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Ecology of Highly Venomous Snakes: the Australian Genus *Oxyuranus* (Elapidae)

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ABSTRACT.—The taipan, ***Oxyuranus scutellatus,*** is a large slender elapid of coastal tropical Australia. The small-scaled snake, ***O. microlepidotus,*** is a similar snake from the arid zone. These are among the most highly venomous snakes in Australia, and probably in the world. We present information on body sizes, sexual size dimorphism, feeding habits, reproductive cycles, fecundity and inferred growth rates, based on dissection of museum specimens and observation of captive snakes.

Adult snakes average approximately 1.5 m SVL in both ***Oxyuranus*** species, and males and females attain similar body sizes. ***Oxyuranus*** species are unique among Australian elapids in feeding exclusively upon endothermic prey. A wide variety of marsupials and rodents is taken: especially ***Rattus villosissimus*** and ***Antechinomys laniger*** by ***O. microlepidotus,*** and ***Melomys*** sp., ***Mus musculus, Perameles nasuta*** and ***Rattus*** spp. by ***O. scutellatus.*** The large body size, highly toxic venom and "snap and release" bite of ***Oxyuranus*** species may be adaptations to feeding on mammalian prey. Over recent decades, taipans have become more common relative to other large elapid species: we suggest that this may be due to the introduction of the toxic cane toad (***Bufo marinus***) as well as habitat modification by agriculture.

Both ***Oxyuranus*** species are oviparous, with mating and oviposition from August to December. Fecundity (7-20 eggs), incubation period (60-80 days), and size at hatching (300-340 mm SVL) are similar in both species. Captive taipans show rapid growth, with sexual maturation as early as 16 months of age in males, and 28 months in females. In several aspects of morphology, ecology and behavior, ***O. scutellatus*** is strongly convergent with an African elapid, ***Dendroaspis polylepis*** (the black mamba).

We have less ecological information about snakes than about any other terrestrial vertebrate group of comparable size. Venomous snakes are particularly poorly-known, and highly venomous species have attracted almost no serious study from ecologists. However, highly venomous snakes are a conspicuous component of the snake fauna in many areas of the world (e.g., Australia, Asia, Africa). Studies of the ecology of such snakes may help us to understand the evolutionary pressures for, and consequences of, the possession of extremely toxic venoms, and epidemiological factors in snakebite. The present paper provides ecological data on two Australian snake species which are among the most highly venomous in the world.

Allowing for venom toxicity and average venom yield per bite, the number of mouse LD_{50} doses per bite is much higher for *Oxyuranus microlepidotus* (218,000) and *O. scutellatus* (94,000) than for any other snakes, including sea snakes, investigated to date (Broad, Sutherland and Coulter, 1979). For example, the bite of *O. microlepidotus* contains about 50 times as many LD_{50} doses as does the bite of the King Cobra (*Ophiophagus hannah*), and about 100 times as many as that of the eastern diamondback rattlesnake (*Crotalus adamanteus*) (Broad, Sutherland and Coulter, 1979).

MATERIALS AND METHODS

The two species which we studied were formerly placed in separate genera: *Oxyuranus scutellatus* and *Parademansia microlepidotus* (e.g., Cogger, 1975). However, strong similarities between these snakes in morphology, venom, behavior and karyotype suggest that they should be placed together in the genus *Oxyuranus* (Covacevich et al., 1981). Both are large,

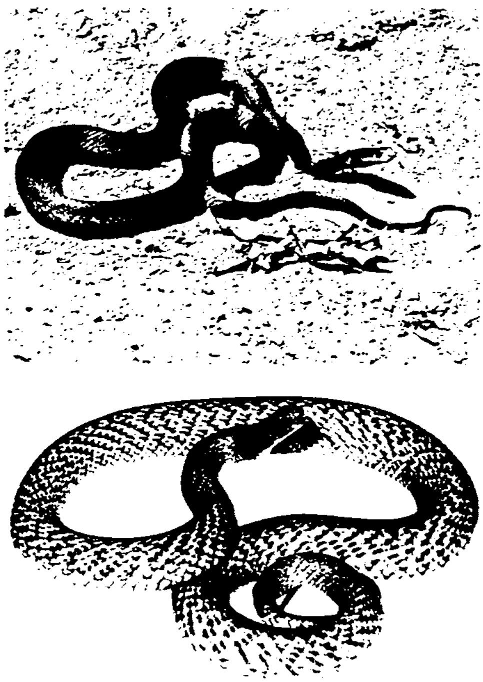

FIG. 1. Upper photograph: Taipan, *Oxyuranus scutellatus*. Lower photograph: Small-scaled snake, *O. microlepidotus*. Photographs by A. Easton, Queensland Museum.

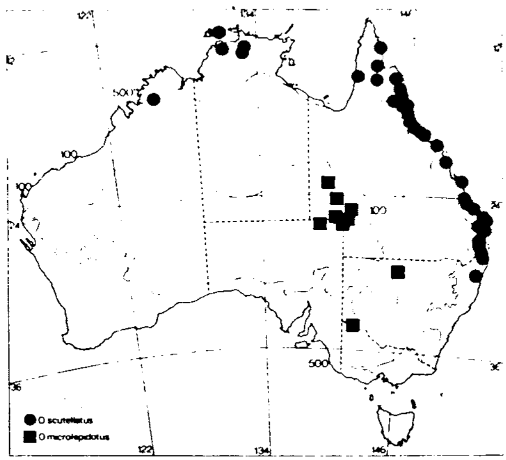

FIG. 2. Geographic distribution of the two *Oxyuranus* species. Circles show *O. scutellatus*, dots show *O. microlepidotus*. Lines are isohyets for annual precipitation (100 mm and 500 mm).

brown, slender-bodied snakes (Fig. 1), and are predominantly diurnal (Covacevich et al., 1981). The snakes differ greatly, however, in geographical distribution. The taipan (*O. scutellatus*) occurs coastally in areas of relatively high rainfall. Taipans attain high densities in sugar-cane fields and their environs. In contrast, the small-scaled snake (*O. microlepidotus*) is restricted to extremely arid inland regions (Fig. 2). Typical habitat for this species is "ashy downs" country which has only sparse, low vegetation.

Published information on the ecology of *Oxyuranus* is scattered and largely anecdotal. Our study summarizes this information, and presents original data based on dissection of all available museum specimens (21 *O. microlepidotus*, 114 *O. scutellatus*) in the collections of the Australian Museum, Queensland Museum (QM), National Museum of Victoria, and South Australian Museum, and recent field work on *Oxyuranus microlepidotus*. The following data were taken from museum specimens: snout–vent length (SVL); sex; reproductive maturity or immaturity (criteria were: males—large testes or opaque efferent ducts; females—gravid, or enlarged oviducts, or ovarian follicles >5 mm diameter); diameters of ovarian follicles or oviducal eggs; and gut contents. In many specimens, the only food items in the alimentary canal were mammalian hairs in the rectum. These hairs were identified using the guide by Brunner and Coman (1974), in conjunction with fur samples from all of the common small mammals within the geographic range of the *Oxyuranus* species. Further data were provided by Charles Tanner, who has bred both *Oxyuranus* species in captivity, and maintained captive *O. scutellatus* over a 20-year period.

RESULTS

Body Sizes.—Table 1 shows that females reach similar body sizes in both species (means of 144 cm, 145 cm SVL), but male taipans grow much larger (mean SVL 156 cm) than male small-scaled snakes (mean

TABLE 1. Sample sizes, body sizes, and sexual dimorphism in body size in adult specimens of two *Oxyuranus* species. All snout-vent lengths (SVL) in cm.

Variable	Species	
	O. microlepidotus	*O. scutellatus*
Sample size ♂♂	13	55
Sample size ♀♀	6	23
Mean SVL ♂ (SE)	132.0 (6.8)	156.4 (3.6)
Mean SVL ♀ (SE)	143.8 (6.3)	145.0 (4.4)
Size range ♂♂	92.0–169.0	78.3–226.0
Size range ♀♀	133.0–170.0	101.4–193.0

SVL 132 cm). The difference in body size between the sexes is close to statistical significance in *O. scutellatus* (N = 55, 23; median test, 1 df, $\chi^2 = 3.1$, $.05 < P < .10$) but not in *O. microlepidotus* (N = 13, 6; median test, 1 df, $\chi^2 = 0.02$). In both *Oxyuranus* species, males mature at much smaller body sizes than do females (Table 1: 92 cm in ♂♂ versus 133 cm SVL in ♀♀ for *O. microlepidotus*; 78 cm in ♂♂ versus 101 cm SVL in ♀♀ for *O. scutellatus*).

Food Habits.—Based on museum specimens, individuals of *Oxyuranus* feed exclusively on endotherms: 18 mammals and one bird were recorded in *O. scutellatus* guts, and nine mammals in *O. microlepidotus* (Table 2). The snakes take a wide variety of mammals, including both marsupials and rodents. Many prey items are large (e.g., a young bandicoot, *Isoodon macrourus*, of 40 gm mass). Kinghorn (1923) reports the occurrence of remains of a quoll, *Dasyurus hallucatus* in the gut of a large taipan (TL 275 cm). Adult quolls attain a mass of approximately 600 gm. Feeding apparently occurs year-round in both *Oxyuranus* species, but sample sizes are too low to reveal any seasonal trends.

Mode of Reproduction.—Both *Oxyuranus* species are oviparous: oviducal eggs of both species were seen in the course of the study. The stage of embryonic development at oviposition was determined for an egg laid by a captive taipan (donated by N. Charles). This embryo (QM J38703) was at stage 28 in the classification of Hubert and Dufaure (1968): the head was large and birdlike and the body tightly coiled.

Size at Hatching.—Several *O. scutellatus* preserved at hatching measured between 30.2 and 32.6 cm SVL. The smallest taipan collected in the field measured 31.5 cm SVL. No small specimens of *O. microlepidotus* have been collected, but fifteen neonates hatched in captivity ranged from 37 to 43 cm total body length. SVL measurements were not recorded, but examination of young taipans shows that 40 cm total length corresponds to 34 cm SVL. Hence, size at birth is similar in the two *Oxyuranus* species. Eggs of *O. microlepidotus* averaged 6 cm × 3.5 cm (Covacevich et al., 1981).

Seasonal Reproductive Timing.—Several large (clearly adult) males of both *Oxyuranus* species possessed small testes and did not contain sperm in the efferent ducts.

Female taipans show clear seasonal variation in ovarian follicle diameters (Fig. 3). Ovigerous females are found from August to November, and post-oviposition specimens with very small follicles (<10 mm) from September to March. Follicles increase in diameter during the first half of the year, but vitellogenesis probably is concentrated close to the time of ovulation (note June specimen with small follicles; Fig. 3).

Data on captive taipans confirm this seasonal schedule of reproduction. Copulation has been observed in August and in early December, and oviposition in October and February (N. Charles, pers. comm.). The interval between copulation and oviposition was 68 days in one case, and 70 days in another. Taipans in the Melbourne Zoological Gardens mated in September and October, and oviposited in November (C. Banks, pers. comm.). Further evidence for this phenology comes from field observations of taipans in coastal north Queensland: ovigerous females may be found (usually basking in "windrows" in canefields) from August to September (K. Day, pers. comm.).

Sample sizes of *O. microlepidotus* are too low to draw any conclusions from field

TABLE 2. Prey items identified from *Oxyuranus* digestive tracts.

Snake species	Prey species	Number of records
Oxyuranus microlepidotus	Marsupials—*Antechinomys laniger*	3
	—dasyurid sp.	1
	Rodents—*Mus musculus*	2
	—*Rattus* sp.	1
	—*R. villosissimus*	2
Oxyuranus scutellatus	Mammal—sp. unknown	1
	Marsupials—*Isoodon macrourus*	1
	—*Perameles nasuta*	3
	Rodents—*Melomys* sp.	4
	—*M. burtoni*	1
	—*M. cervinipes*	1
	—*Mus musculus*	5
	—*Rattus sordidus*	1
	—*R. tunneyi*	1
	Bird—sp. unknown	1

samples (Fig. 3). Fortunately, data are available on captive snakes (C. Tanner, pers. comm.). Attempted courtship has been recorded in January, February, March, September, October and December, and mating has been seen in March and October. Oviposition occurred twice in December, once in November and once in March (the two latter records from the same female, in successive years).

Incubation Periods.—One clutch from a captive taipan hatched in late April (69 days after oviposition), when incubated at room temperature (probably 25°–30°C, N. Charles, pers. comm.). Other clutches hatched in January, after 64 to 68 days incubation (R. W. Dunn and C. Banks, pers. comm.). Eggs of *O. microlepidotus* hatched in February, 66 days after laying (Covacevich et al., 1981).

Clutch Sizes.—Fecundity data for *O. scutellatus* are shown in Figure 4. Clutch size ranged from 7 to 17 eggs, with a mean of 11.4 (SEM = 1.3, N = 8). Fecundity was independent of maternal body size (r^2 = 0.23, 7 df, n.s.). Captive taipans produced clutches of 7 eggs (including one infertile), 15 eggs (all fertile), 10 eggs and 19 eggs (N. Charles, pers. comm.; C. Banks, pers. comm.). Clutch sizes of captive *O. microlepidotus* were as follows: 20, 19, 12, 15 (including two infertile), and 15 (at least ten infertile). The mean of these five records is 16.2 (SEM = 1.5).

Seasonal Abundance.—Figure 5 shows that taipans may be collected throughout the year, but are taken most commonly in late winter and spring (Aug.–Oct.).

DISCUSSION

One corollary of highly toxic venom in snakes is great public interest in these species. In the case of the taipan, this public interest has stimulated several zoos to include taipans in their exhibits. At least three such zoos have successfully bred taipans, as have private reptile-keepers (Barnett, 1978; N. Charles, pers. comm.). Hence, despite the comparative scarcity of *Oxyuranus* in museum collections, a great deal is known about reproduction of *O. scutellatus* in captivity. The small-scaled snake (*O. microlepidotus*) is less well-known; live specimens did not become available to scientists until 1975 (Covacevich and Wombey, 1976), and few specimens of this species have been collected (Table 1). Our information on *O. microlepidotus* reproduction is entirely due to Charles Tanner's success in breeding captive specimens.

Body Sizes.—Both *Oxyuranus* species

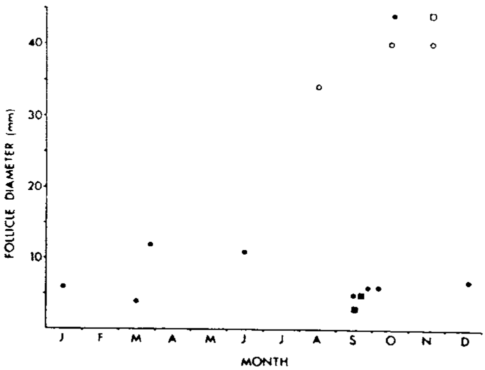

FIG. 3. Seasonal changes in diameter of the largest ovarian follicle, or oviducal egg, in *Oxyuranus scutellatus* (circles and dots) and *O. microlepidotus* (squares). For *O. scutellatus*, dots show ovarian follicles, and circles show oviducal eggs. For *O. microlepidotus*, solid squares show ovarian follicles, open squares show oviducal eggs.

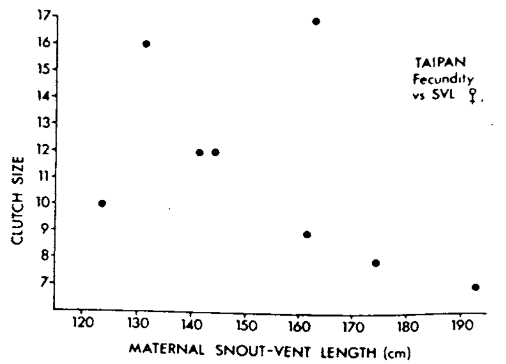

FIG. 4. Relationship between maternal body length and clutch size in *Oxyuranus scutellatus*.

rank among the largest Australian elapids; *O. scutellatus* probably attains greater body sizes than does any other species. This large body size may be an adaptation to feeding on large prey (mammals; see below).

The trend for sexual size dimorphism in taipans (♂♂ average 156 cm SVL, ♀♀ average 145 cm: Table 1) may be related to the occurrence of male combat in this species. Combat in captive taipans has been noted by Worrell (1970), and field observations by Hosmer (1953) strongly suggest male combat behavior (although the sexes of the snakes involved were not determined). Among snakes in general, there is a strong correlation between male combat behavior, and sexual size dimorphism in which the male is the larger sex (Shine, 1978*a*). Male combat and male superiority in body size are common among large Australian elapids (e.g., Shine, 1977*a*, 1978*b*).

Food Habits.—The specialization of *Oxyuranus* upon mammalian prey (Table 2) is consistent with observations on captive snakes (C. Tanner and N. Charles, pers. comm.) and with previous reports (Kinghorn, 1923; Thomson, 1935; Garnet, 1968; Worrell, 1970; Gow, 1976, 1980; Barnett, 1978; Stackhouse, 1978; McPhee, 1979; Broad et al., 1979; Covacevich et al., 1981). The suggestion that young taipans may feed on skinks as well as mammals (Kinghorn, 1923; Gow, 1976; Barnett, 1978) is not supported by gut contents analyses (Table 2) or by observations in captivity: young taipans are attracted to small moving prey, but will not attack ectotherms (N. Charles, pers. comm.).

This specialization of *Oxyuranus* upon mammalian prey is unique among Australian elapid snakes. Extensive data on food habits are available for 28 elapid species (Shine, 1977*b*, 1980*a*, *b*, and unpublished data). Mammals comprise less than 10% of the prey items taken in all but six of these 28 species. The six mammal-eating species are a diverse group: *Tropidechis carinatus* (48% of prey items recorded were mammals), *Hoplocephalus stephensi* (44%), *Pseudechis guttatus* (39%), *Acanthophis antarcticus* (32%), *Pseudonaja textilis* (25%) and *Echiopsis curta* (14%). The vast majority of mammals taken by all these species are introduced house mice, *Mus musculus*. In contrast, *Oxyuranus* species consume a wide range of mammalian prey (Table 2). The large size of some prey items reflects the large body size of the snakes. The only Australian snakes likely to overlap significantly in diet with *Oxyuranus* are the pythons. However, the marked differences in foraging strategies between the two types of snakes—fast-moving, venomous, usually diurnal versus slow-moving, constricting, usually nocturnal—may well result in differences in prey types taken.

We interpret the following characteristics of *Oxyuranus* as adaptations to feeding on mammals:

(a) Large body size—enabling large prey to be eaten.
(b) High venom toxicity—enabling *Oxyuranus* to feed on large prey (e.g., rats) which must be immobilized rapidly, before they can injure the snake.
(c) Immediate release of prey after strike—unlike other Australian elapids, *O. scutellatus* do not retain their initial hold on the prey until struggling ceases: the prey is released instantly after the strike.

The "strike and release" bite of *Oxyuranus*, like high venom toxicity, may be an adaptation to the retaliatory ability of mammalian prey. Fleay (1981) describes how a large taipan was killed by a rat which was held by the snake for a few seconds after the intial strike.

Although both *Oxyuranus* species feed on a wide variety of mammals (Table 2), the difference in habitats occupied by *O. microlepidotus* and *O. scutellatus* means that there is little overlap in the prey species taken. The small-scaled snake lives in arid regions of unpredictable rainfall, where small mammals (especially *Rattus villosissimus*) undergo massive periodic fluctuations in abundance (e.g., Watts and Aslin, 1981). In contrast, taipans exploit relatively high-rainfall areas where mammalian densities are high and relatively constant (Watts and Aslin, 1981). This apparent difference in food supply may not always be the case: in the first detailed notes on the taipan, Thomson (1935, p.730) describes this species as being numerous "only . . . where there exist extensive colonies of a *Rattus*, apparently *R. villosissimus*, which forms its chief food source. The taipan frequents holes in the ground in the country infested by the rats." This situation is exactly that characteristic of present-day populations of *O. microlepidotus*.

The specialization of taipans on mammalian prey means that these snakes have been little-affected by the introduction of marine toads, *Bufo marinus*, into northeastern Australia in the 1930's. Snakes attempting to eat toads are killed by the toads' toxins (Covacevich and Archer, 1975), with the result that most large elapids apparently have decreased in numbers wherever the toads have invaded, especially in cane-growing areas of Queensland. There has been no apparent decline in taipan numbers over the same period (K. Day, pers. comm.).

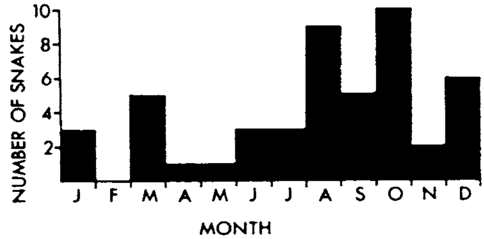

FIG. 5. Seasonal abundance of taipans, *Oxyuranus scutellatus*, represented in museum collections.

This apparent shift in species composition of the snake fauna after introduction of *Bufo* is an interesting phenomenon, but a difficult one to quantify. We have examined Queensland Museum accession records to determine relative number of different snake species registered from coastal Queensland (less than 200 km from the coast) over the period 1911 to 1982. If the introduction of *Bufo marinus* has depressed densities of large frog-eating elapids (*Acanthophis antarcticus, Pseudechis australis, P. porphyriacus, Pseudonaja textilis*), but not of *Oxyuranus*, then this trend should be reflected in the number of taipans registered relative to the numbers of the other large elapids. The data are consistent with the prediction of increased relative numbers of taipans following the introduction of cane toads in 1935 (Fig. 6). A significant change in relative numbers of taipans registered occurred between the 1940's and the 1950's (testing 1911–1940 versus 1941 to present, Mann-Whitney U test, $U = 0$, $N_1 = 4$, $N_2 = 4$, $P = .01$). An alternative test also

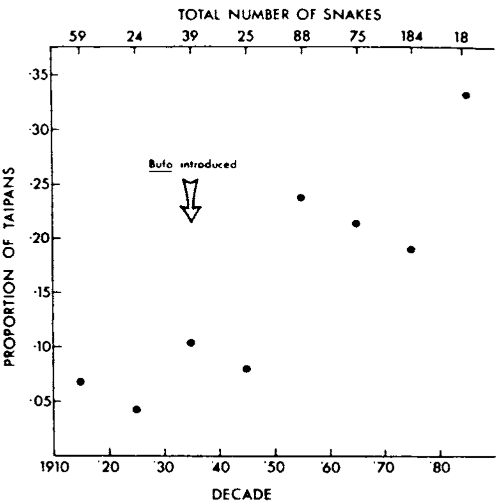

FIG. 6. Number of taipans registered in Queensland Museum over the period 1911 to present, as a proportion of the total number of large elapids registered. Data from coastal Queensland (200 km from coast) only. Arrow shows time when *Bufo marinus* was introduced.

reveals a significant increase in relative taipan numbers with time (taking 1911–1920 as zero, 1921–1930 as 1, etc.; $r^2 = .78$, $N = 8$, $P < .01$). However we cannot be sure that this change in taipan numbers is due to *Bufo marinus;* agricultural clearing has drastically affected coastal Queensland over this period. Clearing by the sugar industry has provided large areas of open habitats and "windrows." This may have increased densities of rats, and hence taipans, while at the same time disadvantaging elapid species that are dependent on forested areas.

Reproduction.—Data presented in this paper are consistent with published reports of reproduction in captive taipans (Table 3), in respect to oviposition dates, clutch sizes, incubation periods, and sizes of eggs and hatchlings. The inference that mating occurs from July to December (based on female reproductive cycles and observations in captivity) is consistent with statements by Slater (1959) and Jones (1977). Hosmer's (1953) observations of probable male combat in taipans occurred in September, and Worrell (1970) notes that combat occurs in spring.

The production of two clutches of eggs within a single summer season is common but certainly not universal in oviparous squamates from warm climates (Fitch, 1970). Most records of captive reproduction in *Oxyuranus* report only a single clutch each year, but examples of two successive clutches have been reported both in *O. scutellatus* (Peters, 1972; clutches in December and January) and *O. microlepidotus* (C. Tanner, pers. comm.; clutches in November and March). Multiple clutches probably are produced in many oviparous Australian elapids during particularly favourable years (e.g., Shine, 1977*c*, 1980*a*, *b*).

Growth Rates.—Observations on captive juvenile taipans consistently reveal rapid growth rates. *Oxyuranus scutellatus* average 31 cm SVL at hatching, and have been recorded to attain lengths of 56 cm SVL in three months (R. W. Dunn and C. Banks, pers. comm.), 74 cm in 5 months (Peters, 1972), 66 cm in 8 months (Slater, 1959) and over 100 cm in 12 months (Peters, 1972). The mean growth rate from these four records is 6.7 cm SVL per month.

We suspect that rapid growth is also attained in the field situation. Direct evidence is lacking, but we note that taipans are found in warm climates, with activity (Fig. 5) and feeding occurring year-round; and of 114 taipans for which data were available, only nine were field-caught snakes less than 100 cm SVL. This scarcity of juveniles suggests that snakes in the field, like those in captivity, grow rapidly through this range of small body sizes. Body-length records for the field-collected juveniles show two groupings: (a) snakes 30 to 40 cm SVL in March–June, undoubtedly recent hatchlings, and (b) snakes 65 to 85 cm SVL in September–November. This latter group is exactly the size one would expect from growth rates in captivity (31 cm SVL at hatching, plus 6.7 cm/month for 7 months, equals 78 cm SVL in October). Thus, these 65 + cm SVL snakes are likely to be in their first year of life.

TABLE 3. Reproduction in captive taipans, *Oxyuranus scutellatus*.

Oviposition date	Clutch size	Egg size (mm)	Egg weight (gm)	Incubation temperature (°C)	Incubation period (days)	Hatchling total length (mm)	Authority
October	7	50–60	—	—		—	Thomson, 1933
July–Aug.	14–18	70	—	32	91–95	318–432	Slater, 1956
January	20	63 × 38	—	27	107	380	Fleay, 1960
—	10–20	<50	—	—	70–98	>559	Worrell, 1970
Nov., Dec., Jan.	13, 18, 22	70	30	27–28	76–82	410–460 (wt. 23–33 gm)	Peters, 1972
December	12, 19	52–72	—	—	64–69	600	Barnett, 1978
—	13–20	52	21–24	—	70	381	Gow, 1980
—	7–20	50–62	—	—	64–68	—	Covacevich et al., 1981
November	10–19	60	33.2	—	64–68	445 (410–510) (wt. 17–23 gm)	R. W. Dunn & C. Banks, pers. comm.
Oct., Feb.	7, 15	—	17–38 ($\bar{x}$ = 32.0, SEM = 0.7)	25–30	69	(wt. 18–26 gm)	N. Charles, pers. comm.

This rapid growth means that sexual maturity may be attained at a surprisingly early age for such a large snake. Male taipans mature at approximately 80 cm SVL, and females at 100 cm (Table 1). If growth rates in captivity are similar to growth rates in the wild, male taipans would attain maturity (first mating) at approximately 16 months of age, and females a year later (28 months). These are exactly the ages at which males and females of captive taipans have first been observed to breed (Peters, 1972; R. W. Dunn and C. Banks, pers. comm.). We infer that taipans, despite their large body size, attain sexual maturity at similar ages as other, smaller Australian elapids (Shine, 1978*b* and subsequent publications). *Oxyuranus scutellatus* also resembles other elapids in the trend for males to mature at smaller sizes, and younger ages, than do females—even though males eventually may grow to be the larger sex. This sexual bimaturism probably reflects different reproductive "costs" in males and females (Shine, 1978*b*).

Overview.—The two species of *Oxyuranus* are similar to each other in body size, diet, fecundity, hatchling size, and incubation period, providing further support for their inclusion in a single genus (Covacevich et al., 1981). At the same time, these two species differ strongly from the other Australian elapids in their specialized diet. We have suggested that *Oxyuranus* characteristics such as body size, venom toxicity and feeding behaviour, reflect adaptations to feeding upon mammalian prey. Although no strong parallels with other Australian elapids are evident, many similarities may be noted between data presented here on the taipan and by Fitzsimmons (1962) on an African elapid—*Dendroaspis polylepis*, the black mamba. These two species resemble each other in body size, general morphology, colour, venom toxicity, "snap and release" bite (in contrast to "chewing" bites in other elapids of both continents), clutch size (9–14 in *Dendroaspis* versus 7–17 in *Oxyuranus*), hatchling size (40–50 cm total length), rapid growth in juveniles, male combat, males growing larger than females, and feeding primarily on mammals. These similarities clearly represent evolutionary convergence rather than taxonomic affinity (Saint Girons and Detrait, 1980).

Acknowledgments.—We dedicate this paper to Charles Tanner, a pioneer of Australian herpetology and the first to breed *Oxyuranus microlepidotus* in captivity. We thank Mr. Tanner for allowing us to use his extensive data on captive *O. microlepidotus*. N. Charles, R. W. Dunn, C. Banks and K. Day offered valuable records of taipan reproduction. G. Ross and L. Hall identified mammalian prey items. A. Greer and H. Cogger (Australian Museum), J. Coventry (National Museum of Victoria) and T. Schwaner (South Australian Museum) gave permission to dissect specimens in their care. This study was supported by the Australian Research Grants Committee.

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