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NOTES ON THE ECOLOGY OF SOME UNCOMMON SKINKS IN THE GREAT VICTORIA DESERT

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ABSTRACT

Understanding rarity is a perplexing problem for ecologists. Here I report limited information and observations on various aspects of the ecology of five species of uncommon skinks, *Cyclodomorphus melanops*, *Eremiascincus richardsoni*, *Lerista desertorum*, *Morethia butleri*, and *Tiliqua multifasciata*, in the Great Victoria Desert of Western Australia. Some possible causes and consequences of rarity are discussed.

INTRODUCTION

Most species of Australian desert lizards I have collected over the past half century are uncommon (Figure 1), making them difficult to study. Regardless of how rareness is defined, most ecologists concur that the majority of species are indeed uncommon (Kunin and Gaston 1997). Magurran and Henderson (2003) distinguished between relatively abundant 'core species,' and uncommon 'occasional species'. Some of the latter are extremely rare to the point of vanishing rareness.

Until recently, inadequate sample sizes have prevented me from doing much with uncommon species, but I have now finally managed to acquire large enough samples to begin to try to understand the ecologies of most of them. A lifetime of dedication and hard work has put me in a unique position to elucidate and understand the ecology of rare species – no one else has ever managed to collect such large samples of uncommon Australian desert lizards. Over the past few decades, I have witnessed metapopulation-like local extinctions and colonization in a few species. I have also captured individuals of a number of species dispersing through habitats that they do not normally occupy. Simply being in an alien habitat is not necessarily a death sentence, as these habitats offer shelter and food – a migrant that succeeds in reaching its correct habitat could also reap the benefits of sweepstakes reproductive success.

Questions that arise include the following: how can rare species find mates and continue to exist? Is rarity an illusion due to cryptic behavior making putative rare species difficult to find? Are species rare because their resources are scarce? Might rare species have narrow tolerances to physical environments? Could predators hold densities of prey species at low levels? Do uncommon species display chronic rarity, or are they ephemeral, sometimes more abundant, and rare only intermittently? Do rare species have narrow geographic ranges, occurring only at a few sites? Are species that are rare locally simply spillover individuals, dispersing from nearby source areas where they are more abundant? How important are rare species to the function and stability of communities?

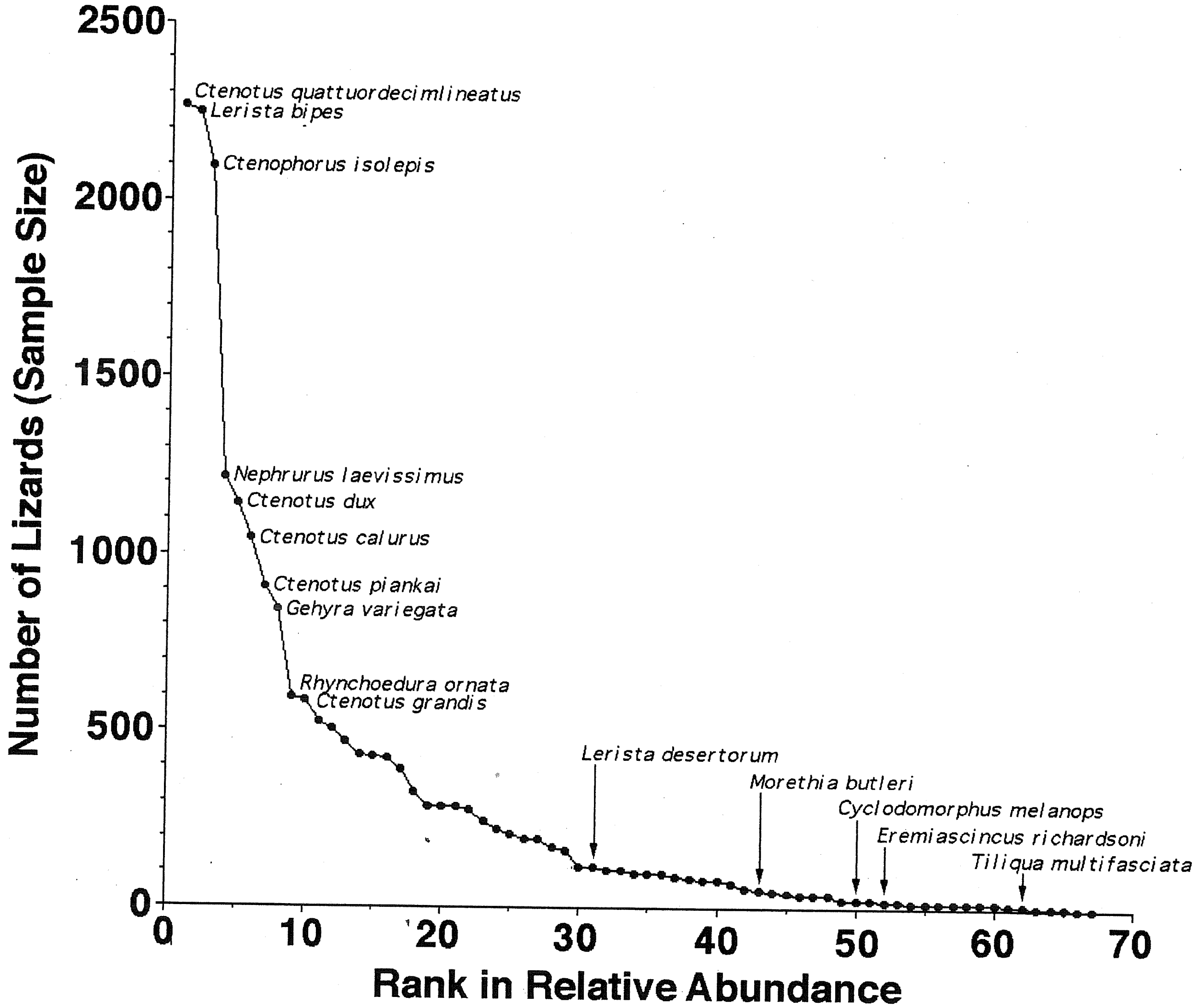

Figure 1. Total number of lizards of 67 species (20,990 individuals) collected on ten desert study sites from 1966 through 2008 plotted against their rank in relative abundance. The ten most common species are named, along with a selected five uncommon to rare skink species considered here. Species are listed along with their abundances in Appendix 1.

Community ecologists, especially Hutchinson (1959) and MacArthur (1955, 1965, 1972) focused attention on community stability, diffuse competition, and species packing. For many species to coexist, many would have to be rare, and these authors have argued that rare species could persist longer in more stable communities. Implicit in this hypothesis is that rare species are a feature of more stable and species-rich communities. Do rare species persist in such communities in spite of their rareness, or does the presence of rare species enhance the biodiversity and stability of ecosystems? Could rare species be uncommon due to diffuse competition from many other, more abundant, species?

In an insightful paper entitled "Rare species: precious or dross?", Main (1982) suggested that ecosystems are like palimpsests and one reason so many rare species exist is that ecosystems have been 'over-written many times after imperfect erasures' (incomplete extinctions). Consequently current ecosystems contain numerous relicts of their predecessors assembled under different conditions. Rare species could be vital to long-term ecosystem sustainability, providing 'insurance' for the delivery of ecosystem functions by alternative means in the event of drastic environmental changes (Main 1982). Unfortunately, Main's interesting hypothesis cannot be evaluated adequately here.

METHODS

Over a 42 year interval, from September 1966 through November 2008, on 11 separate research expeditions, I have spent 41 months (1256 days) in the field studying lizards, mostly at 10 study sites during Springs in the Great Victoria Desert (GVD) of Western Australia (Pianka 1986). A few specimens were also captured outside the GVD. Up until 1979, all lizards were collected by hand, and data were obtained on date and time of activity, ambient air temperature, active body temperature, habitat and microhabitat. Active body temperatures were taken with thin bulb Shultheiss cloacal thermometers immediately upon capture. Ambient air temperatures were taken at chest height at capture with the same thermometer. Lizards were collected and preserved, and then measured and dissected later in the laboratory to obtain dietary and reproductive information. All specimens are permanently lodged in the Los Angeles County Museum of Natural History, the Western Australian Museum, or the Texas Memorial Museum. Scant data available for some of these uncommon skink species were summarized in Pianka (1986). Beginning in 1989, most lizards were collected at three study sites, the B-area (138 km. E. Laverton, Lat. 28° 13.5' S, Long. 123° 35.5' E), the L-area (40 km. E. Laverton, Lat. 28° 31' S, Long. 122° 45' E), and Redsands, also known as the R-area (138 km. E. Laverton, Lat.

28° 12' S, Long. 123° 35' E), using pit traps (62,226 pit trap days), which augmented sample sizes with more limited qualitatively different information. Pit-trapped lizards provided no data on microhabitat, thermal relations, or time of activity, but were useful for analyses of diet and reproduction.

Food items within stomachs were sorted and identified among 21 categories, mostly arthropod orders. Prey items were counted and volumes estimated to the nearest cubic millimetre for each category. Volumes were estimated either by volumetric displacement or by placing a one millimetre thick layer of material over square millimetre grid paper and counting squares occupied to approximate total volume. Each lizard's counted stomach contents were kept individually and stored in ethanol. Dietary niche breadths were estimated using the inverse of Simpson's (1949) index of diversity [$D = 1/ \Sigma p_i^2$], where p_i is the proportion by volume of food items in stomachs based on all prey categories.

Here, I report augmented ecological information on the following uncommon desert skinks: *Cyclodomorphus melanops* (N=27), *Eremiascincus richardsoni* (N=22), *Lerista desertorum* (N= 117), *Morethia butleri* (N=67), and *Tiliqua multifasciata* (N=11).

RESULTS

Time of Activity and Thermal Relationships

Most of these skinks were active during the warmer springtime-early summer months of October through February. In the following, all times are decimalized in metric units to facilitate computation of statistics.

In this study of five species (Table 1), *Cyclodomorphus* had the highest active body temperatures ranging from 31.6 to 37.7°C, with a mean of 34.8°C. The nocturnal species *Eremiascincus* had the lowest active body temperature, ranging from 24 to 27°C, averaging 26.2°C. All *Lerista desertorum* were pit trapped and no data on time of activity or body temperature were obtained for this fossorial species although most species of *Lerista* are believed to be largely nocturnal or crepuscular (J. Dell, pers. comm.).

Habitat and Microhabitat

In the GVD, lizards recognize four

Table 1. Average ambient air temperature, mean active body temperature, and average time of activity for four species with data (sample sizes in parentheses).

Species	Air Temperature (N)	Body Temperature (N)	Time (N)
Cyclodomorphus	29 (4)	34.8 (3)	13.57 (5)
Eremiascincus	25.5 (7)	26.2 (6)	16.64 (7)
Morethia	28.7 (15)	33.6 (11)	10.02 (16)
Tiliqua	26.33 (3)	32.4 (3)	11.45 (4)

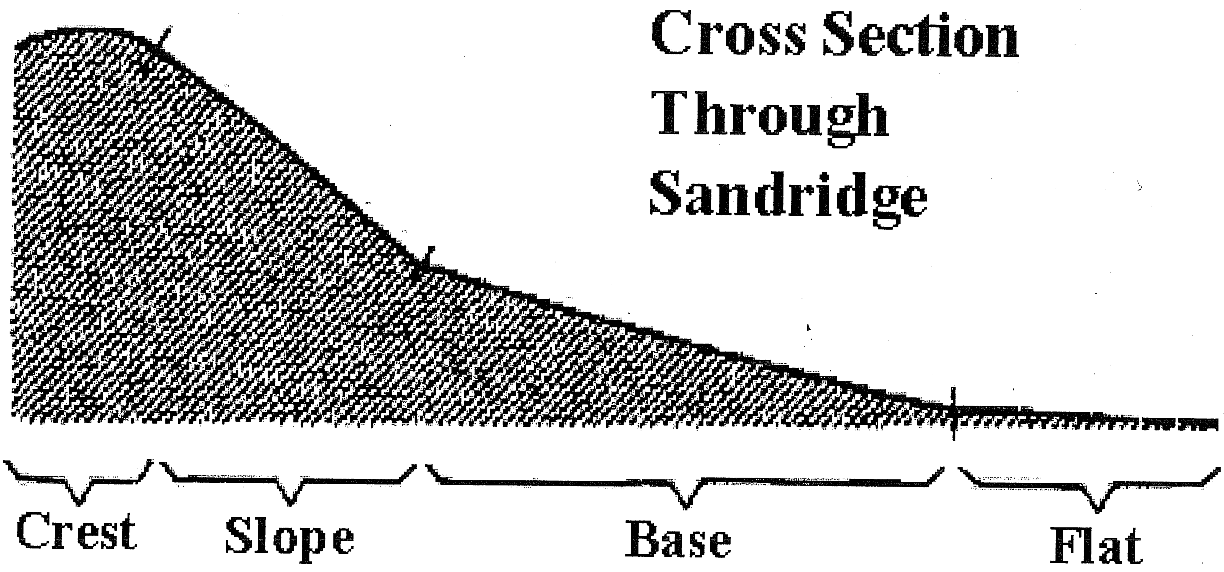

Figure 2. Cross section through a sandridge with four habitat types marked.

different habitat types, flat, base, slope, and crest (Figure 2).

Cyclodomorphus are found both on flat sandplain areas and sandridge crests and are strongly associated with large long unburned spinifex grass hummocks (*Triodia basedowi*), which they seldom leave and through which they appear to "swim". *Eremiascincus* are nocturnal, spending daylight hours in small side out pockets of large burrows, their diurnal retreats — several were found emerging from a large rabbit warren shortly after dusk on May 5, 1967 on the Y-area (Pianka 1986). *Lerista desertorum* are fossorial, usually associated with sandridges and often under fallen litter beneath Marble Gum (*Eucalyptus gonglyocarpa*) trees. *Morethia butleri* are diurnal, usually found in litter underneath large bushes or Marble Gum trees, both on flat sandplains and on sandridges. Least known is the large skink *Tiliqua multifasciata*, all of which were diurnal, most were found on spinifex flats although a few were on sandridges. Habitat niche breadth is narrowest for *Tiliqua* and broadest for *Lerista desertorum* (Table 2).

Anatomy

The five species of skinks considered here vary widely in size, the smallest (*Morethia butleri*) has an SVL of 42.7 mm, while the largest (*Tiliqua multifasciata*) averages 211 mm in SVL. *Cyclodomorphus melanops* and *T. multifasciata* have relatively short limbs and tails. *L. desertorum* is an elongate burrower with reduced vestigial fore and hind limbs and toes. The other two species, *Eremiascincus richardsonii* and *Morethia butleri*, are more like other lizards morphologically with considerably longer limbs and tails relative to their snout-vent lengths (Table 3).

Table 2. Percentages of lizards found in various habitats (Sample sizes in parentheses). Lizards found at an interface between habitats are split between both. Habitat niche breadths calculated with the inverse of Simpson's (1949) index of diversity, $1/\Sigma p_i^2$, where p_i represents the proportion of animals in habitat *i*.

Species	Flat	Base	Slope	Crest	Total	Habitat NB
Cyclodomorphus	30.4 (7)		13.1 (3)	56.5 (13)	23	2.33
Eremiascincus	30.0 (6)		15.0 (3)	55.0 (11)	20	2.41
L. desertorum	2.9 (2)	18.6 (13)	21.4 (15)	57.1 (40)	70	2.45
Morethia	11.1 (4)	52.8 (19)	16.7 (6)	19.4 (7)	36	2.81
Tiliqua	63.6 (7)		9.1 (1)	27.3 (3)	11	2.05

Table 3. Average snout-vent length (SVL in mm), fore leg length (FLL) as a proportion of SVL, hind leg length (HLL) as a proportion of SVL, mean length of intact non-regenerated tails (in mm), and mean body weight (in grams). Sample sizes are given in parentheses.

Species	SVL (N)	FLL (N)	HLL (N)	Tail L. (N)	Weight (N)
Cyclodomorphus	85.1 (20)	.155 (10)	.200 (10)	75 (11)	7.7 (20)
Eremiascincus	71.6 (19)	.288 (9)	.395 (9)	102 (4)	8.34 (19)
L. desertorum	77.6 (114)	.039 (31)	.164 (31)	75.98 (54)	3.68 (114)
Morethia	42.7 (64)	.273 (43)	.401 (43)	62.3 (26)	1.55 (62)
Tiliqua	211 (10)	.186 (9)	.185 (9)	97.4 (9)	205.7 (10)

Diets

Tiliqua are omnivores, but are largely herbivorous (Shea 1994; Hutchinson 1993). Of the five species considered here, they have the most specialized diet, eating 71.7% plant material by volume (Table 4), mostly seeds and fruits. *Cyclodomorphus* feeds primarily on spiders, orthopterans, beetles, and termites, and has a dietary niche breadth of 4.98. Jones (1992) and McAllister et al. (1993) reported on gastrointestinal parasites of *Cyclodomorphus* and *Tiliqua*. *Eremiascincus* and *Morethia* have somewhat broader dietary niche breadths of 6.65 and 6.70, respectively, preying on a wide variety of arthropods. The fossorial *Lerista desertorum* has the broadest dietary niche breadth of 7.36, probably not surprising as diversity and abundance of small prey items is usually greater compared to larger invertebrates (J. Dell, unpublished data).

Despite their abundance in Australian deserts, ants were represented by low volumes in stomachs of all five species in this study, in keeping with findings of Morton and James (1988) and Twigg *et al.* (1996), who found that ants were infrequently consumed by many desert species with the exception of a few dietary specialized ant-eating agamid lizards.

Table 4. Proportions of different prey categories by volume in stomachs.

Species/ Prey Category	*Cyclodo-morphus*	*Eremia-scincus*	*Lerista desertorum*	*Morethia butleri*	*Tiliqua*
Centipedes	0.009	0.108	0.028	0	0.010
Spiders	0.312	0.092	0.052	0.268	0
Scorpions	0	0	0.020	0.019	0
Ants	0.007	0.031	0.004	0.005	0.006
Wasps	0	0.019	0.004	0.090	0
Orthopterans	0.130	0.101	0.012	0.139	0.021
Thysanura	0.024	0.009	0.096	0.121	0
Blattaria	0.024	0.118	0.092	0.049	0
Mantids/ Phasmids	0	0	0	0	0.002
Beetles	0.133	0.307	0.128	0.015	0.134
Isoptera	0.254	0.026	0.108	0.141	0.015
Hemiptera	0.048	0.028	0.020	0.010	0.017
Diptera	0.005	0	0.004	0	0
Lepidoptera	0.010	0.087	0	0	0
Insect Eggs	0	0	0.004	0	0
Larvae	0.005	0	0.088	0.015	0.002
Other Insects	0.019	0.024	0.036	0.110	0.004
Vertebrates	0.002	0.007	0	0	0
Vegetation	0	0	0.012	0	0.717
Unidentified Other	0.019	0.043	0.292	0.020	0.072
Total Volume of Prey, cc.	5.863	4.241	2.5	2.060	19.542
Dietary Niche Breadth	4.98	6.65	7.36	6.70	1.86
Number of Stomachs	27	22	117	67	11

Reproduction

Samples were too few to infer very much about reproduction. Males of all species outnumbered females in pit traps (sex ratios, proportion of males averaged across all species = .758 ± 0.017), suggesting that males may move more often and/or farther than females. *Cyclodomorphus* and *Tiliqua* are live bearers (Shea 1994; Hutchinson 1993), the other three species lay eggs (Greer 1989). One *Cyclodomorphus* female collected on 12 December 1978 contained 3 eggs in her oviducts, which constituted 18.6 % by volume of her total body weight, presumably this allocation would increase substantially with embryonic growth before young reached full term. One *Eremiascincus* female collected on 19 January 1979 contained 5 oviductal eggs, which comprised 11.4 % by volume of her body weight.

DISCUSSION

In addition to the five species of skinks discussed here, many other lizard species, including some agamids, pygopodids, geckos, other skinks, and varanids, are also uncommon (Appendix 1). A few of these, such as *Ctenophorus clayi*, *C. nuchalis*, *Diplodactylus damaeus*, and *Rhynchoedura ornata*, display ephemeral booms and busts which are frequently associated with previous episodic rain events. Other cases of apparent chronic rarity, including *Ctenophorus fordi*, *C. scutulatus*, *Lophognathus longirostris*, *Ctenotus greeri*, *C. leae*, *C. leonhardii*, *Diplodactylus ciliaris*, *Nephrurus vertebralis*, and *Varanus gilleni*, appear to be episodes of dispersal.

Cyclodomorphus melanops are elongate lizards with reduced limbs, presumably an evolutionary response favoring movement through dense vegetation. They require extremely large old long-unburned spinifex grass hummocks. Spinifex is the dominant vegetation at most of my study sites, yet *Cyclodomorphus* appear to be rare, suggesting that microhabitat availability itself cannot be limiting. Nor is food limitation likely since this species consumes a wide variety of arthropods. Perhaps they have poor hunting ability because their reduced limbs results in slow movement. Even if food items are abundant, prey must be encountered and caught. Although no data are available on predation, predators could hold population densities down as these skinks would be exceedingly vulnerable when outside of the protection of grass hummocks. Even when inside hummocks, they might easily fall victim to large snakes. Because they are small live bearers, their fecundity is low, which could also be a factor contributing to their rarity.

At my desert study areas, *Eremiascincus richardsonii* dig their own small tunnels on the sides of large deep burrows dug by rabbits and Perenties (*Varanus giganteus*). Such large burrows are few and far between, suggesting that populations of these nocturnal skinks could be limited by availability of these diurnal retreats. From 1995 to 1998, eight individual *E.richardsonii* were trapped along the same short stretch on the crest of a sandridge at Redsands, whereas pit traps on crests of other sandridges nearby captured only three *Eremiascincus*, suggesting that spatial distributions of this species are patchy and clumped. Thus, *Eremiascincus* may be locally relatively more abundant than they are across the landscape at large.

Based on numbers pit trapped, *Lerista desertorum* is the most abundant of these five species, and it also is the most generalized, with the broadest habitat and dietary niche breadths. Its burrowing habits presumably confer protection from predation. It would be interesting to know whether such generalists with broad niches tend to be more abundant than more specialized species.

Morethia are usually found in the litter under Marble Gum trees, a place difficult to install and maintain pit traps and drift fences. They have relatively broad habitat and dietary niche breadths. Their apparent rarity could be an illusion due to cryptic behavior making this species difficult to capture.

Like *Cyclodomorphus, Tiliqua* are elongate lizards with reduced limbs, facilitating movement through dense vegetation. However, due to their short limbs they are very slow moving and vulnerable when out in the open, and would be easy picking for avian predators, which could keep population densities low (Aumann 2001). They are also eaten by Australian Aborigines (Fyfe 1986; Bird *et al.* 2005). As with *Cyclodomorphus*, their low fecundity could also contribute to their rarity.

No general explanation for rarity may exist, but rather each species may have its own idiosyncratic reasons for being uncommon. Many of the possible factors that could contribute to rarity remain to be evaluated, and the difficulty of studying uncommon species remains a formidable challenge to ecologists.

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APPENDIX 1

List of species and their relative abundances, ranked from most abundant to rarest.

Species	Sample Size	Species	Sample Size
Ctenotus quattuordecimlineatus	2263	*Varanus tristis*	104
Lerista bipes	2249	*Delma butleri*	98
Ctenophorus isolepis	2097	*Varanus brevicauda*	97
Nephrurus laevissimus	1214	*Ctenotus leonhardii*	97
Ctenotus dux	1142	*Diplodactylus elderi*	88
Ctenotus calurus	1047	*Lophognathus longirostris*	85
Ctenotus piankai	905	*Nephrurus levis*	78
Gehyra variegata	842	*Ctenophorus scutulatus*	77
Rhynchoedura ornata	596	*Diplodactylus strophurus*	70
Ctenotus grandis	585	*Morethia butleri*	67
Diplodactylus conspicillatus	526	*Pygopus nigriceps*	51
Menetia greyi	505	*Lialis burtonis*	44
Gehyra purpurascens	468	*Lerista muelleri*	40
Ctenophorus nuchalis	431	*Diporiphora winneckei*	35
Egernia striata	428	*Heteronotia binoei*	35
Ctenotus pantherinus	425	*Cyclodomorphus melanops*	27
Ctenotus hanloni	396	*Ctenotus leae*	25
Ctenotus colletti	392	*Ctenotus atlas*	23
Egernia inornata	329	*Eremiascincus richardsoni*	22
Ctenotus ariadnae	287	*Diplodactylus stenodactylus*	17
Ctenophorus clayi	286	*Diplodactylus pulcher*	16
Ctenotus helenae	285	*Nephrurus vertebralis*	16
Ctenotus brooksi	274	*Ctenophorus reticulatus*	14
Ctenotus schomburgkii	242	*Delma nasuta*	14
Moloch horridus	222	*Caimanops amphiboluroides*	13
Varanus eremius	205	*Varanus caudolineatus*	12
Cryptoblepharus buchananii	193	*Egernia depressa*	12
Pogona minor	192	*Tiliqua multifasciata*	11
Diplodactylus ciliaris	169	*Varanus giganteus*	10
Diplodactylus damaeus	161	*Tiliqua occipitalis*	6
Lerista desertorum	117	*Ctenotus greeri*	5
Varanus gouldii	116	*Varanus gilleni*	2
Ctenophorus fordi	107	*Egernia kintorei*	1