

# BODY TEMPERATURE STUDIES IN SOUTH AFRICAN LIZARDS

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On a visit to the Union of South Africa from October, 1958 to May, 1959, I investigated body temperatures in free living lizards in the field and captives in outdoor cages. Most intensive work was done at Johannesburg in the Transvaal and at Twee Rivieren in the Gemsbok Game Reserve in the Kalahari Desert. It should be pointed out for persons unfamiliar with South Africa that Johannesburg is at an elevation of 6,000 feet in the grass veld, a region of frequent summer rainfall and brisk winters, with frost and occasional light snowfall. The active season for reptiles extends over a period of about 8 months. The Kalahari locality is high desert (4,000 feet) of low relief, dissected by dongas of pale sand and hardpan and ridged with rust-coloured dunes and low rock outcrops. It is a region of uncertain rainfall of less than 10 inches a year. Winters are cool but less severe than at Johannesburg. Vegetation is chiefly open desert scrub of stiff, small leafed, thorny bushes and coarse grasses, with trees (acacias and others), largely confined to the dongas.

Information was sought on species differences in body temperatures of normal activity and maximum temperature tolerance of lizards exposed to direct sunlight. The "normal activity" range is defined by Cowles and Bogert (1944)<sup>1</sup> as the thermal range extending from the resumption of ordinary routine (after the animal has ceased basking, in the case of diurnal forms) and terminating at a point just below the level at which high temperatures drive the animal to shelter.

Two species, the Yellow-throated Plated Lizard (*Gerrhosaurus flavigularis*) and the Common East African Chameleon (*Chameleo dilepis*) were studied intensively in outdoor cages to test possible effects of removal of the parietal or "third" eye on thermoregulation. Although results were negative, information was gained on the thermal characteristics of individual lizards kept simultaneously under uniform conditions over a period of nearly 6 months, mid October, 1958 to early April, 1959.

The *Gerrhosaurus* study also made possible a comparison in the same individuals between body temperatures sought during periods of activity with those accepted during periods of seclusion. Such data were collected at times when the environmental temperatures available to the animals in their cages permitted thermal selectivity. The body temperatures of the lizards in hiding were thus not imposed.

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1. Important literature on temperature responses of reptiles is cited in the bibliography.

With the exception of a brief study of the temperature responses of two Namaqua Chameleons (*Chameleo namaquensis*), caged with the *C. dilepis*, all other lizards studied were investigated in the field.

## METHODS

In the field, lizards were procured for temperature records in several ways. Some were caught with a short-shanked fine copper wire (Eakin, 1957) or thread noose attached to a slender stick about 5 feet long. Others, difficult to noose, were killed with 22 calibre dust shot or were stunned with a heavy rubber band cut from an automobile tire inner tube and fired from the thumb (Brain, 1959).

Lizards in outdoor cages at Johannesburg were provided areas of light and shade and places of retreat. The chameleons were kept 8 to 10 to a cage. The larger animals had approximately 3 to 4, and the smaller ones,  $1\frac{1}{2}$  cubic feet of space per lizard. The sides and tops of the cages were of window screening and the floor was covered with soil. Tufts of grass, branches and rocks provided cover. Water was always available and live grasshoppers were offered as food. From time to time water was sprinkled into the cages to help maintain a moist atmosphere. The *Gerrhosaurus* were housed 1 to 4 per cage in 9 glass-sided screen top containers that measured 12 x 30 x 12 inches deep. The substratum was of sand in which they frequently buried themselves and a small box at the shaded end offered shelter for individuals on the surface. Drinking water was always available and the lizards were fed termites, mealworms, and grasshoppers. A hard board hood, open at one end, was used to cover the cages when it rained and at night, and served to shade the south end of the cage in bright sun. The long axis of the cages was oriented in a north-south direction, with the north end exposed to the sun (Southern Hemisphere). The sides and top of the open end of the hood were extended with a 4 inch wide strip of triple thickness window screening to provide a zone of weak shade between the end of the cage exposed to full sunlight and that in deep shadow. The lizards had, therefore, a step-wise choice in light intensity and a range in temperature during the day that extended well above and below that usually found in active surface-dwelling individuals.

Critical maximum temperature tests were performed in the Kalahari Desert on recently caught animals. They were tied loosely around the waist on a foot length of heavy thread and staked out in full sunlight on a grass mat on level ground. Body temperature was recorded (1) when the animal was first placed in the sun (2) when it began to pant, and (3) at the first sign of paralysis of the hind legs, which was regarded as the critical maximum temperature. Nearly all lizards recovered fully upon being placed in the shade. Exceptions are noted in Table 1.

All temperatures were taken with a quick-recording Schultheis thermometer designed and described by Bogert (1949). In the field, only records obtained promptly following capture were considered valid. When a lizard's normal pattern of activity was disturbed for several minutes by difficulties in capture, it was not considered a suitable subject for a temperature record. In the field, air in the occupied stratum (thermometer bulb shaded) and surface temperatures (bulb shallowly buried) were occasionally recorded. All temperatures of normal activity were taken with the same thermometer.

## RESULTS

*Body temperatures of normal activity.* Among the lizards studied the mean body temperature of normal activity seemed to be correlated with the amount and intensity of sunlight in the occupied stratum and the habits of the animals with respect to exposure to the sun.

At Twee Rivieren in the Kalahari Desert, the lacertids (*Scaptira* and *Eremias*), fast, agile, ground dwellers, had the highest mean  $38.0 \pm C^{\circ}$ , Fig. 1). They frequented exposed, well-illuminated ground where there was scant shade. The Namaqua Sand Lizard (*Eremias namaquensis*) and the Ocellated Sand Lizard (*E. lineo-ocellata*) appear to be the ecological equivalent of members of the American Whiptail genus (*Cnemidophorus*), found chiefly in arid southwestern United States and Mexico. They closely parallel these lizards in their ground dwelling habits, coloration, slim form, alert manner, nervous shaking of the forelimbs and habit of dashing quickly from bush to bush.

Nearby the Common Striped Skink (*Mabuya striata*), with a mean  $2^{\circ}C$  lower, was usually associated with acacia trees along the main wash. It was seen both on the ground and in the trees, usually where shade was prevalent, a cooler micro-environment than that occupied by the lacertids. This skink, an adept climber, readily escapes superheating of the ground yet is able to continue above ground activity, by ascending trees.

At Jackson's Drift near Johannesburg, a much cooler environment, the species (at least at the time of my study) spent much time basking and sought exposed rock surfaces rather than trees.

In the Kalahari, the Ground Gecko (*Chondrodactylus angulifer*) was found at night along the border of the main wash, usually above the bottom and in open desert scrub. As is to be expected in nocturnal ectotherms, the body temperature was close to that of the air, averaging over  $10^{\circ}C$ . lower than that of the other desert species studied. Geckos as a group have had a long history of nocturnality and thermal conservatism.

All the *Chondrodactylus* were found standing or walking in stilted fashion with the body held well off the ground.

This species seems to be the ecological counterpart of the American genus *Coleonyx*. Although lacking movable eyelids and having a chunkier head and broader shorter toes, it is similar in its terrestrial habits and general form and colour. It carries its body well off the ground, with tail curled.

The Yellow-throated Plated Lizard and the Common East African Chameleon, studied in the outdoor cages, occur naturally around Johannesburg. The former inhabits grassland. Its slim form, short legs, sinuous snake-like method of locomotion, and yellow dorsolateral stripes facilitate concealment in and rapid movement through grass. The places where it occurs are, in general, less subject to intense illumination than are those occupied by the lacertids or the skink and the mean preferred temperature was correspondingly lower. In proportions, presence of folds on the sides of the body, osteoderm development, tongue action, and habitat, this species resembles members of the American anguid genus *Gerrhonotus*.

The Common East African Chameleon of the bush and grass velds, although ranging into areas of relatively high temperature, proved to be thermally conservative. It not only had a mean some 7 degrees below that of the lacertids, but it was active over a much wider temperature range. Thermal conservatism is correlated in this species with plant dwelling habits. It lives chiefly in the air well above the ground, in an environment of shade and high humidity. It moves slowly and relies on cryptic colour and form and stealthy behaviour in procuring food and escaping its enemies.

Despite the extreme specializations of its relatives for arboreal life, the Namaqua Chameleon (*Chameleo namaquensis*) of arid southwestern Africa, frequents the ground. It is less flattened than most chameleons and has a brown and beige pattern that harmonizes with its desert surroundings. The mean of the normal activity range in two captives was 2.3 degrees higher than that of the Common Chameleon in keeping with its ground dwelling habits.

It would be desirable to obtain temperatures of both species of chameleons in the field to see if consistent differences are to be found.

A significant difference of 1.0°C ( $P = .001$ ) was found between the mean body temperature of Common Striped Skinks in the Kalahari Desert and those at Jackson's Drift. Although the localities are at approximately the same latitude, there are marked differences in climate, as pointed out earlier. Microhabitats also differ. At the former locality the lizards live among rocks and grass and seem not to be especially attracted to trees, whereas at Twee Rivieren they seek out isolated trees (*Acacia giraffae*, etc.) where they establish large colonies.

In view of the interruption of activity on the high veld by summer rain-fall and cold winter months, lizards at Jackson's Drift have less opportunity

for activity than those in the Kalahari Desert. At the former site, heat may often be at a premium for a sun basking reptile, whereas in the Kalahari the possibility of excessive exposure must exist. Perhaps the lower mean in the Kalahari animals represents acclimation to high environmental temperatures. A recent experiment by Wilhoft and Anderson (1960) on the Western Fence Lizard (*Sceloporus occidentalis*) lends support to this interpretation. In the fence lizard, forced exposure to the mean of the normal activity range (35.0°C.) was followed by a depression of 3.5°C. in the selected mean when the lizards were allowed to regulate their temperature in a thermal gradient. Animals subjected to 25° and 12°C. displayed no lowering of temperature in the gradient.

It would be desirable to repeat this study to exclude the possibility that some aspect of temperature recording technique influenced results. Thermometer variation is ruled out because the same instrument was used throughout.

The co-existence of the lacertids at the Kalahari locality is noteworthy. The existence of three closely related ground-dwelling species of similar size and proportions, and preferred body temperature in an open and floristically simple habitat, offers an unusual opportunity for study of species interaction, competition, and niche specificity. The following impressions are set forth in the hope of stimulating work on this problem.

Separation on the basis of thermal preferences with associated differences in time of daily activity, as noted by Inger (1959) in Bornean skinks, does not apply here. Choice of substratum, however, may be a factor in separating two of the species.

Although overlapping some in their spatial relations, the two *Eremias* seemed to be well separated by the colour and perhaps also the texture of the soil. The reddish *lineo-ocellata* was most abundant in areas of loose orange sand and uncommon on the firm, nearly whitish soil of the dry river bottom. The buff-coloured *namaquensis*, on the other hand, was seldom seen in areas occupied by *lineo-ocellata*. Overlap occurred especially in zones of gradation in soil texture and colour along the sides of the main wash and its tributaries.

Apportionment of the habitat by *Scaptira* and *E. namaquensis*, however, cannot be explained on this basis. They both seemed to favour hardpan and the edges of the dunes near the wash bottom where their pale colour blended well with background and where they intermingled freely. Study of food habits and timing of breeding may clarify this problem. Copulation was often observed in *Eremias* but was not seen in *Scaptira*.

#### INDIVIDUAL DIFFERENCES IN BODY TEMPERATURE

To the present time most studies of body temperatures of normal activity have been based on pooling of temperature data from groups of individuals

captured or shot in the field or tested in the laboratory. Little attention has been given to individual temperature characteristics. Procurement of reliable data of this sort on free-living lizards is difficult because it depends on chance recaptures of marked animals<sup>2</sup>. Therefore, such studies must usually be carried out in outdoor enclosures or in the laboratory.

An attempt was made to get information on individual temperatures in the Yellow-throated Plated Lizard and the Common Chameleon in order to test possible effects of shielding or removal of the parietal eye on thermoregulation. Although no change was detected when the eye was covered or removed, a byproduct of the study was the accumulation of temperature records on individual lizards over a 5 to 6 months' period. Although a long term study, the number of records procured for each individual was not as great as one might desire because temperature recording had to be curtailed to minimize disturbance of behaviour and irritation of the cloaca by frequent insertion of the thermometer and because of the sheer effort involved in studying, simultaneously, some 50 animals (only records on selected surface-active individuals are shown).

Body temperatures can, of course, be taken continuously by means of a thermocouple wired into the body of the animal. Although this technique can supply valuable detail, it has the disadvantage in a long-term investigation of providing voluminous data, difficult to analyze because of its sheer bulk. In the present study, the spot-check method seemed adequate to determine whether shifts in mean temperatures had occurred.

The precision with which some stenothermic reptiles maintain their body temperature within narrow limits, implies the existence of a central nervous system control center comparable in refinement to that of warm blooded animals.

When one considers that such reptiles depend on external sources of heat and regulate their temperature by locomotor movement and body orientation, within a frequently changing thermal mosaic, it is not surprising that fluctuations occur. Indeed, one might expect their body temperature to be more variable than it is. Behavioral control in thermally labile surroundings, involving problems of lag, over- and under-shooting, and unpredictable environmental changes, is likely to be crude compared to physiologic control, even given a highly perfected regulatory center.

One might predict, therefore, that there would be a better chance of demonstrating significant individual differences in the preferred body temperature of even the most highly stenothermic reptile than there would be in detecting such differences in the normal body temperature of almost any warm blooded animal. Selective pressure to produce and maintain precision in the

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2. The Marine Iguana (*Amblyrhynchus cristatus*) of the Galapagos Islands would appear to be an ideal subject. Individuals in some populations are abundant and tame.

maintenance of a constant body temperature would seem to be less in animals accustomed to environmentally induced temperature fluctuations than in those in which the tissues have become adapted to a constant internal climate. Genetic changes modifying the preferred temperature of the former would be less physiologically disrupting than in the latter. If this view is correct, it can be expected that among ectotherms eurythermal species would display greater individual differences than stenothermal ones and that, in general, such differences would increase with increasing eurythermy.

Contrary to expectation, no significant differences in the mean of the normal activity range was found in the moderately stenothermic *Gerrhosaurus*, despite the fact that the sample included both sexes and young and old individuals. Temperatures were taken over most of the season of activity for the species in nature and, judging from temperatures obtained in field animals, they appear to closely approximate those of individuals in the field. In 8 animals, for each of which over 75 records are available, mean temperatures ranged from 33.8 to 35.1°C., a difference of only 1.3°C. (not statistically significant).

The Common East African Chameleon, a more eurythermal species, showed statistically significant differences between the extreme individuals. In 11 selected animals, the range was from 29.1 to 32.2°C, a difference of 3.1°C. ( $P = .02$ ).

The high temperature animal was a male, the low temperature one, a female. They measured 72 and 74 mm. respectively, on November 10, 1958 at the beginning of the experiment, and 82 and 108, respectively at the end (March, 1959), the male growing more slowly than the female (.07 mm. as compared with .27 mm. per day). In a study of locomotor activity carried on in conjunction with the temperature work, the activity index for the female was twice that of the male. I can find nothing in these data to explain the observed thermal difference. It is tempting to speculate that it reflects differences based on different "thermostat" settings in the brain.

*Body temperature differences in secluded and active lizards.* — Pre-occupation of herpetologists with temperatures of the normal activity range has resulted in little attention being given to the body temperatures of lizards that have sought cover. It is usually assumed that, except for occasional individuals that have paused briefly in the course of routine activity, such ensconced animals are resting and are no longer actively thermoregulating.

The thermal characteristics and degree of alertness of such individuals has become of special interest in view of evidence for an increase in time spent abroad on the surface of the ground in temperate zone lizards that have been deprived of their parietal eye (Stebbins and Eakin, 1958). Such increased exposure implies extension of the time spent at temperature levels of normal activity and thus an exaggeration of exposure to heat if it can

be shown that secluded lizards average significantly lower temperatures than exposed ones.

It is not safe to conclude that when a lizard buries itself in the soil it promptly stops thermoregulating or that a low body temperature necessarily ensues. Buried Western Fence Lizards (*Sceloporus occidentalis*) in thermal gradients in the laboratory adjust body temperature to some extent by locomotor movements beneath the sand. In the field, the Lesser Earless Lizard (*Holbrookia maculata*) may delay emergence until it has reached a temperature well within its normal activity range (Bogert, 1959). Nonetheless, one may expect to find, on the average, that retreat is accompanied by a fall in body temperature.

Fitch (1956 : 448) found that free-living Five-lined Skinks (*Eumeces fasciatus*) in Kansas that had sought shelter, displayed a wider range in body temperature than those exercising control and a mean some 5°C. lower. I have obtained similar results with caged *Gerrhosaurus flavigularis* reported on here (Fig. 2). Surface active individuals averaged 34.3°C. (range 21 to 41°C.); secluded individuals 29.9°C. (17 to 40°C.). All temperatures of secluded individuals were recorded at times when the temperature gradient in their cages offered thermal levels well within the normal activity range.

*Critical maximum temperature tolerance.* — Species tested are listed in Table 1. The geckos had a lower critical maximum than the others, in keeping with their thermal conservatism. There are too few records to adequately compare the skink with the lacertids. The data suggest that the latter may be the more resistant to high temperature.

It is noteworthy that panting did not occur in *Mabuya striata*. In future tests further attention should be given to this point.

## SUMMARY

A study of the body temperatures of normal activity was made in the following South African lizards, arranged in order of preferred temperature from lowest to highest: Gekkonidae — *Chondrodactylus anguilifer*\*; Chameleontidae — *Chameleo dilepis*, *C. namaquensis*; Gerrhosauridae — *Gerrhosaurus flavigularis*; Scincidae — *Mabuya striata*\*; Lacertidae — *Eremias lineocellata*\*, *E. namaquensis*, *Scaptira suborbitalis*\*. In *Gerrhosaurus flavigularis* and *Chameleo dilepis* sufficient temperatures were obtained in captives to compare temperature preferences of individual lizards. Significant differences were found in *Chameleo* but not in *Gerrhosaurus*. Maximum temperature tolerances were determined in the species above marked with an asterisk and in the geckos *Pachydactylus bibroni*, *P. capensis*, and *Ptenopus garrulus*. The lacertids were more heat resistant than were the geckos. Preferred body temperatures seem to correlate with the amount and intensity of sunlight in



the occupied stratum and the habits of the animals with respect to exposure to the sun.

A comparison between body temperatures of surface-dwelling and secluded *Gerrhosaurus flavigularis* in a thermal gradient revealed that this species is more eurythermal when inactive than when active on the surface and that it averages a higher preferred temperature above ground.

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Dr. Elizabeth Scott and Mr. William Loughman carried out the statistical tests.

TABLE I.

Critical Maximum Temperature Tolerance in South African Lizards.

Species	Age and sex	Time (p.m.)	Temperature °C.		
			Starting	Panting	Critical maximum
<i>Eremias lineo-ocellata</i>	ad. M.	2 : 22– 2 : 34	37.0	41.5	44.7
	ad.	1 : 55– 2 : 00	35.7	43.7	46.0
	ad.	2 : 07– 2 : 12	35.6	44.1	45.1
	ad.	2 : 36– 2 : 40	37.7	43.0	46.7
<i>Scaptira suborbitalis</i>	ad. M.	3 : 05	34.6	43.4	46.0
<i>Mubaya striata</i>	im.	2 : 28– 2 : 44	37.5	none	44.9
	ad.	1 : 35– 1 : 41	36.0	none	44.5
	ad. F. (gravid)	2 : 48– 2 : 52	34.5	none	42.5
<i>Chondrodactylus angulifer</i>	ad.	1 : 36– 1 : 39	36.3	38.1	43.7
	im.	1 : 46– 1 : 50	36.7	39.0	43.0
	ad. M.	2 : 57– 3 : 04	35.4	36.5	42.5
	ad. M.	2 : 40– 2 : 48	32.0	32.4	42.5
<i>Pachydactylus bibroni</i>	ad.	3 : 50– 4 : 00	33.8	37.3	43.4
	ad.	2 : 05– 2 : 08	35.6	38.4	41.0 Died
	ad.	12 : 55– 1 : 00	33.6	37.7	41.6
	ad.	1 : 05– 1 : 10	35.3	39.3	43.0
<i>Pachydactylus capensis</i>	ad.	1 : 27– 1 : 30	35.8	37.8	42.6 Died
<i>Ptenopus garrulus</i>	ad.	—	37.7	none	43.4

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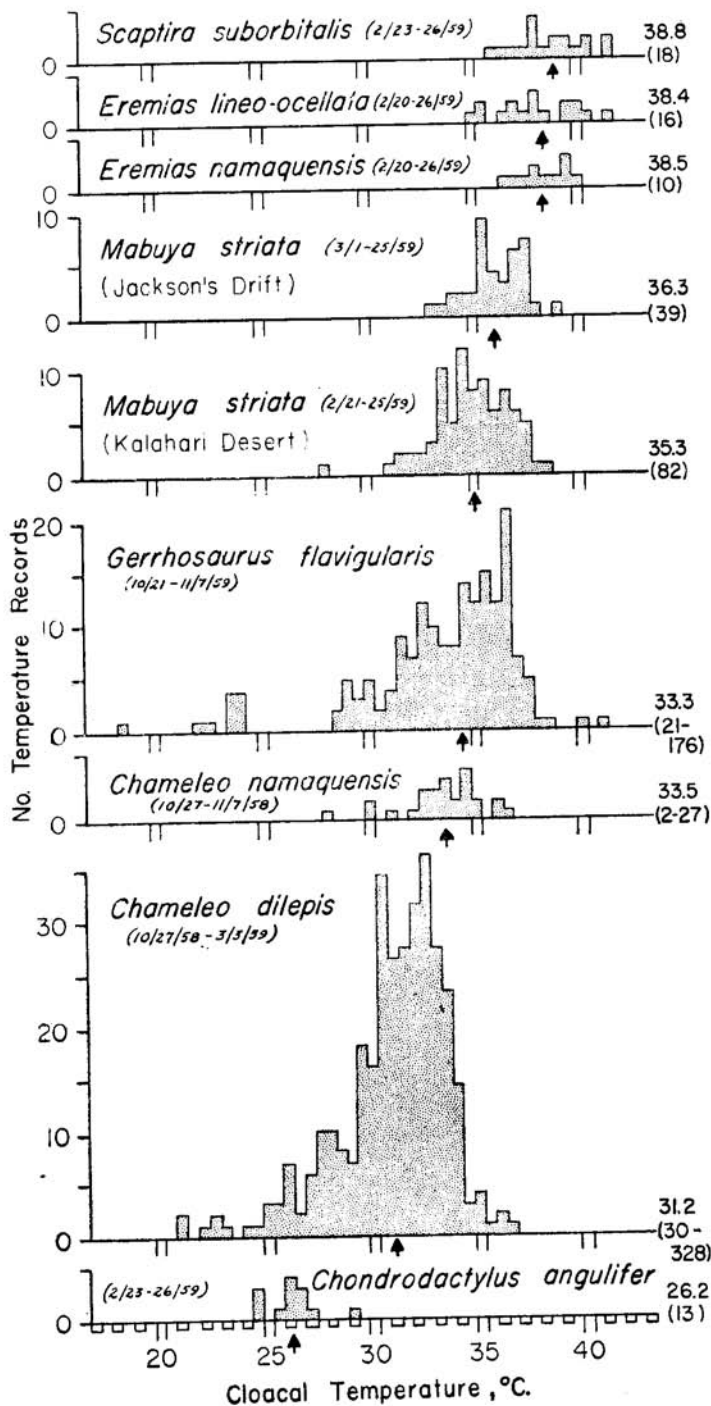
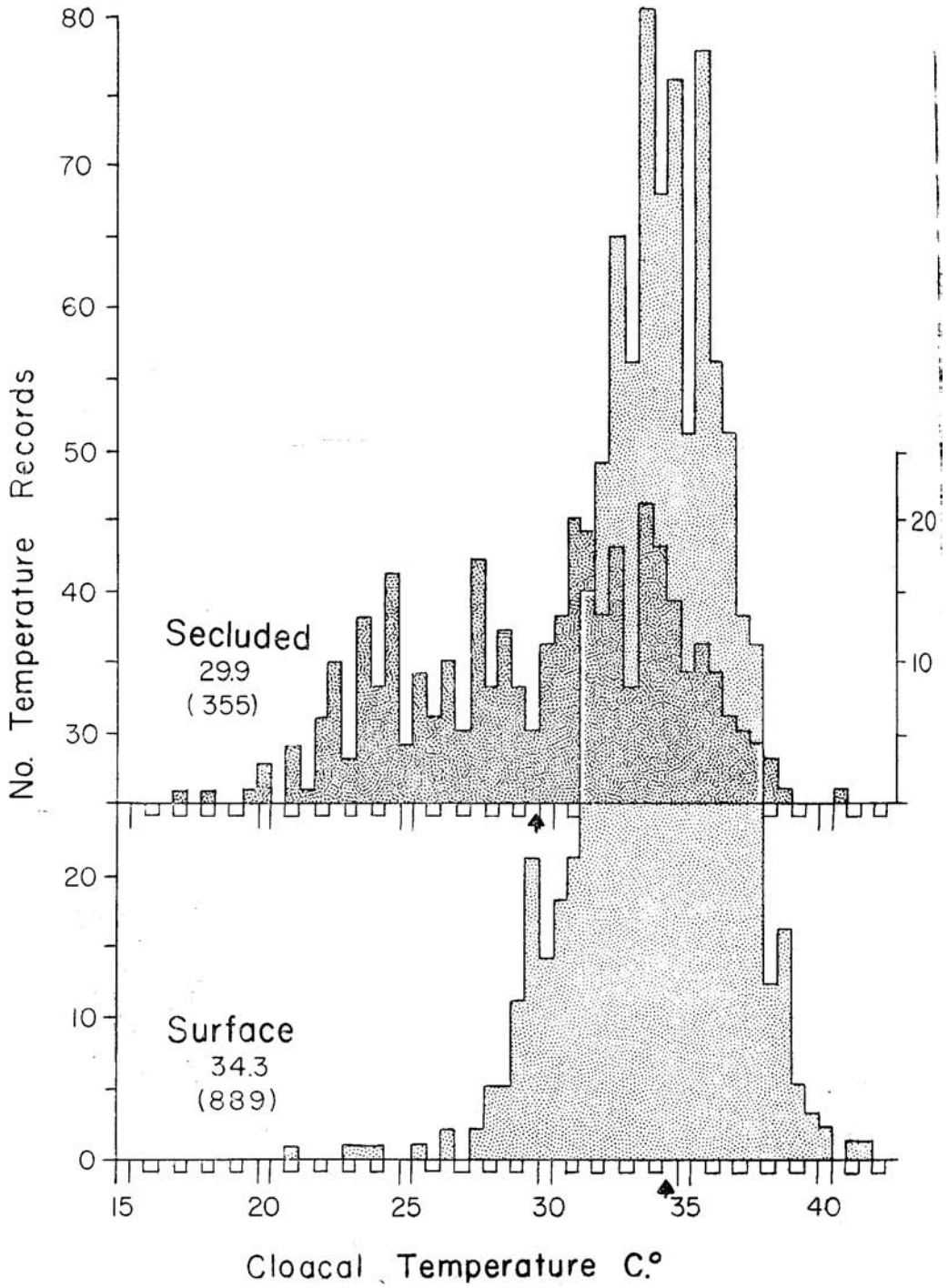


Fig. 1.—Body temperatures of lizards active on the surface of the ground, arranged in sequence from lowest to highest mean temperature of the normal activity range. Temperatures of *Chameleo dilepis*, *C. namaquensis*, and *Gerrhosaurus flavigularis* are of captives in outdoor cages. The others are of lizards caught in the field. With the exception of *Gerrhosaurus* and *Chameleo*, the numbers at the right of each graph are (top to bottom) the mean and the total number of individuals studied. The third number, given for *Gerrhosaurus* and *Chameleo*, is the total number of temperature records. Small numbers in parentheses are dates when temperatures were recorded.



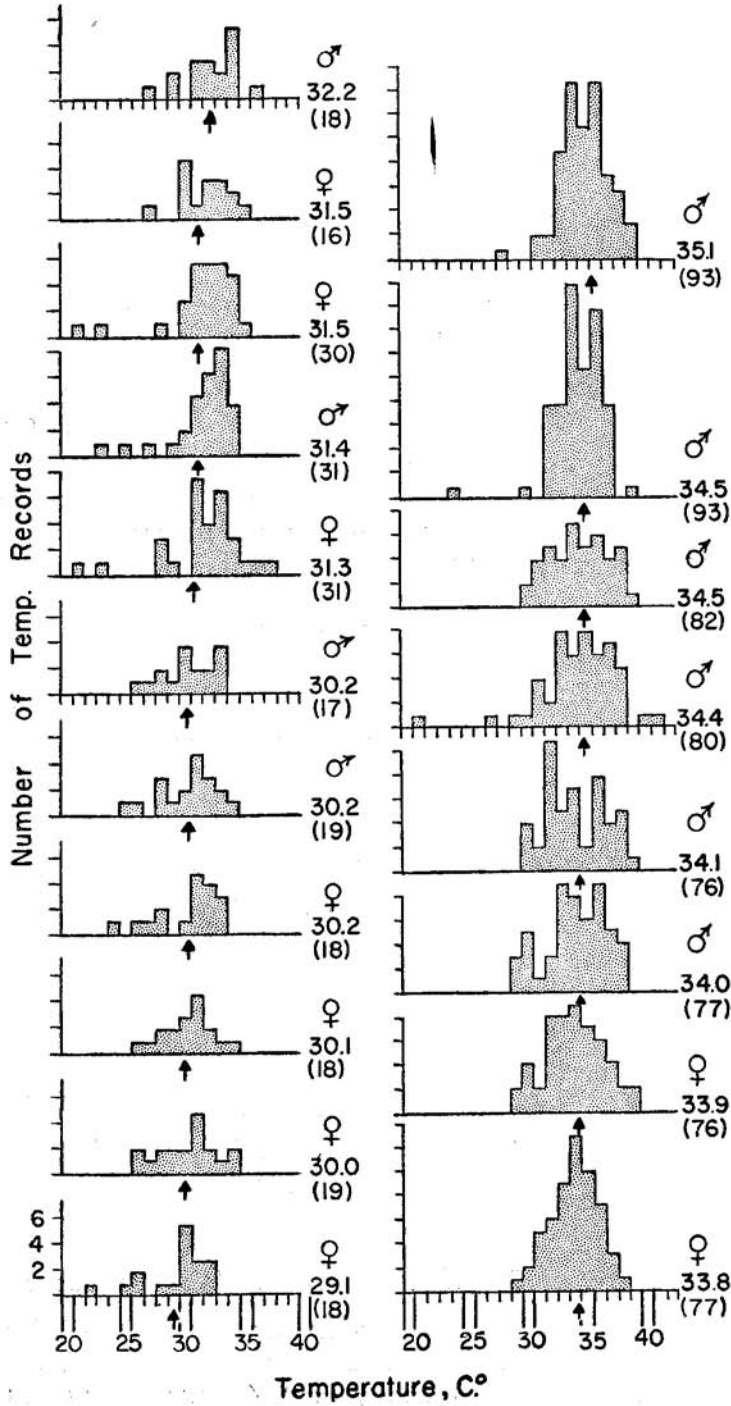


Fig. 3.—Individual body temperature records of normal activity in *Chameleo dilepis* (left column) and *Gerrhosaurus flavigularis* (right column). Numbers on right in parentheses are total numbers of records. Other numbers are means.