Ecology of the Agamid Lizard *Amphibolurus isolepis* in Western Australia

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The geographic distribution of *Amphibolurus isolepis* covers much of the desert interior of Australia, except for certain rocky areas. *A. isolepis gularis* usually occurs in desert habitats with a sandy, reddish colored substrate. Ants constitute most of its food, but numerous other arthropods, various plant materials, and an occasional lizard are also taken. Foraging individuals usually sit-and-wait in the open spaces between shrubs where they make short forays after prey items. Actvity is year around; in warm months, daily activity is distinctly bimodal, whereas in colder months the lizards are most active during midday. Cloacal body temperatures average 10° C higher than ambient air temperatures, indicating that these reptiles employ incident radiation and the substrate to maintain their body temperature. Both air and body temperatures recorded for lizards in the shade when first sighted are significantly higher than those recorded for animals in the sun. Body temperatures of active lizards show a decided seasonality, being much lower during winter.

Females lay at least two clutches of eggs each season, with late clutches averaging nearly one egg larger than early clutches. Eggs are laid from September through early February. Clutch size is correlated with female body size. Hatchlings grow rapidly, reaching adult size and breeding in their first spring at an age of from six to nine months. There may be an annual turnover of adults, but this is still uncertain. Potential predators and competitors are described and briefly discussed. Certain ecological similarities and differences between *A. isolepis* and *Uta stansburiana* and *Callisaurus draconoides* are indicated, and it is suggested that the the former two species are both relatively "*r* selected."

Introduction

RECENTLY revised by Storr (1965), the lizards of the *Amphibolurus maculatus* species group constitute some of the most conspicuous of all Australian desert reptiles and they are certainly among the most abundant. Yet very little about their biology has been reported. Storr (1965) briefly discussed longevity and habitat preference; Licht *et al.* (1966) studied various aspects of thermoregulation in *Amphibolurus "maculatus"* (probably *A. isolepis*); and Cogger (1969) examined the population ecology of the closely related *Amphibolurus fordi* in western New South Wales. Bradshaw (1965), Heatwole (1970), and Pianka (1971) have described the ecology of certain other Australian *Amphibolurus.*

The geographic range of *A. isolepis* (Fig. 1) covers most sandy portions of the Australian desert interior.

Methods

During a 16 month field study in Western Australia, my wife Helen and I made numerous observations on *A. i. gularis* (Sternfeld) (Fig. 2), mainly on eight major study areas in the Great Victoria Desert and surrounding regions. Exact locations, descriptions, lizard and bird species lists, and other information about these areas have been published elsewhere (Pianka, 1969a, 1969b, 1971; Pianka and Pianka, 1970a, 1970b). Our collection of over 500 specimens has been donated to the Los Angeles County Museum of Natural History.

Whenever possible, we recorded the following for each lizard observed: date, time, ambient air temperature (at chest height above ground, in shade), approximate size, exact microhabitat location when first sighted and subsequent movements. As many lizards as possible were collected, using tech-

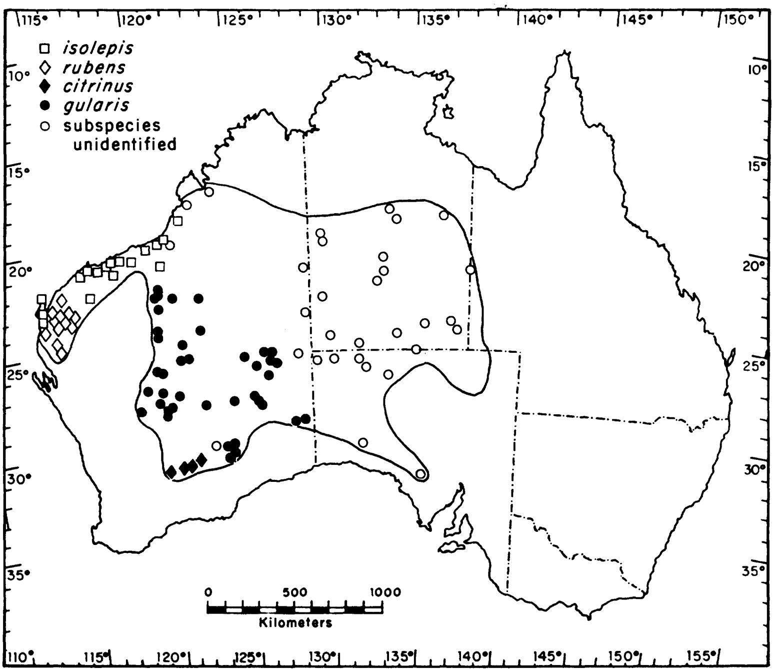

Fig. 1. Geographic distribution of various races of *Amphibolurus isolepis*. Recorded localities are shown with symbols, and probable limits of range outlined. Based on Storr (1965), personal records, museum collections and the literature.

niques such as shooting with .22 caliber dust shot or BB guns or digging specimens out of burrows. Sex, wet weight, snout-vent length (SVL), and tail length were recorded, and body temperatures (BTs) of active lizards were taken with Shultheis cloacal thermometers, usually within a few seconds of shooting. Lizards badly damaged were not used. Preserved material provided data on gonad condition and stomach contents. Prey items were counted for each stomach, except for ants and termites (here standards were obtained by direct count and used to make estimates of the number per stomach). Volumes of prey items were estimated as follows: Intact stomachs were submersed in water in a small graduated cylinder and the volume displacement estimated to the nearest 0.1 cc. The volume of the empty stomach was similarly determined after the contents had been removed and subtracted from the first measurement to yield the total volume of food actually in the stomach. Approximate volumes of individual prey items were then estimated visually to the nearest 0.01 cc, by the proportion of a given stomach's total food volume occupied by that prey item.

RESULTS

Habitat and Microhabitat

The major habitats of *A. i. gularis* are in the sandy deserts, usually in those areas covered by reddish sands. The species occurs both on sandplains and on stabilized longitudinal sandridges which characterize much of the desert interior of Australia. Typically the vegetation is dominated by perennial grasses (*Triodia basedowi* and/or *Triodia pungens*). Various shrubs (such as *Grevillea* spp. and *Hakea* spp.) and trees (*Acacia* spp. and *Eucalyptus* spp.) may or may not be present.

A. i. gularis is a lizard of the open spaces; individuals are usually found in the open between shrubs and grass tussocks, or during the heat of midday, in the open shade adjacent to a plant. When approached and pursued, the lizards make long, often zigzag, runs, tending to stay in the open. Only when repeatedly pursued will they actually run into a bush or grass tussock, within which they move quite clumsily compared to other lizards such as skinks and varanids (Pianka, 1969a, b). In these respects this agamid is

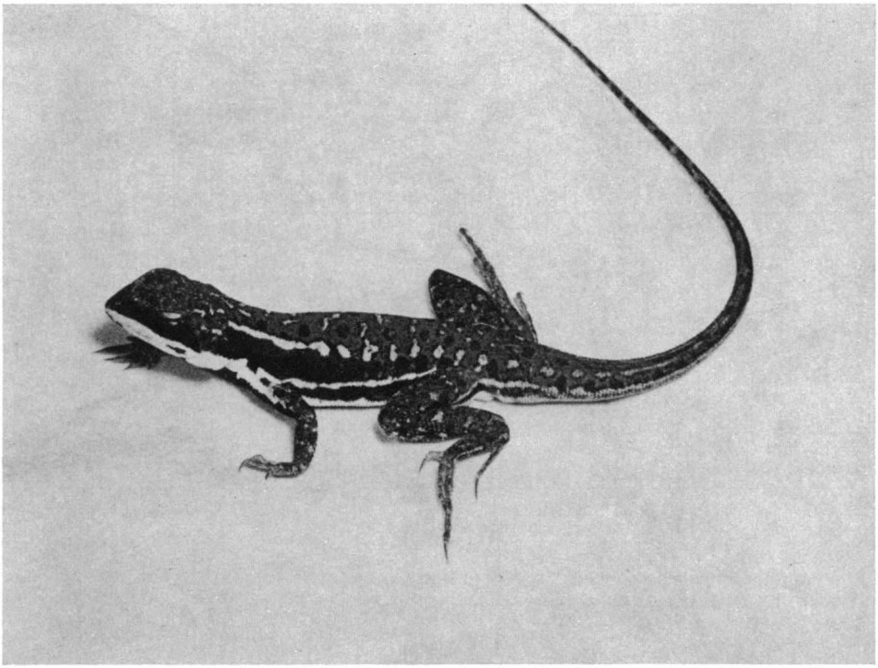

Fig. 2. Adult male *Amphibolurus isolepis gularis* from 34 km west of Lorna Glen Homestead, Western Australia (59 mm SVL). Dorsal ground color reddish brown with small spots of black; legs and dorsum spotted with larger patches of black and pale yellow or beige (the latter occasionally coalesce to form a weak pale dorso-lateral band); mouth, shoulder region, and pale lateral stripe are bright yellow, bounded above by a broad band of black.

reminiscent of the North American iguanid *Callisaurus draconoides.* In the morning, when environmental temperatures are still low, basking individuals will sometimes retreat directly into burrows. Of some 437 active lizards observed under natural conditions before they began taking evasive action, 195 (44.6%) were in the open sun or open shade. Another 166 (37.9%) were first sighted either in the sun or shade adjacent to a *Triodia* tussock. The remaining 76 (17.5%) were in miscellaneous other microhabitat locations, such as underneath various shrubs and trees.

Daily and Seasonal Patterns of Activity

Although the lizards are active all year long, the daily pattern of activity varies predictably with the seasons (Fig. 3). In autumn and winter, they are most active during midday, whereas in the spring and summer there is a distinct bimodality in daily activity, with decreased activity during midday. Mayhew (1964, 1968), Tinkle (1967), and Pianka (1969b) have documented similar seasonal shifts in time of activity in other lizard species.

Mean BT of 511 active lizards was 37.7° C (standard deviation (S) $= 2.32$), whereas mean air temperature at the time of capture of 535 lizards was only 26.8° C ($S = 5.25$), an indication that the lizards depend on substrate temperatures and incident solar radiation for their heat source. Nevertheless there is a highly significant correlation between air temperature and body temperature ($r = .51$, $P < .001$), showing that air temperatures do reflect ambient thermal conditions (presumably air temperatures taken closer to the ground would be even more strongly correlated with BTs). There is a significant difference (t-test, $P < .01$) between BTs of lizards first sighted in the sun ($\bar{x} = 37.3$, $S = 2.29$, S. E. $= .127$, and $N = 328$) and in the shade ($\bar{x} = 38.7$, $S = 2.51$, S. E. $= .195$, and $N = 66$). A similar statistically significant difference exists (t-test, $P < .01$) between the air temperatures recorded for lizards in the sun ($\bar{x} = 25.3$, $S = 4.98$, S. E. $= .266$, and

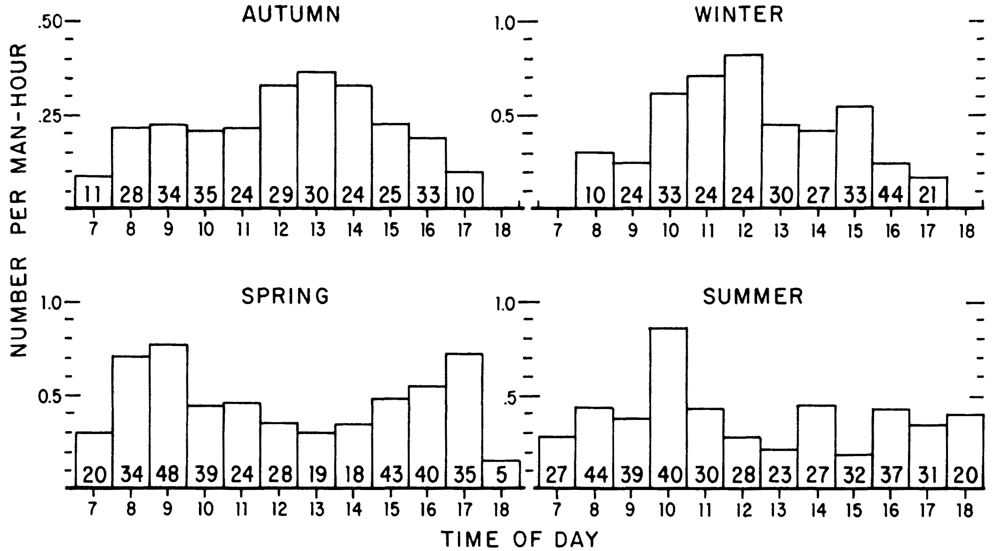

Fig. 3. Number of lizards collected per man-hour of effort in each of four seasons (see text). Numbers within bars indicate number of man-hours expended at each time of day. Seasons as in Table 3.

N = 350) and those in the shade ($\bar{x} = 29.9$, $S = 4.02$, S. E. = .478, and $N = 71$). Fig. 4 gives frequency distributions of BTs of undisturbed lizards first sighted in the sun or shade.

Licht *et al.* (1966), using a thermal gradient, recorded the following preferred body temperature (PBT) statistics for *Amphibolurus "maculatus"* (probably *A. isolepis*)' $\bar{x} = 37.0$, $S = 1.28$ (with 15 observations on each of six specimens, for a total N of 90). Both the overall mean and variance of BTs in nature are significantly (t and F-tests, $P < .05$) higher under natural conditions than

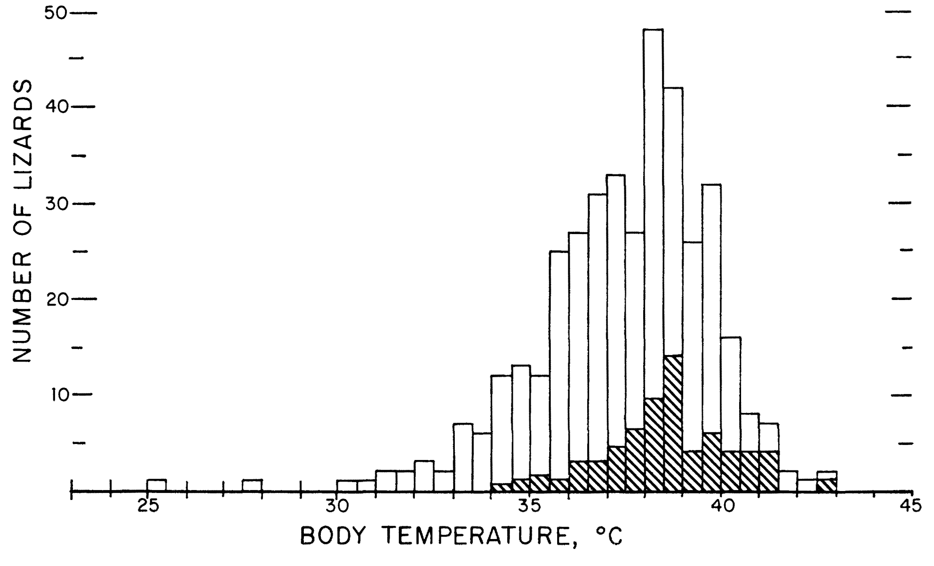

Fig. 4. Frequency distributions of BTs of lizards first sighted in sun (open bars) and shade (hatched bars). Statistics included in text.

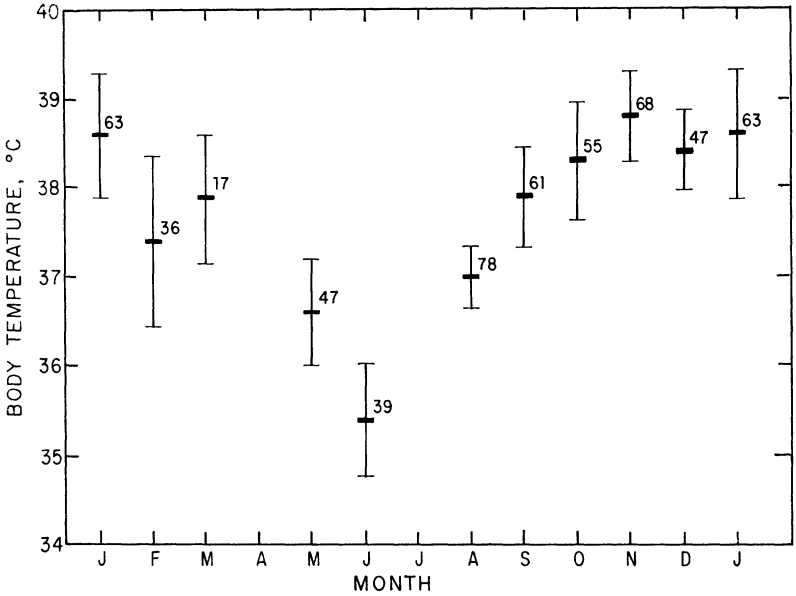

Fig. 5. Active body temperature statistics by months, showing seasonal progression. Horizontal bars represent means; vertical lines plot 2 standard errors on either side of mean. Numbers indicate sample sizes.

in a thermal gradient, suggesting that these lizards are less able to stay within their preferred range in nature (see also Pianka, 1971).

BTs of active lizards collected during May and June (late autumn-early winter in the southern hemisphere) were significantly lower than BTs of lizards collected during the spring and summer months (Fig. 5). Thus while *A. i. gularis* during the cold winter months are relatively less able to attain high BTs, they are nevertheless active. It appears that active field BTs are generally *higher* than the PBT (37.0° C) during warmer months, but lower than the preferred level during cooler months. It would be interesting to know whether PBT changes seasonally in these lizards as it does in *Sceloporus undulatus* (Ballinger *et al.*, 1969). [Licht *et al.* (1966) did not indicate precise collection dates for their experimental animals.]

Food

These lizards forage in typical agamid fashion, by "sitting-and-waiting" for prey to move within range. They sometimes pursue large prey items for several meters, but usually do not move that far. As is usually the case in lizards which forage by sitting-and-waiting, it is impossible to distinguish "feeding time" from time spent on other activities. Almost all feeding is done in the open.

Ants constitute the most important prey item, by both numbers and volume (Table 1). Ninety-four percent of the lizards with food in their stomachs contained at least some ants. However, a wide variety of other arthropods are also consumed. One specimen had eaten a very small baby skink (*Ctenotus pantherinus ocellifer*), and several stomachs contained pieces of plant materials (leaves, flowers, and grass seeds). Nearly half the termites were found in the stomachs of only 26 lizards, collected shortly after cyclone Elsie (Jan. 1967) when isoptera were swarming. The preceding demonstrates that these lizards are fairly opportunistic feeders, taking whatever prey items are available within a broad range of types and sizes (Table 2). This is consistent with what is known about feeding habits in many other species of lizards (Hotten, 1955; Pianka, 1969b).

Reproduction

There is a pronounced sexual dimorphism in color in *A. i. gularis*, with males (Fig. 2) being much more conspicuous and colorful

TABLE 1. STOMACH CONTENTS OF 511 *Amphibolurus isolepis gularis*. VOLUMES IN CC.

	No.	Vol	% By Vol	Frequency
Centipedes	20	1.60	1.44	3.9
Spiders	40	1.62	1.47	7.2
Scorpions	10	0.14	0.13	1.6
Ants	12,014	56.79	51.44	94.3
Other Hymenoptera	164	6.27	5.68	15.9
Grasshoppers	74	6.44	5.83	13.9
Roaches	8	0.84	0.76	1.4
Phasmids and Mantids	6	0.49	0.44	1.2
Beetles	70	2.99	2.71	10.9
Termites	477	7.28	6.59	8.4
Homoptera and Hemiptera	416	8.91	8.07	36.4
Flies (Diptera)	5	0.46	0.42	1.0
Butterflies and Moths	5	0.43	0.39	0.8
Insect Pupae	1	0.01	0.01	0.2
All Insect Larvae	139	4.40	3.99	11.7
Unidentified Insects	53	1.84	1.67	10.4
Lizards	1	0.80	0.72	0.2
Plant Materials	36	1.01	0.91	7.0
Sand		8.09	7.33	60.1

TABLE 2. PREY SIZE DISTRIBUTION, GIVING NUMBER OF PREY ITEMS OF A GIVEN VOLUME (IN MM^3).

Size	No.
under 10	10,213
10	2,585
20	511
30	205
40–50	168
60–90	81
100–200	59
over 200	8

than females. Females are cryptically colored, with a reddish brown ground color dorsally, speckled with small spots of beige and tiny black dots.

Testes size, an indicator of spermatogenesis, suggests that males are in breeding condition from very early spring (August) through midsummer (January). Fig. 6 shows the testicular cycle. Females deposit eggs from September through early February. The percentage of females with enlarged ovarian and/or oviducal eggs rises sharply in September, drops in October, rises again slightly in November and falls in December, rising once

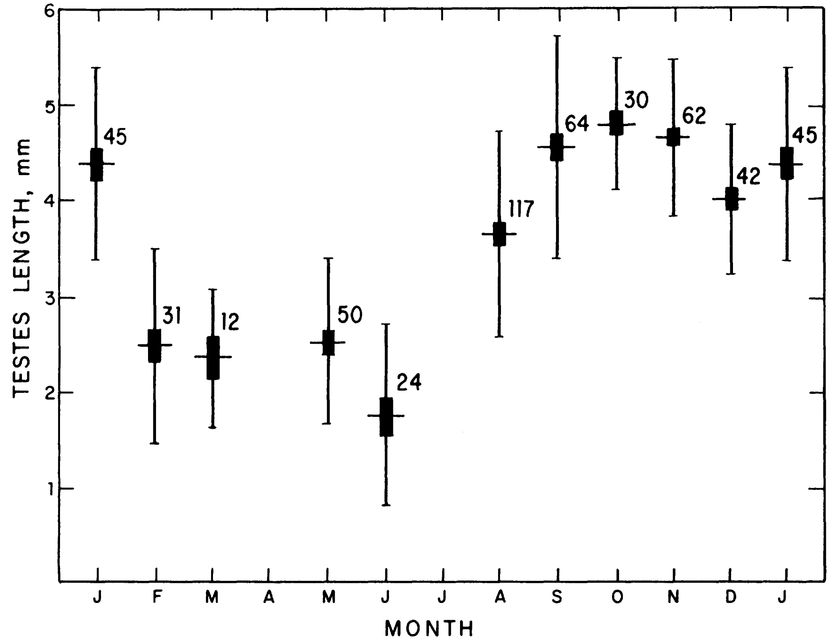

Fig. 6 Variation in testis length by months, showing male breeding cycle. Means plotted as horizontal lines; one standard error of mean and one standard deviation on either side of mean indicated with heavy and light vertical lines, respectively. Numbers indicate sample sizes.

TABLE 3. NUMBER OF GRAVID FEMALES, TOTAL NUMBER OF FEMALES, AND PERCENTAGE OF GRAVID FEMALES, BY MONTHS. NOTE BIMODAL DISTRIBUTION OF GRAVID FEMALES IN TIME.

	Winter		Spring			Summer			Autumn		
	Jun	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	May	Total
No. of gravid females	0	1	27	12	19	6	25	12	0	0	102
Total No. of females	9	22	34	31	41	29	34	24	12	21	267
% gravid	0.0	4.5	79.4	38.7	45.3	20.7	73.5	50.0	0.0	0.0	

more to a high level in January (Table 3). These data suggest that at least two and possibly three clutches are laid each reproductive season. Five females had enlarged yolky follicles in their ovaries and shelled eggs in their oviducts simultaneously, a further indication of two clutches. Clutch size varied from 1–6, with a mean of 3.33 eggs per clutch (108 clutches). Early clutches, *i.e.,* those estimated using females gravid from August through December, were significantly smaller (t-test, $P < .05$) than late clutches (estimated from females gravid during January and February); see Table 4. This increase in clutch size may be possible because females have grown during the interim between clutches. Fig. 7 shows that larger females tend to lay more eggs than smaller females; moreover, females laying late clutches are appreciably larger than those laying early clutches. The smallest gravid female observed measured 51 mm SVL.

Hatchlings emerge in two waves, one during January and February, and a second during April and May. They grow rapidly, with the majority reaching adult size in time to enter the breeding population the following spring (Fig. 8). Hence many individuals reach sexual maturity and breed at an age of from 6 to 9 months. On the basis of size frequency distributions through time, Storr (1965) suggested that there may be an annual turnover of adults in this species. Data gathered during this study are in reasonable agreement with Storr's hypothesis (Fig. 8), but without mark and recapture data, one cannot be certain that this is the case.

Predators and Competitors

Varanus eremius (and probably *Varanus gouldi flavirufus*) preys on adult *A. i. gularis* (Pianka, 1968, 1970a). Other predators no doubt include the pygopodid lizard *Lialis burtoni,* snakes, and various raptorial birds. Hatchling *A. isolepis* are extremely tiny (*ca.* 25 mm SVL, 0.1 g.) and could easily fall prey to a wide variety of smaller predators, conceivably even large spiders and small lizards.

At least nine, and sometimes as many as 20, other diurnal species of lizards often occur in ecologic sympatry with this species (Pianka, 1969a). Only two congeners are usually found with *A. isolepis*: *A. barbatus minor* and *A. inermis.* Both forms are considerably larger as adults, but there is probably some competition between juveniles of the larger species and adult *A. isolepis.* There is broad overlap in the diet of all three species (Pianka, 1971, and unpubl. data). On one study area, the closely related *Amphibolurus fordi* (in the same species group as *A. isolepis*) occurred with *A. isolepis,* but *fordi* occupied the sandridges, while *isolepis* occurred largely on the interdunal sandplains. Soulé (1966)

TABLE 4. FREQUENCY DISTRIBUTIONS AND STATISTICS FOR EARLY AND LATE CLUTCHES. OVERALL STATISTICS GIVEN AT BOTTOM. $\bar{x}$ = MEAN, SE = STANDARD ERROR OF MEAN, S = STANDARD DEVIATION, N = SAMPLE SIZE.

	Clutch Sizes						Statistics			
No. of clutches	1	2	3	4	5	6	$\bar{x}$	SE	S	N
Early (Aug–Dec)	2	13	37	11	4		3.01	0.10	0.82	67
Late (Jan–Feb)	2	3	8	18	7	3	3.88	0.19	1.20	41
Overall	4	16	45	29	11	3	3.33	0.10	1.06	108

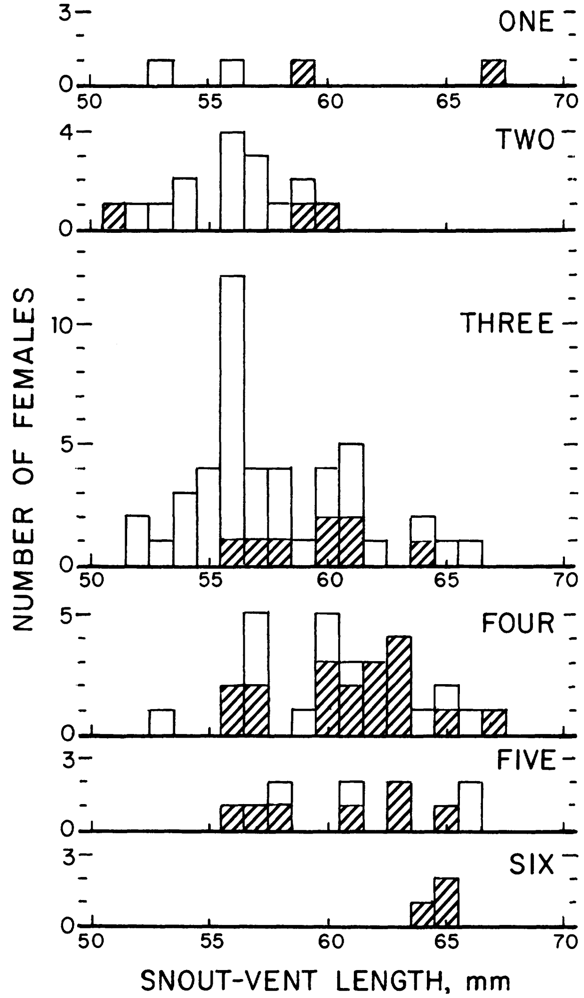

Fig. 7. Size frequency distributions (SVL) for females carrying varying numbers of large ovarian and/or oviducal eggs. Clutches of lizards collected during January and February (late clutches in Table 4) are crosshatched, showing that females tend to be larger later in season. The 67 mm female with only one egg had probably already deposited most of her clutch. Smallest gravid female measured 51 mm SVL.

and Schoener (1969) noted that, in insular populations of *Uta stansburiana* and *Anolis*, adult body size decreases as a function of the number of closely related competing species. Table 5 summarizes data for *A. i. gularis*, with no such trend being apparent in this mainland form.

Discussion and Conclusions

There are certain similarities between the ecology of *A. i. gularis* and that of the North American desert iguanid *Uta stansburiana*, particularly in the southern parts of the latter species' range. *U. stansburiana* has been studied in detail by Tinkle (1967, and included references) and his colleagues. *A. isolepis* and *U. stansburiana* are both small, abundant lizards. Both are active all year long and grow rapidly, reaching adult size and breeding during their first year. Populations of both species appear to have essentially an annual turnover. Both species are sexually dimorphic, lay multiple clutches of eggs and would appear to be relatively "*r* selected" lizards (MacArthur and Wilson, 1967; Pianka, 1970b). On the other

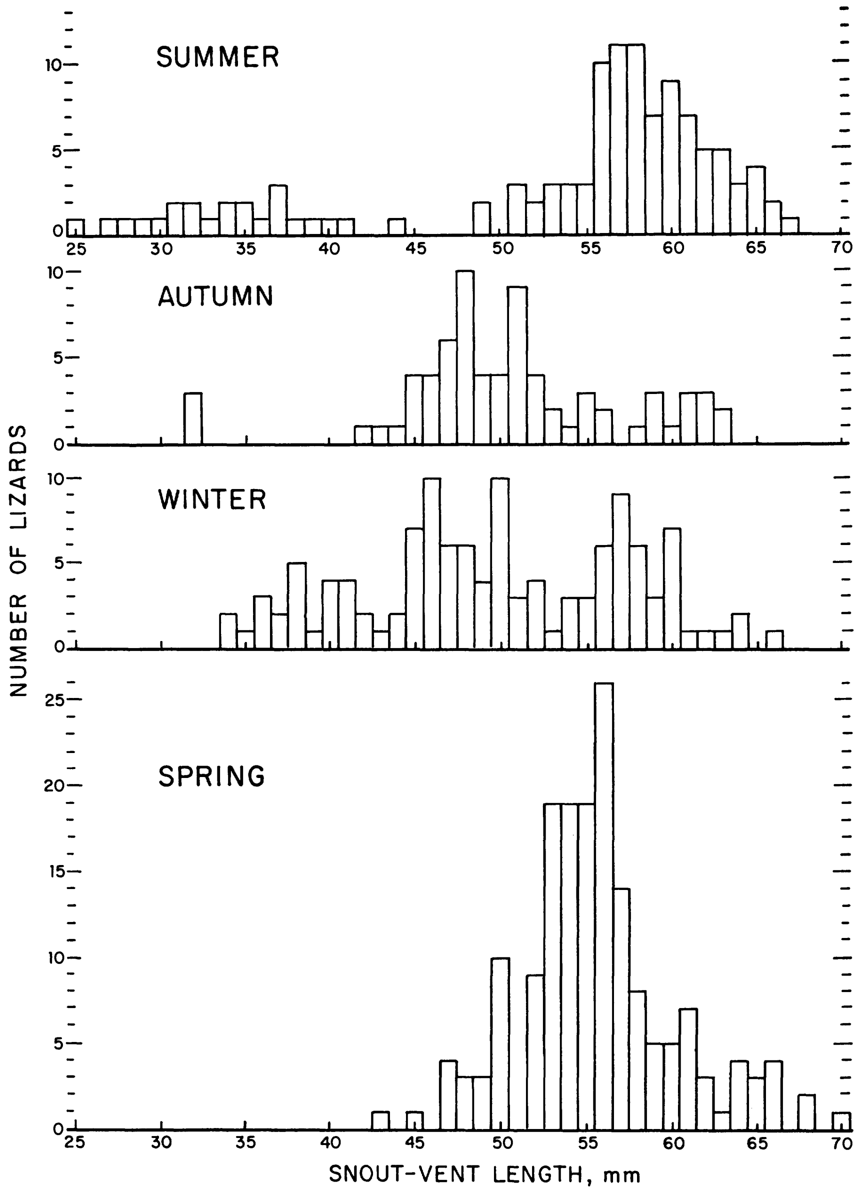

Fig. 8. Frequency distributions of snout-vent length by season (as in Table 3), showing rapid growth of hatchlings. Virtually all animals in spring populations are reproductive. See text.

hand, there are also fundamental differences between these two forms; *A. isolepis* forages in the open spaces between plants, whereas *U. stansburiana* spends most of its time in the shelter of shrubs. Correlated with this difference in space utilization, escape responses differ markedly in the two species. The agamid normally makes long zig-zag runs and tends to stay in the open, while the iguanid usually simply moves into a nearby burrow underneath the shrub. Elsewhere I have demonstrated that relative hind-leg length is often correlated with the frequency of use of open spaces between plants (Pianka, 1969b, 1971, 1972). This correlation also applies to the present comparison. As indicated earlier, 45% of 437 undisturbed *A. isolepis* were in the open sun or open

TABLE 5. NUMBER OF SYMPATRIC AGAMID AND *Amphibolurus* SPECIES OCCURRING ON SEVEN STUDY AREAS, WITH MEAN SNOUT–VENT LENGTHS (IN MM) OF *Amphibolurus isolepis*. N = SAMPLE SIZE, $\bar{x}$ = MEAN SVL, $\bar{x}_{1/3}$ = MEAN OF LARGEST THIRD OF SAMPLE.

Area	No. of Agamid Species	No. of *Amphibolurus* Species	Snout–Vent Length		
			N	$\bar{x}$	$\bar{x}_{1/3}$
M	6	4	48	57.6	65.1
D	6	3	93	54.1	60.1
E	8	5	82	51.2	56.4
L	4	3	55	56.8	62.4
G	5	4	113	52.7	59.1
N	2	2	20	52.7	58.6
Y	4–5	4	10	53.5	60.7

shade when first observed; the hindleg length averages 99.8% (± 0.27) of the SVL in this species. Only 26% of some 789 *U. stansburiana* were first found in the open (Pianka, unpubl. data); hindleg length in this species averages only 74.1% (± 0.28) of SVL. In contrast, some 83% of 447 *Callisaurus draconoides* were in the open when first sighted (Pianka, unpubl. data); hindleg length in *Callisaurus* averages 94.3% (± 0.34) of SVL. Hence, in terms of its "place niche" (Pianka, 1969b), *A. isolepis* appears to be intermediate between *Uta* and *Callisaurus*.

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