

The Ecology of *Moloch horridus* (Lacertilia: Agamidae) in Western Australia

ERIC R. PIANKA AND HELEN D. PIANKA

Observations on the ecology of the Australian agamid, *Moloch horridus*, are described, and the literature on the species is reviewed. Its geographic distribution, which embraces most of the desert interior of Australia, corresponds closely to the distribution of sandy soils. With respect to food, *Moloch* is among the most specialized of lizards, since analysis of the stomach contents of 103 specimens revealed almost nothing but very small ants (*Iridomyrmex*). *Moloch* has a bimodal seasonal pattern of activity, with reduced activity in mid-winter and mid-summer. Evidence is presented for a spring breeding season, during which time individuals travel over great distances, probably increasing their chances of making mating contacts. At least some ovarian eggs become enlarged and yolked in autumn, but, since there is no evidence for autumnal oviducal eggs or egg laying, either sperm storage or arrested embryonic development may occur during the winter. Egg deposition occurs in the spring or early summer. Clutch size varies from three to ten, with a mode of eight. Females reach nearly twice the body weight of males. Natural longevity is often at least six years. Predators on the species include aborigines, bustards, and probably raptors and snakes.

The ecology of *Moloch* is compared with that of its North American ecological analogue *Phrynosoma platyrhinos*. Although these two ant specialists are morphologically similar, there are a number of striking differences in their ecologies, which can be explained, in part, by the differences between the Australian and the American desert environments.

INTRODUCTION

ALTHOUGH *Moloch horridus* Gray is one of the more familiar agamid lizards in Australia, and certainly the most bizarre, little is known of its behavior, natural history, and ecology. "Mountain devils" are very difficult to find in any numbers and most of what is known is based upon a few captive individuals. During a 16 month field study in the Australian deserts, we made a concerted effort to find and observe this species. Our observations are presented here along with a summary of what is known about *Moloch*.

Moloch was first exhibited in London by John Gould in 1840; this specimen was described and figured by Gray in 1841. Giles (1889:10) mentioned *Moloch* and reproduced Gray's figure. Saville-Kent (1897) discovered that they fed almost exclusively on ants and made other observations on their behavior and egg laying in captivity. Saville-Kent first noted the striking morphological similarity between *Moloch* and the North American iguanid genus *Phrynosoma*. On the basis of

this similarity in body form, he predicted that *Phrynosoma* would be found to be an ant eater and his prediction proved correct. Davey (1923) discovered that his pet *Moloch* would accept only one (*Iridomyrmex rufoniger*) of eight species of ants occurring around Melbourne. Davey also made reference to the "hygroscopic nature" of the skin of *Moloch*, a phenomenon later analyzed more completely by Bentley and Blumer (1962). Locality data has been provided by Davey (1923), Kinghorn (1924, 1945), Lockwood (1964), Loveridge (1934), Lucas and Frost (1896), Ride *et al.* (1962), Slater and Lindgren (1955), Sterling and Zietz (1893), Thomson and Hosmer (1963), and Zietz (1914). Several papers have dealt with aspects of egg laying and incubation in nature (White, 1947) and in captivity (Sporn, 1955, 1958, 1965), and with thermoregulation in nature and captivity (Licht *et al.*, 1966). Sporn's long-term studies have provided valuable information on breeding, feeding, growth, and longevity in captivity.

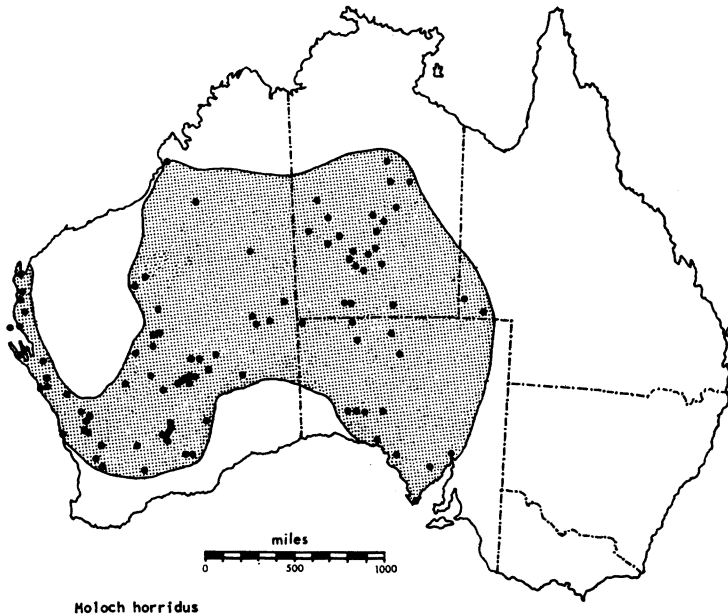


Fig. 1. Collection localities of *Moloch horridus* (closed circles). Hypothetical geographic distribution shown by stippling.

DISTRIBUTION AND HABITAT

The geographic distribution of *Moloch* is usually given as "the inland desert parts of Western Australia (W. A.), South Australia (S. A.), the Northern Territory, and Queensland," but no one has yet published a range map. During the course of this study, we visited all the state museums in Australia and collated nearly all locality data. Fig. 1 shows localities specific enough to be plotted as closed circles. The stippled area represents a hypothetical geographic distribution, based upon considerations of habitat and autecology as well as proximity to recorded localities. Exact localities are listed in the APPENDIX.

It is nearly certain that records from the Perth and Adelaide regions are due to human transportation, and they are therefore not plotted. Other problematical specimens are not so easily dismissed. Two records from the "Nullarbor Plain" are not precise enough to be plotted, but raise the question of whether or not *Moloch* exists on the Nullarbor. There are good records from Ooldea, S. A., and Queen Victoria Spring, W. A., both of which are just off the edge of the plain and in decidedly different soil and vegetation zones. It is only after considering habitat (below) that we conclude that *Moloch* probably does not occur on the Nullarbor

Plain. While there are only a few records from the entire Great Sandy Desert region, habitat considerations make it nearly certain that *Moloch* occurs throughout this vast uninhabited and unknown region. Although there is no record of the species from northwestern New South Wales, it is possible that it occurs there.

A comparison of the distribution as depicted in Fig. 1 with existing soil and vegetation maps (Prescott, 1944; Wood and Williams, 1960) indicates that the species exists in two quite different habitats: the sandplain and sandridge deserts of "The Centre," and the mallee belt of southwestern W. A. Of the 106 *Moloch* we have collected, 104 were found on relatively sandy soils—either on sandplains, sandridges, or on sandy loams. (This is in part due to the fact that tracks are easier to follow in sandy areas, and often our specimens were located by tracking.) Habitat vegetation in most cases consisted of spinifex grass tussocks (*Triodia* spp.) with scattered acacia (commonly referred to as "mulga") and eucalypt bushes and trees. However, several *Moloch* were taken in mallee eucalypt and low acacia shrub with little or no spinifex, and two of our specimens were found crossing the road in mulga areas with soft soils. *Moloch* has also been

reported from stony soils in the extreme southwestern portion of its range near York and Dryandra, W. A. (Licht *et al.*, 1966; A. R. Main, pers. comm.). However, it appears that over most of its geographic range, *Moloch* does not occur in stony "mulga" country or on mountain slopes. Strong evidence that the species does not inhabit areas with tightly-packed soils comes from the lack of any records from the extensive rocky Pilbara-Hammersley region of W. A., an area which has not been neglected by lizard collectors. It is nearly certain that there is a real gap in *Moloch's* geographic range here. This fact also suggests that *Moloch* may not occur on the relatively stony soil of the Nullarbor Plain proper. The distribution of *Moloch* coincides more closely to the distribution of sandy and sandy loam soils (see Prescott, 1944; Stephans, 1956 for soil maps) than with any climatological field.

FOOD AND FEEDING BIOLOGY

Moloch thrive on ants and have distinct preferences as to the species accepted (Saville-Kent, 1897; Davey, 1923, 1944; and others). Sporn (1955) noted that his *Moloch* would accept six different species of ants but refused stinging species. However, most of these observations were made upon captive specimens, often many miles from their natural habitat. We examined the stomach contents of 103 *Moloch* preserved shortly after capture. The sample included animals from a variety of habitats, and many different geographic localities, which had been collected over the entire seasonal range of conditions.

The stomachs of this diverse series contained only ants and a few tiny objects such as small stones, sticks, minute flowers and small insect eggs (probably objects being carried by the ants and only eaten "accidentally"). At least three different species of ants, all very small, are represented in the stomachs examined. The estimated volume per ant varies only from .002 to .005 cc. William L. Brown (pers. comm.) indicates that all are probably species of *Iridomyrmex*, a genus still in need of revision.

The literature on *Moloch* is replete with estimates of rates of feeding, varying from 24 to 45 ants per min (White, 1947; Davey, 1923). Estimates of the total number of ants eaten per meal by an individual range from 675 (Davey) to 1000-1500 (Saville-Kent). Two of the largest stomachs we examined con-

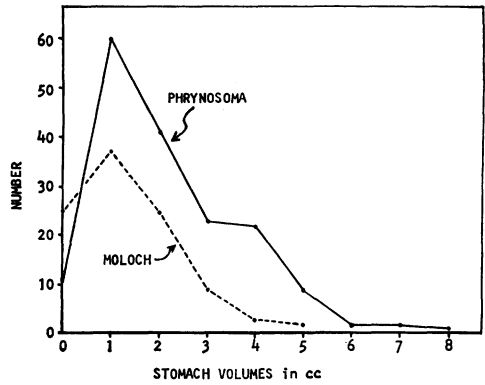


Fig. 2. Distribution of stomach volumes in 171 *Phrynosoma platyrhinos* and 72 *Moloch horridus*.

tained about 2500 very tiny black ants, probably the "spinfex ant," *Iridomyrmex flavipes* [= *rostronotus*] (W. L. Brown, pers. comm.). The stomach capacity of *Moloch* is large, but in only an occasional individual in our series did the stomach appear filled to capacity. Fig. 2 shows the frequency distribution of stomach sizes.

Moloch fecal pellets are very distinctive; these glossy, black, perfect prolate spheroids are often found in neat piles either in the open or amongst sparse vegetation. Individuals have specific defecation sites, apparently separate from their "basking" sites, and tracks and accumulations of fecal matter indicate that they often return to such a spot several days in succession.

SEASONAL ACTIVITY AND REPRODUCTIVE BIOLOGY

Moloch have a pronounced seasonal activity pattern, reflected in the frequency distribution of the dates of collection (Table 1), which indicates two annual periods of activity and two of relative inactivity. During the coldest months (June and July) and the hottest months (January and February), *Moloch* seldom move (*i.e.*, their tracks are seldom seen) and are only rarely collected. There is a three month autumnal activity period (March, April, and May) and a five month activity period spanning late winter, spring, and early summer (August through December), during which mating and egg deposition take place. During hot summer days, *Moloch* may retreat into shallow underground burrows; we discovered a juvenile female in a

TABLE 1. THE NUMBERS OF *Moloch* COLLECTED DURING EACH MONTH OF THE YEAR, AND THE NUMBER OF DAYS SPENT IN THE FIELD.

	No. Days in Field	No. <i>Moloch</i> Collected	No./Day	Museum Records	Tot. No. Collected	
Jan	26	2	0.08	5	7	Summer
Feb	20	0	0.00	8	8	
Mar	15	8	0.53	4	12	
Apr	2	0	0.00	13	13	Autumn
May	17	21	1.24	9	30	
June	14	0	0.00	1	1	Winter
July	0	0	0.00	3	3	
Aug	17	15	0.88	2	17	
Sept	16	31	1.94	10	41	Spring
Oct	26	7	0.27	5	12	
Nov	30	11	0.37	6	17	
Dec	24	9	0.38	6	15	Summer
TOT.	207	104		72	176	

burrow and an adult male near another burrow in late November. These burrows clearly fit each animal and were no doubt excavated by them.

During the summer and autumn months, *Moloch* are sedentary, an individual's movements generally being restricted to an area about 20–30 ft on a side. Within this area there will usually be one of more ant trails, a defecation site, and several small bushes with scattered dead leaves and/or loose *Triodea* tussocks beneath them. These lizards spend the night and the heat of mid-day within the protective cover of such shrub complexes (sometimes actually within a loose spinifex tussock), and will often take refuge in them upon the approach of a predator (as evidenced by fresh tracks). Tracks and observations on several individuals suggest the following general pattern of daily activity: The animal first walks a short distance into the sun from the shrub(s) under which it has spent the night. After basking and “bellying-down,” the lizard attains an active body temperature and begins to move. Often an individual will then walk 5–10 m to its defecation site, defecate, and return by nearly the same route to the shrub complex, stopping to feed at an ant trail somewhere along the way.

In contrast to the relatively sedentary summer–autumn existence, *Moloch* move over much greater distances during August and September. It is not uncommon to encounter

fresh “cross-country” tracks in the early spring, when we often followed relatively straight tracks for linear distances of up to 500 ft. Such increased movements could be a means of increasing the probability of contact between individuals, conceivably for the purpose of mating. On 25 August 1967 we observed one small aggregation of two males and two females in an area immediately adjacent to and beneath a large shrub. Tracks clearly indicated that all four individuals had travelled varying distances (150–250 ft) toward and converged upon this shrub from different directions, all in less than 24 hr (winds had erased all tracks the day before). Evidence of a similar gathering was observed on another area, also in August, although we were able to collect only two of these individuals, both males. Tracks indicated the presence of two other much larger individuals (probably females) and showed that considerable mingling had occurred. In spite of concerted efforts, we were unable to find evidence of such aggregations at any other time. The above two cases are striking because of their rarity and their simultaneous occurrence, and we are inclined to interpret them as “mating contacts.”

Our observations suggest that mating occurs in the springtime, during late August. Sporn (1965:159), however, asserted that his captive *Moloch* “become sexually active and mate in the late summer and during the

TABLE 2. STATISTICS ON TESTES VOLUMES OF ADULT MALES DURING DIFFERENT MONTHS, MEASURED BY VOLUME DISPLACEMENT (mm³). \bar{x} = mean, S = standard deviation, S.E. = standard error of mean, N = sample size (number of testes).

	\bar{x}	S	S.E.	N
Mar	95.8	24.7	7.12	12
May	102.5	29.0	8.36	12
Aug	108.0	30.5	6.83	20
Sept	104.1	24.4	4.69	27
Oct	82.5	17.1	8.54	4
Nov	74.6	29.1	8.78	11
Dec	47.5	15.0	7.50	4

warm days of early autumn, from late March to late April." It is difficult to resolve this apparent discrepancy in the absence of actual field observations of copulation. We therefore measured, by volumetric displacement, the testes volumes of our 46 adult males. Testes size has been found to be indicative of the peak period of spermatogenesis in *Uma* and *Urosaurus* (Mayhew, 1965, 1966; Asplund and Lowe, 1964). In our samples, testes are large during the months of May, August, and September (Table 2). The testes of individuals collected during late August are largest and were noted to be of a distinctly more reddish hue than those of specimens taken during other months. In themselves, these data are inconclusive, so we performed a similar analysis on the ovaries of our 46 adult females. Large, yolked, ovarian follicles also occur in May, August, and September, but oviducal eggs occur only from late August through December. Hence our data indicate that in the Great Victoria Desert, W. A., some *Moloch* mate during August and September. Perhaps others breed during the autumnal period of activity, even though we noted no evidence of this in the field. The occurrence of enlarged testes and ovarian follicles during May (9 of 13 females collected in May had yolked ovarian eggs over 6 mm in diameter) supports Sporn's observations of mating in the early autumn. If a female were able to mate in either autumn or early spring (or both), she would be prepared to receive sperm at all times of activity, except perhaps during the egg-laying season.

Twenty-five records of the date of egg deposition break down as follows: late October (6), early November (8), late November (5), early December (3), late December (3) (Sporn, 1955, 1958, 1965; White, 1947; and our data). Neither egg laying nor oviducal

eggs have ever been recorded during the short Australian winter (June and July). We suggest that if autumnal insemination occurs (which seems very likely) either the sperm are stored or embryonic development is arrested during the winter months. Sperm storage has been reported for *Uta stansburiana* (Cuellar, 1966) and *Hemiergis peronii* (Smyth and Smith, 1968). To our knowledge, no one has reported evidence of enlarged yolked ovarian eggs in any lizard so well in advance of egg deposition.

It is reasonably certain the *Moloch* usually lay only a single clutch of eggs annually. Sporn (1965) reported that one of his females deposited two clutches in one year on October 25 and December 29th. The fact that these two dates are among the earliest and the latest of 25 records (above) suggests that double clutches might ordinarily not be frequent in nature.

Clutch size in *Moloch* varies from three to ten, with a mode of eight eggs per female. Most females lay from six to eight eggs per clutch (Fig. 3). White (1947) and Sporn (1955, 1965) have described excavation of the egg chamber and deposition of the eggs. Sporn (1965) allowed five clutches laid in captivity to hatch normally and recorded incubation periods of from 90 to 132 days (average 115 days).

THERMOREGULATION

The significance of field studies on reptile body temperature has recently been the subject of debate (see Heath, 1964; Soulé, 1963; and Licht *et al.*, 1966). It is usually accepted that, while field body temperatures do not provide direct information on "preferred body temperatures," they do reflect the all-important compromise between the preferred body temperature and the range of environmental temperatures available. Licht *et al.*

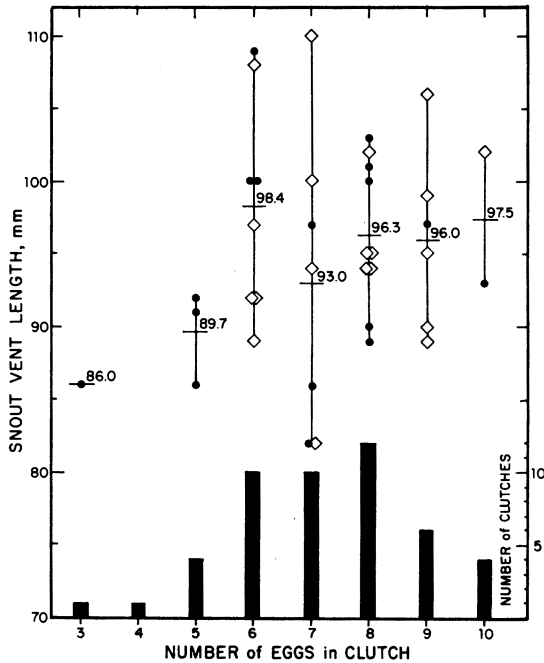


Fig. 3. Clutch sizes recorded in 37 female *Moloch horridus* plotted against snout-vent length. Oviducal eggs depicted by circles, enlarged ovarian eggs by diamonds. Mean snout-vent length of females for each clutch size is shown by a horizontal bar. Frequency distribution of clutch sizes at bottom of figure includes 11 literature records of clutches laid, but for which no snout-vent lengths of the females are available. Mean clutch size from these data is 7.23 eggs.

(1966) demonstrated that the variance in body temperature in nature is almost always greater than the same measure as determined by means of thermal gradient chambers in the laboratory. Indeed, the difference between the means and variances of active body temperatures in nature and those preferred in the laboratory thermal gradient may be ecologically the most significant thermoregulatory parameters possible. Such statistics reflect a wide variety of ecological activities and provide a convenient and readily obtainable measure of the particular compromise reached by a given species.

Licht *et al.* (1966) also provided preliminary data on the thermal relations of *Moloch*, and give the mean and variance of its body temperature in a thermal gradient and in nature. Although the sample size is small, their data show that the standard deviation of body temperature in nature (3.38) is greater than in any other Australian lizard they studied. In sharp contrast, the standard deviation in body temperature recorded in their thermal gradient (1.17) was similar to that of many other lizard species (Licht *et al.*, 1966).

During the course of the present study, we recorded body temperatures of 83 active *Moloch*. W. R. Dawson and G. M. Storr provided a further six records. These data are plotted against the ambient air temperature (4 ft above ground, shaded bulb) in Fig. 4. It is apparent from this graph that there is a correlation between air temperature and body temperature ($r = .625$, $P < .01$). The mean body temperature is slightly lower and the variance somewhat smaller than the same measures as determined in nature by Licht *et al.* (1966). We discuss these data further in the concluding section of this paper.

VARIATION, SIZE, GROWTH, AND AGE

While we have not engaged in any elaborate study of variation, we have noticed that, although the configuration of blotches on the dorsum appears to be fairly invariable, abdominal patterns differ markedly in every individual. Dorsal color differences between individuals occur, however, and appear to be correlated with the color of the sands from which an animal is taken. Red-backed individuals usually are found on red sands,

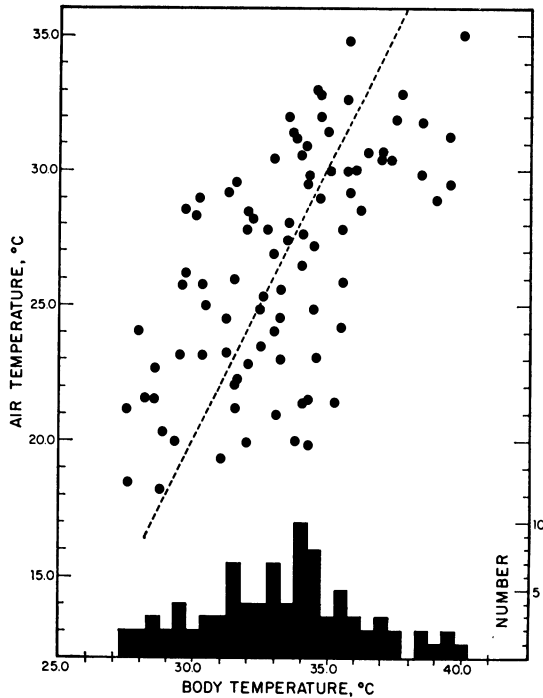


Fig. 4. Plot of ambient air temperature versus body temperature of 89 active *Moloch horridus*. Histogram at bottom of figure shows frequency distribution of body temperatures. Correlation coefficient of +0.63 is significant at the $P < .01$ level.

brown-backed ones on the mallee brown soils, while yellow-backed animals are often found on the yellow sandplains and dunes.

As noted by White (1947) and others, *Moloch* can change their colors rapidly in a chameleon-like fashion. There are two basic color phases, a "dark" phase in which the ground color becomes greenish and the blotches olive, and a "light" phase with the ground color yellowish and the blotches either reddish, brownish, or yellowish (as indicated above). The dark phase is invariably assumed by cold or inactive animals while the light phase is only taken on by active warm specimens. However, an active individual can change its color fairly rapidly and it is often difficult to ascertain whether a specimen has darkened in response to the observer's approach. We have watched these lizards "escape" into shady spots and darken from a bright yellow and rufous red to a dull gray-green and olive-brown within a few minutes.

There is a pronounced sexual size dimorphism in *Moloch*, with adult females being larger and often stouter than adult males.

This is shown graphically in Fig. 5. Whereas adult females are from 80 to 110 mm in snout-vent length and weigh from 33 to 88.7 g, adult males are all under 96 mm in snout-vent length and never weigh more than 49 g. There is no noticeable size difference between hatchling males and females.

Sporn (1955, 1958, 1965) gave growth rate figures over a 5-8 year period for several captive specimens. His valuable data showed that during the first year, males and females grow at about the same rate, but after that females grow faster than males. He also showed that *Moloch* continued to grow until at least their fifth year. Sporn (1965) has kept individuals under close observation for as long as eight years, and considers it highly likely that *Moloch* live up to 20 years in nature.

Polymodal analysis of snout-vent length frequency distributions for both males and females, using the method outlined in Cassie (1954), demonstrates six size groups in each sex, which correlates well with Sporn's observations and suggests a natural longevity of at least six years. A slowing of the growth

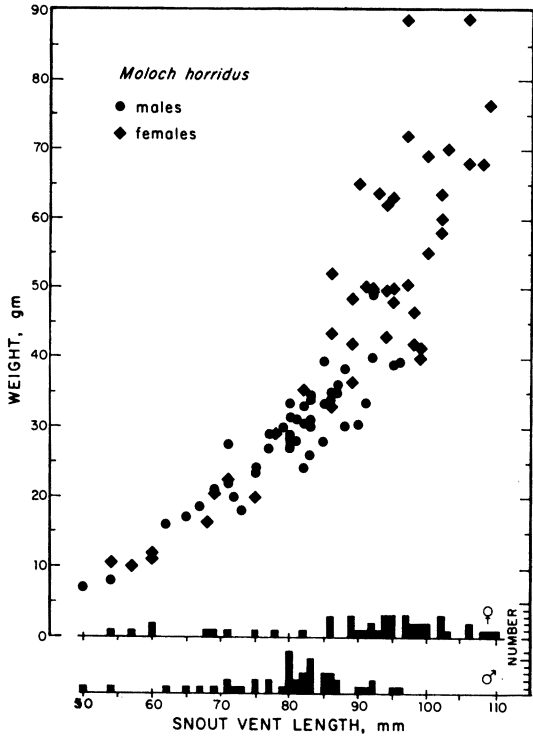


Fig. 5. Plot of snout-vent length versus weight, illustrating sexual size dimorphism in *Moloch horridus*. Male and female snout-vent length frequency distributions are given at bottom of figure.

rate with age would no doubt obscure any older age classes.

PREDATION

Moloch has highly characteristic ambulatory movements, walking in short, slow, jerky steps. When approached by a human, an individual will usually freeze, often halfway through a step, with its tail held high. In this stance, the lizard strongly resembles a small dead, thorny plant and is easily overlooked. Hence, while *Moloch* might be relatively easy to detect by predators using smell, they are probably more difficult to locate by a predator dependent upon sight. Only when the human "predator" is so close that a *Moloch* is aware it has been discovered will the lizard move to the nearest shrub or other cover.

Only two predators have actually been recorded for *Moloch*, the Australian desert aborigines (Lockwood, 1964) and the bustard, *Eupodotis australis* (Serventy, 1966:112). Both hunt by sight. It seems likely that raptors, also dependent upon sight, constitute the

most important source of mortality. *Moloch's* behavior and mode of progression provide for excellent camouflage and are also suggestive of constant distant vigil. Sporn (1955) observed that *Moloch* have very keen vision, and that a flying bird is seen from a long distance. The dingo and the fox, both introduced, could conceivably be present-day predators on *Moloch*. It has been suggested that snakes would have difficulty swallowing *Moloch* because of their spines (LeSouef, cited [incorrectly] by White, 1947, as LeSouef, 1937. Proc. Roy. Soc. N.S.W.), but large snakes would probably have little trouble eating small specimens. Cogger (1967:40) discussed the spiny knob on the back of *Moloch's* neck as follows: "It can be seen from the plate [a photograph of *Moloch*] that a large thorny hump projects from the lizard's neck and biologists have long been curious about its function. It has been suggested that it is a store of fatty tissue on which the Devil can draw when food is scarce, but specimens starved in captivity rarely show any diminution in the size of their hump. On the other

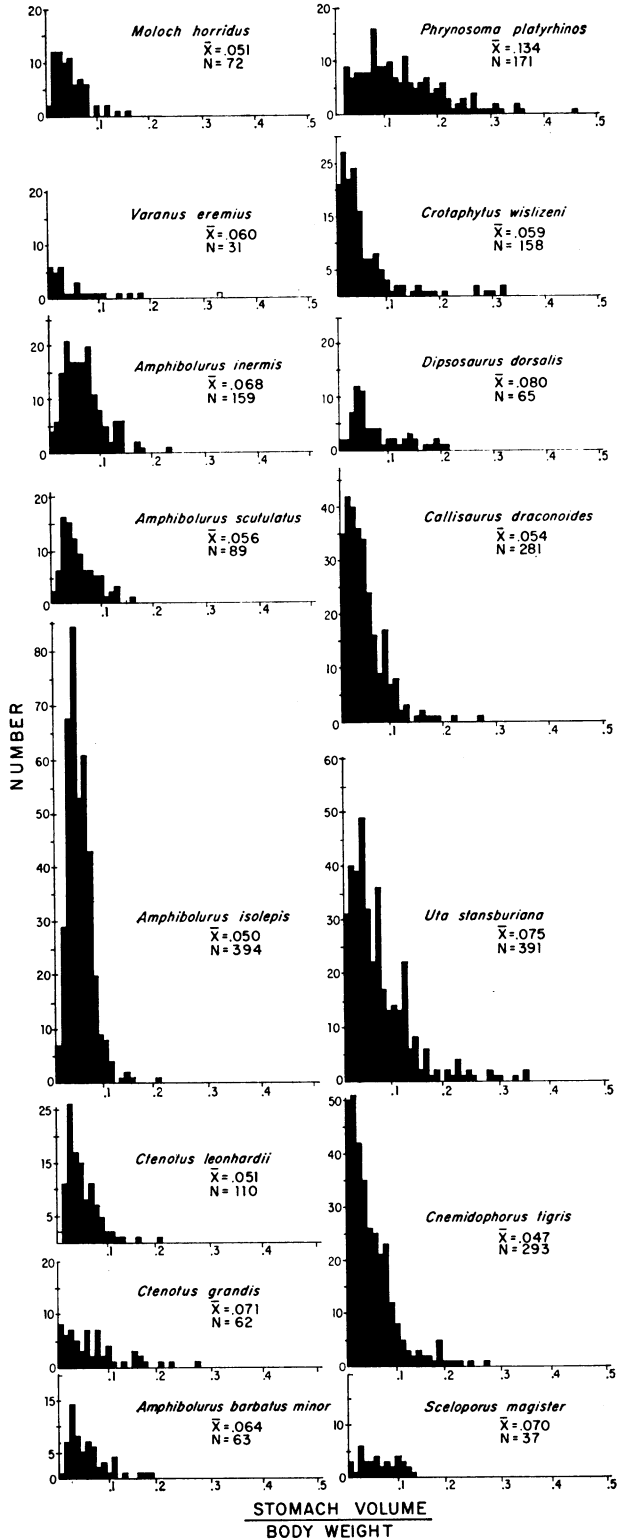


Fig. 6. Ratios of stomach volume to body weight in a variety of North American and Australian desert lizard species. Approximate ecological equivalents are arranged opposite one another. The mean ratio for each species is listed below the species name.

TABLE 3. BODY TEMPERATURES OF ACTIVE LIZARDS IN NATURE FROM NORTH AMERICAN AND AUSTRALIAN DESERTS. Crude ecological equivalents are listed opposite each other. \bar{x} = mean, S = standard deviation, N = sample size.

NORTH AMERICAN				AUSTRALIAN			
	\bar{x}	S	N		\bar{x}	S	N
<i>Cnemidophorus tigris</i>	39.5	1.8	1848	<i>Ctenotus leonhardii</i>	38.0	1.9	92
<i>Uta stansburiana</i>	35.3	2.4	778	<i>Amphibolurus isolepis</i>	37.7	2.3	511
<i>Crotaphytus wislizeni</i>	37.3	2.4	150	<i>Varanus eremius</i>	37.3	3.1	36
<i>Phrynosoma platyrhinos</i>	34.4	3.6	132	<i>Moloch horridus</i>	33.3	2.9	89
<i>Callisaurus draconoides</i>	38.5	2.6	235	<i>Amphibolurus scutulatus</i>	38.9	1.9	81
<i>Sceloporus magister</i>	35.0	1.6	36	<i>Amphibolurus barbatus minor</i>	34.8	3.6	63
<i>Dipsosaurus dorsalis</i>	40.2	2.3	43	<i>Amphibolurus inermis</i>	36.1	3.8	129
<i>Urosaurus graciosa</i>	36.1	1.5	32	<i>Diporiphora winneckei</i>	33.5	3.1	31
<i>Uma scoparia</i>	37.3	2.2	30	<i>Amphibolurus fordi</i>	36.9	2.2	104
<i>Xantusia vigilis</i>	29.3	2.0	20	<i>Heteronota binoei</i>	27.0	3.5	25
<i>Coleonyx variegata</i>	29.6	2.3	32	<i>Rhynchoedura ornata</i>	27.4	2.9	237
<i>Heloderma suspectum</i> ¹	28.7	2.4	55	<i>Egernia kintorei</i>	25.2	—	1

¹ From: Bogert and Del Campo (1956).

hand, when alarmed the Thorny Devil pulls its head protectively down between its front legs, leaving the head-like hump in the position normally occupied by the head itself. This habit has led to the suggestion that the hump is a false head used to divert a predator's attention from the real one, but as it is rare to see a *Moloch* with a damaged hump, it would appear that the primary function of the hump—if, indeed, it has one—is still unknown." Cogger perhaps overstated the objections to the "false head theory" by failing to note that most predation is on an all-or-none basis. It is worth noting that the hump could serve to deter predators without becoming damaged as in the case of any predator that normally takes its prey intact (*i.e.*, snakes and bustards).

COMPARISON WITH THE AMERICAN IGUANID *Phrynosoma platyrhinos*

Our initial interest in the agamid *Moloch* stemmed from the striking similarities between it and the North American iguanid genus *Phrynosoma*; the two seemed to be obvious ecological equivalents. Both are highly specialized and morphologically unique members of their families. The two families are close, but the agamids are considered to be a more recent and more "advanced" family than the iguanids. Members of the two groups are never found together, and zoogeographers think that the iguanids radiated early, and were later replaced by agamids in the old world, Africa, and Australia, leaving

iguanids only in the New World and Madagascar (with a probable trans-Pacific colonization of Fiji) (Darlington, 1957; A. S. Rand, pers. comm.). In any case, both *Phrynosoma* and *Moloch* are evidently quite old genera, with a long history of adaptation in arid regions.

In addition to their superficial morphological likeness, both *Phrynosoma* and *Moloch* exist on diets consisting largely of ants. The senior author studied the ecology of *P. platyrhinos* in western North America, and attempted to integrate aspects of its anatomy, behavior, diet, and thermoregulation (Pianka, 1965, 1966). Since it is of interest to apply these same considerations to *Moloch*, the conclusions of the *P. platyrhinos* study are restated.

The proportion of the stomach volume to the volume of the entire body is greater in *P. platyrhinos* than in any other species of North American desert lizard (Fig. 6). The variance in body temperature of active *P. platyrhinos* taken in nature is also significantly greater than that of any other North American desert lizard (Table 3), an indication that this species allows its body temperature to fluctuate widely under natural conditions. Such "relaxed thermoregulation" presumably allows the animals to spend less time moving into or out of the sun and shade, and therefore provides them with more time for other activities such as feeding. *Phrynosoma* does almost all of its foraging in the open sun between shrubs. Because

ants are small and contain a large component of unusable chitin, large numbers of them must be consumed and an ant specialist must therefore possess a large stomach. The fact that ants usually occur in clumped spatial distributions and therefore constitute a concentrated food source is another important consideration; it has been argued that food specialization can only evolve under such conditions (MacArthur, 1961; MacArthur and Pianka, 1966). Thus, in order to make most efficient use of the concentrated, but at the same time chitinous food supply, *P. platyrhinos* has evolved a large stomach and "relaxed" its thermoregulation. Foraging lizards find an ant trail or nest and essentially gorge themselves. Furthermore, and importantly, the entire ecology is dependent upon the animal's cryptic coloration, heavy body, and spines, for these provide some measure of immunity to predation, the risks of which are likely to be increased during long periods in the open. Lastly, a slowness or a reluctance to move, even when threatened with predation, could be advantageous, since moving would attract the predator's attention and negate some or all of the safety derived from cryptic coloration. The above line of reasoning can be applied in nearly every particular to *Moloch*, which has evolved completely independently of *Phrynosoma*.

Given the preceding facts and interpretations concerning *P. platyrhinos*, Pianka (1966) predicted that if these two ant specialists were as similar as it seemed, the variance in body temperature of *Moloch* in nature might be expected to be significantly greater than that of most other Australian desert lizards. Table 3 summarizes the data relevant to this prediction. Note that the standard deviation of active *Moloch* body temperatures in nature is intermediate among those Australian desert lizards for which there are data. This suggests either that the *Phrynosoma* theory presented above is incorrect or that there is some major difference between the ecologies of *Moloch* and *Phrynosoma*.

A second prediction would be that the proportion of stomach to body volume should be greater in *Moloch* than in other Australian desert lizards. Fig. 6 demonstrates that this is not true. A comparison of the stomach volumes of *Moloch* with those of *Phrynosoma* (Fig. 2) indicates that the considerably smaller iguanid (mean weight = 16.5 g, N = 167)

has in fact a larger stomach than the heavier agamid (about twice the weight, mean weight = 38.2 g, N = 75). Again these data indicate that there is something faulty with the preceding generalizations concerning ant specialization.

Before making suggestions as to possible reasons for these discrepancies, it might be useful to review briefly the basic ecological differences between *P. platyrhinos* and *M. horridus*. 1) *Phrynosoma* consumes 87% ants by number but only 56% by weight (volume), while *Moloch* eats nothing but ants; thus *Moloch* is substantially more specialized with respect to food than *Phrynosoma*. 2) *P. platyrhinos* is smaller, flatter, and less spiny than *Moloch*. 3) There is no sexual size dimorphism in *P. platyrhinos*, as there is to a pronounced degree in *Moloch* (see Fig. 4). 4) *Phrynosoma* is a more active animal than *Moloch*. Whereas the former species often makes a short rapid run to elude predators, the latter seldom even attempts to move quickly. 5) There are at least 14 known species of *Phrynosoma*, many with rather restricted geographic ranges (Reeve, 1952), whereas *Moloch* is a wide-ranging monotypic genus. 6) *Phrynosoma* does nearly all its foraging in the open sun (Pianka, 1965); in contrast, *Moloch* seems to feed in either the sun or open shade with approximately equal frequency.

In addition to these differences between the lizards, there are several striking differences between the Australian and the North American desert environments. There are considerably more trees and hence more shade in the Australian desert, suggesting that cooler substrate temperatures may always be within easy reach. Ranges in temperature on an annual, monthly, or daily basis are generally lower in the Australian than in the North American deserts. Another difference, more difficult to document but certainly of no small importance to the present problem, concerns the abundance of ants. Our impression is that there is a much larger standing crop of ants in Australian than in North American deserts. (This can be demonstrated by allowing a drop of blood or some other food to fall to the ground. Australian ants quickly find such a "bait" and on occasion one must race to get to a wounded lizard before ants cover it. North American desert ants on the other hand take considerably longer to locate an attractive

food object and never actually compete for a wounded lizard.) Correlated with this, but also deriving from differences in the behavior of the ants is the fact that the Australian ants constitute a spatially more concentrated food source than do the American ants. Dense trails of ants, from 2 to 3 cm wide, running from bush to bush (or grass clump) are a regular element of the Australian desert. It is probable that it is this exceptionally dense concentration of ant food which has been the major factor allowing *Moloch* to evolve such an extraordinarily high degree of dietary specialization.

Consider first the fact that *Moloch* apparently does not allow its body temperature to fluctuate to the degree that *Phrynosoma* does. There are several plausible explanations why this might be. Although air temperature means and variances are similar for both species, there is some evidence that substrate temperatures are not. The greater biomass of ants and their relative accessibility in both sun and shade almost certainly provides *Moloch* with a greater opportunity to regulate its body temperature than *P. platyrhinos*. Also, all else being equal, a heavier, more spheroidal animal is better buffered from environmental thermal flux than a lighter and more flattened one. Given the fact that *Moloch* eats a smaller volume of food per feeding than *P. platyrhinos*, even at the same prey density it should not be necessary for it to spend such long periods eating; *Moloch* might therefore have more time available for other activities, including thermoregulation.

The second discrepancy (*i.e.* the smaller stomach in *Moloch*) is difficult to resolve. *Moloch* could have lower energy requirements than *Phrynosoma*; this is suggested by the former's generally lower activity. However, if metabolic rates and energy requirements are similar in the two species, then either 1) *Moloch* must be more efficient at converting ants into usable materials (for instance, it could harbor gut bacteria with chitinases; this would be a reasonable adaptation for such an extreme food specialist), or 2) *Moloch* could process its food at a faster rate than *P. platyrhinos* (*i.e.* it might ingest and defecate more often). Some combination of these possibilities would seem to be the most likely situation, with, for instance, *Moloch* being both more efficient and also having a proportionately lower energy budget.

We must now unfortunately resign ourselves to a less than complete answer and hope that someone with access to these animals and the necessary physiological tools will undertake investigation of some of the problems raised by this investigation. There are a number of reasons why *Moloch* would make ideal lizards for a detailed populational study, including their large size, individual markings, relatively long-lived and fairly sedentary existence, and readily quantified ingestion and egestion. Furthermore, *Moloch*'s tracks on sand are highly distinctive, and can easily be followed to determine the movements of an individual.

APPENDIX

List of Locality Records

Abbreviations used: AM (Australian Museum), NTM (Northern Territory Museum), NMV (National Museum of Victoria), SAM (South Australian Museum), QM (Queensland Museum), WAM (Western Australian Museum), and ERP (personal collection). Only one record is given for each locality. Latitude and longitude of most localities can be located in the gazetteer of Australia published by the Office of Geography, Department of Interior, 1957.

NORTHERN TERRITORY: NTM R3230 (Aileron); AM R18677 (Alice Springs); QM J7218 (nr Alice Springs); QM J11445 (150 miles W Alice Springs); SAM R2682 (Banka Banka); NMV D5605 (Barrow Creek); NTM R3229 (Barkley Highway); NTM R2095 (Corandirrk Homestead, nr Tanami Wildlife Sanctuary, 21° 32'-½' S × 130° 57' E); AM R17611 (Curtain Springs); ERP 9766 (21 miles E Curtain Springs); NTM R1633 (No. 3 Bore, Hamilton Downs, 23° 05' S × 133° 06'-½' E); NTM R2344 (5 miles S No. 3 Bore, Hamilton Downs); WAM R21457 (Frewena); QM J11013 (near "Harts Bluff"—probably should be Haast's Bluff); SAM R80-81 (Hermannsburg); SAM R305 (MacDonnell Ranges); NTM R3547 (Papunya); NTM R3231 (Tanami Wildlife Sanctuary, 20° 52' S × 130° 33' E); ERP 9882 (20 miles SE Tanami); NMV D7888 (Tea Tree Well); NMV D8030 (Tennant's Creek); QM J7316 (nr Tennant Creek); NTM R2149 (Yuendumu, 22° 16' S × 131° 48' E); WAM R21522 (Warrabri).

QUEENSLAND: SAM R73 (Birdsville); AM R13907 (Camp 19, Simpson Desert Expedition).

SOUTH AUSTRALIA: SAM R4843 (Archaringa Creek); SAM R3218 ("Adelaide"); NMV D10903 (Ernabella Mission); SAM R1751 (Everard Ranges); SAM R897 (Findon); SAM R1200 (Fowler's Bay); NMV D5411 (Gawler Ranges); AM R7639 (Immarna); SAM R8395 (Kimba); SAM R1493 (Koonibba); NTM R1536 (Lambina); SAM R2148 (Mile End); SAM R5337 (Mount Davies, Tomkinson Ranges); SAM R2346 (Nullarbor Plain); AM R10171 (Ooldea); SAM R3213 (Ooldea soak); NMV R10859 (Port Augusta); SAM R898 (360 miles N Port Augusta); NMV R10849 (Port Lincoln); SAM R869 (Wynbring, E. W. Railway); SAM R1550 (Yantanabie).

WESTERN AUSTRALIA: SAM R4844 (Barrow Range); SAM R4840 (Barrow-Everard Range); NMV R13769 ("Barton, W.A."—probably Barton, S. A.); WAM R27736 (Boologooroo); NMV D4402 (Broome); AM R9637 (Bruce Creek); WAM R2312 (Bunjil); WAM R19596 (15 miles SE Cardabia); WAM R21557 (Carnarvon); WAM R21959 (Caron); NMV D3478 (Coolgardie); WAM R21990 (9 miles W Coolgardie); WAM R28152 (16 miles SW Coolgardie); WAM R21991 (20 miles S Coolgardie); ERP 10919-20 (22 and 28 miles ESE Coolgardie); WAM R13859 (Cosmo Newberry via Laverton); WAM R19597 (27 miles E Cosmo Newberry); WAM R12787 (Dryandra); WAM R26003 (Dryandra State Forest); SAM R1377 (Fraser Range); WAM R17346 (28 miles W Fraser Range HS); WAM R27256 (35 miles N Galena); WAM R13540 (Giles Meteorological Station); QM J10253 ("Gilesmet Stn."—probably Giles Meteorological Station); SAM R1392 (Gullwa Station, 100 miles from Geraldton); NMV R8317 (Gwalia); WAM R29573 (Joanna Springs); WAM R17664 (Jurien Bay); WAM R25374 (Kalbarri); WAM R5152 (Kalgoorlie); ERP 10918 (21 miles N Kalgoorlie); WAM R2919 (Kurrawang); WAM R20702 (14 miles S Lake Throssel); WAM R21603 (Lake Varley); WAM R23907 (Laverton); ERP 12488 (15 miles WSW Laverton); ERP-7 specimens (24 miles ENE Laverton); ERP 13175 (18 miles ENE Laverton); ERP 11149 (31 miles ENE Laverton); NMV R10851 (Lawlers); WAM R20554 (Learmonth); ERP-13 specimens (21 miles W Lorna Glen HS); WAM R25625 (Meadow Station); WAM R27745 (Merolia Station); ERP 10046 (9 miles NNE Millrose HS); ERP 10191 (17 miles ENE Millrose HS); NMV R10855 (Mount Morgan); WAM R21953 (half way between Moora and Dalwalinu); WAM R20242 (Moreland HS); WAM R27737 (Mullewa); WAM R26760 (near Murchison River mouth); WAM R16937 (14 mi. E mouth Murchison River); NMV D3 ("Nullarbor Plain, W.A."); ERP 10460 (½ mile S Pithara); ERP 11715 (69 miles NNE Sandstone); ERP-9 specimens (33 miles SW Sandstone); WAM R21745 (Shark Bay); NMV R10860 (Swan River); AM R10432 (Southern Cross); WAM R22165 (Warburton Ranges); WAM R22100 (presumably Warburton Ranges); WAM R22025 (Warburton Mission); WAM R14634 (28 miles NNW Warburton Mission); WAM R19595 (Warroora); WAM R26881 (54 miles E Wiluna); ERP 10921 (6 miles N Wubin); ERP 10269 (24 miles NE Wubin); ERP 12828 (12 miles NW Agnew); ERP-55 specimens (5 miles NE Dunges Table Hill); ERP 11132 (18 miles S Neale Junction); WAM R3887 (Well 10, Canning Stock Route); WAM R29650 (2 miles E Wyalkatchem).

ACKNOWLEDGMENTS

H. G. Cogger, J. Coventry, J. M. Dixon, D. Howe, F. J. Mitchell, G. M. Storr and J. F. Woods provided locality data and/or access to the collections under their care. Mr. B. Hart of the Northern Territory Administration's Animal Industry Branch helped with permits and provided storage space in Alice Springs. The Department of

Zoology, University of Western Australia served as a base of operations and allowed access to the library and computing center. Funds for this study were granted by the National Institutes of Health and the National Science Foundation. Drs. R. H. MacArthur and A. R. Main co-sponsored the senior author's postdoctoral fellowship and provided helpful suggestions. Drs. A. S. Rand, H. F. Recher, and D. E. Willard read the manuscript and made numerous useful suggestions.

LITERATURE CITED

- ASPLUND, K. K. AND C. H. LOWE. 1964. Reproductive cycles of the iguanid lizards *Urosaurus ornatus* and *Uta stansburiana* in southeastern Arizona. *J. Morphol.* 115:27-34.
- BENTLEY, P. J. AND F. C. BLUMER. 1962. Uptake of water by the lizard, *Moloch horridus*. *Nature* 194:699-700.
- BOGERT, C. M. AND R. MARTIN DEL CAMPO. 1956. The gila monster and its allies. The relationships, habits, and behavior of the lizards of the family Helodermatidae. *Bull. Am. Mus. Nat. Hist.* 109:1-238.
- CASSIE, R. M. 1954. Some uses of probability paper in the analysis of size-frequency distributions. *Austral. J. Mar. Freshw. Res.* 5:512-522.
- COGGER, H. 1967. Australian reptiles in colour. Reed and Reed. Sydney, Wellington, Auckland.
- CUELLAR, O. 1966. Delayed fertilization in the Lizard *Uta stansburiana*. *Copeia* 1966(3):549-552.
- DARLINGTON, P. J., JR. 1957. Zoogeography: the geographical distribution of animals. John Wiley and Sons, Inc. New York.
- DAVEY, H. W. 1923. The moloch lizard, *Moloch horridus* Gray. *Victorian Nat.* 40:58-60.
- . 1944. Some lizards I have kept. *Ibid.* 61:82-84.
- GILES, E. 1889. Australia twice traversed. Sampson Low, Marston, Searle and Rivington. London.
- GRAY, J. E. 1841. Appendix. In: *Journal of two expeditions in northwest and western Australia*. G. Grey, pp. 440-441.
- HEATH, J. E. 1964. Reptilian thermoregulation: evaluation of field studies. *Science* 146:784-785.
- KINGHORN, J. R. 1924. Reptiles and batrachians from South and Southwest Australia. *Rec. Austral. Mus.* 14:163-183.
- . 1945. The Simpson Desert Expedition, 1939. Scientific reports: No. 3. Biology, reptiles and amphibians. *Trans. Roy. Soc. S. Australia* 69:3-9.
- LICHT, P. *et al.* 1966. Observations on the thermal relations of Western Australian lizards. *Copeia* 1966(1):97-110.
- LOCKWOOD, D. 1964. The lizard eaters. Cassell Australia Ltd., Melbourne, Australia.
- LOVERIDGE, A. 1934. Australian reptiles in the Museum of Comparative Zoology, Cambridge, Massachusetts. *Bull. Mus. Comp. Zool.* 77:243-383.

- LUCAS, A. H. S. AND C. FROST. 1896. Reptilia. In: Report on the work of the Horn scientific expedition to central Australia. Pp. 112-151. Dulau, London.
- MACARTHUR, R. H. 1961. Population effects of natural selection. *Am. Nat.* 95:195-199.
- AND E. R. PIANKA. 1966. On optimal use of a patchy environment. *Ibid.* 100:603-609.
- MAYHEW, W. W. 1965. Reproduction in the sand-dwelling lizard *Uma inornata*. *Herpetologica* 21:39-55.
- . 1966. Reproduction in the psammophilous Lizard *Uma scoparia*. *Copeia* 1966(1): 114-122.
- PIANKA, E. R. 1965. Species diversity and ecology of flatland desert lizards in western North America. Ph.D. thesis, Univ. Wash., Seattle, Washington. (Diss. Abstr. 27:334-335B.)
- . 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* 47:1055-1059.
- PRESCOTT, J. A. 1944. A soil map of Australia. Commonwealth Austral. Coun. Sci. Ind. Res. Bull. No. 177, pp. 1-15.
- REEVE, W. L. 1952. Taxonomy and distribution of the horned lizard genus *Phrynosoma*. *Univ. Kans. Sci. Bull.* 34:817-960.
- RIDE, W. D. L. *et al.* 1962. Bernier and Dorre islands (Fauna Bull. 2). Fish. Dep., Perth, West Australia.
- SAVILLE-KENT, W. 1897. The naturalist in Australia. London.
- SERVENTY, V. N. 1966. A continent in danger. Andre Deutsch, London.
- SLATER, P. AND E. LINDGREN. 1955. A visit to Queen Victoria Spring, January 1955. *West. Austral. Nat.* 5:10-18.
- SMYTH, M. AND M. J. SMITH. 1968. Obligatory sperm storage in the skink *Hemiergis peronii*. *Science* 161:575-576.
- SOULÉ, M. 1963. Aspects of thermoregulation in nine species of lizards from Baja California. *Copeia* 1963(1):107-115.
- SPORN, C. C. 1955. The breeding of the mountain devil in captivity. *West. Austral. Nat.* 5:1-5.
- . 1958. Further observations on the mountain devil in captivity. *Ibid.* 6:136-137.
- . 1965. Additional observations on the life history of the mountain devil, *Moloch horridus*, in captivity. *Ibid.* 9:157-159.
- STEPHANS, C. G. 1956. A manual of Australian soils. 2nd. ed. Commonwealth Austral. Coun. Sci. Ind. Res. Melbourne, Australia.
- STERLING, E. C. AND A. ZEITZ. 1893. *Vertebrata*. *Trans. Roy. Soc. S. Australia* 16:154-176.
- THOMSON, D. F. AND W. HOSMER. 1963. A preliminary account of the herpetology of the Great Sandy Desert of central Western Australia. *Roy. Soc. Victoria* 77:217-237.
- WHITE, S. R. 1947. Observations on the mountain devil (*Moloch horridus*). *West. Austral. Nat.* 1:78-81.
- WOOD, J. G. AND R. J. WILLIAMS. 1960. Vegetation. In *The Australian environment*. Pp. 67-84. Commonwealth Austral. Coun. Sci. Ind. Res. Melbourne Univ. Press, Melbourne, Australia.
- ZIETZ, F. R. 1914. Lacertilia from central Australia. *Trans. Roy. Soc. S. Australia* 38:440-444.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF TEXAS, AUSTIN, TEXAS 78712.