Comparative Ecology of Two Lizards

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The ecology of the Australian agamid *Amphibolurus inermis* is described and compared with that of its North American ecological analogue, the iguanid *Dipsosaurus dorsalis.*

Although broadly similar, there are a number of striking differences in the ecologies of these two lizards. The agamid is a rather generalized omnivore, while the iguanid is a specialized herbivore. *A. inermis* has a much lower average preferred (36.4° C) and active (36.8° C) body temperature than *D. dorsalis* (38.6° C and 41.0° C, respectively). The former species is also active year around and has a substantially longer breeding season.

An individual *A. inermis* digs many shallow burrows; *Dipsosaurus* individuals normally excavate a single deep burrow, often used as a thermal retreat. Both species frequently climb into vegetation when ground temperatures become very hot, presumably a behavioral avoidance of thermal extremes.

Clutch size ranges from two to six in *A. inermis* ($\bar{x}$ of 96 clutches = 3.43) and from three to eight in *Dipsosaurus. A. inermis* females may sometimes lay two or more clutches per season, but it is unlikely that individual female *Dipsosaurus* ever produce more than a single clutch annually.

Possible reasons for these differences are discussed.

INTRODUCTION

An apparent ecological similarity between the Australian desert agamid *Amphibolurus inermis* (De Vis) (Fig. 1) and the North American iguanid *Dipsosaurus dorsalis* Baird and Girard has frequently been noted [e.g., Bradshaw (1965), Licht *et al.* (1966), and Warburg (1965)], although the ecologies of the two species have never been subjected to any detailed comparison.[1] This is the second in a series of papers comparing the ecologies of phylogenetically different, but ecologically similar, species of lizards. The first was a treatment of the agamid *Moloch horridus* and the iguanid *Phrynosoma platyrhinos* (Pianka and Pianka, 1970). Future papers will treat *Amphibolurus isolepis, A. scutulatus,* and *Callisaurus draconoides* (Pianka, in prep.).

During an 18 month field investigation in the deserts of Western Australia, I made numerous observations on *A. inermis*; these are reported here and compared with similar observations on *Dipsosaurus*. (The resulting collection has been donated to the Los Angeles County Museum of Natural History.) Both the Australian and the North American study systems and study areas are described elsewhere (Pianka, 1965, 1967, 1969a, 1969b).

DIET

Perhaps the single most characteristic feature of the ecology of *Dipsosaurus* is its diet, which alone distinguishes it from 11 other, often ecologically sympatric, species of lizards (Pianka, 1965, 1966). Except for the rock-dwelling chuckwalla (Johnson, 1965), it is the only largely herbivorous American desert lizard. A sample of 65 collected over a two-year period (from March through late August) contained 94.2% vegetable materials by volume (Table 1). Similar percentages (80–95%), although from smaller samples, were reported by Norris (1953), who noted distinct seasonal changes in the composition of the diet as well.

During the spring months, *Dipsosaurus* relies heavily on the flowers of the creosote bush, *Larrea divaricata*, an extremely seasonal food supply which blooms regularly and profusely during April and May. Norris (1953:268) was greatly impressed with the intricate relationship between this plant and *Dipsosaurus*. My own observations suggest that the lizard's temporal pattern of activity,

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[1] Mayhew (1963) compared *Dipsosaurus* with *A. pictus*, which is closely related to *A. inermis*.

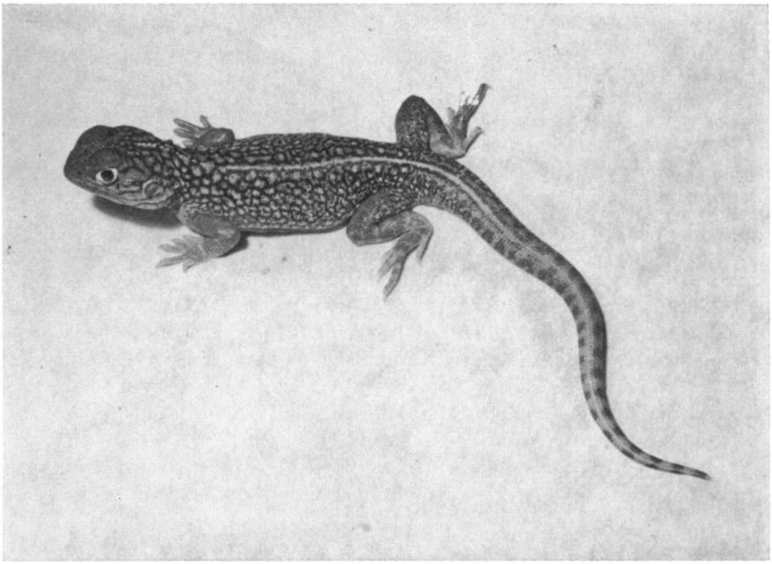

FIG. 1. Adult male *Amphibolurus inermis* (120 mm snout-vent), from 27 km south of Atley homestead, Western Australia.

which is the most seasonal of any flatland desert lizard in the Mojave or Sonoran Desert, is closely geared to the availability of *Larrea* flowers. On regular visits to study areas from March through August, I noted a distinct May peak in the number of *Dipsosaurus* observed. Later in the summer, the lizards eat a variety of other plants, and appear to be considerably less active.

Asplund (1967) examined the stomach contents of 19 *D. dorsalis* collected in southern Baja California during the August rainy season and found 46% animal material by dry weight. Thus no more than 54% of the diet (by weight) of these particular lizards could have constituted plant matter. Asplund noted that 12 juveniles contained 68% animal material whereas seven adults contained only 41% animal matter. Four of these seven adults contained mostly plant materials. Large body size has often been correlated with herbivory in lizards (Szarski, 1962; Ostrom, 1963; and Sokol, 1967), although there are many large carnivorous lizards as well (*e.g. Varanus* and *Tupinambis*). Asplund's (*op. cit.*) observation that juvenile *Dipsosaurus* eat a greater proportion of insects than adults may be yet another reflection of this trend; perhaps "herbivorous" lizards often change during ontogeny from being relatively insectivorous as juveniles to being relatively herbivorous as adults. Mayhew (1968:251) noted a similar dietary shift in the agamid *Uromastix*.

Hotten (1955) distinguished four kinds of dentition in North American iguanid lizards: herbivorous, ant-eating, and two pre-

TABLE 1. SUMMARY OF STOMACH CONTENTS OF 65 *Dipsosaurus dorsalis*. Two stomachs were empty. Volumes measured in cm^3. Frequencies based on 63.

Food	No.	Vol.	% Total Vol.	Frequency
Animal				
Ants	40	0.5	0.23	3.2
Wasps	2	0.4	0.18	3.2
Mantids	1	0.1	0.05	1.6
Beetles	22	1.7	0.78	25.4
Diptera	101	1.1	0.50	6.4
All insect larvae	2	0.3	0.14	3.2
Unidentified insects	78	1.9	0.87	28.6
Plant				
Floral parts	603	78.4	35.88	71.4
Vegetative parts	1833	88.9	40.69	77.8
Unidentified plant materials		38.5	17.62	71.4
Unidentifiable debris		6.7	3.07	25.4
TOTALS	2718	218.5		

daceous types; *Dipsosaurus* has teeth adapted for herbivory, *i.e.,* strongly compressed laterally, highly cuspate, sharp and bladelike.

The foregoing suggests that, although *Dipsosaurus* on occasion does prey upon animals, the adult diet in nature usually consists predominantly of plant materials. (In captivity, *Dipsosaurus* thrives on a diet of mealworms, crickets, and fruity baby food.)

A. inermis is evidently a more generalized feeder than *Dipsosaurus.* Bradshaw (1965) examined the stomach contents of an unspecified number of *A. inermis* and emphasized that there are "considerable quantities of insect material always present at all times of the year." He did note, however, that during the spring months, following rain, this species "apparently utilizes to some extent in its diet the petals of a small compositae." Bradshaw did not give percentages or otherwise indicate the extent of herbivory in *A. inermis.*

Stomach contents of 156 *A. inermis* collected over the entire seasonal range of conditions are summarized in Table 2. Only 24.3% of the diet by volume consists of vegetative materials; a wide variety of arthropods comprises 71.9% of the stomach contents by volume. The diet is fairly diverse at all times of year. Although *A. inermis* is less of an herbivore than *Dipsosaurus,* it is one of the most herbivorous of Australian desert lizards (Pianka, 1968, 1969b, 1970, and in prep.). The only other desert species known to eat over 20% plant materials by

TABLE 2. SUMMARY OF STOMACH CONTENTS OF 159 *Amphibolurus inermis.* Three stomachs were empty. Volumes measured in cm^3. Frequencies based on 156.

Food	No.	Vol.	% Total Vol.	Frequency
Animal				
Centipedes	10	5.76	3.95	6.4
Arachnids	20	1.59	1.09	6.4
Acarina	2	0.07	0.05	1.3
Ants	1872	22.96	15.76	77.6
Wasps and bees	132	10.41	7.14	19.2
Grasshoppers	37	10.06	6.90	14.7
Roaches	4	0.45	0.31	1.9
Phasmids and mantids	2	0.55	0.38	1.3
Neuroptera	1	0.15	0.10	0.6
Coleoptera	147	13.59	9.33	39.1
Isoptera	2755	24.25	16.86	20.5
Homoptera and hemiptera	70	4.90	3.36	23.1
Diptera	4	0.24	0.15	2.6
Insect eggs	7	0.02	0.01	1.3
All insect larvae	79	8.91	6.12	19.9
Unidentified insects	14	1.01	0.69	9.0
Lizards	1	0.20	0.12	0.6
Plant				
Floral parts	79	7.90	5.42	74.4
Vegetative parts		27.53	18.91	
Sand, bark and other debris		5.87	4.03	26.2
TOTALS	5236	145.60		

TABLE 3. BODY TEMPERATURE STATISTICS FOR THE TWO SPECIES, WITH SOURCES. BT = body temperatures of active lizards in nature, PT = preferred body temperatures recorded in a thermal gradient, x̄ = mean, S = standard deviation, N = sample size.

	x̄	S	N	Source
Dipsosaurus dorsalis				
BT	42.1	—	64	Norris (1953)
BT	41.1		332	Mayhew (1964)
BT	39.4	—	28	Brattstrom (1965)
BT	40.0	2.3	60	This paper
Overall BT	41.0	—	484	
PT	38.5	—	19	DeWitt (1963, 1967a)
PT	38.6	1.8	2144	This paper
Amphibolurus inermis				
BT	36.1	—	40	Bradshaw (1965)
BT	39.3	1.2	47	Licht *et al.* (1966)
BT	36.1	3.8	129	This paper
Overall BT	36.8	—	216	
PT	36.4	2.4	225	Licht *et al.* (1966)

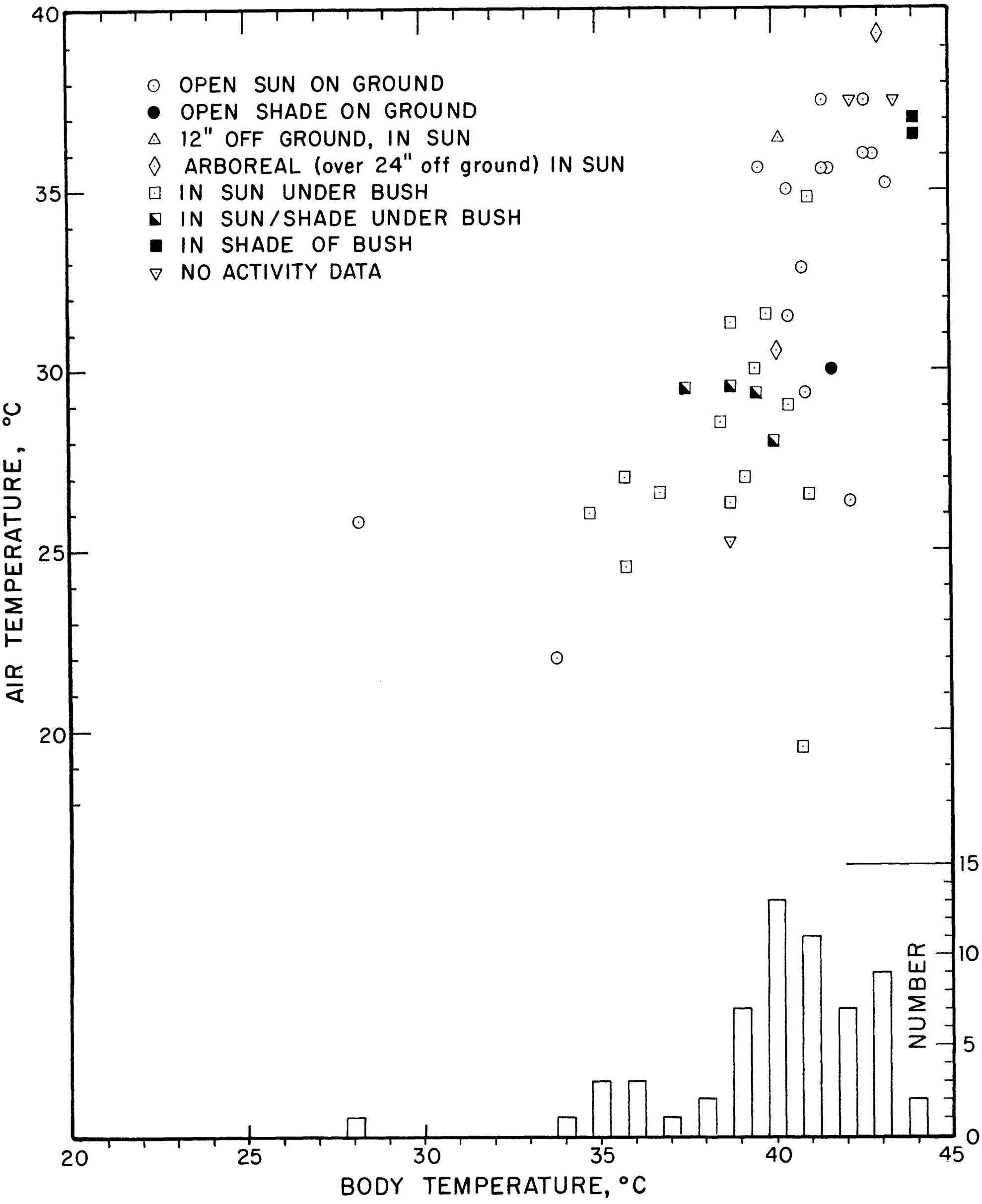

Fig. 2. Plot of air temperature versus body temperature of 49 active *Dipsosaurus dorsalis*. Histogram of active body temperatures at bottom of graph.

volume are *Amphibolurus barbatus minor*, *A. reticulatus*, and *Tiliqua occipitalis*.

Thermoregulation and Temporal Activities

Norris (1953) emphasized that *Dipsosaurus* voluntarily attain extremely high body temperatures in nature. He found one animal with a cloacal temperature of 46.4° C, and the mean of his 64 records was 42.1° C. (Mayhew (1964) recorded an even higher voluntary body temperature of 47° C.) Mayhew (1964), Brattstrom (1965), and I recorded somewhat lower body temperatures, with means, respectively, of 41.1° C (332 records), 39.4° C (28 records), and 40.0° C (60 records). Figure 2 is a plot of air temperature (1 m above ground, shaded bulb)

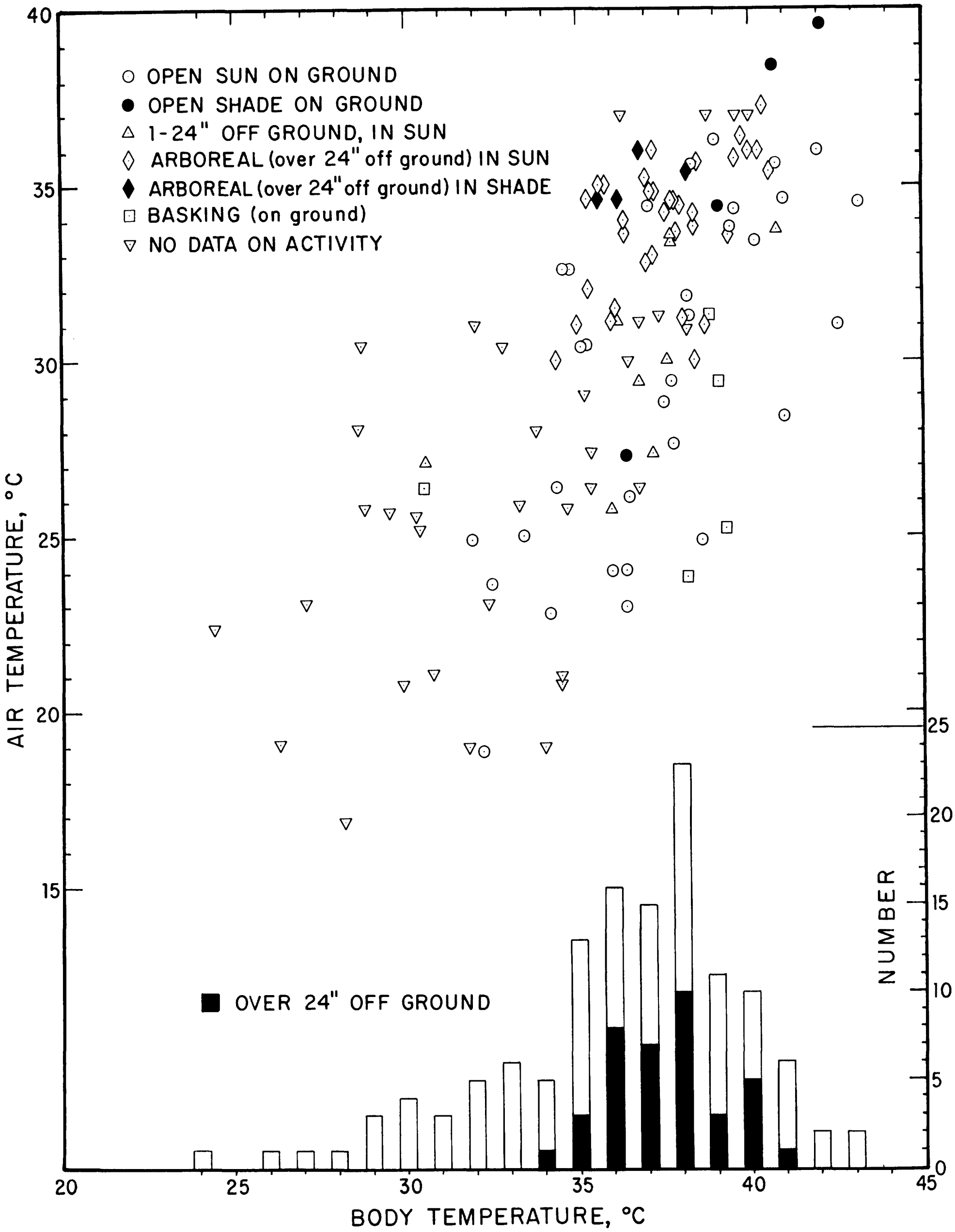

Fig. 3. Plot of air temperature versus body temperature of 123 active *Amphibolurus inermis*. Frequency distribution of active body temperatures at bottom of graph.

against body temperature for 49 active *D. dorsalis*. Table 3 gives statistics computed from these and other data. DeWitt (1963, 1967a, 1967b) recorded a mean preferred body temperature (MPT) in a thermal gradient for *Dipsosaurus* of 38.5° C. Using seven recently captured spring specimens (total of 2144 observations), I obtained an MPT of 38.6° C. Thus the discrepancy between the MPT and the mean body temperature in nature (MBT) is about 2.4° C. There is, however, no significant difference between the variance in BT and PBT by an F-test. McGinnis and Dickson (1967) studied thermo-

TABLE 4. RANGES OF BODY TEMPERATURES (°C) OBSERVED FOR LIZARDS OF EACH SPECIES UNDER DIFFERENT DIURNAL THERMAL CONDITIONS, WHILE ENGAGED IN PARTICULAR ACTIVITIES. Means for *A. inermis* are given in parentheses.

Activity	*Dipsosaurus dorsalis*[1]	*Amphibolurus inermis*[2]
Emergence	38–42	27.6–30.4 (29.0)
Basking		27.6–35.0 (32.2)
Foraging	41–43.8	34.0–40.3 (36.7)
Arboreal	41–44.8	35.4–43.8 (39.0)
Mid day rest	41–45	
Retreat		39.2 (39.2)

[1] from Norris (1953)
[2] from Bradshaw and Main (1968)

TABLE 5. NUMBERS OF *Amphibolurus inermis* OBSERVED, THE NUMBER OF DAYS IN FIELD, AND THE NUMBER OBSERVED PER DAY

Month	No. Observed	Days in Field	No. Day
Jan	24	26	0.92
Feb	12	20	0.60
Mar	11	15	0.73
Apr	7	2	3.50
May	17	17	1.00
June	8	14	0.57
Aug	26	17	1.53
Sept	1	16	0.06
Oct	8	26	0.31
Nov	7	30	0.23
Dec	39	24	1.63
TOTALS	160	207	

regulation of free *Dipsosaurus* in nature by means of telemetry.

The highest body temperature recorded in nature for *A. inermis* is 43.8° C (Bradshaw and Main, 1968). The mean of 129 active body temperatures I measured was only 36.1° C (Fig. 3, Table 3), substantially lower than the means recorded for *Dipsosaurus*. An F-test shows that the variance in body temperature in nature is significantly ($P < .01$) greater in *A. inermis* than in *D. dorsalis* (Table 3).

Licht *et al.* (1966) measured the preferred body temperature of *A. inermis* in a thermal gradient. Using 15 observations on each of 15 animals (225 in all), they calculated an MPT of 36.4° C with a standard deviation of 2.39. The difference between this mean preferred temperature and the mean body temperature recorded in nature (36.1° C from Fig. 2 and 36.8° C from Table 3) is slight. However, an F-test shows that the variances of the two measures are significantly different ($P < .01$), indicating that in nature these lizards are relatively less able to stay within their preferred range.

Bradshaw and Main (1968) developed the thesis that, in nature, *A. inermis* are forced to spend long periods at body temperatures higher than their preferred temperature, and that behavioral avoidance of extremely high environmental temperatures is an important aspect of their ecology. However, as may be seen from Table 3, this is much more pronounced in *Dipsosaurus*. Both species climb, and during the midday are frequently seen in bushes, on fence posts, or on dead tree trunks several feet above the ground. Cowles (1946) commented on this behavior in *D. dorsalis* and suggested that it might be related to thermoregulation as well as feeding. Soulé (1968) recorded significantly lower body temperatures in arboreal than in terrestrial *Sator grandaevus*. Bradshaw and Main (1968), however, recorded a significantly higher mean body temperature for arboreal *A. inermis* than for terrestrial individuals. Fig. 3 indicates that *A. inermis* climb over 60 cm (24 in) above ground only when air temperatures exceed 30° C. However, in my sample (data of Fig. 3), the mean body temperature (37.6° C ± 0.5) of 40 terrestrial animals is not significantly different from the mean body temperature (37.4° C ± 0.3) of 38 arboreal lizards.

Both *D. dorsalis* and *A. inermis* show distinct diurnal changes in body temperature which are accompanied by associated changes in behavior (Table 4). For any behavioral sequence, the agamid invariably has a lower body temperature than the iguanid.

A. inermis is active all year long (Table 5) whereas *D. dorsalis* is active for only seven months of the year, hibernating from October to late March (Moberley, 1963). In another paper (in prep.), I relate differences in thermal relations of North American and Australian desert lizards to the foregoing difference in seasonal duration of activity.

HABITAT, MICROHABITAT, AND BURROWS

Both *D. dorsalis* and *A. inermis* usually occur in very open, hot, and arid situations. Thus, both species frequently encounter extremely high environmental temperatures, a paucity of suitable thermal retreats, and severe water shortages (see Norris, 1953; Bradshaw, 1965; and Warburg, 1965). Although the plant species and plant life forms in North American and Australian desert habitats are usually quite disparate (Pianka, 1969a), the physical extremes encountered by each species have presumably been rather similar.

Microhabitats occupied by the two species are roughly comparable; both lizards are most common in open sandy areas, spending time both in the open and underneath or up in the foliage of various perennials. However, comparative hindleg lengths (see "anatomical considerations") suggest that *A. inermis* may stay closer to cover more of the time than does *Dipsosaurus.*

D. dorsalis and *A. inermis* both dig their own burrows. The former species usually digs a single, deep and fairly complicated burrow in a central location (Norris, 1953), while the latter normally digs up to six or eight simple, relatively shallow,dead-end burrows in different parts of its home range (White, 1949; pers. observ.). *Dipsosaurus* employs its deep, cool burrow as a thermal retreat during the hottest part of the day (Norris, 1953). The shallow burrows of *A. inermis* are seldom used in this way, as these lizards frequently spend the hottest portion of the day on a perch a meter or more above ground. *A. inermis* uses its burrows primarily as nocturnal retreats and in predator escape.

REPRODUCTION

Norris (1953) reported maturing ova (presumably yolked) in *Dipsosaurus* from April through July, a period of about four months. He stated that these lizards lay 3–8 eggs at a time. Probably only one clutch is laid per season. Young *Dipsosaurus* emerge in August.

Bradshaw (1965) found female *A. inermis* with yolked ova from September through the end of February; I have collected gravid females from early October through February. Hence the time during which females are or may become gravid in *A. inermis* is at least five, and probably six, months. Bradshaw (1965) recorded a mean clutch size of 3.2 (72 records); I found a mean clutch of 4.1 (range = 2–6; N = 24), resulting in a combined mean of 3.43 eggs per female (96 records). As several of my females had both large yolked ovarian follicles and oviducal eggs at the same time, some *A. inermis* may lay two or more clutches per season. Fig. 4 shows the relationship between female snout–vent length and clutch size, as well as the frequency distribution of clutch sizes observed in this study.

Information available on testicular cycles corroborates and confirms the temporal patterns suggested by female cycles. Norris (1953:273) and Mayhew (1964) presented data for male *Dipsosaurus*; in Table 6, I list similar data and statistics for male *A. inermis.*

Male *A. inermis* defend territories during the spring months (breeding season). I observed two males fighting during November 1966 near Hermannsburg in central Australia. White (1949) described a territorial encounter between males in detail. Norris (1953) described a similar fight between two male *Dipsosaurus,* and noted that they frequently break their opponent's tails during such clashes. Carpenter (1961) studied social behavior in *Dipsosaurus* in some detail.

ANATOMICAL CONSIDERATIONS

A. inermis is a smaller but stockier lizard than *D. dorsalis.* Both species have a short, blunt head when compared with other iguanids and agamids (Fig. 1), presumably related to their herbivorous and burrowing habits. Relative hindleg length in certain lizards has been correlated with the percentage of individuals first observed in the open spaces between plants (Pianka, 1969b; in prep.). *Dipsosaurus* has a proportionately longer hindleg (72% of snout–vent) than *A. inermis* (59% snout–vent), suggesting that the former species spends more of its time in the open. Of 102 *Dipsosaurus,* 53 were in the open when first sighted (52%), whereas only 38 out of 100 *A. inermis* were in the open (38%).

PREDATORS

Raptors, snakes, and large lizards are the major lizard predators on both continents. I have found *A. inermis* in the stomachs of *Varanus eremius* (Pianka, 1968), *Varanus gouldi* (Pianka, 1970), and some of the large desert elapid snakes. Young *D. dorsalis* are known food items of large *Crotaphytus wislizenii* (Pianka, 1965); presumably rattle-

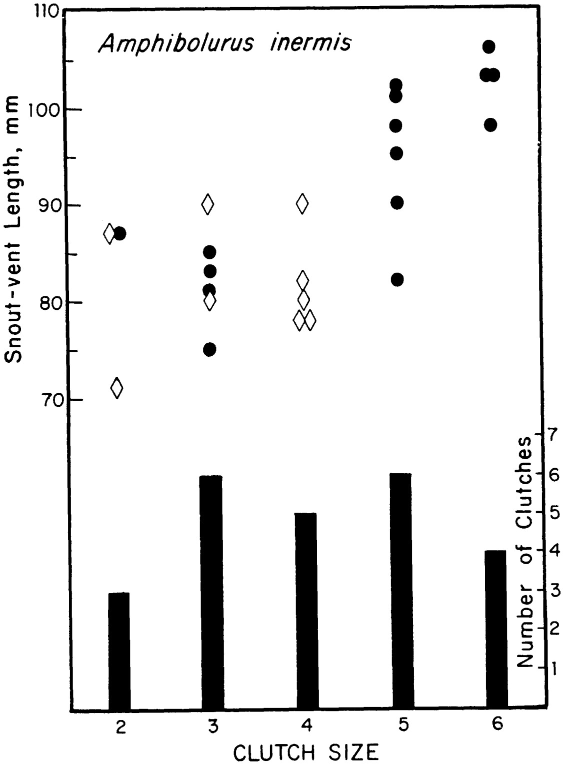

FIG. 4. Clutch sizes of 24 female *Amphibolurus inermis* plotted against snout-vent length, showing that larger females tend to lay more eggs per clutch. Oviducal eggs depicted by circles, yolked ovarian eggs over 4 mm in diameter by diamonds.

snakes and other snakes constitute important predators on *Dipsosaurus* as well. Both *A. inermis* and *D. dorsalis* often retreat at the approach of humans and usually move into their burrows. However, *A. inermis* must fall easy prey to snakes and digging lizards such as *V. gouldi* because their burrows are usually simple dead-ends. In contrast, *Dipsosaurus* burrows, with their multiple openings, usually offer a second chance of escape. Brattstrom (pers. comm.) indicates that *Dipsosaurus* burrow systems often have one tunnel close to the surface, which is used in an emergency as a predator escape route.

COMPETITION

For several reasons, *Dipsosaurus* probably encounters less direct interspecific competition with other lizards than *A. inermis.* The former species has a more restricted diet and seldom occurs in ecologic sympatry with more than nine other lizard species, none of which are congeneric (Pianka, 1967). However, *A. inermis* has a diet which overlaps broadly with that of many other lizards and it frequently occurs in sympatry with up to 20–30 other species, often with three other species of *Amphibolurus* (Pianka, 1969a). Thus one would predict that biotic factors should be relatively more important to an understanding of the agamid's ecology than to that of the iguanid.

DISCUSSION AND CONCLUSIONS

A. inermis is ecologically similar to *D. dorsalis* only in the sense that it is closer, in a number of different ways, to *Dipsosaurus* than is any other Australian desert lizard [except, perhaps, for the closely related *Amphibolurus reticulatus,* which usually occurs in a different habitat than *A. inermis* (Pianka, 1969a; Storr, 1966)]. Numerous differences between the ecologies of the two forms have been detailed on previous pages. Some of these stem directly from differences in the physical environments on

TABLE 6. DATA AND STATISTICS ON THE TESTES LENGTHS (IN MM) OF MALE *Amphibolurus inermis*, BY MONTHS. x̄ = mean, S = standard deviation, S.E. = standard error of mean, N = sample size (number of testes).

	Jan	Feb	Mar	Apr	May	June	Aug	Sept	Oct	Nov	Dec
0.5	2		4	2	2	2					
1.0	8	5	2	10	4	6					
2.0	1		3		7		3	1			
3.0	1		5		5	2	2	1	3		
4.0	4				3		4			2	
5.0	5	2		2	2		9		2	2	8
6.0	5	2					1			1	6
7.0	8						1			3	7
8.0											1
x̄	4.2	3.0	1.8	1.5	2.4	1.3	4.3	2.5	3.8	5.6	6.1
S	2.5	2.4	1.1	1.5	1.3	0.9	1.3	0.7	1.1	1.3	1.0
S.E.	0.4	0.8	0.3	0.4	0.3	0.3	0.3	0.5	0.5	0.5	0.2
N	34	9	14	14	23	10	20	2	5	8	22

the two continents, while others may be attributed to differences in the biotic environments in the respective deserts.

Differences in seasonal duration of activity and reproductive schedules, including the probable second clutch of *A. inermis*, are directly traceable to the milder thermal climate of the Australian desert. The slightly larger clutch size of *Dipsosaurus* is probably a simple result of its larger body size. Although complexly determined, it is also possible that the difference in thermal relations of the two species can be attributed to climate (Pianka, in prep.). However, thermoregulatory differences may also be due, at least in part, to the different biotic matrix in which each species finds itself.

No Australian desert plant is quite as suitable for food specialization as the North American *Larrea divaricata*; there is no perennial dicot in Australia as abundant and widespread or so predictable in its flowering. As a result, even though *A. inermis* probably faces greater competitive pressures than *Dipsosaurus*, it has a fairly broad food niche.

Grazing herbivores range less widely than most carnivores of the same body weight, due to differences in concentrations of their foods (McNab, 1963; Schoener, 1968). Because of this fact, *Dipsosaurus* individuals presumably do not need to range as far from their burrows as do individuals of *A. inermis* in order to gather food enough to sustain themselves. The iguanid can put all of its "burrow-digging" energy into one central complex burrow; whereas the agamid, which must range more widely to gather its insect food, digs several simpler burrows in different parts of its home range. Lower risks of predation resulting from a complex central burrow with multiple openings could therefore be one of the factors favoring the evolution of herbivory in lizards. To the extent that hindleg length determines a lizard's maximum speed (R. C. Snyder, pers. comm.), the evolution of the hindleg can be related to diet and the distance the individual ranges from its burrow as well as the percentage of time spent in the open.

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