Life on the Lowest Branch: Sexual Dimorphism, Diet, and Reproductive Biology of an African Twig Snake, *Thelotornis capensis* (Serpentes, Colubridae)

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Measurement and dissection of 144 twig snakes (*Thelotornis capensis*) from southern Africa provided data on morphology, sexual dimorphism, food habits, and reproductive biology of this species. Twig snakes are extremely elongate arboreal species that remain immobile for long periods and ambush passing vertebrates. Both sexes attain sexual maturity at about 60 cm snout–vent length, at around three years of age [based on growth rates from Jacobsen's (1980) mark-recapture study]. Maximum size is about 80 cm SVL in both sexes, and this lack of size dimorphism is consistent with published reports of male-male combat in this taxon. Males have longer tails, smaller heads, and thinner bodies (and hence, weigh less) than do females at the same body length. Reproductive cycles are highly seasonal in both sexes. Testes in adult males are turgid in spring (the mating season) but flaccid over most of the rest of the year. Females undergo vitellogenesis in spring, ovulate in late spring, and oviposit in summer. Clutch sizes ranged from 4–7 eggs, with a mode of 6.

The diet of *T. c. capensis* is diverse: of 56 prey items, most were lizards (63%), frogs (27%), and snakes (8%). Only a single bird was recorded in a dissected twig snake. Approximately half of all prey items were arboreal taxa (e.g., chamaeleons, dwarf day geckos), with the rest being terrestrial in habit (e.g., brevicepid frogs). Thus, we infer that *T. capensis* often forages from a relatively low perch, which enables it to detect and seize terrestrial as well as arboreal prey. An ontogenetic increase in the proportion of terrestrial prey was evident, but even the largest snakes took many arboreal prey items. Larger snakes took larger prey, and the relationship between prey size and snake body length differed between the sexes, in concert with the observed sexual dimorphism in relative head size. Our results generally agree with those of previous studies on the biology of twig snakes; the most surprising result from our work is that a snake with extreme morphological and behavioral modifications for arboreal life nonetheless feeds to a large degree on terrestrial prey.

ONE of the most remarkable examples of convergent evolution in reptiles involves extremely slender arboreal "vine snakes" from four distantly related colubrid lineages. These four genera (*Ahaetulla* in Asia, *Oxybelis* and *Uromacer* in the neotropics, and *Thelotornis* in Africa) have independently evolved a bizarre suite of traits that includes modifications of morphology (elongation of the head and body, cryptic coloration, large eyes, binocular vision) as well as behavior (diurnality, prolonged immobility, rigid tongue extension, lateral head-swaying, reliance on ambush predation). These distinctive features of vine snakes may be adaptations for the detection and capture of active prey on unstable substrates such as leaves, twigs, and branches (Henderson and Binder, 1980). Available data indicate strong ecological similarities among all four genera of vine snakes (especially, specialized diets based on small agile arboreal lizards), but anecdotal reports suggest that the African taxon (*Thelotornis*) differs significantly from the other genera in dietary composition, as well as in being venomous (Henderson and Binder, 1980). Information on the ecology of *Thelotornis* thus may illuminate the adaptive significance of vine snake morphology and behavior, as well as clarifying the ecological correlates of arboreality in snakes (Shine, 1983; Lillywhite and Henderson, 1993).

MATERIALS AND METHODS

This paper provides information on the morphology, diets, and reproductive biology of one species of vine snake (the twig snake, *Thelotornis capensis*) in southern Africa, based on measurements and dissections of preserved specimens in the collections of the Transvaal Museum and the Port Elizabeth Museum, Republic of South Africa. Most of the specimens we examined belonged to the subspecies *Thelotornis capensis ca-*

pensis and came from the Transvaal, Natal, Zululand, and Swaziland. Additional data on diet and reproduction came from four specimens of *Thelotornis capensis oatesii* collected in Zambia. The northern regions of South Africa inhabited by *Thelotornis* mainly comprise savannah woodland (commonly called bushveld or moist woodland). This habitat type merges into mopane veld along the Limpopo Valley, arid woodland in eastern Swaziland, and the thicket of the Indian Ocean Coastal Belt in northern Natal. Together, these habitats comprise the Kalahari-Highveld regional transition zone and the Tongala-Pondoland regional mosaic of White (1983). All of these veld types are covered by scrub woodland (dense, but rarely closed-canopy), with most larger plants approximately 7 m high. The climate is subtropical, typified by hot wet summers and mild dry winters, except at higher elevations. Winter (July) mean minima average around 6–10C, and summer (Jan.) maxima average approximately 27–32C (Schultze and McGee, 1978). Annual rainfall averages 350–1000 mm, decreasing to the west, and falls mainly as intense thunderstorms between Oct. and April (Jacobsen, 1980).

Preserved specimens of *T. c. capensis* (45 adult females, 33 adult males, and 62 juveniles) were measured and dissected, as follows. We recorded snout–vent length (SVL), tail length, head length (from the posterior margin of the lower jaw to the tip of the snout), head width (at the widest point), eye diameter, body width (diameter at midbody), and body mass. The specimen was opened with a midventral incision, and any prey items in the alimentary canal (including the hindgut) were removed for later identification and measurement. Sizes of relatively undigested prey (lengths, widths, masses) were determined directly, and reconstituted sizes of more fully digested prey items were determined by comparison with similar-sized intact specimens in the collection of the Port Elizabeth Museum. Sex and reproductive status of the snakes were determined by visual inspection of the gonads. Males were considered mature if they had enlarged, turgid testes and/or white, thickened efferent ducts (indicating the presence of sperm). Females were classed as mature if they had thick muscular oviducts, vitellogenic ovarian follicles, and/or oviductal eggs.

RESULTS

Sexual dimorphism.—Sex differences in adult body lengths were negligible. Both sexes attained sexual maturity at slightly less than 60 cm SVL and grew to around 80 cm SVL (Table

TABLE 1. SAMPLE SIZES AND SEXUAL DIMORPHISM OF ADULT TWIG SNAKES, *Thelotornis c. capensis*, EXAMINED IN THE TRANSVAAL MUSEUM AND THE PORT ELIZABETH MUSEUM. SVL = snout–vent length. See text for statistical tests.

Trait	Adult males	Adult females
Sample size	32	42
Range of SVLs (cm)	58–80	59.5–82.5
Mean SVL (cm, ± SD)	69.0 (± 6.47)	71.3 (± 5.91)
Range of head lengths (mm)	27.1–36.3	28.8–38.0
Mean head length (mm, ± SD)	31.3 (± 2.57)	33.3 (± 2.31)
Range of head widths (mm)	9.9–15.6	11.5–18.3
Mean head width (mm, ± SD)	13.6 (± 1.60)	14.4 (± 1.84)
Range of body widths (mm)	8.4–14.6	9.0–17.3
Mean body width (mm, ± SD)	10.9 (± 1.71)	12.0 (± 1.66)
Range of tail lengths	35.4–50.5	31.0–48.4
Mean tail length (cm, ± SD)	41.8 (± 4.36)	39.8 (± 3.67)
Range of body mass (g)	37–180	49–130
Mean body mass (g, ± SD)	77.2 (± 33.1)	80.4 (± 18.2)

1). Mean body lengths thus did not differ significantly between the sexes (unpaired $t = 1.62$, 72 df, $P = 0.11$). However, our data showed significant differences in body proportions between the sexes. Analysis of covariance, with sex as the factor and SVL as the covariate, showed that males had longer tails than did females at the same SVL (Fig. 1; slopes homogeneous $F_{1,37} = 0.31$, $P = 0.58$; intercepts $F_{1,38} = 25.90$, $P < 0.0001$). Similarly, males had smaller heads than did females of equivalent body lengths (Fig. 1; slopes homogeneous $F_{1,44} = 0.02$, $P = 0.88$; intercepts $F_{1,45} = 22.69$, $P < 0.0001$) and weighed less than did females at the same length (ln mass vs SVL: slopes heterogeneous $F_{1,32} = 5.08$, $P < 0.032$). No sex difference was apparent in relative head width (slopes homogeneous $F_{1,33} = 0.80$, $P = 0.38$; intercepts $F_{1,34} = 1.24$, $P = 0.27$), relative body width (slopes homogeneous $F_{1,32} = 3.38$, $P = 0.08$; intercepts $F_{1,33} = 2.45$, $P = 0.13$), or relative eye diameter (slopes homogeneous $F_{1,32} = 0.30$, $P = 0.59$; intercepts $F_{1,33} = 0.01$, $P = 0.94$).

Because of these sex differences in body proportions, adult males and females differed significantly in mean values for head length (Table

Fig. 2. Seasonal variation in sizes of the largest ovarian follicles (circles) and oviductal eggs (dots) in twig snakes, *Thelotornis capensis*.
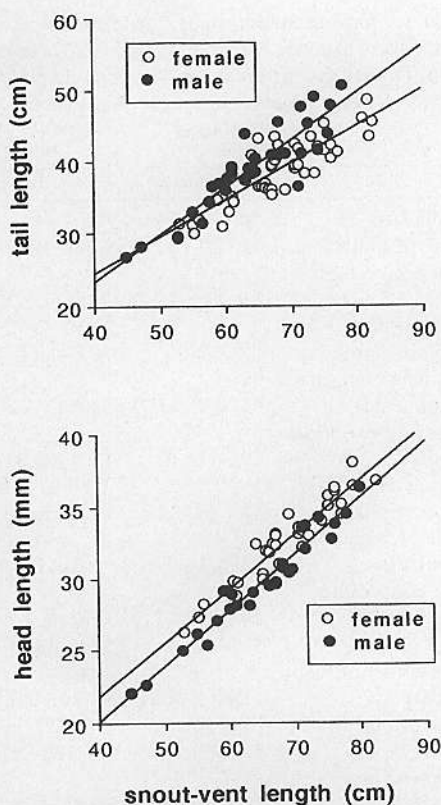

Fig. 1.   Sexual dimorphism in twig snakes, *Thelotornis capensis*. Compared to conspecific males, female twig snakes have shorter tails relative to body length (upper graph) and larger heads relative to body length (lower graph). Lines are fitted by least-squares regression. See text for statistical results.

1: unpaired t = 2.74, 47 df, $P < 0.01$) and body width (t = 2.29, 47 df, $P < 0.03$: note that the relevant ANCOVA reported above was close to statistical significance). Mean tail lengths did not differ significantly between the sexes (Table 1: t = 1.77, 53 df, $P = 0.08$), because of two opposing factors: males averaged slightly shorter in SVL but had longer tails relative to body length.

Reproductive biology.—Four females contained oviductal eggs with thick shells, indicating oviparity. Three of these animals each contained six eggs, and the third had seven. The eggs ranged from 28 × 10 mm to 34 × 14 mm in size, and averaged approximately 30 × 12 mm (2.8 g). Relative clutch mass (RCM) was estimated for one female that oviposited shortly before being killed and preserved (Transvaal Museum # 63629). This snake measured 67 cm
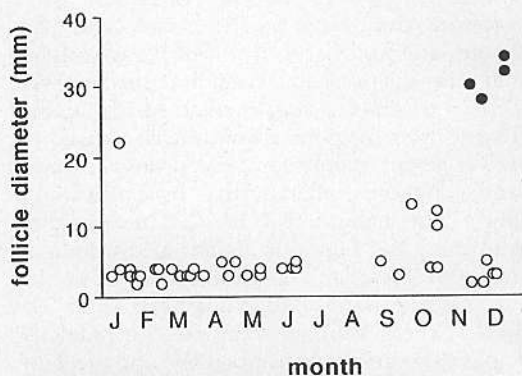
SVL and weighed 65 g; it produced six eggs weighing 4.9–5.3 g (Haagner and Els, 1987). Thus, we estimate RCM as $30.6/65 = 0.47$ (or, if clutch mass is included in the denominator as well as the numerator, 0.32). Another captive female that laid 10 eggs had a much higher RCM (0.94: G. Haagner, pers. comm.). Four other adult females contained vitellogenic ovarian follicles > 10 mm in length, with probable clutch sizes of six (three animals) and four (one animal). All of these reproductive females were collected over the period Sept. to Jan.: ovarian follicles were < 6 mm in all specimens collected in the rest of the year (Fig. 2). Thus, female reproductive cycles are synchronous and highly seasonal. In contrast, three adult female *T. c. oatesii* collected in winter (July) in Zambia had large vitellogenic follicles (maximum diameters 16–27 mm), suggesting that reproduction may commence earlier (or extend year-round) in this tropical region. Of 13 adult female *T. c. capensis* collected over the period Oct. to Dec., when we could class them unequivocally as either reproductive or nonreproductive, only seven showed vitellogenic follicles or oviductal eggs (Fig. 2). Hence, it seems that adult females of this race may reproduce less than annually.

All adult males collected in spring (Sept.–Oct.) had turgid testes, and their efferent ducts contained abundant sperm. Most of the males collected at other times of year had flaccid testes, with no sperm in the efferent ducts. However, we recorded turgid testes and sperm in some males collected in late winter. Occasional males collected in late spring (Nov.) and early summer (Dec.) also contained sperm in the efferent ducts but had small flaccid testes. These data suggest that male reproductive cycles in *T. capensis* are strongly seasonal, with testicular recrudescence

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in winter, spermiation in early spring, and testicular regression in late spring.

Seasonal distribution of captures.—Collection data indicated that the twig snakes in museum collections had been collected throughout the year, with no obvious bias towards a particular season (n = 2–16 snakes per month). Contingency table tests showed that the numbers of snakes collected did not deviate significantly from the null hypothesis of equal proportions of captures in each season (spring Sept. to Nov., summer Dec. to Feb., autumn March to May, winter June to Aug.: $\chi^2 = 6.84$, 3 df, $P = 0.07$) and that the relative numbers of juvenile vs adult snakes were approximately constant throughout the year ($\chi^2 = 3.40$, 3 df, $P = 0.33$). However, the proportion of collected snakes that contained identifiable prey items in their alimentary tracts was lowest in winter (three of 19 snakes) and highest in summer (18 of 37) and showed significant monthly variation ($\chi^2 = 22.7$, 11 df, $P < 0.02$).

Food habits.—Fifty-six prey items were removed from 50 *T. c. capensis* and in approximately equal proportions from adult males (11 of 33 snakes) and adult females (21 of 45). These data do not suggest any difference in feeding frequency between the two sexes ($\chi^2 = 0.09$, 1 df, $P = 0.77$) or between adults (32 of 78 snakes) and juveniles (18 of 63; $\chi^2 = 0.81$, 1 df, $P = 0.37$). Most *T. c. capensis* with prey contained only a single identifiable item, but six snakes contained two prey items each. Of these six, one contained two chamaeleons (*Bradypodion setaroi*) and one a skink (*Mabuya striata*) and a gecko (*Lygodactylus capensis*). The other four *T. c. capensis* with multiple prey items each contained a squamate reptile and an amphibian (and see below for multiple prey in *T. c. oatesii*).

Table 2 shows that the diet of *T. c. capensis* is very diverse and is composed primarily of lizards (63%), frogs (27%), and snakes (8%). Only a single bird was recorded (Table 2). However, the lizards consumed ranged from slow-moving arboreal taxa (chamaeleons) to fast-moving terrestrial species (e.g., *Nucras*; Table 2). The frogs were similarly diverse, with treefrogs (*Chiromantis*) as well as fossorial species (*Breviceps*; Table 2). Approximately equal numbers of arboreal and terrestrial prey were taken, and no sex difference was evident in this respect. The nonvertebrate items we recorded in guts (Table 2) were small and probably taken as secondary prey. However, the hindgut of one adult twig snake (SVL 66 cm) contained large numbers of termite alates, with no obvious vertebrate remains.

TABLE 2. Prey Items Identified from Alimentary Tracts of Preserved Twig Snakes, *Thelotornis c. capensis.*

Prey species	Number of prey items	Number of snakes containing that prey type
Frogs		
Frog sp.	4	4
Brevicepidae		
Breviceps sp.	2	2
Breviceps adspersus	3	3
Ranidae		
Tomopterna cryptotis	1	1
Rhacophoridae		
Chiromantis xerampelina	3	3
Lizards		
lizard sp.	1	1
Agamidae		
Acanthocerus atricollis	1	1
Agama aculeata distanti	1	1
Chamaeleonidae		
chamaeleon sp.	1	1
Bradypodion setaroi	4	3
Chamaeleo dilepis	3	3
Gekkonidae		
gecko sp.	1	1
Lygodactylus capensis	6	6
Lacertidae		
Nucras ornata	1	1
Scincidae		
skink sp.	3	3
Mabuya sp.	2	2
Mabuya depressa	3	3
Mabuya striata punctatissimus	1	1
Mabuya striata striata	1	1
Mabuya varia	1	1
Varanidae		
Varanus albigularis	1	1
Snakes		
Colubridae		
colubrid sp.	1	1
Duberria lutrix	1	1
Lycodonomorphus rufulus	1	1
Philothamnus hoplogaster	1	1
Bird		
Vidua regia (shaft-tailed whydah)	1	1
Other		
Termite alates	1	1
Insect remains	4	4
Plant material	1	1
Soil and debris	2	2

Although these may have been primary prey (note a similar record by Loveridge, 1953), we chose to omit these items from our analyses.

Three of the four *T. c. oatesii* from Zambia also contained prey. One of these snakes had a *Chamaeleo dilepis* and a large grasshopper in the stomach and snake scales in the lower gut; another had skink scales in the gut; and the third contained a chamaeleon and an adult *Gerrhosaurus multilineatus*.

Many of the prey items were large relative to the size of the predator. For 21 prey items for which we recorded both snake mass and prey mass, the relative prey mass averaged 19% (SD = 16%), with a range from 1–50%. This ratio was not correlated with absolute size of the snakes (vs SVL: n = 21, r = 0.25, P = 0.27). Most prey items were swallowed headfirst (34 of 38 items for which direction of ingestion could be determined, = 90%).

An ontogenetic shift in prey types and prey sizes was evident. Small twig snakes fed exclusively on lizards (snakes < 50 cm SVL contained five dwarf day geckos, one chamaeleon, and one skink) whereas larger snakes had a more diverse diet. Contingency-table analysis showed significant differences in relative numbers of reptiles vs frogs in twig snakes of different 10-cm SVL classes (χ^2 = 13.37, 5 df, P < 0.021). Prey sizes also shifted with increasing size of the snake. Juvenile twig snakes ate smaller prey items than did adult conspecifics, in terms of both length (mean for juveniles = 39.9 mm SVL, SD = 15.2, n = 15, vs mean for adults = 109.9 mm, SD = 107.6, n = 14; unpaired t = 2.49, 27 df, P < 0.02) and mass (mean for juveniles = 4.3 g, SD = 4.4, n = 9, vs mean for adults = 13.4 g, SD = 8.85, n = 12; unpaired t = 2.83, 19 df, P < 0.011).

No differences in dietary composition were apparent between adult males and females (4 × 2 contingency table, using major prey categories: χ^2 = 1.18, 3 df, P = 0.76). Likewise, although adult males tended to take smaller prey, on average, than did females (mean prey SVL = 82.3 mm, SD = 74.9, n = 8 for males, vs 146.7 mm, SD = 139.7, n = 6 for females; mean prey mass = 11.6 g, SD = 9.59, n = 6 for males, vs 15.3 g, SD = 8.5, n = 6 for females), these differences between the sexes were not statistically significant (SVL unpaired t = 1.12, 12 df, P = 0.28; mass unpaired t = 0.71, 10 df, P = 0.50). Nonetheless, closer analysis revealed a significant difference between males and females in the relationship between predator size and prey size. Prey width increased significantly with snake SVL in adult males (r = 0.82, n = 6, P < 0.05) but not in adult females (r = 0.62,

n = 7, P = 0.14). A heterogeneity of slopes test, with sex as the factor, SVL as the covariate, and prey width as the dependent variable, showed that the slope of the relationship between prey width and SVL differed between adult males and females (slopes $F_{1,12}$ = 6.07, P < 0.03). However, no difference in relative prey widths between male and female snakes was apparent if we used head length (rather than SVL) as the covariate in this analysis (slopes $F_{1,10}$ = 1.69, P = 0.22; intercepts $F_{1,11}$ = 0.54, P = 0.48).

DISCUSSION

In general, our results are consistent with earlier reports on the biology of *Thelotornis*. For example, several authors have commented on the highly seasonal reproductive cycle in this species, with mating in spring and oviposition in midsummer (e.g., Wilson, 1965; Broadley, 1966). A single report of male-male combat in autumn (May: Haagner, 1990) is the only record of reproductive activity outside this period. The lack of strong seasonality in collection dates for museum specimens of twig snakes is surprising, in view of field studies showing considerable seasonal variation in habitat selection and activity levels (Wilson, 1965; Jacobsen, 1980). Previous studies are consistent with our own in terms of reproductive output, but other authors have reported larger clutch sizes (usually around six eggs, but up to 18; Bennefield, 1982; Branch, 1988) and egg sizes (approximately 36 × 16 mm, 5 g; Dyer, 1979; Broadley, 1982; Haagner and Els, 1987, vs 30 × 12 mm, 2.8 g in our data). The difference in egg sizes may be at least partly due to uptake of water after oviposition. The largest clutch (18 eggs: Bennefield, 1982) is the only reproductive record for the eastern race *Thelotornis capensis mossambicana*, and may reflect geographic variation in this trait.

There are no previously published data with which to compare our information on sexual dimorphism in *T. capensis*. The longer tails of male than female twig snakes are not surprising (see also Jacobsen, 1980), because this phenomenon is common in snakes (King, 1989; Shine, 1993). The lack of sexual dimorphism in adult body sizes is more interesting, in that females exceed males in body size in most snake taxa (Shine, 1994). Nonetheless, our data on twig snakes fit well with a previously documented pattern: males tend to grow at least as large as females in snake species that show male-male combat (Shine, 1978, 1994). Combat behavior between rival males of *T. capensis* has been reported both in the field (Haagner, 1990) and in captivity (Bennefield, 1982; for descriptions of

combat in the congeneric *Thelotornis kirtlandi*, see also Mangili, 1956). Thus, the relatively large average body size of adult male *Thelotornis* may be a trait that has evolved through sexual selection for success in male-male combat (Gibbons, 1972). At first sight, it might seem that the significant divergence in relative head sizes between the sexes could also be attributed to selection for success in male-male combat (as in lizards; Vitt and Cooper, 1985). However, this hypothesis is unlikely to be valid, because males have not been reported to bite each other during combat bouts (Bennefield, 1982; Haagner and Els, 1987) and males have smaller, not larger, heads. Instead, such head-size divergence probably reflects differential selection on males and females with respect to prey-handling and prey ingestion (Shine, 1991). In keeping with this interpretation, male and female twig snakes differ in the sizes of prey they ingest relative to their own body length but not relative to their head length (see above). There is no evidence of a corresponding sex difference in prey types.

The significant sex difference in body shape in *T. capensis* (females are thicker and more heavy-bodied than conspecific males) is a particularly interesting result, given that the extremely elongate morphology of this taxon, relative to other snakes, suggests that there has been intense selection for an attenuate shape. Such a shape may minimize circulatory problems (Lillywhite and Henderson, 1993), as well as enable the snake to approach a potential prey item along a slender branch without alerting the prey (Sweeney, 1961; Henderson and Binder, 1980). Although such shape differences among the sexes may be relatively widespread in snakes (Shine, 1993), this seems to be a clear-cut case of a trade-off between two conflicting optima. A more thickset build in females is likely to be favored by fecundity selection (because the resultant increase in abdominal volume allows an increase in clutch mass) but opposed by selection for foraging efficiency. It would be instructive to compare foraging effectiveness of male and female twig snakes under various conditions to test the hypothesis that the females' thicker build compromises foraging success.

Published accounts of dietary composition in *Thelotornis* disagree in important respects. Several authorities have suggested that twig snakes specialize on arboreal prey items (notably, chamaeleons and birds: e.g., Broadley, 1982; Marais, 1992). However, lists of specific prey items generally consist primarily of lizards, frogs, and occasional snakes (see Appendix 1). Only a single mammalian prey item (a banana bat) has been reported (Broadley, 1966). Although it is

clear that *Thelotornis* do consume chamaeleons and birds; it also seems clear that their diet is more diverse, and less concentrated on arboreal taxa, than has generally been believed (Table 2, Appendix). Instead, twig snakes (especially large animals) seem to feed at the ground-tree interface, rather than strictly in the trees. In keeping with this inference, Jacobsen (1980) reported that most twig snakes perched < 1.5 m from the ground, in small shrubs, for most of the active season. From these low perches, the snakes can ambush passing terrestrial prey that are seized either while the snake's hindbody remains anchored in the shrub or by dropping to the ground upon the prey (Broadley, 1966; Jacobsen, 1980; W. D. Haacke, pers. comm.). The co-occurrence of terrestrial and arboreal prey within single stomachs of *Thelotornis* supports the idea that these snakes scan both arboreal and terrestrial habitats and are prepared to attack whatever prey they detect.

The apparent scarcity of birds in the diet of *Thelotornis* (Table 2, Appendix) deserves special mention. First, it means that the common name of "bird-snake" is certainly inappropriate (Loveridge, 1953). Second, it means that hypotheses interpreting *Thelotornis* behaviors (tongue extension, gular inflation) as "strategies" to attract birds (Goodman and Goodman, 1976) are unlikely to be correct. Third, it supports Shine's (1983) prediction that "the apparently high incidence of bird-eating in arboreal snakes might not be supported by more detailed studies, because authors perhaps suggest that a snake preys on birds simply because the snake is arboreal." Overall, birds appear to be relatively rare prey items for most snake species—presumably because they are difficult to capture (see also Luiselli and Rugerio, 1993). A recent record of a *Thelotornis* eating a bird that was entangled in a mist set (Braunlich and Bohme, 1991) reinforces the notion that twig snakes will eat birds but find them hard to catch.

The high dietary diversity of *Thelotornis* means that this species differs from the other vine snakes, which all have relatively specialized diets. Henderson and Binder (1980) had noted the atypical nature of *Thelotornis* in this respect but thought that its greater trophic breadth resulted from the inclusion of large numbers of chameleons and endotherms in the diet. Instead, our data suggest that the high dietary diversity of *Thelotornis* results from the inclusion of many terrestrial ectotherms, notably amphibians, as well as arboreal prey. Mammals and birds are taken only rarely, and chamaeleons are taken no more often than other types of lizards (Table 2. Appendix). Similarly, the large

relative prey sizes of *T. capensis* offer a contrast to the situation in other vine snakes. Within the genus *Oxybelis*, elongate vine snakes tend to consume smaller prey items than do more heavy-bodied forms, perhaps because of physical limitations on the maximum size of ingestible prey (Henderson, 1982; Henderson et al., 1988).

Twig snakes appear to be relatively unspecialized, and similar to other kinds of snakes, in prey size (the prey items taken by twig snakes cover a wide size range, and include small as well as relatively large prey); dietary breadth (the diet of *T. capensis* is no more specialized than are the diets of many sympatric snakes such as *Psammophis* spp.; Broadley, 1982; Jacobsen, 1980); feeding rates [the proportion of preserved snakes containing prey in twig snakes (36%) was similar to that in several other species of African snakes that we have examined; unpubl. data]; RCMs (the two RCM estimates for this species span most of the range reported for other oviparous snakes; Seigel and Fitch, 1984); movements [home ranges of *T. capensis* (mean = 4.6 ha; Jacobsen, 1980) fall within the range reported for similar-sized snake species; Macartney et al., 1988]; reproductive rates (the proportion of reproductive females in our samples was similar to many types of snakes in this respect; for a review, see fig. 4 in Shine, 1986); and growth rates and maturation. Based on size-specific growth rates of recaptured snakes (mean = 0.32 mm/day: Jacobsen, 1980) combined with our data on size at maturity, we calculate that sexual maturation (first mating) is attained in both sexes of *T. capensis* at about 30 months of age (i.e., in the third spring after they hatch). These snakes would thus fall into Parker and Plummer's (1987) category of "late-maturing temperate colubrids," a category that also contains *Carphophis vermis*, *Coluber constrictor*, *Diadophis punctatus*, *Masticophis taeniatus*, and *Pituophis melanoleucus*. Because these species include taxa both larger and smaller than *T. capensis*, it seems that ages at maturation in twig snakes, although later than in many snakes, are not exceptional.

Overall, our data suggest that the extreme morphological and behavioral specializations of twig snakes have not been accompanied by any pronounced modifications of dietary habits or reproductive biology. Despite its extraordinarily attenuate form and unusual foraging mode, the diet of *T. capensis* is broad in terms of both prey types and relative prey sizes. Similarly, the reproductive output, growth rates, and age at maturation in *T. capensis* appear to be similar to those of other snake species from comparable climatic zones. Perhaps the most surprising as-

pect of our results has been the importance of terrestrial prey items in this highly arboreal snake. This study thus provides a cautionary tale: it may be difficult to predict dietary habits purely from morphological features and observations of habitat selection. Published reports of habitat selection by this species consistently refer to its arboreality, and even a cursory glance at the morphology of *T. capensis* suggests that it is superbly adapted for life in the trees. Nonetheless, our data suggest that the primary trophic specialization of this taxon is actually a lack of specialization—the simultaneous utilization of arboreal and terrestrial prey. Many African habitats contain low densities of snakes, perhaps because of high predation rates on these animals (Janzen, 1976). Thus, the primary advantage of arboreality in twig snakes—and hence, the selective force for evolution of the vine snake morphology—may be protection from predators, rather than access to arboreal prey as stressed by Henderson and Binder (1980). By foraging at the ground-tree interface, twig snakes can utilize a broad prey resource (arboreal as well as terrestrial animals) while remaining camouflaged from potential prey or predators and in a good position for rapid escape (either arboreal or terrestrial). The causal link between ecology and morphology may thus be rather different in twig snakes than in their ecological analogues from other parts of the world.

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APPENDIX. PUBLISHED RECORDS FOR PREY ITEMS OF *Thelotornis* SPECIES.

Prey species	Locality	*Thelotornis* species	Authority
Frogs			
Brevicepidae			
Brevicepes adspersus	Zimbabwe	*capensis*	Broadley, 1966
Breviceps mossambicus	Nchingidi, Tanzania	*capensis*	Loveridge, 1942
Breviceps mossambicus (3)	Cholo, Mocambique	*capensis*	Loveridge, 1953
Breviceps mossambicus	Mocambique	*capensis*	Broadley, 1966
Breviceps poweri	E. Zambia	*capensis*	Wilson, 1965
Ranidae			
Arthroleptis stenodactylus (2)	Mocambique	*capensis*	Broadley, 1966
Arthroleptis xenodactyloides	Mocambique	*capensis*	Broadley, 1966
Phrynobatrachus sp.	Mocambique	*capensis*	Broadley, 1966
Phrynobatrachus perpalmatus	Mtimbuka, Malawi	*capensis*	Loveridge, 1953
Ptychadena oxyrhynchus	Cholo, Mocambique	*capensis*	Loveridge, 1953
Rana sp.	Mocambique	*capensis*	Broadley, 1966
Rana sp.	E. Zambia	*capensis*	Wilson, 1965
Bufonidae			
Bufo sp. (2)	Hanha, Angola	*capensis*	Bogert, 1940
Lizards			
Agamidae			
Acanthocerus atricollis	Buta, Zaire	*kirtlandii*	Loveridge, 1942
Acanthocerus atricollis	Zimbabwe	*capensis*	Broadley, 1966
Agama sp.	E. Zambia	*capensis*	Wilson, 1965
Agama kirkii	Mocambique	*capensis*	Broadley, 1966
Chamaeleonidae			
chamaeleon	Zambia	*capensis*	Johnsen, 1962
chamaeleon	Zambia	*capensis*	Vessey-Fitzgerald, 1958
Brookesia platyceps (2)	Rungwe, Tanzania	*capensis*	Bogert, 1940
Brookesia nschisiensis (2)	Mocambique	*capensis*	Loveridge, 1953
Chamaeleo d. dilepis (3)	Mocambique	*capensis*	Loveridge, 1953
Chamaeleo dilepis (4)	Lake Sibaya, Natal	*capensis*	Bruton and Haacke, 1980
Chamaeleo dilepis	East Africa	?	Loveridge, 1923
Cordylidae			
Cordylus tropidosternum	Chowe, Mocambique	*capensis*	Loveridge, 1953
Gekkonidae			
Lygodactylus capensis	Zimbabwe	*capensis*	Broadley, 1966
Lygodactylus angularis	Cholo, Mocambique	*capensis*	Loveridge, 1953
Gerrhosauridae			
Gerrhosaurus nigrolineatus	E. Zambia	*capensis*	Wilson, 1965
Gerrhosaurus validus	Zimbabwe	*capensis*	Broadley, 1966
Lacertidae			
Ichnotropis capensis	Zambia	*kirtlandii*	Broadley, 191
Nucras taeniolata ornata	Zimbabwe	*capensis*	FitzSimons, 1939

APPENDIX. CONTINUED.

Prey species	Locality	*Thelotornis* species	Authority
Scincidae			
Mabuya maculilabris	Buta, Zaire	*kirtlandii*	Loveridge, 1942
Mabuya striata	NE Transvaal, South Africa	*capensis*	Maberley, 1948
Mabuya varia	Zimbabwe	*capensis*	FitzSimons, 1939
Mabuya varia	Mtimbuka, Malawi	*capensis*	Loveridge, 1953
Mabuya varia	Cholo, Mocambique	*capensis*	Loveridge, 1953
Snakes			
Colubridae			
Dispholidus typus	Transvaal, South Africa	*capensis*	Haagner and Clark, 1992
Philothamnus carinatus	Lukolela, Zaire	*kirtlandii*	Bogert, 1940
Philothamnus neglectus	Nyange, Tanzania	*capensis*	Barbour and Loveridge, 1928
Philothamnus angolensis (2)	Cholo, Mocambique	*capensis*	Loveridge, 1953
Typhlopidae			
Rhinotyphlops mucruso	East Africa	?	Loveridge, 1923
Birds			
nestling weavers (2) (*Spermophaga ruficapilla*)	Buta, Zaire	*kirtlandii*	Loveridge, 1942
finch or weaver feathers	Kitaya, Tanzania	*capensis*	Loveridge, 1942
Mammals			
Banana bat (*Pipistrellus narus*)	Zimbabwe	*capensis*	Broadley, 1966
Other			
termites	Cholo, Mocambique	*capensis*	Loveridge, 1953