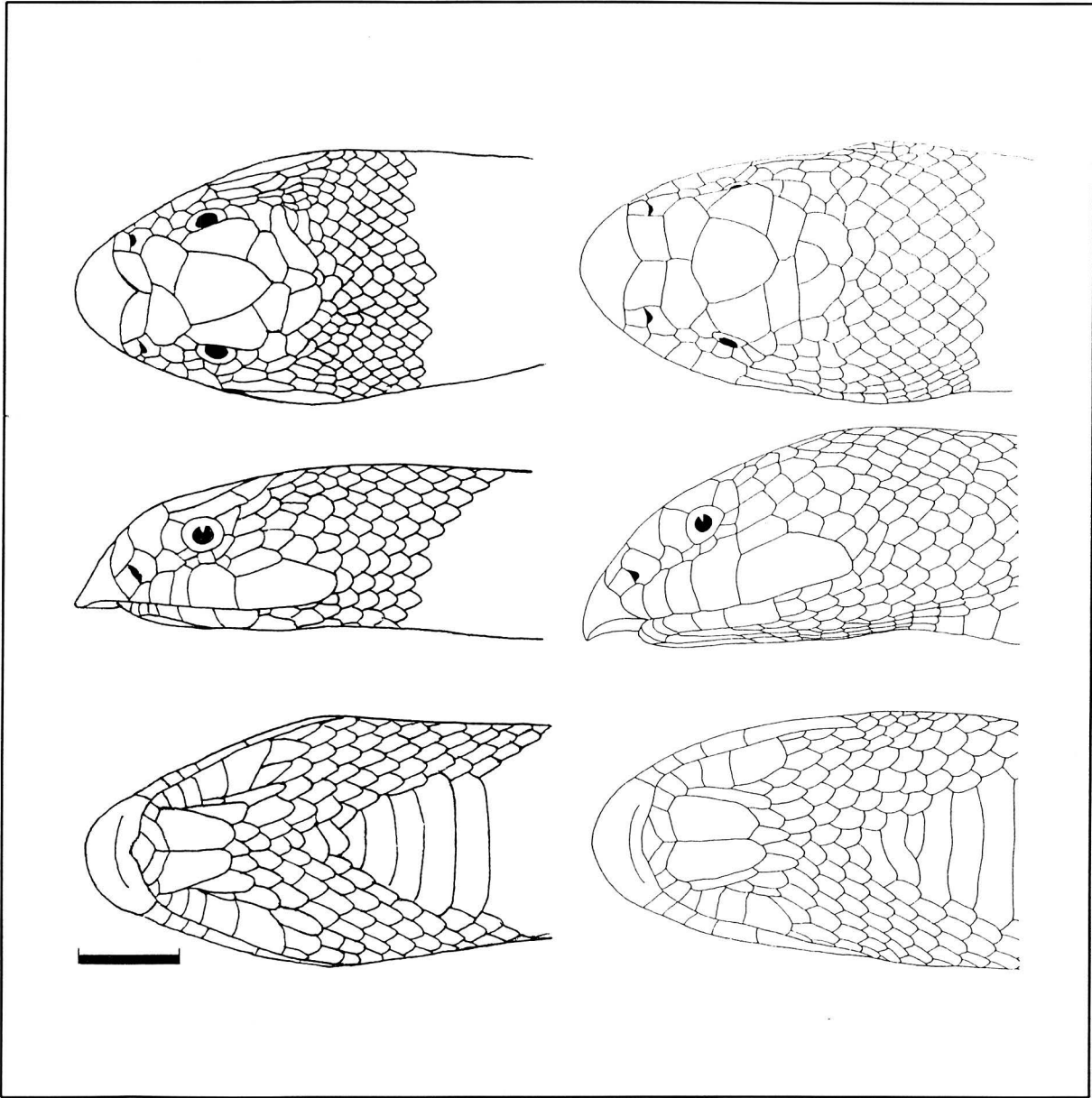


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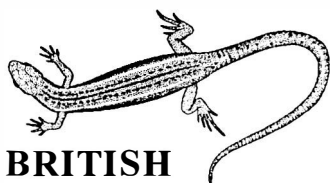
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A REVISION OF THE AFRICAN GENUS *SCAPHIOPHIS* PETERS (SERPENTES: COLUBRIDAE)

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Analysis of the geographical variation in the genus *Scaphiophis* suggests that *S. raffreyi* Bocourt should be reinstated as a full species, with *S. calciatti* Scortecci as a synonym. In *S. albopunctatus* Peters there are ring clines in counts of midbody scale rows and ventrals, the terminal populations in northern Zambia and southwestern Tanzania showing no overlap in these counts.

INTRODUCTION

Peters (1870) described the new genus and species *Scaphiophis albopunctatus* on the basis of a single juvenile specimen from Keta, Ghana, although Loveridge (1936; 1957) subsequently caused confusion by citing the type locality as "Kita, Guinea" (= Kita, Mali) and led Villiers (1962) to give the range as extending as far west as Mali.

Bocourt (1875) described *S. raffreyi*, based on a large adult specimen from Ethiopia, but Boulenger (1894) placed it in the synonymy of *S. albopunctatus*.

Scortecci (1928) described *S. calciatti* on the basis of a juvenile specimen from Eritrea, but Loveridge (1936) suggested that it was a synonym of *S. raffreyi*.

Parker (1949) considered the Eritrean-Ethiopian populations subspecifically distinct on the basis of their higher counts for midbody scale rows and ventrals. This taxonomic arrangement has subsequently been generally accepted.

About seven years ago, I was struck by the pronounced differences in the above scale counts between material from southern Zaire (Shaba Province) and northern Zambia on the one hand and specimens from the Rukwa Valley in southeastern Tanzania on the other, although they are only 200 km apart. I have subsequently collected data for most of the available material.

MATERIAL AND METHODS

Most of the available material was examined or data were obtained from the relevant institutions, the total sample consisted of 230 specimens. Preliminary analysis was based on the number of scale rows at midbody and ventral counts, but several other characters were investigated. Ventrals were counted using the Dowling (1951b) system and dorsal scale row reductions expressed using the Dowling (1951a) formula.

The following acronyms are used to indicate the institutions holding *Scaphiophis* material: AMNH = American Museum of Natural History, New York; BH = material examined by B. Hughes in West African

Universities; BM = Natural History Museum, London; CM = Carnegie Museum, Pittsburgh; FSM = University of Florida, Gainesville; IFAN = Institut Fondamental d'Afrique Noire, Dakar; IRScNB = Institut Royal des Sciences Naturelles de Belgique, Brussels; MCZ = Museum of Comparative Zoology, Harvard; MNHN = Museum National d'Histoire Naturelle, Paris; MSNG = Museo Civico di Storia Naturale di Genova "Giacomo Doria"; NHMAA = Natural History Museum, Addis Ababa; NMK = National Museum of Kenya, Nairobi; NMZB = Natural History Museum of Zimbabwe, Bulawayo; PEM = Port Elizabeth Museum; RGMC = Musée royal de l'Afrique Centrale; TM = Transvaal Museum; UMMZ = University of Michigan, Ann Arbor; USNM = National Museum of Natural History, Washington, D.C.; VW = Van Wallach Collection; ZFMK = Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; ZMB = Zoologisches Museum, Humboldt Universität, Berlin.

RESULTS

CHARACTER ANALYSIS

1. *Midbody scale rows.* Table 1 shows the variation in five populations of *Scaphiophis*. *S. raffreyi* is readily distinguished from the *S. albopunctatus* population with the highest counts (south-east), the Coefficient of Difference being 1.43. The south-east and south-west populations are even better distinguished, with a CD of 2.73, but they are connected by a ring cline encircling the Zaire lowland forest block and the highlands bordering the western rift valley.

In the small sample of *S. raffreyi* there is sexual dimorphism in midbody scale counts, males having 25-27 rows and females 27-31.

In *S. albopunctatus* the mid-dorsal scales are about one and a half times as long as wide, whereas in *S. raffreyi* they are about three times as long as wide.

2. *Ventral counts.* Table 2 shows the variation in the five populations of *Scaphiophis*, with the sexes shown separately. In this case the population of *S.*

Population	<i>N</i>	Range	Mean	SD
<i>ALBOPUNCTATUS</i> :				
SOUTH-WEST: Gabon, Congo, Southern Zaire, Northern Zambia	102	19-21	20.72	0.72
NORTH-WEST: Ghana, Togo, Benin, Nigeria, Cameroun, Chad, Central African Republic	34	19-25	22.03	1.29
NORTH-EAST: Northern Zaire, Southern Sudan, Uganda	41	19-25	22.80	1.66
SOUTH-EAST: Kenya, Tanzania	43	23-25	24.65	0.72
<i>RAFFREYI</i> :				
Ethiopia, Eritrea, Eastern Sudan, Northeast Uganda	23	25-31	27.39	1.20

TABLE 1. Range of variation in counts of midbody scale rows in five populations of *Scaphiophis*. *N* = number of specimens

Population	Males				Females			
	<i>N</i>	Range	Mean	SD	<i>N</i>	Range	Mean	SD
<i>ALBOPUNCTATUS</i> :								
SOUTH-WEST	43	170-184	175.33	3.04	56	189-204	198.45	4.26
NORTH-WEST	18	174-191	182.83	5.69	17	192-216	203.35	6.64
NORTH-EAST	16	183-201	189.56	4.27	25	197-228	216.00	5.61
SOUTH-EAST	19	186-195	189.47	2.87	23	207-221	211.61	3.38
<i>RAFFREYI</i>	6	204-216	211.00	4.20	17	225-243	234.53	5.43

TABLE 2. Range of variation in ventral counts for five populations of *Scaphiophis* (as in Table 1).

Population	Males				Females			
	<i>N</i>	Range	Mean	S.D.	<i>N</i>	Range	Mean	SD
<i>ALBOPUNCTATUS</i> :								
SOUTH-WEST	45	58-72	66.93	2.60	56	52-62	56.91	2.70
NORTH-WEST	18	53-76	64.00	6.63	16	50-64	57.00	4.05
NORTH EAST	16	63-74	69.00	2.92	25	51-72	60.72	4.78
SOUTH-EAST	20	62-73	67.35	2.72	22	49-60	56.18	2.74
<i>RAFFREYI</i> :	6	72-79	76.00	2.53	13	55-68	63.77	3.65

TABLE 3. Range of variation in subcaudal counts for five populations of *Scaphiophis* (as in Table 1).

albopunctatus with the highest counts (north-east) is separated from *S. raffreyi* by a CD of 2.53 in males and 1.68 in females. The south-east and south-west populations are again readily distinguished by CD's of 2.39 in males and 1.72 in females. In this case the counts for the north-west population are intermediate and those for the north-east population are higher than those of the south-east.

3. *Subcaudal counts.* *S. raffreyi* has higher average counts than *S. albopunctatus* in both sexes, but there is great overlap in the ranges. There is no significant geographical variation in *S. albopunctatus*.

4. *Scale row reduction formulae.* Three specimens of *S. albopunctatus* have the following formulae:

NMZB-UM 32859 female, Musosa, Zaire:

21 4+5(136) 19 (196)
4+5(138)

NMZB-UM 32858 female, Mweru Wantipa, Zambia:

23 5+6(12) 21 4+5(151) 19 (197)
5+6(13) 5+6(146)

NMZB 209 female, Kilifi, Kenya:

27 6+7(8) 25 -6(118) 23 5+6(166) 21 4+5(199)
6+7(8) -6(118) 5+6(176)
20 (212)

A specimen of *S. raffreyi* has the following formula:

NMZB 11789 female, Meki, Ethiopia:

29 6+7(15) 27 26 5+6 (142) 23
6+7(15) -2(122) 2+3 & 5+6(142)
4+5(211) 21 (229)
-5(211)

All the scale row reductions are lateral. The higher number of scale rows anteriorly in *S. raffreyi* and the eastern populations of *S. albopunctatus* is considered to be a derived character (Marx & Rabb, 1972).

5. *Number of loreals.* *S. raffreyi* usually has a single loreal (76.5%), rarely two (13%), very rarely 0, 3 or 4. *S. albopunctatus* has 1-3 loreals, two being most common.

6. *Colouration.* *S. albopunctatus* is light brown to grey-brown above, the juveniles with white stippling which disappears in the adult. Most adults have some irregularly scattered dark brown spots, more numerous posteriorly.

S. raffreyi is usually red-brown above, uniform or with a few dark spots posteriorly. Juveniles are pale blue-grey above, each scale black at the base and brown at the apex, giving a speckled effect.

7. *Skull and Dentition.* Bourgeois (1968) described and illustrated the skull of a *S. albopunctatus* from Zaire. She recorded the numbers of teeth as: maxillary 15, palatine 9, pterygoid 8, dentary 18.

Garth Underwood has reported on the skulls of two *S. albopunctatus*, BM 98.1.8.12 (female, Mgana, Kenya) and BM 94.2.10.4 (male, Ugogo, Tanzania, [broken, data in square brackets]), left/right: "The toothless stretch at each end of the maxilla is unusual: (blank equiv. 3 tooth places) 9 teeth (blank equiv. 5) [(3/2) 12/14 (3/3)].

The expanded maxillary process at the anterior end of the palatine bone is unique (both). It lacks a foramen for the maxillary branch of nerve V, a minor but not rare condition. Teeth: (blank equiv. 4) 9 [left broken/ (3) 10]. The choanal process is narrow and of full length. Palatine-ptyergoid contact end to end.

Pterygoid 9 [8/10]. Dentary (blank 1) 17 [(1/1) 20/19]. Articular and splenial bones are without foramina (both). The shapes of these two bones are somewhat different in the Mgano and Ugogo specimens, but symmetrical within each.

The very large premaxilla separates the nasals (both); not seen elsewhere. The nasals have facets which articulate with the frontal; this is usual. The septomaxillae have unusually large facets for the frontal.

The sphenoid of the broken specimen has a broad sella turcica. The foramen for the left cerebral artery is much wider than the left; this is usual. The Vidian canals open anteriorly inside the sphenoid margin. Just above the anterior opening of the Vidian canal is a foramen which I believe is for the retractor branch of nerve V4, what Rieppel (1979) calls the constrictor internus dorsalis (CID) nerve. This arrangement is usual in colubrids. There is a canal for nerve VI passing on either side of the sella turcica to open over the anterior end of the Vidian canal. The posterior lateral parts of the sphenoid are greatly expanded, which obscures the features there. There appears to be a common tunnel for the cerebral artery and the palatine branch of nerve VII.

The stapes shows no signs of reduction in size; it does in some other burrowing snakes. In each the fenestra ovale lies between pro- and opisthotic. The foramina in the exoccipital bones are similar in *Scaphiophis* and *Spalerosophis*, but may be like this in many other snakes."

Scortecci (1928) reported fewer teeth on all bones in the type of *S. calciattii*, i.e. seven, five, three and twelve respectively. However, NMZB 11789, a *S. raffreyi* from Meki, seems to have had a similar number of teeth to *S. albopunctatus* (thirteen, seven, seven and sixteen respectively). The rounded toothless anterior tip of the dentary bone is very noticeable. In this genus the small teeth barely penetrate the thick pleated buccal membrane and the teeth are easily lost when the membrane is removed. As the tooth sockets are very shallow, apparently Scortecci (1928, pl. vii) did not count the empty sockets in the skull of the 370 mm juvenile type of *S. calciattii*. Scortecci also showed fused frontal bones in his illustration of the skull of *S. calciattii*; the frontals seem to be partially fused in NMZB 11789. As in *S.*

albopunctatus, the nasals are separated by a posterior extension of the premaxilla.

8. *Precaudal vertebra*. (Form of description follows Auffenberg, 1963): *S. raffreyi* (NMZB 11789) - middle precaudal vertebrae without well developed hypapophyses; centrum somewhat conical from below, without subcentral ridges. The haemal keel is flattened, but terminates in a prominent spatulate tip near the condyle. The paradiapophyses are provided with two well-developed articular facets, without a projected parapophysial process. The cotyle is round. The condyle is on a short neck, directed posteriorly. The neural canal is round from the front. The neural arch is moderately long, without epizygapophysial spines. The neural spine is slightly longer than high, overhanging both anteriorly and posteriorly. The zygosphene is shallowly hollowed crenate. The prezygapophyses are oval to subtriangular. The accessory processes are moderately developed, directed laterally and blunted.

This vertebra was compared with specimens from *Coluber constrictor* (NMZB 5438 - Florida), *C. (Haemorrhois) hippocrepsis* (NMZB-UM 4578 - Morocco), *C. rogersi* (NMZB-UM 6871 - Egypt), *Meizodon semiornata* (NMZB 10161 - Mozambique) and *Spalerosophis diadema* (NMZB-UM 6865 - Egypt): it shows greatest similarity to the last of these. *S. diadema* differs in having a distinct haemal keel, the cotyle is horizontally oval, the zygosphene is crenate and the prezygapophyses are oval.

9. *Internal anatomy*. The jaw muscles are described and illustrated by Haas (1931). Garth Underwood has dissected a *S. albomaculatus* (BM 98.1.8.12) and a *S. raffreyi* (BM 1973.3257, female, Lake Chamo) and reports as follows (organ positions with reference to ventrals, *S. raffreyi* figures in parentheses): ventrals 207 (228), heart tip V38 (43), trachea to V39 (46), tip of liver V51 (58), systemic arches join at V39 (46). In each the entry of the trachea into the right lung is subterminal. There is a small left lung, not more than 1V long. The vascularisation of the lung fades out in the roof of the narrow trachea. The thyroid lies between four thymus bodies, two on each side. These features are primitive for higher snakes.

The above character analysis facilitates the compilation of the following key to the identification of the two taxa of *Scaphiophis*.

Midbody scale rows 19-25; ventrals 170-201 in males, 189-228 in females; dorsum grey-brown.....

S. albopunctatus Peters.

Midbody scale rows 27-31 (rarely 25); ventrals 204-216 in males, 225-243 in females; dorsum red-brown in adults.....*S. raffreyi* Bocourt.

SCAPHIOPHIS ALBOPUNCTATUS PETERS,
GREY BEAKED SNAKE

Scaphiophis albopunctatus Peters, 1870: 645, pl. i, Fig 4 (Type locality: Keta, Ghana); Bocourt, 1875: art.

3; Mocquard, 1887: 77 (var. *nigropunctatus*); Boulenger, 1894: 254; Bocage, 1895: 102 & 1896: 83; Boulenger, 1896b: 641 & 1897: 279; Tornier, 1897: 71; Boulenger 1902: 446; Werner, 1907: 1873; Sternfeld, 1908: 243; Pellegrin, 1909: 204; Boulenger, 1911: 165, 1915a: 209, 1915b: 626 & 1915c: 649; Chabanaud, 1916: 372 & 1917: 11; Boulenger, 1919: 25 & 1920: 285; Schmidt, 1923: 90, pl. viii; Loveridge, 1928: 53; Haas, 1931: 396; Witte, 1933: 91; Loveridge, 1936: 255; Pitman, 1938: 122, pl. viii, Figs. 3 & 4, col. pl. H, Fig. 3; Vesey-FitzGerald, 1958: 46, pl. 16; Hughes & Barry, 1969: 1018; Cahill, 1971: 233; Vesey-FitzGerald, 1975: 14, pl. iii; Joger, 1982: 331; Hughes, 1983: 354.

Scaphiophis albopunctatus albopunctatus Witte, 1953: 208, Fig. 66; Loveridge, 1955: 46 & 1957: 264; Broadley & Pitman, 1960: 442; Robertson, Chapman & Chapman, 1962: 429; Witte, 1962: 100, Fig. 57; Doucet, 1963: 257; Villiers, 1963: 122, Fig. 161-162; Thys van den Audenaerde, 1965: 379; Witte, 1966: 75, pl. iv, Fig. 1; Bourgeois, 1968: 252, Fig. 109-111 (skull); Broadley, 1971: 81, pl. 9; Pitman, 1974: 113, pl. H, Fig. 3; Spawls, 1978: 5.

Description. Rostral very large, wedged between the internasals, which are usually shorter than the prefrontals; frontal large, longer than broad; parietals fragmented, usually an anterior pair, a lozenge-shaped interparietal and a group of 2 to 5 posterior parietals; nostril pierced between anterior and posterior nasals; loreals 1-3, usually 2, superposed; preoculars 1-2; suboculars 2-3; postoculars 2-3; anterior temporals 4-6, posterior temporals not differentiated; supralabials five, (very rarely six), fifth very long; infralabials 7-9, the first pair in contact behind the mental, the first 2-5 in contact with the single pair of large chin shields. The inside of the upper lip has a flange into which the lower jaw fits with valve-like precision.

Midbody scale rows 19-25, smooth with paired apical pits; ventrals 170-201 in males, 189-228 in females; anal divided; subcaudals 53-76 in males, 49-72 in females.

Size. Largest male (Loveridge, 1928 - Shinyanga District, Tanzania) 949 + 206 = 1155 mm; largest female (MNHN 1904-66 - Upper Nile Province, Sudan) 1302 + 210 = 1512 mm.

Colouration. Grey-brown above, white below. The juveniles are usually heavily speckled with white above, whereas adults usually have scattered large dark dorsal spots, which may be confluent.

Behaviour. There is little information available on this fossorial species. Vesey-FitzGerald (1958: 47) has described its threat display: "The snake will grimace by expanding the lips, opening its mouth, and extruding the tongue. The inside of the mouth and the tongue itself are deep blue. Against this dark

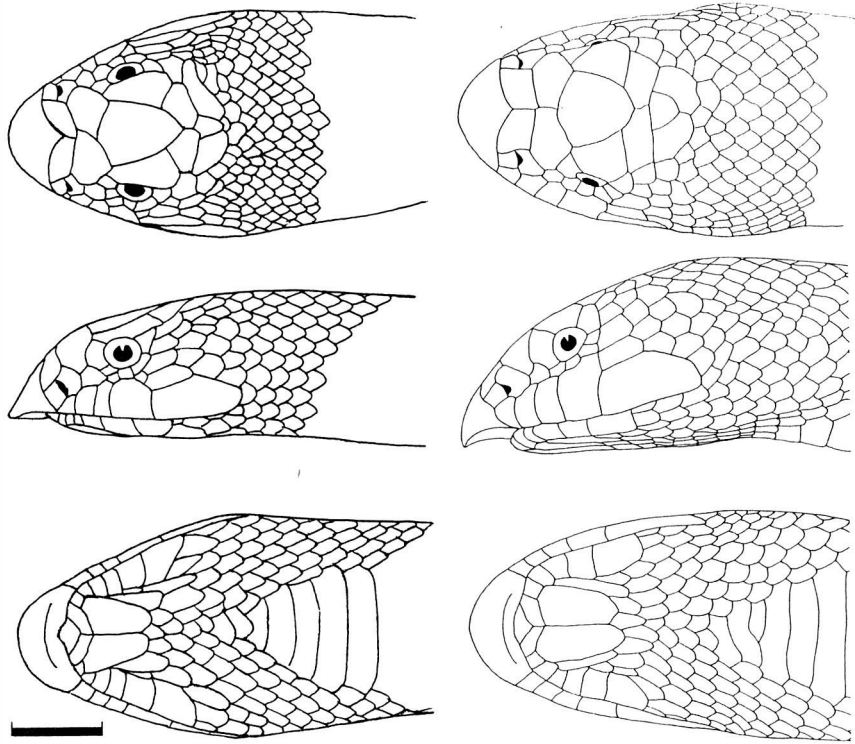


FIG. 1. Dorsal, lateral and ventral views of the head of (left) *Scaphiophis albopunctatus* (NMZB-UM 32858 - Mweru Mantipa, Zambia) and (right) *Scaphiophis raffreyi* (Type: MNHN 4331 - Debre Tabor, Ethiopia). Scale bar = 1cm.

background the hawk-like beak is seen to full advantage. After this preliminary warning, the snake may strike with such violence that its whole body nearly leaps off the ground, and in fact if the teasing is continued, a sort of wild dance is enacted, which one can easily imagine might have a most terrifying effect on a possible enemy." Two stages in the display are illustrated (Vesey-FitzGerald, 1958, pl. 16 & 1975, pl. iii)

Cahill (1971) has described the efficient way in which this snake kills mice in an artificial burrow by crushing them against the tunnel wall with its muscular body. The prey is never taken into the jaws until it is dead.

Diet. In the Rukwa valley Robertson *et al.* (1962) found four newborn rats in a 384 mm snake and an adult rat in a 774 mm snake (snake measurements from field note book in NMZB).

Habitat. Robertson *et al.* (1962) collected 27 of their 32 specimens in the open mixed woodland fringing the Rukwa flood-plain grasslands in southwestern Tanzania. Most of the recorded localities in Kenya and Tanzania seem to be in dry savanna, varying from miombo woodland to *Acacia-Commiphora* deciduous bushland and thicket (White, 1983). However, the habitats on the Kenya coast are much more moist and a Gede specimen was found crawling on the forest floor.

In northern Zambia and southeastern Zaire (Shaba Province) this snake inhabits moist Zambezian miombo woodland, then it seems to occur in the Guineo-Congolian mosaic of lowland rain forest and secondary grassland (? cultivation) which encircles the main Congo lowland forest block and extends west to Ghana. In the environs of Kinshasa it occurs equally in savanna and forest (Thys van den Audenaerde, 1965). In Nigeria and Benin *S. albopunctatus* also occurs in Sudanian woodland with abundant *Isoberlinia*.

Distribution. (Fig. 2). Northern Zambia and southern Zaire, northwest through Congo, Gabon, Cameroun, Nigeria, Benin and Togo to Ghana, east through Chad, Central African Republic, northern Zaire and southern Sudan to Uganda. Southern Kenya, western Tanzania and extreme eastern Zaire at Uvira on the northwest shore of Lake Tanganyika (so presumably present in southern Burundi).

Recorded localities. GHANA: Keta (Peters, 1870) ZMB 6945 (type). TOGO: Agou RGMC 73-14-R-16; Ezime, Atakpame USNM 223899-901; Tohoun IFAN 50-4-34. BENIN: No locality MNHN 1904-117; Agouagou (Chabanaud, 1917) MNHN 1916-156, 157, 200; Ajuda (Bocage, 1895, 1896); Parakou USNM 199603; Segbana USNM 199602. NIGERIA: No locality BM 1940.2.1.8; BH C30A2; Bauchi AMNH 96112; Ibi BM 1916.11.6.9; Ilorin BM 1916.11.6.10; Jos BM 1966.352; Kankiya RGMC 28342, 28348;

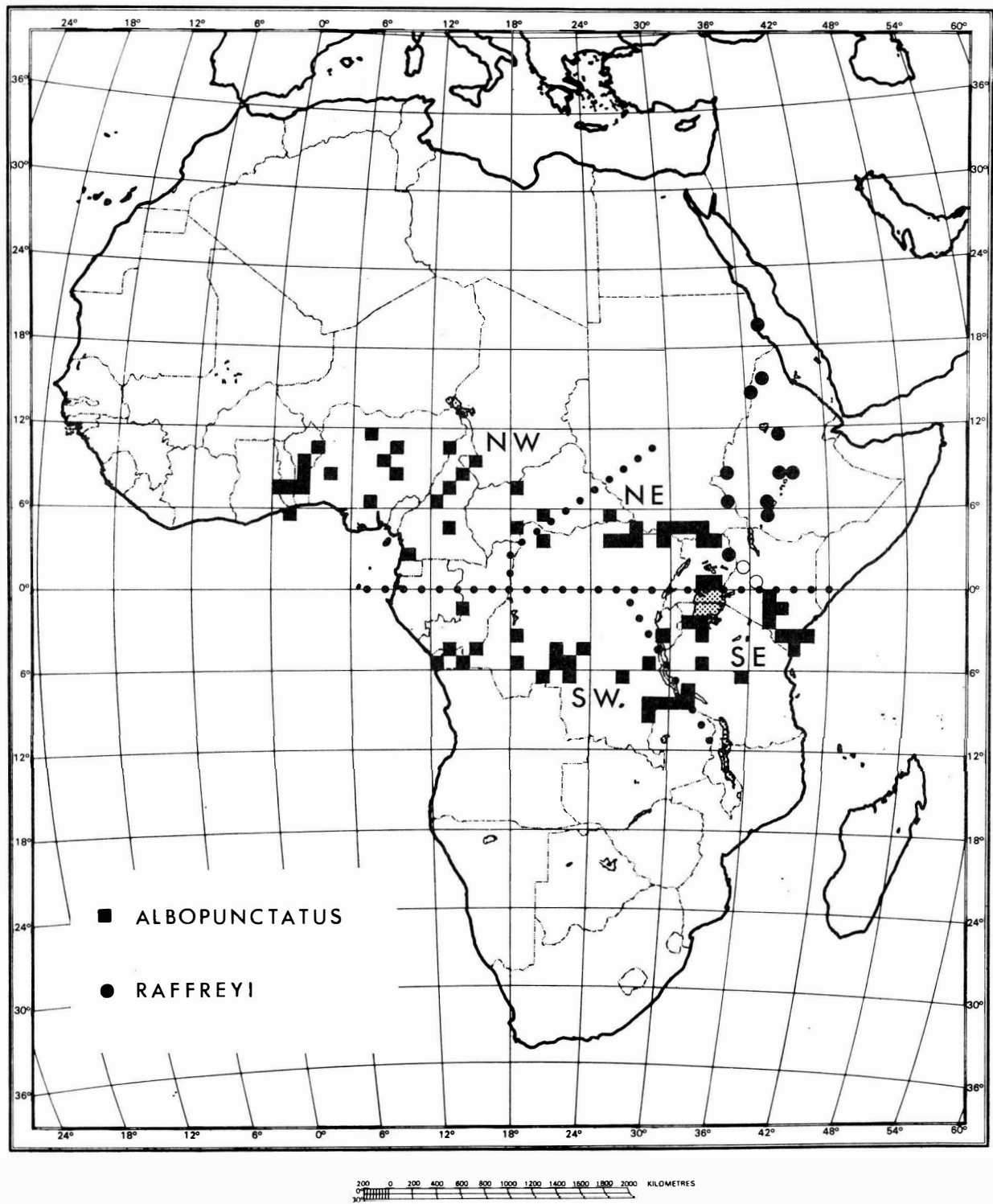


FIG. 2. Distribution of two species of *Scaphiophis*. Open symbols indicate unverified literature records. The dotted lines separate the four populations of *S. albopunctatus* for which data for midbody scale rows and ventrals are presented separately.

- Nsukka (Cahill, 1971); Zaria BM 1975.608. CAMEROON: Duma ZMB 20708; 30 km E of Kribi MCZ 44242; Mokolo Mts MNHN 1962.12; Tcholliré (Joger, 1982) ZFMK 20216-7; Tibati IFAN 51-5-12; Touboro MNHN 1962.11; Wakwa, Ngaoundéré MNHN 1972, 139-140. CHAD: Maillao MNHN 1978.1831; Mayo-Kebbi MNHN 1965.42. CENTRAL AFRICAN REPUBLIC: Bambari MNHN 1991.346; NW of Damara MNHN 1991.374; Gribingui river MNHN 1921.17. GABON: Diélé (Mocquard, 1887) MNHN 1886.221. CONGO: Brazzaville MNHN 1965.14, 1966.726, 1987.1643. ZAIRE: Api RGMC 1022; Avakubi (Boulenger, 1919); Bagbele (Witte, 1966) CM 69270; RGMC 30734-45; Banana (Witte, 1933) RGMC 2479; Bas Congo RGMC 10717, 10726; Bulape AMNH 104101; USNM 167085-9; Dika (Witte, 1933) RGMC 3537; Faradje (Schmidt, 1923) AMNH 12151; Gangala na Bodio RGMC 20164; Kabalo (Witte, 1933) RGMC 4243; Kafumba UMMZ 172970; Kalina RGMC 14679, Kananga (Lulubourg) MCZ 42948; RGMC 2810, 12019, 74-13-R-74; Karawa Mission USNM 236653; Kasai BM 97.1.30.7; Kilwa RGMC 11653; Kina RGMC 9367-8; Kinshasa (Leopoldville) PEM 3355; RGMC 1275, 11577, 14580, 14588-9, 14935, 27204, 27215, 27270-81; VW 1167, 1240; Kinsuka VW (x3); Kisangani (Stanleyville) (Boulenger, 1919); Kwango (Boulenger, 1897) RGMC 38; Lubondaie Tshimbu RGMC 21076; Luebo RGMC 2757; Lusambo RGMC 16533; Makaw River, Kasai RGMC 21121; Mauda (Witte, 1933) RGMC 3352; Mbanza Ngungu (Thysville) RGMC 10741; Misumba RGMC 15589; Musosa (Witte, 1933) NMZB-UM 32859; TM 38157; Niangara (Schmidt, 1923) AMNH 12146-7, 12149; RGMC 3235; Niemba-Lukaga Confluence RGMC 1988, 1994; Nyunzu RGMC 9791; Poko (Boulenger, 1919) RGMC 1758; Pweto BM 1901.2.12.97; RGMC 256; Tanganika district RGMC 433; Tshanga RGMC 14826; Tshikaji, Kasai RGMC 74-13-R-11, 35-6, 45, 71, 77 & 120; Tshikapa (Witte, 1933) RGMC 2412; Uvira MNHN 1950.72; Zemio (Boulenger, 1894) BM 84.5.2.15. SUDAN: Juba ZFMK 29568; Kagelu ZFMK 26069; Lerwa MCZ 53394; Nimule MCZ 53395; Torit (Loveridge 1955) MCZ 53396-9; Upper Nile MNHN 1904-66. UGANDA: Budini (Pitman, 1975) NMZB 182; Busoga NMK 491; Bussu (Boulenger, 1911; Pitman, 1975) BM 1911.7.8.10-11, UMMZ 61227; Eastern Province BM 1931.10.1.1; Kaliro AMNH 63773. KENYA (Spawls, 1978): Gede NMK 2563, 2804, 3193, 3195 (2); Ithumba BM 1966.64; Kiboko Range Station NMK 2951(2), 3003; Kibwezi (Sternfeld, 1908) ZMB 22476(2); Kilifi BM 1955.1.12.12-13; NMZB 209; Kwale BM 1966.63; Malindi NMK 1410-1; Mazinga Hill, Voi NMK 1568; Mgana BM 98.1.8.12; Ngomeni, Kitui NMK 1568; OI Doinyo Sabuk NMK 1575; Voi AMNH 61635; NMK 1422, 1505; Sakoke Forest (Loveridge, 1936) MCZ 39953-4. TANZANIA: Dodoma (Loveridge, 1928) MCZ 23068; USNM 72469; Kafukola (Robertson *et al.*, 1962) MCZ 54581; NMZB 664-5; TM 25304, 25586; Kapenta, Kapombo & Kinambo (Robertson *et al.*, 1962); Kipangate (Robertson *et al.*, 1962) MCZ 54079; Kizumbi, Shinyanga (Loveridge, 1928) MCZ 23069; Lake Rukwa MCZ 53115, 54078, 54080; NMZB 1756; ZMB 16111; Machaka MCZ 54579-80; Malombe (Robertson *et al.*, 1962); Milepa NMZB 666; Mwanza ZMB 16820; Nkulukulu Mbuga (Robertson *et al.*, 1962); Tabora (Tornier, 1897) ZMB 10377; Tumba NMZB 668; Ugogo (Boulenger, 1896) BM 94.2.10.4; Utundu, S.W. Nyanza (Tornier, 1897) ZMB 13275; Zimba ZMB 23473. ZAMBIA (Broadley, 1971): Buleya IRScNB 5055; Chansa, Masanka Flats PEM 1435/65; Mbala (Broadley & Pitman, 1960) CM 59030; IRScNB 4223, 4224(8), 4230(2), 4233(2), 5056(3), 8745; Mukupa Katundula (Broadley & Pitman, 1960) IRScNB 8743(3); Mweru-Wantipa IRScNB 4229, 4231(4); NMZB-UM 32858.
- SCAPHIOPHIS RAFFREYI* BOCOURT,
ETHIOPIAN BEAKED SNAKE
- Scaphiophis raffreyi* Bocourt, 1875: art. 3 (Debre Tabor, Ethiopia); Loveridge, 1936: 256.
- Scaphiophis albopunctatus* (not Peters) Fischer, 1885: 100, pl. iii, Fig. 6; Boulenger, 1896a: 553; Emmrich, 1985a: 68 & frontispiece; 1985b: 40, pl. 8.
- Scaphiophis calciattii* Scortecci, 1928: 300, Fig. 5, pl. vii, Figs. 2-5. (Cunana Region, Eritrea); 1930: 201.
- Scaphiophis albopunctatus raffreyi* Parker, 1949: 62; Emmrich, 1985a: 68.
- Description.* Head scalation similar to *S. albopunctatus*, except that a single loreal is usual and infralabials average a little more numerous, i.e. 8-11. Midbody scale rows 27 in males (25 in one from Khor Okwat), 27-31 in females, smooth with weakly developed paired apical pits; ventrals 204-216 in males, 225-243 in females; anal divided; subcaudals 72-79 in males, 55-68 in females.
- Size.* Largest male (NHMAA606 - Gambela, Ethiopia) 1050 + 270 = 1320 mm; largest female (BM 1973.3258 - Arba Minch, Ethiopia) 1220 + 260 = 1480 mm.
- Colouration.* Red-brown above, usually uniform, but with some dark spots posteriorly in the type specimen, ventrum white. Juveniles pale blue-grey above, speckled darker (Emmrich, 1985a: frontispiece).
- Behaviour.* Emmrich (pers. comm.) caught a 110 cm adult at Meki in May 1982 and noted that in captivity it killed mice by clumsily pressing them against the ground with its body. Only about one in ten attempts to pin down prey was successful. It detected prey by scent rather than vision.
- Habitat.* Ionides (in Pitman, 1974) dug a 1423 mm female *Scaphiophis* from an abandoned termitarium at Baringo in northwestern Kenya. Emmrich (pers. comm.) recorded a juvenile caught at Meki during ploughing.

Most records of *S. raffreyi* are from the Ethiopian rift valley: deciduous mixed savanna woodlands (1300–1400 m) in the south (Lake Chamo and Arba Minch) and *Chrysopogon/Dactyloctenium* grasslands (1300–1760 m) further north (Meki, Nazaret, Ouardji and Welenchiti). From western Ethiopia there is a series from Gambela (515 m in *Hyparrhenia* grassland) and one from Tulu Walel (formerly broadleaf forest, but now intensively cultivated). Two of the earliest records are from altitudes of 2500 m, the type from Debre Tabor (broadleaf forest) and a specimen from Rappe (coniferous forest), habitats not substantiated by recent material. The Eritrean records are from *Sorghum* grasslands at approx. 1000 m. (Data on natural vegetation from the National Atlas of Ethiopia, 1988).

The northernmost record is from Khor Okwat on the Red Sea in Sahel semi-desert grass/shrubland. The southernmost specimen examined is from Moroto in the Karamoja District of northeastern Uganda in the Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket (White, 1983). *Scaphiophis* records from this habitat in northwestern Kenya (Baringo and Kerio Valley) are provisionally assigned to *S. raffreyi*, pending the collection of voucher specimens.

Distribution. (Fig. 2) Eastern Sudan, Eritrea, Ethiopia from the rift valley westwards, northeastern Uganda and probably northwestern Kenya as far south as Baringo.

Recorded localities. SUDAN: Boma National Park Base Camp NMK 0/2889; “Kor Ofat, Egypt” = Khor Okwat MNHN 1909.159; Nubia (Fischer, 1885). ERITREA: Barentu (Scortecci, 1930) MSNG 40756 (2); Cunana Region (Scortecci, 1928). ETHIOPIA: Arba Minch BM 1973.3258; Debre Tabor (Bocourt, 1875) MNHN 4331 (type); Gambela (Emmrich, 1985a) NHMAA 606, 708, 877–8; West of Lake Chamo BM 1973.3257; Meki (Emmrich, 1985) NMZB 11787–9; Ouardji MNHN 1905–197; Rappe (Boulenger, 1896); Tulu Walel ZFMK 16812; Welenchiti BM 1916.6.24.8–9. UGANDA: No locality BM 1909.10.30.31; Moroto NMK 0/1028. KENYA. Baringo (Ionides, pers. comm. to Pitman, 1974); Kerio Valley (Spawls 1978).

DISCUSSION

The relationships of *Scaphiophis* are uncertain. Bogert (1940) placed it in his monotypic Group XI, one of the groups distinguished by vertebral hypapophyses absent posteriorly, sulcus spermaticus not forked and no grooved maxillary teeth.

Taub (1967) investigated labial glands in the Colubridae and noted that *Scaphiophis* shared with *Ari zona*, *Eirenis* and some *Elaphe* “... a primarily mucous supralabial gland with occasional serous cells interspersed among the mucous lobules. The numerous lobules open into the oral cavity via several ducts.” The last three above-mentioned genera were assigned to the Tribe Colubriini by Dowling & Duellman (1978), al-

though they included *Scaphiophis* in the Tribe Pseudaspidini of the Subfamily Lycodontinae. McDowell (1975) considered *Scaphiophis* to be closely related to *Argyrogena fasciolata* (Shaw), which in turn he considered to be a specialised relative of *Coluber ravergeri* and *Spalerosophis diadema*, both of which have a Duvernoy’s gland. Branch (pers. comm., 1978) examined the everted hemipenis of a Nigerian *Scaphiophis* (BM 1975.608) and also noted its resemblance to the hemipenis of *Argyrogena fasciolata* (Shaw), described by Wilson (1967).

It seemed that *Scaphiophis* should be assigned to the Tribe Colubriini, so a spine was prepared from a *Scaphiophis raffreyi* (NMZB 11789) and a precaudal vertebra closely resembles that of *Spalerosophis diadema*, illustrated by Schatti (1986), although the haemal keel is weakly developed. This affinity was confirmed by comparison with vertebrae from five colubrine species.

Skulls were prepared of both *Scaphiophis* species. The striking feature of the interior of the mouth is the heavily pleated blackish buccal membrane, through which the small teeth barely penetrate. This resembles the interior of the mouth of *Dasypeltis*, described and illustrated by Gans (1952). There is a pronounced flange on the inside of the upper lip into which the countersunk lower jaw fits tightly. A less well developed pleated buccal membrane was noted during the preparation of a skull of *Spalerosophis diadema*.

The skull of *S. raffreyi* (NMZB 11789) resembles that of *S. albopunctatus* illustrated by Bourgeois (1968) in most respects, but the nasals are larger and in good contact with the frontals (which are partially fused), separated by a posterior prolongation of the premaxilla. Many teeth were lost during preparation of the skull and determination of the number of teeth is difficult due to the shallowness and irregular spacing of the tooth sockets.

Minton (1966) recorded behaviour in Pakistan *Spalerosophis atriceps* reminiscent of that used by *Scaphiophis* to kill mice. “[Captive specimens] feed well on mice, young rats and sparrows. The prey tends to be small in proportion to the size of the snake. Usually the snakes press struggling animals against the floor or wall of the cage with a coil; occasionally they employ true constriction”.

Underwood (1967) thought that there were probably no fossorial Colubrids, but *Scaphiophis* seems to be the exception, which may have arisen from an isolated southern population of ancestral *Spalerosophis* stock.

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THE EFFECT OF SURGICALLY IMPLANTED TRANSMITTERS UPON THE LOCOMOTORY PERFORMANCE OF THE CHECKERED GARTER SNAKE, *THAMNOPHIS M. MARCIANUS*

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The effect of both surgery and implanted transmitters upon sprint time of *Thamnophis m. marcianus* from two populations was assessed under laboratory conditions using a circular race-track. The mean sprint times of snakes before surgery were 7.52 s (SE = 0.393, $n = 8$) and 9.69 s (SE = 0.358, $n = 5$) for the Arizona and Texas populations, respectively. Mean sprint times of the same snakes following surgery were 7.55 s (SE = 0.387, $n = 8$) for the Arizona population and 9.83 s (SE = 0.408, $n = 5$) for the Texas population. A repeated measures ANOVA indicated that sprint time for both non-surgery and surgery treatments did not differ significantly. Transmitter treatments consisted of implanting transmitters equalling 10% or 15% of the snake's body mass. The mean sprint times for snakes receiving either 10% or 15% transmitter treatments were statistically compared to the mean sprint time of snakes receiving the surgery treatment. A two-way ANCOVA accounting for body mass indicated that the mean sprint time was significantly reduced for snakes carrying implanted transmitters equal to 15% of their body mass. These results suggest that surgical techniques have no effect upon locomotory performance and that implanted transmitters for radiotelemetry of snakes should probably not exceed 10% of the snake's body mass.

INTRODUCTION

Many studies of snake behaviour and ecology have used either ingested or surgically implanted transmitters (e.g. Osgood, 1970; Fitch & Shirer, 1971; Parker & Brown, 1972; Landreth, 1973; Brown & Parker, 1976; Nickerson *et al.*, 1978; Jacob & Painter, 1980; Reinert & Kodrich, 1982; Reinert, 1984*a,b*; Reinert *et al.*, 1984; Shine & Lambeck, 1985; Burger & Zappalorti, 1988; Reinert & Zappalorti, 1988*a,b*; Plummer, 1990). However, implanting transmitters surgically into the coelomic cavity of a snake may be the preferred method for radiotelemetry because it circumvents the many problems associated with ingested transmitters (Reinert & Cundall, 1982; Lutterschmidt & Reinert, 1990).

Although surgical implantation methods are commonly used, the effects of these methodologies upon snake behaviour and locomotory performance have never been experimentally evaluated. Transmitter packages having an approximate mass 10% of the snake's body mass have been assumed to have little or no effect upon snake behaviour (Pisani *et al.*, 1987). However, Shine (1988) recently proposed that transmitters with a mass less than 5% of a snake's mass are more appropriate. Reinert (1992) has also suggested that transmitters implanted in the coelomic cavity should probably not exceed 5% of a snake's body mass.

Because data on how transmitter mass may reduce snake locomotor ability are unavailable, I have evaluated the effect of transmitter mass upon locomotory performance to determine a critical transmitter mass for surgical implantation.

MATERIALS AND METHODS

Thirty-six checkered garter snakes, *Thamnophis m. marcianus*, were collected from Graham County, Arizona and Lubbock County, Texas. Only male snakes were used for experimentation to eliminate possible variation due to sex. Snakes were housed in separate 3.78 l plastic cages and acclimated to laboratory conditions (24.0±2.0 °C and a light and dark cycle of LD 12 hr:12 hr) for approximately 6 months. Snakes were maintained on a diet (30% of the snake's body mass weekly) of bullfrog tadpoles, *Rana catesbeiana*, and water *ad libitum*.

Each snake was randomly selected for one of three experimental groups: (1) non-surgery, and then surgery with no implanted model transmitter (i.e. repeated measures design); (2) surgical implantation of model transmitter equal to 10% of the snake's body mass; (3) surgical implantation of model transmitter equal to 15% of the snake's body mass. Surgical procedures were as described by Reinert & Cundall (1982). Experimental groups receiving surgery were allowed 24 hr before testing. Model transmitters consisted of a small steel rod coated with a 1:1 mixture of beeswax and paraffin. These models were designed to simulate actual size, shape, and mass of transmitter packages. The possible effects of an antenna, which would normally be placed longitudinally under the skin, was not used and therefore not evaluated.

Locomotory performance was assessed by determining burst or sprint speed (Garland & Arnold, 1983; Ford & Shuttlesworth, 1986). Sprint speed was deter-

mined by the time required to crawl a distance of 3.0 m around a circular racetrack similar to that described by Ford & Shuttlesworth (1986). Because distance (3.0 m) remained constant for all trials, the variable of time (not rate or speed) was used for treatment comparisons. Time (s) was measured to the nearest 0.01 s for each snake in three different trials to calculate an average sprint time.

Trials were conducted under standard conditions of light and temperature (25.0 ± 2.0 C). Snake body temperatures ($\bar{x} = 24.7$, $SE = 0.06$, $n = 85$) were also kept constant and measured before all trials to avoid possible temperature effects upon metabolism and locomotory performance (e.g. Heckrotte, 1967; Stevenson *et al.*, 1985).

A model I, two-way ANOVA with repeated measures was used to first examine possible surgical effects upon sprint time in both populations by comparing non-surgery and surgery (with no implanted transmitter) treatments. The surgery group was then used as a control for a second comparison to determine if sprint time differed among the implanted transmitter groups (10% and 15% of body mass).

The experimental design consisted of preliminary tests (*t*-test) to first determine if transmitters of 15% body mass affected locomotory performance. Because sprint speeds of the 15% transmitter group were significantly reduced in comparison to the surgery group, the next experimental group (transmitters 10% of body mass) was investigated.

Final statistical comparisons consisted of a model I, two-way analysis of covariance with repeated measures to determine differences in sprint time among experimental groups for both the Arizona and Texas populations. The analysis of covariance eliminated possible effects of body size upon sprint speed (e.g. Heckrotte, 1967; Seigel *et al.*, 1987; Jayne & Bennett, 1990a). An *a posteriori* test (SAS, 1988) of adjusted means assessed differences among all experimental groups for each population. All data were analyzed using SAS (1988). The assumption of similar slopes among treatments and populations was met for the ANCOVA analysis (Figs. 1A and 1B).

RESULTS

Surgical methods described by Reinert & Cundall (1982) and the implantation of transmitters (10% of body mass) into the coelomic cavity had no effect upon sprint time in *Thamnophis m. marcianus*. The mean sprint times of snakes without surgery for both Arizona and Texas populations were 7.52 s ($SE = 0.393$, $n = 8$) and 9.69 s ($SE = 0.358$, $n = 5$), respectively. Mean sprint times for the same snakes following surgery were 7.55 s ($SE = 0.387$, $n = 8$) in the Arizona population and 9.83 s ($SE = 0.408$, $n = 5$) in the Texas population (Table 1). A repeated measures two-way ANOVA indicated that sprint times for non-surgery and surgery

Treatment	Arizona population	Texas population
Non-surgery	7.52 (0.393, 8)	9.69 (0.358, 5)
Surgery only	7.55 (0.387, 8)	9.83 (0.408, 5)
Surgery and 10% MT	6.87 (0.311, 7)	10.23 (0.644, 3)
Surgery and 15% MT	10.45 (0.776, 8)	12.47 (0.531, 5)

TABLE 1. Non-adjusted mean sprint times (s) with SE and n for each treatment of the two populations. The implantation of a model transmitter (MT) 10% and 15% of the snake's body mass is indicated by 10% MT and 15% MT.

treatments did not differ significantly (Treatments: $F_{1,22} = 0.04$, $P > 0.05$; Population: $F_{1,22} = 29.08$, $P < 0.001$; Treatments $\times$ population: $F_{1,22} = 0.02$, $P > 0.05$).

Sprint time for the surgery treatment was then statistically compared to the sprint time of snakes receiving 10% and 15% transmitter treatments. A two-way ANCOVA accounting for body mass indicated that the mean sprint time differed significantly among treatments (Table 2). A multiple comparisons test for adjusted means indicated that sprint time was significantly reduced for snakes carrying implanted transmitters 15% of their body mass. Both the surgery and 10% transmitter treatments significantly differed from the 15% transmitter treatment but not from each other. In order to examine possible variation of the linear relationship due to the volumetric function of mass, the same analysis was conducted using the cube root of body mass (per. comm. G.D. Schnell). Because the same results were obtained, all results are reported in mass (not the cube roots of mass), for the sake of convenience.

The Arizona and Texas populations were analyzed as separate populations (and not grouped) due to preliminary tests indicating significantly different sprint times between the populations ($t = 3.76$, $df = 11$, $P < 0.01$). However, each population demonstrated similar responses to each of the experimental treatments (Figs. 1A and 1B).

Source	df	SS	MS	F	P
Treatment	2	48.26	24.13	19.13	0.0001
Population	1	72.57	72.57	57.53	0.0001
Treat. x Pop.	2	1.74	0.87	0.69	0.5085
Mass	1	21.04	21.04	16.68	0.0003
Error	29	36.58	1.26		
Total	35	180.17			

TABLE 2. A two-way ANCOVA table showing respective F and P values accounting for mean sprint time and mass as the covariate.

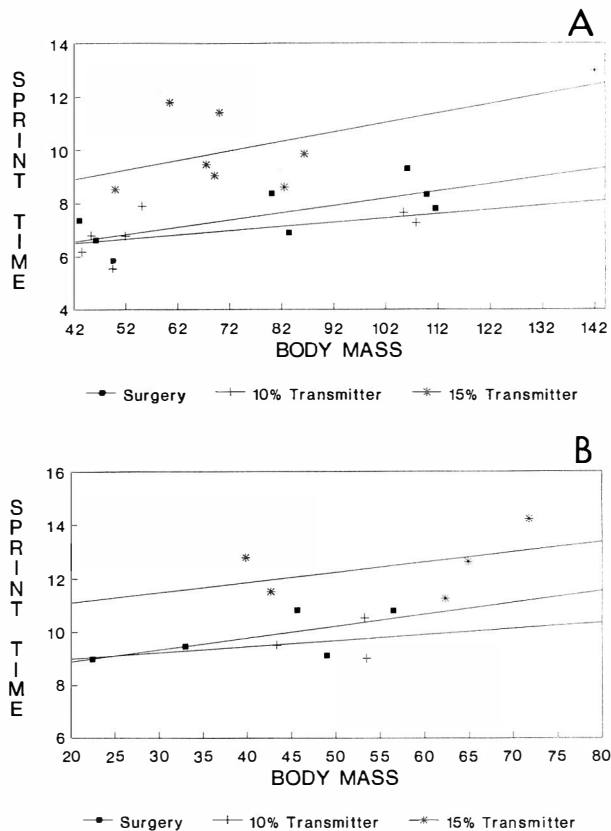


FIG. 1. Body mass (g) plotted against sprint time (s) showing similar slopes for the surgery, 10% transmitter, and 15% transmitter treatments. A, relationship between body mass and sprint time for all treatments in the Arizona population; B, relationships for the Texas population.

DISCUSSION

Snake ecologists have questioned the possible influences of transmitters upon behaviour. My own concerns and speculation of experimental bias have been: (1) a possible reduction in survivorship of individuals carrying transmitters due to an inability to successfully escape predators, (2) a lowered success rate in capturing prey for snakes that demonstrate an active foraging strategy, and (3) a reduction in home-range and movement patterns which may also affect other aspects of a snake's ecology (e.g. energetics and reproduction). In support of these concerns, Jayne & Bennett (1990b) and Garland *et al.* (1990) have shown that individual differences in locomotor performance of *Thamnophis* affect survival. Secondly, relationships between locomotor capacity and foraging behaviour have also been demonstrated (Huey *et al.*, 1984).

Although transmitters equal to 15% of a snake's body mass significantly reduced locomotor performance, neither surgical procedures nor implanted transmitters equal to 10% of a snake's body mass affected sprint time. These findings may help in addressing concerns of snake ecologists who use surgically implanted transmitters.

Until recently, a critical mass for transmitters (10% of the snake's body mass) has been assumed to have a limited effect upon locomotor ability (Pisani *et al.*, 1987; but also see Shine, 1988). Results of this study support Pisani *et al.* (1987) and indicate that critical mass (i.e. mass which will significantly reduce "sprint speed") of transmitter packages may be between 10% and 15% of a snake's body mass.

Ford & Shuttlesworth (1986) found similar results for juvenile garter snakes, *Thamnophis marcianus*. Sprint speed of snakes with a food bolus equal to 10% of their body mass did not significantly differ from snakes with no ingested food items. However, sprint speed was significantly reduced by the ingestion of a food bolus 30% and 50% of the snake's body mass. Garland & Arnold (1983) also showed that sprint speed of juvenile *Thamnophis elegans* was not affected by a "full stomach" (i.e. ingestion of food items between 17.6 - 26.9% of body mass). Unlike Ford & Shuttlesworth (1986) and Garland & Arnold (1983), my results indicate a significant reduction in sprint speed with a 15% increase in body mass. However, a direct comparison between my results and these studies may not be appropriate. The difference in results may simply suggest that snakes may be able to carry a greater mass within its stomach without a reduction in sprint speed. Therefore, surgically implanting a transmitter into the coelomic cavity may have a greater effect upon sprint speed than if the same transmitter mass was ingested. However, gravid garter snakes (*Thamnophis marcianus*) can carry a clutch mass 24% of their body mass before a significant reduction in locomotor ability occurs (Seigel *et al.*, 1987).

In summary, my results suggest that transmitter packages having a mass equal to and possibly less than 10% of the snake's mass do not reduce a snake's sprint speed. However, several other aspects of snake behaviour also should be considered when determining the mass and size of a transmitter. Although a certain size transmitter package may not affect sprint speed, it may alter endurance, the passage of material through the digestive tract, and possibly thermoregulatory behaviour. Such factors have not been evaluated by this study and should be of concern to investigators using surgically implanted transmitters. In order to circumvent possible influences upon snake behaviour, I suggest that the smallest transmitter package (that can meet the experimental needs) should be used for telemetric studies of snakes. Such practices may limit possible behavioural biases until the effects of surgical methods and implanted transmitters can be fully evaluated.

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THE DIET OF ADULT *TUPINAMBIS TEGUIXIN* (SAURIA: TEIIDAE) IN THE EASTERN CHACO OF ARGENTINA

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Analysis of the number, weight and volume of food items in the digestive tracts of 70 teiid lizards, *Tupinambis teguixin*, were obtained during spring-summer from areas neighbouring El Bagual Ecological Reserve in northeastern Argentina. The food items revealed the species to be a widely-ranging opportunistic omnivorous forager. *Tupinambis* consumed a large proportion of fruits, invertebrate and vertebrates. The species forages in both terrestrial and aquatic habitats, but no evidence was obtained for arboreal feeding habits. A sample of 27 to 49 digestive tracts is sufficient to reveal 80-90% of the prey types in the diet.

INTRODUCTION

Tupinambis teguixin, the black tegu lizard, is a member of the abundant fauna of South America characterized by large adult size, relatively small hatchling size, sexual dimorphism as adults, large clutch size and reproduction limited to a brief breeding season (Yanosky & Mercolli, 1992a). However, no detailed study of this lizard's diet has been published. Some ancillary information has been published about prey items in *Tupinambis*, based on data obtained in the wild or in captivity (see review in Mercolli & Yanosky, in press). Only a thesis by Herrera (1980) offered data on feeding habits during a drought period in Venezuela, and we earlier reported some prey items described within an ethological framework (Mercolli & Yanosky, 1989).

Little is known about the ecology of Argentinian lizards (Vega *et al.*, 1988). Knowledge about this teiid lizard is needed because of its importance in economic, social and cultural aspects of South American human societies (Fitzgerald *et al.*, 1991; Yanosky & Mercolli, 1992a) and for this reason special conservation emphasis is now being directed towards *Tupinambis* species. Recently, the diet for *T. rufescens* has been reported (Williams *et al.*, 1990).

The study had the following aims: (1) to determine the food items taken by this terrestrial teiid lizard in the humid Chaco forest community, (2) to broaden our knowledge about the food web, and (3) to offer minimum, reliable sample sizes to determine food habits. This lizard is an intensive forager in the sense of Anderson & Vitt (1990), and relies on chemical cues for feeding (Cooper, 1990; Yanosky *et al.*, 1993).

MATERIALS AND METHODS

STUDY AREA

The study area is in the eastern-humid Chaco district of the Chaco province (Cabrera & Willink, 1973). All specimens were collected from adjacent areas to El

Bagual Ecological Reserve (26° 59' 53" S, 58° 56' 39" W) in northeastern Argentina. The area is characterized by flooded savannas and forests, subject to cyclic fires and flooding (Neiff, 1986). The soils, originating from volcanic ash of northwestern Argentina, are planosoles, gley-humid and alluvial with poor drainage, and influenced by Bermejo River lowlands (Helman, 1987). The El Bagual Ecological Reserve annual mean temperature is 22°C with a maximum average of 27°C and minimum of 17°C. Extreme recorded temperatures ranged from - 2 to 45°C and there is a marked rainy season (November-April) with an annual rainfall of 1200 to 1900 mm.

FIELD TECHNIQUES

Between November 1990 and March 1992, seventy adult tegu lizards ranging from 290 to 480 mm snout-vent length were bought from local professional hunters in the department of Laishi (province of Formosa). These specimens were harvested under the regulations for a species listed in Appendix II of CITES and no individuals were killed specifically for the purpose of this study. Lizards were killed in the field by hunters, and the skins removed for trading. Specimens were not obtained during winter months (Yanosky & Mercolli, 1992b). Hideless carcasses were stored in 10% formalin within six hours of harvest. Each specimen was later eviscerated, labelled and returned to 10% formalin.

LABORATORY TECHNIQUES

Total digestive tract contents were analysed for each specimen because important prey were found from the rectum to the oesophagus. The contents of the preserved alimentary tract were emptied into bowls for collection of data and identification. Non-food items (parasites, inorganic material) were separated and recorded.

Where possible, food items were identified to species, but the lowest useful taxonomic level was order/

FOOD TAXA	Frequency		Number		Weight		Volume	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
<i>PLANTAE</i>								
Tomatillo	1	1.40	47	1.25	29.0	0.65	25.0	0.64
Coquito	5	7.14	84	2.25	297.0	6.65	279.5	7.12
Granadilla	2	2.80	27	0.73	11.5	0.25	9.5	0.24
Congorosa	2	2.80	151	4.04	71.5	1.60	71.0	1.81
Ñangapiri	2	2.80	28	0.75	7.0	0.15	6.5	0.17
Aguay	2	2.80	6	0.16	4.5	0.10	3.4	0.09
Mora	15	21.42	1263	33.80	353.5	7.91	30.8	7.85
Pindó	23	32.85	244	6.53	1198.0	26.82	994.2	25.40
Higuerón	9	12.85	359	9.60	85.5	1.91	77.1	1.90
Tala	8	11.42	140	3.75	27.5	0.61	24.5	0.60
Guabiyú	11	15.71	106	2.84	43.5	0.97	37.0	0.90
Palma	17	24.28	222	5.94	516.0	11.55	448.6	11.43
Cocú	1	1.40	2	0.05	0.5	0.01	0.3	Trace
Others	9	12.85	116	3.10	49.5	1.10	50.1	1.27
Seeds	9	12.85	75	2.00	10.0	0.22	7.4	0.18
Vegetal matter	62	88.57	-	-	281.6	6.30	271.1	6.90
<i>INVERTEBRATES</i>								
Crustacea	11	15.71	21	0.56	45.5	1.01	39.40	0.99
Gastropoda	48	68.57	379	10.14	289.3	6.47	272.20	6.94
Araneae ad.	13	18.57	26	0.70	26.5	0.59	26.30	0.68
Araneae ootheca	11	15.71	13	0.35	10.0	0.22	8.90	0.23
Miriapoda	6	8.57	17	0.45	4.5	0.10	3.20	0.08
Lepidoptera ad.	2	2.80	2	0.05	1.0	0.02	0.60	0.01
Lepidoptera pupae	2	2.80	2	0.05	2.0	0.04	1.80	0.04
Lepidoptera larvae	18	25.71	56	1.50	90.1	2.01	73.05	1.87
Coleoptera								
- Carabidae	5	7.14	11	0.29	5.0	0.11	3.80	0.09
- Chrysomelidae	1	1.40	1	0.02	0.5	0.01	0.20	Trace
- Coccinellidae	1	1.40	1	0.02	0.5	0.01	0.30	Trace
- Scarabeidae	1	1.40	1	0.02	0.5	0.01	0.30	Trace
- Others	28	40.00	54	1.44	29.5	0.66	25.20	0.64
- Larvae	1	1.40	1	0.02	9.5	0.21	10.50	0.27
Hemiptera	1	1.40	2	0.05	2.5	0.05	1.50	0.03
Homoptera	3	4.28	3	0.08	3.5	0.07	2.60	0.06
Orthoptera								
- Proscopidae	2	2.80	2	0.05	1.5	0.03	2.20	0.05
- Others	14	20.00	27	0.72	30.5	0.68	34.50	0.88
Hymenoptera								
- Vespidae	2	2.80	4	0.11	1.0	0.02	0.70	0.01
- Formicidae	3	4.28	4	0.11	1.5	0.03	1.30	0.03
Blattaria	7	10.00	11	0.29	10.5	0.23	9.40	0.24
Odonata	1	1.40	1	0.02	0.5	0.01	0.30	Trace
Unidentified insects	9	12.85	154	4.12	8.5	0.19	6.40	0.16
<i>VERTEBRATES</i>								
Pisces	4	5.71	10	0.27	85.5	1.91	74.10	1.87
Amphibia-Anura	19	27.14	49	1.31	475.0	10.63	409.6	10.44
Reptilia								
- Serpentes	4	5.71	4	0.11	60.5	1.35	56.50	1.44
- Sauria	1	1.40	1	0.02	20.5	0.45	20.00	0.52
Aves adults	2	2.80	5	0.13	50.0	1.12	46.00	1.17
Aves eggs	1	1.40	1	0.02	68.0	1.52	56.00	1.42
Mammalia								
Rodentia	4	5.71	4	0.11	145.5	3.26	123.80	3.20
Unidentified vertebrate	1	1.40	1	0.02	1.0	0.02	0.50	0.01
TOTALS	-	-	3738	100.00%	4466.5	100.00%	3924.8	100.00%

TABLE 1. Composition of food records for 70 black tegu lizards examined. Volume is measured in cm³ and weight in g. Scientific names appear in Appendix 1. Trace = less than 0.01. Ad. = adults.

	Frequency		Number		Weight		Volume	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Plantae	7	100.0	2870	76.8	2986.1	66.8	2613.2	66.6
Invertebrates	68	97.1	793	21.2	574.4	12.9	525.1	13.4
Vertebrates	31	44.3	75	2.0	906.0	20.3	786.5	20.0
Totals	-	-	3738	100.0	4466.5	100.0	3924.8	100.0

TABLE 2. Composition of food records for 70 black tegu lizards summarized in the three greatest taxonomic groups.

family. The developmental stage of invertebrates was also recorded (e.g. larvae, adults).

Each digestive tract was processed in the manner reported by Korschgen (1980). After weighing and measuring the volume of the tracts, the contents were washed in tap-water over a 0.5 mm sieve that removed small particles. Items were separated by size, and the smallest were identified under a binocular dissecting microscope. For each food type, volume, mass and frequency (Pianka, 1971) were calculated.

Absolute frequencies represented the total number of lizards that contained a particular item and relative frequencies were based on the total number of the lizards in the sample.

Food items were sorted into the following categories; (1) trophic levels (producer, primary/secondary consumer, omnivore, detritivore) and (2) life-forms (aerial, arboreal, terrestrial). Data files were prepared for individual gut contents. These files were then randomly selected in order to determine a minimal sample representative of cumulative prey items (Margalef, 1980).

RESULTS

All digestive tracts of the 70 tegu lizards examined contained food. The incidence of "non-food" items was low except for parasites. One female contained a stone-like piece of compact red soil and this contributed 14.3% by weight (2 g) and 11% by volume (1.5 cm³) to food contents of that individual. Internal parasites were found in 69 animals (98.6%) and though most were located in the intestines, they were present throughout the alimentary canal. Parasitic load was 2.35 ± 1.84 g and 2.11 ± 1.83 cm³ per individual (Three percent was the percentage to total weight and volume).

Most prey items were undigested, which allowed individual identification and inclusion in the analysis. A few insects and vertebrates (flesh) were unidentified, which contributed to 0.16% and 0.01% of the total volume, respectively.

Table 1 lists thirteen invertebrate orders that can be identified into 19 lower taxonomic groups; 6 taxonomic groups for vertebrates, 13 fruit species, in addition to ootheca, seeds, plant material and other fruit.

Total diet mass consisted of 69% plant matter and 33% animal matter (Table 2). Almost identical percentages were found for the total diet volume, 66.5% plant matter, and 33.5% animal matter. Plant material (stems, leaves, and vegetation remains) was the most frequent item recorded (89.57%), followed by snails (68.57%), Coleoptera (52.85%), pindó fruits (32.85%) and anura (27.14%). Weight values revealed that, pindó fruit were most important with 26.8%, followed by palm fruits (11.5%), anura (10.63%), and mora (7.9%). Volumetrically, the spectrum is in the same decreasing order, but for total biomass consumed, vertebrates were more important than invertebrates.

Table 3 shows numerical, weight and volumetric values for trophic levels of the most assignable food items. *Tupinambis teguixin* feeds predominantly on producers. Primary consumers follow in numerical importance, but when weight/volume is considered, secondary consumers are more important than primary consumers. Predation on omnivorous species is not important in this lizard's diet.

Large proportions of the diet of *Tupinambis teguixin* are flying/arboreal invertebrates, but this does not suggest that the lizard feeds in arboreal situations. This species is predominantly terrestrial though some

	Number		Weight		Volume	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Primary producer	2870	79.6	2986.1	68.7	2613.2	66.5
Animal detritivore	39	1.1	101.0	2.3	188.0	4.7
Primary consumer	454	15.1	580.9	13.4	520.2	13.2
Secondary consumer	121	3.4	646.6	14.9	568.9	14.5
Omnivore	29	0.8	32.0	0.7	36.7	0.9

TABLE 3. Trophic levels of assignable prey items.

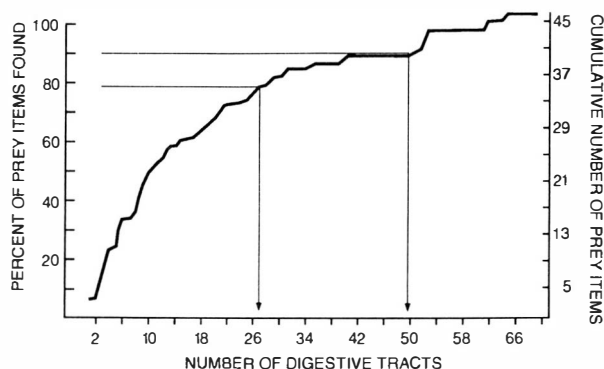


FIG. 1. Cumulative number and percentage of prey items found for *Tupinambis* diets. Arrows indicate the minimum sample sizes needed to estimate 80% and 90% of the diet.

arboreal habits have been reported by Yanosky (1991). In addition, all fruits found in stomachs of these lizards belong to trees with fruits that fall to the ground when ripe. Birds eaten by this lizard were tinamous chicks, probably eaten while in the nest. Tinamous are terrestrial and poor fliers. The lizards appear to be entering shallow waters to prey upon fish, crabs and snails. Snail shells with operculae were found intact in the gut.

Fig. 1 shows the percentages assignable to the total cumulative prey items. A sample of 27 specimens estimates 80% of items in the diet, while a sample of 49 specimens estimates 90%.

DISCUSSION

Tupinambis teguixin does not consume local crops as commonly believed and should not be considered a potential pest. Our data do not indicate that the species is a scavenger as suggested by Donadio & Gallardo (1984).

Measures of potential prey availability were not made because previous literature suggested the *T. teguixin* occupies an intricate position in the food web (Donadio & Gallardo, 1984). Based upon total food consumption by this lizard, it is clearly omnivorous. *Tupinambis* could be considered a "keystone" species because of its size and trophic level, for complete removal of it could have a cascading effect on the food web (Vitt, *in litt*). At our site *Tupinambis teguixin* is 71% herbivorous and 29% carnivorous. Lepidopteran larvae found within digestive tracts were all characterized by irritant hairs. We presume that this teiid is immune to any toxins released by the hairs of these larvae.

The foraging mode, related to prey eaten by lizards (rodents, lepidopteran larvae, spiders, beetles and anurans) suggests a broad foraging strategy as a means of obtaining food, a common feature of teiid lizards (Anderson & Vitt, 1990; Pianka, 1970). Foraging mode in these lizards is a primitive trait and the diet is a consequence of their foraging mode, body size, and prey availability where they are studied. All fruits recorded in this study (which fall when ripe) together

with flying insects that rest at ground level suggests that this species feeds on the ground, not in trees. In addition, presence of complete snail shells with operculae suggest that these items are ingested without chewing, as reported by Gudynas (1981).

In summary our analysis indicates that *Tupinambis teguixin* is a food generalist and omnivore, that feeds on medium and large-sized arthropods, vertebrates and vegetative parts (stems, leaves, but principally fruits). Principal food items (Petrides, 1975) were fruits, snails, coleopterans, lepidopterans, anura and rodents. Several other food items of very low frequency were also present, suggesting they are occasionally ingested by this opportunistic teiid lizard.

Finally, a sample of 50 specimens is required to obtain a spectrum representing 91% of the diet. Our data supports the national effort to cover major gaps in the biology of *Tupinambis* lizards as stated by Dirección Nacional de Fauna Silvestre (1991).

ACKNOWLEDGEMENTS

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APPENDIX 1

SCIENTIFIC NAMES FOR FRUIT-PLANTS MENTIONED IN THE TEXT.

Aguaý (*Chrysophyllum gonocarpum*: Sapotaceae)
 Cocú (*Allophylus edulis*: Sapindaceae)
 Coquito (*Trithrinax campestris*: Palmeras)
 Congorosa (*Maytenus ilicifolia*: Celastraceae)
 Granadilla (*Schinus longifolia*: Anacardiaceae)
 Guabiyú (*Eugenia pungens*: Mirtaceae)
 Higuera (*Ficus monckii*: Moraceae)
 Mora (*Chlorophora tinctoria*: Moraceae)
 Ñangapirí (*Eugenia uniflora*: Mirtaceae)
 Palma (*Copernicia alba*: Palmeras)
 Pindó (*Syagrus romanzoffianum*: Palmeras)
 Tala (*Celtis spinosa*: Ulmaceae)
 Tomatillo (*Solanum* sp.: Solanaceae)

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TREE AND SUBSTRATE SELECTION IN THE SEMI-ARBOREAL SCINCID LIZARD *EUMECES LATICEPS*

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Broad-headed skinks occupied a range of substrates during the daily activity period. Although they foraged and engaged in social behaviour on the ground, two-thirds of individuals were initially observed on trees and other vertical surfaces. In using both trees and ground as sites for foraging and social activities, these skinks are similar in microhabitat use to trunk-ground anoles. Substrate occupation differed significantly between adults and juveniles, adults occurring more frequently on oaks and ground, juveniles on walls, pine trees, and palmettos. Adult males and females had substantially, but not quite significantly different substrate distributions. The lizards occupied oak trees much more frequently than expected by chance, strongly preferring them to palmettos and pines. There is some evidence that they may actively avoid pines. No significant differences were detected in perch height among age and sex categories during the daily activity period, but sample sizes were small and differences might occur at other times of day or in other seasons.

INTRODUCTION

Numerous studies have been published on habitat selection among arboreal lizards in the polychrid genus *Anolis* (e.g. Rand, 1964, 1967; Andrews, 1971; Schoener & Schoener, 1971a,b). Most of these studies have dealt with differences in habitat distribution among species. Studies of the ecological distribution of arboreal lizards in the United States are few (e.g. Vitt, Van Loben Sels, & Ohmart, 1981); these also deal with differences in microhabitat among species. A group of North American lizards that contains species that tend to be arboreal, at least much of the time, is the scincid genus *Eumeces*. Here we report preliminary data on habitat selection in the broad-headed skink, *Eumeces laticeps*, studied in the southern part of its range during the breeding season in May and later in activity season in July.

Over its wide geographical range in the eastern United States, the broad-headed skink, *E. laticeps*, occupies forests having diverse soil types and moisture conditions (Cooper & Vitt, 1987a). This species forages on the ground and trees (Vitt & Cooper, 1986) and uses trees to escape from terrestrial predators, for shelter sites, and for nest sites. Here we provide data showing a strong preference for oaks and a preliminary characterization of the degree of arboreality, as indicated by perch height and types of substrates occupied by broad-headed skinks when first observed during the period of maximum daily activity.

METHODS

All observations were made on Kiawah Island, Charleston County, South Carolina between 1000 and 1530 hr (EDST) on 13-14 July 1982 and on 13 and 14 May 1983. The habitat was edificarian, consisting of a mixture of buildings, forest, and edge. To find lizards we walked slowly through each area once, attempting to carefully scan all trees, walls, ground, bushes, and other substrates in the area. Substrates on which lizards were observed were categorized as trees, other vertical surfaces such as walls, ground, and other. We also recorded perch height when first sighted for many individuals.

To obtain data to test the relationship between lizards and tree types, the number of large trees (diameter ≥ 15 cm) were counted in an open, wooded region of unmeasured area (approximately 2 ha) supporting a dense population of lizards on Seabrook Island, Charleston County, South Carolina on 13 May 1987. This area was a disturbed, largely cleared site surrounded by climax forest. After counting the trees, one of us surveyed the area once for skinks either on trees when first observed or fleeing to trees when disturbed, noting the types of trees for each lizard.

Significance of differences in (1) substrate types among age and sex groups and (2) occupation of tree species by lizards from randomness were assessed by chi-squared tests. We examined the data on perch height for differences between sexes and age groups of

lizards and between tree types by conducting Mann-Whitney U tests. All statistical tests were two-tailed with $\alpha=0.05$.

RESULTS AND DISCUSSION

SUBSTRATES OCCUPIED

Nearly two-thirds of broad-headed skinks were observed on trees and other vertical surfaces (sample sizes given in Fig. 1). Forty-two percent were on oaks and 22 percent were on other vertical surfaces, giving a total of 65 percent on trees and vertical surfaces during the daily activity period in May and July. The other 35 percent were on the ground. Our observations suggest that many adults spend the night in trees or logs and descend to the ground early in the daily activity period. During the day, the lizards move across the ground and climb trees other than the ones in which they spent the night. During June and early July, females spend most of their time in cavities of trees guarding their eggs (Vitt & Cooper, 1985). Broad-headed skinks are semiarboreal because much of their foraging and social behavior occurs on the ground (Vitt and Cooper, 1986; Cooper, unpublished data). However, most individuals, especially adults, spend their nights and a substantial fraction of their days in trees. *Eumeces laticeps* is similar in its relative use of ground and trees to the trunk-ground ecomorph of anoles (Williams, 1972, 1976).

Statistical association between lizards and substrate types could not be assessed because data on numbers and areas of the various types of substrates were not collected. However, it was possible to compare the distributions of substrate types occupied among age and

sex groups. Comparison of the distributions of adult males, adult females, and juveniles on substrates shows an apparently greater diversity of substrate types for juveniles (Fig. 1). If the 'other' substrate category is omitted and the pine, wall and palmetto categories are pooled to meet the requirements for minimal expected frequencies, there is a significant difference among the distributions for the age and sex categories ($\chi^2=12.74$, $df=4$, $P<0.05$).

The major difference is between adults and juveniles, with a greater proportion of juveniles being observed on the pooled wall, palmetto, and pine category, i.e. vertical surfaces other than oaks, and lower proportions of juveniles being found on oaks and on the ground (Fig. 1). The statistical test underestimates the true difference due to the higher proportion of juveniles than adults occurring on 'other' substrates. Observations in the other category were as follows: adult males, none; adult females, one in a snake's mouth; and juveniles, two trapped in spider webs, one on a grapevine, and one on a human body (it had crawled onto a person who was standing still). Predations by spiders, in a reversal of the predator-prey relationship between spiders and older immature and adult skinks, may be a major source of mortality to hatchling skinks.

Further examination of the data required additional pooling to attain the minimal expected cell frequencies for chi-squared tests. A comparison of male and female distributions was conducted using two substrate categories, ground and a pooled vertical category (all tree types and walls). Although the distributions differ substantially, they do not differ significantly ($\chi^2=4.56$, $df=1$, $P=0.07$). Even using the Fisher exact test, which is sometimes preferred with small sample sizes, the difference is not quite significant ($P=0.057$). It would not be surprising if a real difference were found using a larger sample size. Females tend to be warier and more difficult to catch than males, in part because they are more often on or close to trees when first observed (Cooper, Vitt, Hedges, & Huey, 1990).

Data for adults were pooled in the three substrate categories used in the initial analysis for comparison with data for juveniles. The pooled adult and juvenile distributions differ significantly ($\chi^2=7.42$, $df=2$, $P<0.05$). The major source of this difference is that juveniles are much more likely than adults to be found on vertical surfaces other than oaks, especially on walls and palmetto trees. When all vertical perches are pooled, including oaks, the distributions of adults and juveniles on vertical surfaces versus the ground do not differ significantly ($\chi^2=1.78$, $df=1$, $P>0.10$). Thus, the primary age difference in microhabitats is that juveniles use a greater diversity of vertical surfaces than adults, not in the tendency to be on the ground or on trees and other vertical surfaces. It is also likely that hatchlings use a greater variety of substrate categories, including some atypical for adults. However, the sample size is too small to test that hypothesis.

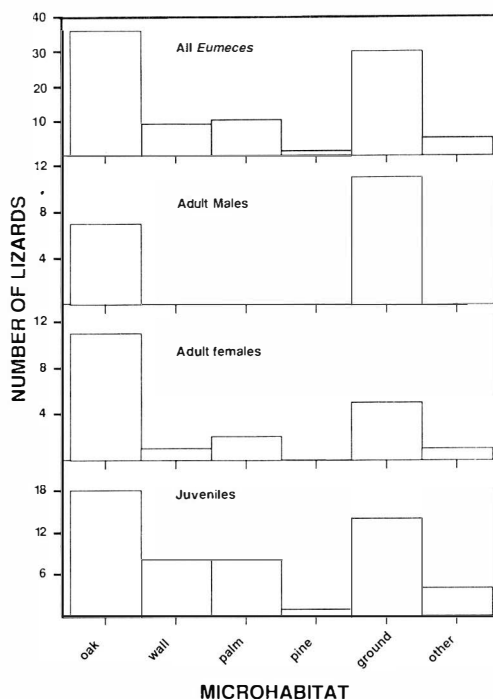


FIG. 1. Substrate types occupied by broad-headed skinks.

Possible reasons for the lower diversity of substrate types in adults include ontogenetic changes in preferences based on fixed developmental programs or learning by juveniles about the suitability of available microhabitats for feeding, climbing, avoidance of predators, etc. This could result in a gradual shift in substrate distribution as the skinks grow and suitable prey and perch sizes change. Another possible contributing factor is the elimination by predators of juvenile skinks that occupy atypical microhabitats.

TREE SPECIES OCCUPIED

At least in the southeastern part of its range, *E. laticeps* has been stated to be closely associated with hardwood trees (Cooper & Vitt, 1987b; Cooper, 1988), but this obvious association has not been demonstrated previously. At the study site there were numerous live oak trees (*Quercus virginiana*), palmettos (*Sabal palmetto*), pines (*Pinus sp.*), and one magnolia (*Magnolia sp.*, Table 1). The uncleared forest contained additional species. In the cleared area the vast majority of *E. laticeps* were initially observed on or fled to live oaks. This agrees with observations made over several years on Kiawah Island and Seabrook Island in both climax forests and partially cleared areas.

However the data are categorized, association between live oaks and lizards was very strong (Table 1). If the single magnolia is dropped from the analysis, leaving three tree categories, skinks were significantly more likely to be found on live oaks than on other trees ($\chi^2=36.81$, $df=2$, $P<0.001$). A slightly higher chi-squared was obtained when the data were analyzed with the single magnolia pooled with the live oaks ($\chi^2=37.84$, $df=2$, $P<0.001$). Lizards were also found at a significantly greater than chance frequency on hardwoods than on palmettos ($\chi^2=26.79$, $df=1$, $P<0.001$) or pines ($\chi^2=11.43$, $df=1$, $P<0.001$).

Taken strictly these data establish only that *E. laticeps* preferentially occupied oaks (hardwoods) in the area observed. However, the data substantiate our strong impression based on longterm observation at numerous sites that broad-headed skinks are found in close association with hardwoods. The precise basis for the preference remains to be determined, but two factors are clearly important: tree size and presence of refuges. The palmettos in the area observed were rela-

tively small, not much over 0.3 m in diameter, which in part may account for the low frequency of use by skinks.

Tree size may have contributed to the observed distribution because many of the live oaks and the magnolia were the largest trees on the site. In many of the largest trees there were holes that offered refuges from predators and potential nest sites. Later in the season, a skink brooding eggs was found in a humus-filled cavity in one of the oaks counted in this study. As both sexes of *E. laticeps* frequently may be observed basking, climbing, foraging, and using holes in oaks, it seems quite likely that the lizards actively select these trees. In contrast to their apparent attraction to oaks and perhaps other large hardwoods, broad-headed skinks may actively avoid pines. Only occasionally have we observed adults or juveniles on pines. On the study site there were numerous pines with diameters greater than those of some live oaks frequented by skinks. An anecdotal observation provides a probable reason for the low frequency of occupancy of pines. An adult male *E. laticeps* observed on 12 May 1987 on Kiawah Island moved from the ground toward a very large pine (diameter >0.75 m) as one of us (WC) slowly approached. The pine was the only tree within 15 m. The male began to climb slowly and with uncharacteristic awkwardness. Broad-headed skinks, including the male, typically climb trees in an upward spiral in the manner of squirrels when attempting to evade pursuing birds or human beings who move around the base. As the male climbed, its progress appeared to be somewhat obstructed by the deep channels between adjacent raised areas of bark. Before the male reached a height of 1 m, its claws failed to grip the slick surface of a raised section of bark, causing the male to fall to the ground. In thousands of observations of *E. laticeps* climbing other types of trees, we have seen no other falls. It is very likely that the surface of large standing pines simply is not suitable for efficient climbing by these lizards.

The situation is less clear for palmettos. In climax forests with large palmettos, we have observed broad-headed skinks climbing large palmettos to the crown while foraging and fleeing from predators. They climb these trees with more finely grained bark normally; they find refuge and may forage among the large leaves of the crown. Undisturbed broad-headed skinks often voluntarily climb palmettos, but appear to use them much less frequently than live oaks, presumably due to the larger size and presence of cavities suitable as refuges and nest cavities in oaks.

PERCH HEIGHT

Perch heights for both sexes of adults and juveniles on various substrate types are presented in Table 2. Perch heights of adult males and females did not differ significantly on oaks (Mann-Whitney $U=18.5$; $n=6, 10$; $P>0.10$). The perch height on oaks of pooled adults was

	Number of trees	Number of lizards
Oak	178	30
Magnolia	1	1
Palmetto	171	1
Pine	66	0

TABLE 1. Numbers of trees and associated *Eumeces laticeps* in an area cleared of underbrush.

	Oak	Wall	Palm	Pine	Ground	Other
Adult male						
$\bar{x}$	0.5	-	-	-	0.0	-
SD	0.3	-	-	-	0.9	-
Adult female						
$\bar{x}$	1.3	1.0	2.0	-	0.0	0.0
SD	1.0	-	0.0	-	0.0	0.0
Juvenile						
$\bar{x}$	1.1	1.4	0.7	1.8	0.0	0.1
SD	0.8	0.9	0.6	-	0.0	1.2

TABLE 2. Substrate types and perch heights (m) occupied by broad-headed skinks.

not significantly different from that of juveniles ($U=130.5$; $n=16$, 18 ; $P>0.10$). Perch heights of juveniles differed slightly on oaks and palms, but the difference did not quite attain significance ($U=53.5$; $n=8$, 18 ; $0.05<P<0.10$). These small samples over a restricted time do not reveal any differences in perch height among age-sex groups, but such differences may exist at other times of day and in other portions of the activity season.

The time of day may have strongly affected the observations of perch height and substrate type because our impression is that broad-headed skinks frequently bask at greater perch height shortly after emergence in the morning before beginning to forage. Shortly after basking on warm days, broad-headed skinks climb down to the ground, where they forage. Therefore, the percentages observed in trees and on the ground vary with time of day. The limited samples also fail to reveal the entire range of perch heights at midday because we have observed adults of both sexes in trees at heights well over 10 m.

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SHORT NOTES

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TROPHIC NICHE OVERLAP IN
SYMPATRIC *TARENTOLA*
MAURITANICA AND *HEMIDACTYLUS*
TURCICUS: A PRELIMINARY STUDY

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The historical centre of Rome is inhabited by two species of gekkonid lizards, *Tarentola mauritanica* and *Hemidactylus turcicus*. These species are sympatric in many areas situated within the urban city centre, and are especially common in the archeological sites with roman age monuments. Because data on the ecology of sympatric populations of these species are absent from the scientific literature, we have carried out field research in order to provide preliminary information on this subject.

The research was conducted between May and September in three very famous archeological areas situated within the centre of Rome: (1) "Roman Forum", (2) "Colosseum", and (3) "Caracalla's Thermae". Areas (1) and (3) were generally sampled in the morning, and area (2) after the sunset.

Data coming from the three localities were pooled because there was not any significant difference either in relative abundance and activity, or in diet composition of lizards (in all cases, overlap between diets of two different population of the same species was >0.95, according to Pianka's (1973) equation).

Geckos were located above-ground (i.e. while basking or climbing on the ancient walls - often in the vicinity of artificial lights - after sunset), or more rarely, below-ground (i.e. while under stones during daylight).

When a lizard was found, it was captured by hand, identified to species, measured for snout-vent length (SVL), and analysed for any food item by collection of faecal pellets. Faecal pellets were collected by placing the geckos into small cages until defaecation occurred. We did not collect any faecal pellets from the soil. Seven *T. mauritanica* and three *H. turcicus*, which were found dead in the field (killed by man and cats), were dissected in order to obtain more food items. After dissection, these specimens were placed in 70% ethanol and deposited in the herpetological collection of one author (LL). Lizards were marked by toe-clipping and set free at the exact capture point. Laboratory examination of both faecal pellets and stomach contents of the few specimens found dead permitted identification (to the lowest taxon possible) of prey eaten by such lizards.

Niche overlap between species was calculated by using Pianka's (1973) symmetric equation (parameter *O*), which yields values ranging from 0 (no overlap) to 1 (total overlap).

In the text the term "fed animals" defines the total number of geckos from which faecal pellets were obtained, plus the total number of geckos found dead with prey in the stomachs.

During our study we examined a total of 243 *Tarentola mauritanica* and 51 *Hemidactylus turcicus*, obtaining 238 and 46 fed animals, respectively. Almost all *H. turcicus* were found after sunset, while *T. mauritanica* showed a diurnal active phase also, though it was more frequently found under sunset. The sample of 243 captures of *T. mauritanica* comprised 167 different individuals, several of which (*n*=24) were recaptured for a total of 76 times. The sample of 51 *H. turcicus* comprised 39 different individuals, of which some specimens (*n*=7) were recaptured a total of 12 times. In most cases, the above-ground *T. mauritanica* were seen while climbing on vertical surfaces (83.9% of the total above-ground sample [*n*=47]). The frequencies of specimens found while climbing on vertical surfaces did not differ significantly between species (χ^2 - test, 2 x 2 contingency table, $\chi^2 = 0.05$, *P*>0.5).

From 238 *T. mauritanica* fed animals we obtained a total of 367 food residues (29 out of which remained unidentified). With regard to *H. turcicus*, we examined a total of 46 fed animals, obtaining 147 food items (31 out of which remained unidentified).

Prey	<i>T.m.</i>		<i>H.t.</i>	
	<i>N</i>	<i>N%</i>	<i>N</i>	<i>N%</i>
Arachnida	97	28.7	22	19.0
Salticidae	24		6	
Thomisidae	31		10	
Lycosidae	3		-	
undetermined	39		6	
Chilopoda	1	0.3	-	
Diptera	83	24.6	21	18.1
Coleoptera	41	12.1	27	23.3
Carabidae	6		2	
Scarabaeidae	4		2	
Curculionidae	5		3	
Tenebrionidae	7		7	
undetermined	19		13	
Homoptera	16	4.7	10	8.6
Lepidoptera	39	11.5	21	18.1
Formicidae	61	18.1	15	12.9

TABLE 1. List of the food items obtained from faecal pellets of *Tarentola mauritanica* (*T.m.*) and *Hemidactylus turcicus* (*H.t.*).

The data given here show that both species feed mainly on arthropods, like several gekkonid species living in other environments (e.g. see Dial, 1978; Pianka & Huey, 1978; Pianka, 1986; Perry & Brandeis, 1992). Both species preyed on the same taxonomic groups (see Table 1), and the diet composition was, on the whole, extremely similar ($O=0.92$). Arachnida, Diptera, Coleoptera, Lepidoptera and Formicidae were common prey items in both *T. mauritanica* and *H. turcicus*. The most relevant characteristics of the diets of either species, however, were: (1) the frequent occurrence of Thomisidae and Salticidae spiders (this finding, though empirically rather predictable, has not been shown previously); (2) the absence of web-spinning spiders and Orthoptera; (3) the relatively high values for ants and flightless insects, representing 59.2% of the diet of *Tarentola mauritanica*, and 55.2% of the diet of *Hemidactylus turcicus*. The diet composition of both *T. mauritanica* and *H. turcicus* indicated a diet based primarily on terrestrial prey, and was relatively similar to *T. mauritanica* populations from the Iberian peninsula, Balearic and Chafarinas islands (Gil *et al.*, 1991). These latter populations were shown to prey on the same major taxonomic groups that were preyed on by our gecko populations in Rome. Moreover, our data seem to indicate that both species are not very selective predators, though the lack of information on the abundance of potential prey types in our study areas makes it impossible to state any firm conclusion on this subject. Individual differences in food habits seem to be rather small in these species (Capula & Luiselli, unpublished data), but this will be analysed in more detail in a further paper.

In conclusion, further studies on sympatric *T. mauritanica* and *H. turcicus* should be done in order to

demonstrate if a strong interspecific competition occurs between these two species. However, the basic conditions needed for the existence of interspecific competition, i.e. identical spatial distribution, very similar activity patterns (Capula & Luiselli, unpublished data) and very similar diet composition (this study), seem to be present, at least in sympatric geckos of the archeological areas of Rome

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BOOK REVIEWS

Snake Life History in Kyoto. Hajime Fukada. (1992). 171 pp. Impact Shuppankai Co. Ltd., Tokyo. (cloth).

Halfway between Tokyo and Hiroshima lies the city of Kyoto, the home of Hajime Fukada, Professor Emeritus and former president of the Herpetological Society of Japan. Cursed with a life-long passion for snakes, Fukada has explored many diverse aspects of serpentine biology, ranging from gland histology to population ecology. Despite having already produced some seventy scientific publications regarding snakes, his tireless studies have further yielded a vast amount of original data and observations which "became too bulky to contribute to journals, and this volume is the result".

Snake Life History in Kyoto reflects the author's comprehensive approach to snake research: topics include the activity patterns of wild snakes, ontogenetic and interspecific comparisons of food habits, growth rates, thermoregulation, locomotion, hibernation and even "peculiar habits". There is, however, little reference to previously published reptile studies in Japan or elsewhere, as Fukada is using this book primarily as a forum for presenting his own detailed observations.

Much of his data derives from a sixteen-year field study of a local free-living community which is predominantly comprised of *Rhabdophis tigrinus*, three *Elaphe* species and *Amphiesma vibakari*. Fukada and his students made up to 244 collecting trips per year in order to monitor these snakes' growth, stomach contents, spatial distribution, survivorship etc. (One hopes that such intensive scientific attention did not influence the community's natural behaviour in any way). A sizeable population of captive snakes provided the opportunity to record behaviours which are difficult to monitor in the field, such as delayed fertilization and the effects of temperature on incubation. The captive population also provided the hatchlings for a bold investigation into dispersal, survivorship and growth of free-living juvenile snakes.

He admits that the methods he employed may seem "classic and out of date", but they do provide some unique insights. For example, he notes dramatic shifts in the diet of *Elaphe quadrivirgata* which were dictated by changing farming practices. This species appears to preferentially consume frogs, but switched its attention to voles when a local decline in artificial irrigation reduced frog numbers. Human activity can also affect the abundance of snakes: it was distressing to note that Fukada's description of the 1960's environmental degradation of his study area is followed by a figure charting the gradual decrease in the size of its snake community.

The text is lucid and packed with information, but a considerable proportion of page-space is devoted to

numerous graphs and tables of almost-raw data. Whilst it is satisfying to note that the sample sizes are consistently large enough to lend statistical credibility to Fukada's findings, the book might have become more reader-friendly had some of the data been consigned to appendices at the back. I would also liked to have seen rather more discussion about the significance of some of the observations. There was no explanation, for example, put forward to explain the pattern of seasonal abundance of all species.

Leaving those criticisms aside, *Snake Life History in Kyoto* is a worthy investment for herpetologists interested in Japanese snakes, and provides useful reference material for ecological studies. Furthermore, small children and eminent herpetologists alike will doubtless enjoy the snake silhouette on every page - if the book is read quickly enough, this snake (species unidentified) is seen to wriggle determinedly up and down the outer margins.

Jennifer Daltry

University of Aberdeen

A Fieldguide to the Amphibians and Reptiles of Madagascar. Frank Glaw & Miguel Vences. (1992). 331 pp. Miguel Vences & Frank Glaw Verlags GbR, Cologne. DM 78, Europe; DM 88, outside Europe (paper).

Madagascar lies just 400 km east of the African coast and is the world's fourth largest island. Its long isolation has resulted in a unique assemblage of plants and animals and as many as 95-99% of the country's amphibians and reptiles may be endemic, occurring nowhere else in the world. Thus, a comprehensive field guide to the herpetofauna of Madagascar has been long awaited and although this present publication only partially fills that role, it is a very worthwhile addition none-the-less.

The authors concede that the book is primarily an identification guide to frogs, with only a brief introduction to the Malagasy reptiles. However, what a guide to frogs it is! The authors have succeeded in producing detailed keys and identification tables based wholly on the external characteristics of live animals. Therefore, albeit with some practice, the reliable identification of almost all life stages should be possible - I remain dubious about the identification of recent metamorphs, which could be confused with smaller species. Also included is a guide to the important features used for frog determinations, therefore simplifying the use of tables and keys. These identification features, which include colour, size, finger discs, nuptial pads, tubercles etc., are well described and, where necessary, illustrated by simple but adequate line drawings.

The main body of the book is taken up by species descriptions. These cover all of the known species and include information on distribution, appearance, habits,

eggs and tadpoles, calls and similar species. Each genus has its own general description together with both an identification table and a detailed key. Whilst these chapters are both informative and well written, I feel that the keys would have benefited from the addition of simple line drawings to clarify difficult couplets.

The section on Malagasy reptiles is, as the authors readily admit, basically an introduction, but a very good one at that. Even though the species descriptions do not provide reliable identifications they are still detailed, following a similar structure to that described for the frogs.

Appendices include taxonomic information, type descriptions and full species lists, including the locations of museums where type specimens are held. Additionally there are several pages devoted to sonograms and oscillograms, which could further aid identification to those with the appropriate sound equipment. Unfortunately however, these latter diagrams are not very clearly linked in with the species description chapters, other than by species name. Whilst the authors claim that the reference list may be missing important papers, I found it to be extremely comprehensive and an excellent start point for those interested in Malagasy herpetofauna.

Finally, the book also contains some 127 colour plates and even though these are not of the best quality, they certainly do reveal the fantastic herpetofaunal diversity that exists on this threatened micro-continent.

In conclusion, what this book offers is a comprehensive identification guide to the frogs of Madagascar, together with a less detailed introduction to the reptiles and a short, but informative, section on conservation. The fact that the authors have taken it upon themselves to publish this book also deserves much credit although their suspicion that only a small number of people are interested in Malagasy frogs and therefore this book is, I hope, unfounded.

Lee D. Brady
University of Kent

ANNOUNCEMENTS

The following applications were published on the 30 September 1993 in Vol. 50, Part 3 of the *Bulletin of Zoological Nomenclature*. Comment or advice on these Applications are invited for publication in the *Bulletin*, and should be sent to the Executive Secretary, I.C.Z.N., c/o The Natural History Museum, Cromwell Road, London, SW7 5BD, UK.

Case 2868

***Hydromantes* Gistel, 1848 (Amphibia, Caudata): proposed designation of *Salamandra genei* Temminck & Schlegel, 1838 as the type species**

Hobart M. Smith. *Department of Environmental, Population and Organismic Biology, University of Colorado, Boulder, Colorado 80309-0334, USA.*

David B. Wake. *Museum of Vertebrate Zoology, University of California, Berkeley, California 94720, USA.*

Abstract. The purpose of this application is to conserve the usage of the name *Hydromantes* Gistel, 1848 for a group of five species of salamanders (family Plethodontidae Gray, 1850) from the mountain areas of north-central and western Italy and southern France; Sardinia; and the mountains of northern and central California, USA. *Hydromantes* is a replacement name which, with one exception (in 1984), has consistently been used during the past 70 years. It is proposed that *Salamandra genei* Temminck & Schlegel, 1838 be designated the type species, in accordance with understanding and usage.

Case 2873

***Emys* Duméril, 1806 (Reptilia, Testudines): proposed conservation**

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Abstract. The purpose of this application is the conservation of the turtle generic name *Emys* Duméril, 1806. This has the senior synonym *Emydes* Brongniart, [1805], which has not been used as a valid name and of which suppression is sought. The type species of *Emys* is *Testudo lutaria* Linnaeus, 1758, long treated as a junior synonym of *Emys orbicularis* (Linnaeus, 1758), the European pond turtle.

THE HERPETOLOGICAL JOURNAL

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(revised January 1992)

1. The *Herpetological Journal* publishes a range of features concerned with reptile and amphibian biology. These include: full papers (no length limit); reviews and mini-reviews (generally solicited by a member of the editorial board); short notes; controversies, under 'Forum' (details available from the Editor); and book reviews. Faunistic lists, letters and results of general surveys are not published unless they shed light on herpetological problems of wider significance.
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3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer (at least near-letter quality, avoid worn ribbons), and double-spaced with wide margins all round. Typesetting is greatly assisted if accepted manuscripts can be supplied on microcomputer diskettes. Authors are therefore strongly encouraged to produce manuscripts using a wordprocessor (preferably on a PC-compatible microcomputer).
4. For all papers the title page should contain only the following: title of paper; name(s) of the author(s); address of the Institution where the work was done; a running title of 5 words or less. The text of the paper should begin on page 2 and be produced in the following order: Abstract, Text, Acknowledgements, References, Appendices. Full papers and reviews should have the main text divided into sections. Short notes (generally less than six manuscript pages and accompanied by a single data set) should be produced as continuous text. The first subhead will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted.
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only be included at cost to the author. If an illustration has more than one part each should be identified as (a), (b), etc. The orientation and name of the first author should be indicated on the back. They should be supplied camera-ready for uniform reduction of one-half on A4 size paper. Line drawings should be drawn and fully labelled in Indian ink, dry-print lettering or laser printed. A metric scale must be inserted in micrographs etc. Legends for illustrations should be typed on a separate sheet.

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Bellairs, A. d'A. (1957). *Reptiles*. London: Hutchinson.

Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared terrapins (*Pseudemys scripta elegans*) in the laboratory. *British Journal of Herpetology* 2, 206–210.

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9. Final acceptance of a paper will depend upon the production by the author of a typescript and illustrations ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.
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