nineteen out of 23 (82%) of the night captures were made either on the night following an afternoon rainstorm, or on the following night (when the humidity ranged from 60 to 95%), although out of a total of 360 night hunts, only 161 (44.6%) were on such nights. Rainfall and high humidity appear to stimulate *H. caudicinctus* to activity.

Nevertheless, this gecko is also active during very dry months. Two specimens were collected in

## **Capture Rates**

Time	17.00-17.59	18.00-18.59	19.00-19.59	20.00-20.59	21.00-21.59	22.00-22.59	23.00-23.59	24.00-06.00
No. Capt.	0	0	8	4	4	5	2	0
Hrs hunte	e <b>d</b> 19	31	49	88	76	56	33	27
Capt. rate	es/hr 0	0	0.163	0.045	0.053	0.089	0.061	0

Table 1. Hemitheconyx caudicinctus capture rates over 24 hr.

February 1981; both were active at night. There was no measurable rainfall that month or the month before. Relative humidity for the specimen collected on 12th February was 29%, and 17% for the one taken on the 27th February; no traceable rain had fallen in 62 and 77 days respectively prior to the date of capture. Joger (1982) reports collecting 3 specimens in January, which is generally the driest month in West Africa. Böhme (1978) suggested that *H. caudicinctus* aestivates during the dry season, relying upon the fat reserves in its tail.

In Wa, nocturnal snake activity was greatly reduced during the dry season. Significant activity during this time was noted for only two species (*Echis ocellatus* and *Telescopus variegatus*), out of the 37 snake species recorded in the area (Spawls, 1992). These two species are essentially inhabitants of the Sahel, which has lower humidity and night

time temperatures than the moister woodland further south.

Table 2 shows temperature and relative humidity data for the 20 captures where at least one temperature value (air, body, substrate) was recorded. The mean midnight temperature at Wa was 25.8 °C. Fifteen captures were made at air temperatures above this. Decline in temperature may explain the apparent cessation of activity after midnight. However, H. caudicinctus can tolerate lower temperatures. Four individuals were taken when the air temperature was below 25.8 °C, all on rainy season nights while feeding on emerging alate termites. In all cases (where recorded) the body temperature was found to lie between the air temperature and the substrate temperature, as is usual for nocturnal reptiles (Pianka, 1977). Werner (1976) notes that, in terms of temperature sensitivity, the optimal range for this species is

Capture Date	Capture Time	Air Temp. °C	Body Temp. °C	Substrate Temp. °C	RH %
04 02 1980	21.30 hrs	28.0	-	-	23
12 04 1980	23.55 hrs	30.1	-	31.1	54
15 04 1980	20.30 hrs	31.6	-	-	56
15 04 1980	21.50 hrs	30.0	-	-	65
08 11 1980	19.00 hrs	28.9	29.2	29.9	64
12 02 1981	19.05 hrs	30.6	31.1	31.8	29
27 02 1981	23.05 hrs	29.8	-	-	17
06 03 1981	19.45 hrs	27.9	28.2	-	64
25 03 1981	22.04 hrs	31.7	-	-	41
27 03 1981	21.10 hrs	24.2	26.6	27.1	75
28 03 1981	22.15 hrs	28.8	-	-	60
28 03 1981	22.25 hrs	28.7	28.8	29.6	60
11 05 1981	19.20 hrs	27.5	28.6	30.1	73
27 05 1981	19.55 hrs	22.2	24.1	-	95
28 05 1981	19.30 hrs	30.3	32.2	-	63
19 06 1981	20.10 hrs	27.2	28.0	29.1	75
02 07 1981	21.20 hrs	24.4	-	-	92
14 07 1981	19.48 hrs	27.6	29.1	30.0	69
17 07 1981	20.15 hrs	22.5	24.6	25.1	93
21 07 1981	19.40 hrs	26.3	-	-	76

Table 2. Hemitheconyx caudicinctus ambient air temperature, body temperature, and substratre temperature.

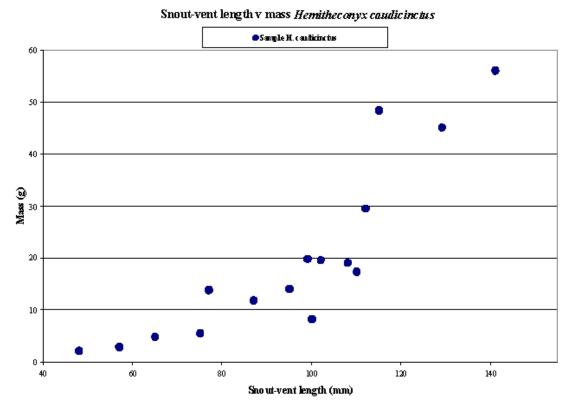


Figure 3. A sample of Meristic data for 15 collected *Hemitheconyx caudicintus*.

28-33 °C; between dusk and midnight the temperature of most nights in Wa was between 26 and 33 °C, with the exception of nights at the end of the rainy season (Spawls, 1992). The individual captured on the night of 17th July 1981 attempted to escape into a hole; Joger (1981) has recorded similar evasion behaviour. The burrows may also be used as heat sources/buffers. Earth temperatures at 30 cm depth at Wa weather station ranged between 27.9 and 33.3 °C over the two years of this study.

# **Meristic Data**

Fig. 3 shows mass against snout-vent length for 15 of the specimens collected. The largest individual was 196 (141 + 55) mm in length; mass was 56.2 g. Loveridge (1947) and Dunger (1968) note larger individuals, of 210 (130+80) and 198 (155+43) mm respectively. The smallest Wa individual was 60 (48+12) mm; tail truncated, mass 2.13 g, captured in late March 1981. This was probably a hatchling, as captive hatchlings were recorded

varying from 1.2-2.5 g and 6.3 to 7.0 total length (Kugler & Kugler, 1984). Eight of the fifteen individuals measured had their original tails; these could be identified as being thin, uniformly banded, 35-43% of total length. Seven individuals had regenerated tails, which were stumpy, grossly swollen, colours discontinuous and less than 30% of total length.

#### Colour

There is some variation in colour amongst the Wa *H. caudicinctus* (Fig. 4). All specimens had a dark patch stretching from the orbit to the nape of the neck and two dark brown or black bars across the dorsal surface. Between these patches, skin colour varied from deep red brown to bright orange, juveniles had a tendency to be orange. The tail was banded in orange, white, black and brown; some juveniles had blue bands. Seven of the 24 individuals had a prominent white dorsal stripe from between the eyes to the base of the tail (see Front Cover, this edtion). One juvenile had a

poorly developed stripe (Fig. 5); sixteen had no stripe. Dunger (1968) states that only males have this stripe, but the gravid female captured was striped. Subsequent examination of specimens in the Natural History Museum (London) indicated that either sex may be striped, or unstriped.

#### **Habitat Selection**

Twenty-three captures were made in flat or gently sloping open savanna; the local habitat. Twenty captures were at distances greater than 500 m from the nearest rock outcroppings; four were more than 5 km from the nearest outcroppings. One specimen was found within the confines of a sheet rock outcrop, but was on soil, not on the actual rock surface. These data conflict with Loveridge's (1947) description of the habitat as 'between



**Figure 4.** Hemitheconyx caudicinctus exhibiting dorsal colour variation.

inside the branch to a height of about 30 cm. The female captured in daytime was dug out of an underground chamber of approximately 20 cm in diameter, at the end of a rodent burrow 1.3 m in length, and with a maximum depth of 60 cm. The final 40 cm of the burrow ascended into the chamber, the top of which was 35 cm below the surface and contained dried grass and rodent fur. In the study area, no *H. caudicinctus* were ever found under rocks or any other ground cover (logs, vegetation heaps, building debris) although a large number of such objects (always over 200 per month, often many more) were routinely turned

rocks', and Dunger's (1968) statement that they are found 'in or near rocks'. Böhme (1975) mentions two specimens found at a fissured stone wall. An average of two hours per week, over 150 hours total, were spent on the granodiorite outcroppings at night, studying a colony of Ptyodactylus ragazzi, but no *H. caudicinctus* were seen on the rocks. They seem to prefer open savanna and are terrestrial, as are other eublepharid geckoes. Rösler (1984) examined the location of H. caudicinctus during unhurried movement, noting that the legs are greatly extended and the ventral surface touches the ground. He concluded that this gecko is strongly adapted to a terrestrial way of life. This is supported by my field observations in Wa, although two captive specimens utilised a hollow branch placed vertically in the cage as a refuge, ascending



**Figure 5.** *H. caudicinctus* juvenile exhibiting prominent white dorsal stripe.

during collecting activities. It would seem that the Wa specimens of *H. caudicinctus* shelter in holes, as does *H. taylori* (Largen & Spawls, 2006).

# **Breeding & Courtship**

Rösler (1983) states that during courtship *H. caudicinctus* uses mostly visual cues, and believes this is characteristic of diurnal species, which initially seems odd considering that in Wa the species appears to be totally nocturnal. Rösler (1983) documents three aspects of courtship behaviour; tail waving, vibration of the body and vibration of the tail. However, the latter two are

presumably audible. Werner (1976) noted that, out of 14 taxa of gecko examined, including four eublepharids, *H. caudicinctus* had the most sensitive hearing.

A female weighing 10.8 g, length 126 (100 + 26) mm, captured on 28th March 1981 laid one egg on 16th April 1981. The egg was 2.3 x 1.2 cm; mass 1.8 g. The eggshell was soft and pliable, as is typical for eublepharid geckoes. The egg was incubated, but failed to hatch. Werner (1972) records an egg size of 2.7 x 1.3 cm. Captive specimens laid five batches of two eggs each in an interval of approximately 6 months (Kugler & Kugler, 1984). Castellenos (2008) states that up to eight clutches a year, of 1 or 2 eggs, may be laid by captive specimens. The specimen donated to the NMZB, collected on 25th March 1981, contained 2 unshelled ova (D. G. Broadley, pers. comm.). Joger (1981) states that the maturation of the eggs takes place during the later half of the dry season (i.e. January to March) and this is supported by Rösler's (1983) records, but the Wa hatchling was captured in late March. Werner's (1972) specimen had laid shortly before 27th December and Kugler & Kugler's (1984) specimens laid their five clutches between April and July. In captivity, H. caudicinctus digs a small hole to deposit its eggs (Rösler, 1983). Egg-laying behaviour in wild specimens is apparently not documented.

# Population Density, Ecology & Diet

In light of the number of specimens collected for the pet trade, some values of the population density of *H. caudicinctus* may be useful. No intensive searching specifically for this species was carried out; all captures were made during general herpetological searching. However, twenty-three of the specimens found were within an area of 9 km<sup>2</sup>, giving a density of 2.5 per km<sup>2</sup>. Seventeen of these were within an area of 2.2 km<sup>2</sup>, and eleven specimens were found in an area of 1 km<sup>2</sup>. This is liable to be an underestimate of the true population density.

Twenty species of lizard were recorded in the Wa area during the survey. Of these, four were geckoes; *H. caudicinctus*, *P. ragazzi*, *Hemidactylus angulatus* and *Tarentola ephippiata*. *P. ragazzi* was found only on sheet rock and inselbergs, it is entirely rupicolous. Only a single specimen of

Tarentola ephippiata was found, it was on a road at night, but this species is normally arboreal, showing a predilection for Fig trees (Dunger, 1968). H. angulatus was common throughout the study area, active at similar times and was also found on the ground. Niche overlap with H. caudicinctus is unlikely, however. H. angulatus is a faster-moving, much smaller species, (the largest individual had a snout-vent length 60 mm and mass 6.2 g), it climbs trees and will live on building walls.

No *H. caudicinctus* were found in the stomachs of the approximately 480 snakes collected in the area, and no evidence of direct predation on the species was found. The individual collected on 11th May 1981 at 19.20 hrs was observed for fifteen minutes before capture, it was on a dirt road close to a barn owl (*Tyto alba*) and a pearl-spotted owlet (*Glaucidium perlatum*). Although these two owl species are known to eat lizards in southern Africa (Maclean, 1985), both birds and the gecko were feeding on emerging alate termites. Captive specimens were fed wild-caught grasshoppers, crickets and termites.

#### Defence

When I approached H. caudicinctus at night with a torch or motorcycle headlamp, they either froze as soon as the beam touched them, or ran away. Those that froze responded when approached closely by either pressing themselves to the ground, or running as I stooped to pick them up. If picked up, they gyrated and some individuals bit. Captive specimens approached in the daylight responded with a threat display. They stood up as tall as possible, stiff-legged, and then slowly curled the tail up into the air, Carpenter & Ferguson (1977) call this the 'high stand and tail wave'. If touched, these geckoes would lash simultaneously with both head and tail at the hand, at the same time producing a single loud hiss. They would then move away obliquely, with mouth open, hissing more quietly. If held, they would bite. Both freshly caught and captive individuals, when biting, would gyrate clockwise and anticlockwise, alternating rapidly; Dunger (1968) noted similar behaviour. A bite from an adult H. caudicinctus on a human hand is strong enough to draw blood; the gyrations with locked jaws can tear human skin; these actions would be an effective defence against a small predator. Violent combat between males, resulting in the death of an individual, has been observed in captivity (Kugler & Kugler, 1984). Rösler (1983) states that during courtship the male frequently bites the female on the tail, sides and neck, sometimes causing wounds.

# Local Knowledge

The Dagarti and Wali people of the Wa area were greatly afraid of this gecko, believing it to be highly venomous. When the specimen was dug out of a hole in daylight, the observers objected strongly to prevent me picking it up. My science students refused to hold or even touch specimens. When asked to explain why I was able to freely handle the specimens, they argued that its venom was selective in whom it could hurt. Durrell (1954) encountered similar arguments regarding a West African skink, Lygosoma fernandi. The Dagarti name for *H. caudicinctus* in Wa is 'Jenibasi', which is said to mean 'your skin drops off'. Local people believed that if this gecko bit someone, the victim's skin would begin to fall off fairly rapidly, and sometimes change colour, to be followed by death. This suggests confusion with some snakes that exhibit tissue destroying venom that causes local discoloration, for example the puff adder, Bitis arietans. However, in much of the Arab world, geckoes are associated with leprosy and skin disease, and thus such local beliefs might be based on observations of geckoes shedding their skin.

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# REFERENCES

- Baker, H. G. (1962). The ecological study of vegetation in Ghana. In: Agriculture and land use in Ghana. J. B. Wills (Ed). London: Oxford University Press.
- Bartlett, R. D. & Bartlett, P. (1999). Leopard and Fat-tailed Geckos. New York: Barron's publications.
- Bauer, A. M., Tchibozo, S., Pauwels, O. S. G., & Lenglet, G. (2006). A review of the gekkotan lizards of Bénin, with a description of a new species of Hemidactvlus (Squamata: Gekkonidae). Zootaxa 1242, 1-20.
- (1975). Zur Herpetofaunistik Böhme, W. Kameruns, mit Beschreibung eines neune scinciden. Bonn. Zool. Beitr. 26, 2-48.
- Böhme, W. (1978). Zur Herpetofaunistik des Senegal. Bonn. Zool. Beitr. 29, 360-417.
- Castellanos, C. (2008). African fat tail gecko Hemitheconyx caudicinctus. www.progeckoes. com/care sheet/fat tail.pdf. (accessed June 2008).
- Carpenter, C. C. & Ferguson, G. W. (1977). Variation and evolution of stereotyped behaviour in reptiles. In: Biology of the Reptilia Volume 7, pp. 335-554, C. Gans (Ed), London: Academic Press.
- Chirio, L & LeBreton, M. (2007). Atlas des reptiles du Cameroun. Paris, Museum national d'Histoire naturelle, IRD.
- CITES (2008). Hemitheconyx. www.cites.org/ resource/quotas. (accessed June 2008).
- Drewes, R. C. (1971). Notes on the distribution of Holodactylus africanus Boettger. African. Nat. Hist. Soc. Natl. Mus. (Nairobi). 28 (126), 1-3.
- Dunger, G. T. (1968). The Lizards and snakes of Nigeria. Part 4: The geckos of Nigeria. The Nigerian Field 33 (1), 18-47.
- Durrell, G. (1954). The Bafut Beagles. London, Rupert Hart-Davis.

- Ineich, I. (1993). *Hemitheconyx caudicinctus*. (Geographic distribution). *Herpetol. Rev.* **24** (2), 67.
- Joger, U. (1981). Zur herpetofaunistik Westafrikas. Bonn. Zool. Beit. 32 (3-4), 297-340.
- Joger, U. (1982). Zur herpetofaunistik Kameruns (II). *Bonn. Zool. Beit.* **33** (2-4): 313-342.
- Kugler, H & Kugler, R. (1984). Nachzucht in zweiter Generation bei Hemitheconyx caudicinctus (Duméril 1851). Salamandra 20 (4), 270-272.
- Largen, M. J. & Spawls, S. (2006). Lizards of Ethiopia (Reptilia Sauria): an annotated checklist, bibliography, gazetteer and identification key. *Trop. Zool.* **19**, 21-109.
- Leaché, A. M., Rödel, M. O., Linkem, C. W., Diaz, R. E., Hillers, A. & Fujita, M. K. (2006). Biodiversity in a forest island: reptiles and amphibians of the West African Togo Hills. *Amph. Rept. Cons.* 4, 22-45.
- Loveridge, A. (1947). Revision of the African lizards of the family Gekkonidae. *Bull. Mus. Comp. Zool.* **98** (1), 1-469.
- Maclean, G. L. (1985). Robert's Birds of Southern Africa. Cape Town: John Voelcker Bird Book Fund.
- Miles, M. A., Thomson, A. G. & Walters, G. W. (1978). Amphibians and reptiles from the vicinity of Boughari, Casamance (Senegal), and the Gambia. *Bull. Inst. Fond. Afrique Noir.* 40. Ser A, 437-456.
- Mohr, P. A. (1971). *The Geology of Ethiopia*. Addis Ababa: Haile Sellassie I University Press.
- Papenfuss, T. J. (1969). Preliminary analysis of the reptiles of arid central West Africa. *Wassmann J. Biol.* 27, 249-325.
- Pianka, E. R. (1977). Reptilian species diversity.In: *Biology of the Reptilia: Volume 7*. pp. 1-34,C. Gans (Ed). London: Academic Press.
- Rösler, H. (1981). Erfolg und Misserfolg bei der Vermehrung von *Hemitheconyx caudicinctus*. *Elaphe* **81**, 49-54.
- Rösler, H. (1983). Ervaringen met de gecko Hemitheconyx caudicinctus (1). Lacerta 42, 8-11.
- Rösler, H. (1984). Ervaringen met de gecko *Hemitheconyx caudicinctus* (2). Voortbeweging en slaapgedrag. *Lacerta* **42**, 170-177.

- Spawls, S. (1992). Activity patterns in nocturnal West African savanna snakes. *J. Herpetol. Assoc. Afr.* **40**, 61-66.
- Survey of Ghana. (1969). Portfolio of Ghana maps. Accra, survey of Ghana.
- Werner, Y. L. (1972) Observations on eggs of eublepharid lizards, with comments on the evolution of the Gekkonoidea. *Zool. Meded.* 47, 211-225.
- Werner, Y. L. (1976) Optimal temperatures for Inner-ear performance in Gekkonid Lizards. *J. Exp. Zool.* **195**, 319-352.
- White F. (1983). The vegetation of Africa, a descriptive memoir to accompany the UNESCO-AETFAT-UNSO vegetation map of Africa. Paris: UNESCO.
- Wills, J. B. (1962). *Agriculture and Land Use in Ghana*. London: Oxford University Press.