AMERICAN MUSEUM NOVITATES

Published by
Number 1358 THE AMERICAN MUSEUM OF NATURAL HISTORY August 21, 1947
New York City

RESULTS OF THE ARCHBOLD EXPEDITIONS. NO. 58

MOISTURE LOSS IN RELATION TO HABITAT SELECTION IN SOME FLORIDIAN REPTILES

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INTRODUCTION

Virtually nothing is known concerning the mechanism of water loss in reptiles. It has been argued (Wetmore, 1922) that any moisture loss is largely through the lungs, since no sweat glands are present on reptiles. However, Noble and Mason (1932) state that moisture may be lost as well as absorbed through the skin of reptiles. Benedict (1932) did not determine how moisture was lost, although he mentions a few bits of evidence bearing on the problem. He also points out that there is rough correlation between carbon dioxide production and vapor output. He found that when the water vapor was measured simultaneously with the heat produced by a snake in an electrical compensation calorimeter, a large output of vapor was evident, "indicating that the major portion, if not all, of the heat produced by the snake left the body by the path of vaporization of water."

Such evidence indicates that water may be lost through the lungs, as well as the skin. In fact there is evidence that at body temperatures approaching the critical maximum some snakes are able to lower their temperatures a few degrees by accelerated breathing with respiratory cooling, doubtless accompanied by vaporization from the lungs. On the other hand Benedict (*supra cit.*) reports the significant observation that, in spite of the absence of sweat glands, there is an unusually large loss of water vapor in snakes just prior to the shedding of

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Fig. 1. Terrain to the northwest of the Archbold Biological Station near Lake Placid, Highlands County, Florida. Timbering operations in the former Pine Flatwoods have resulted in the removal of most of the trees beyond the railroad track in the foreground. Relatively few reptiles except *Sceloporus woodi*, *Eumeces inexpectatus*, and *Coluber constrictor priapus* occur in such disrupted habitats.

Fig. 2. View to the east of the Archbold Biological Station, showing the scrub forests, with pine and palmetto interrupted by fire lanes. Several species of reptiles occur in this habitat, *Sceloporus woodi* being the most abundant.

the skin. In one of his experiments the water output of a boa about to shed increased from 5 to 11 grams per kilogram of body weight. This may indicate only a temporary loss of water through the skin, a loss that perhaps is more closely associated with the complex physiological processes involved in ecdysis.

Hall and Root (1930) desiccated a few amphibians and reptiles under controlled conditions and found that the amount of water loss was variable, being greatest in the salamander and least in the alligator. Although they tested but one representative of each group, they drew the conclusion that the lower in the phylogenetic series an animal is, the greater is the influence of low humidity upon its temperatures. Noble and Mason (1932), however, point out that there are vast differences between individual species of reptiles belonging to the same suborder. They do not describe the techniques they employed, but they report that lizards absorb moisture through their skin, and that species living in damp habitats both lose and absorb greater amounts of moisture than those frequenting arid regions. Moreover, they state that there is little correlation between water loss and skin structure except that the most impervious skins are provided with the thickest horny layer.

It is no simple task to determine whether heat is more important than moisture as a factor limiting distributions; optimum conditions for a reptile's activity may indeed be dependent more often upon both, as well as upon other factors. However, it is well known that even in the tropics both amphibians and reptiles are more difficult to find during the dry season than they are at other times of the year, even though there may be no significant drop or rise in atmospheric temperatures. In temperate regions reptiles are not abroad during periods of cold, and relatively few species are abroad during the driest months. In general more species are seen and adult individuals tend to be more abundant, even in deserts, during the wettest periods of the warm months. Whether moisture is lost in greater quantities through the lungs or through the skin, it is of interest to ascertain the differences that may exist among species living in various habitats in the same region. The purpose of these experiments, therefore, was to measure the moisture loss in as many species of Floridian reptiles as possible under conditions that would permit comparisons.

REGION AND TERRAIN

It is important that ecological experiments with reptiles be carried out with freshly captured specimens. Relatively few species can easily be maintained under conditions in captivity that permit them to thrive. Commonly reptiles secured from dealers are emaciated or in such poor physical condition that they are unlikely to survive under experimental conditions tolerated by healthy animals. For this reason it was imperative that experiments be carried out in a region where reptiles could not only be observed in the field, but where they could be transferred immediately to the laboratory. Such requirements were met at the Archbold Biological Station,[1] which is situated 7 miles south of the town of Lake Placid in southern Highlands County, Florida. For several years over a thousand acres of land (figs. 1, 2) comprising the area controlled by the Biological Station have been relatively undisturbed, although fire lanes have been cut in the vegetation and drainage ditches have been dug at the lower portions of the land. These ditches empty into Lake Annie, a

[1] Much of the cost entailed in carrying out these investigations was borne by the Archbold Expeditions of the American Museum of Natural History. In addition we are greatly indebted to Mr. Richard Archbold for his hospitality, his innumerable courtesies, and his constant assistance and advice in designing laboratory apparatus, for which he supplied much of the material. For their help in securing live reptiles we are similarly grateful to members of his staff, including Messrs. Frank Rinald, S. H. Walter, Dennis Hinchey, Winston Kelsey, Ben Kline, Melvin Purviss, Thomas Browning, Tom Barnes, and Scofield Williams. Thanks are due Mr. Leonard Brass for his courteous help in drawing up our plans. Dr. A. F. Carr, and Dr. Coleman J. Goin of the University of Florida, as well as Mr. Ross Allen of Silver Springs, all of whom are well acquainted with the herpetofauna of Florida, were extremely helpful in offering suggestions concerning collecting techniques and other information. To them our thanks are gratefully acknowledged.

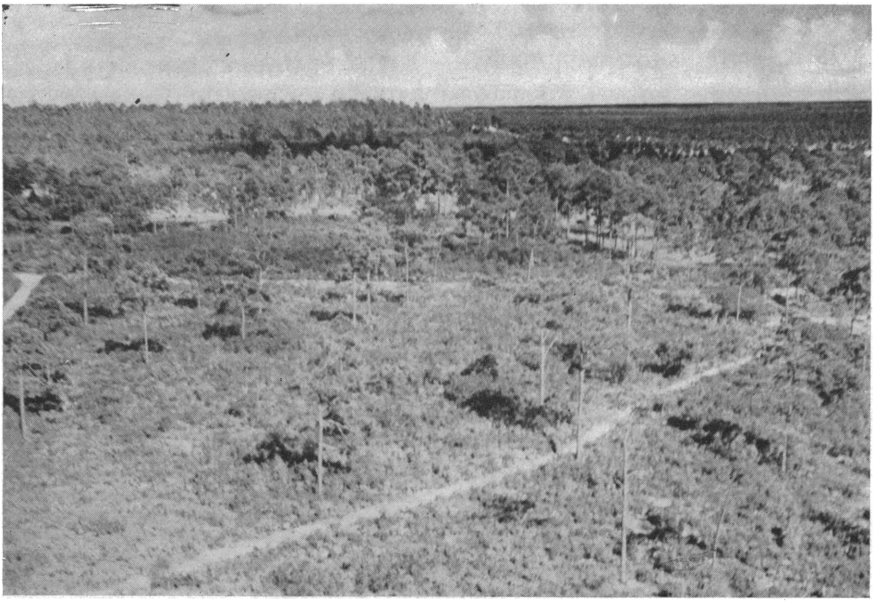

Fig. 3. Red Hill, at the horizon to the left looking east from the Archbold Biological Station, rises to a maximum elevation of 222.2 feet and marks the southern end of the Highlands Ridge of central Florida. South of this hill the relatively dry ridge drops off abruptly to the Pine Flatwoods, and Wet Prairies of the Everglades. *Rhineura floridana, Neoseps reynoldsi, Coluber flagellum, Coluber constrictor, Gopherus polyphemus,* as well as several other reptiles, occur in this habitat.

pond approximately a mile north of the Biological Station. Red Hill (fig. 3), at the eastern edge of the land owned by the Station, rises to a maximum elevation of 222.2 feet above sea level and marks the southern end of the Highlands Ridge of Central Florida. South of Red Hill the land is lower, with a rather abrupt change from the "Scrub Forests" (which Davis, 1943, fig. 71, includes in the southern end of the Highlands Ridge in his map of the vegetation of southern Florida) to the Pine Flatwood Forests, Wet Prairies, and Inland Swamps of the ill-defined region known as the Everglades. West of the Archbold Biological Station most of the timber has been cut from the Pine Flatwoods, although a few small hammocks remain. Two small pools, one of them partially excavated, are on the property of the Biological Station.

Climatic records for Highlands County over a period of 37 years have been taken at Avon Park, which lies roughly 25 miles in air-line distance north of Lake Placid. As reported by the United States Department of Agriculture (1941), the mean annual precipitation is 52.12 inches. The maximum (air) temperature is 102° F. (40° C.) and the minimum 21° F. (−5.5° C.)

APPARATUS AND METHODS

Owing to wartime scarcities of materials our apparatus was in part improvised with the equipment available at the Archbold Biological Station. A chamber in which temperatures could be controlled and maintained at suitable levels was prepared by Mr. Richard Archbold who conceived the ingenious notion of converting a well-insulated butcher's display case (fig. 4) that he had on hand. The case, except the doors, on the upper portion was constructed of sheet iron glazed with white enamel, with the inner wall insulated from the outer wall. Sliding doors on the upper portion were made of wood, with inner and outer panes of glass holding an insulating layer of air in between. Hinged insulated doors on the lower portion opened on the floor of the case. Inside, the chamber was divided into an upper and a lower compartment by a shelf comprised of metal grills permitting free circulation of the air. Boards were placed on this shelf in such a manner that only the ends of the shelf were open.

An electrical heating element, thermostatically controlled, was installed in the lower compartment at one end, with an electric fan behind it. The fan, maintained at a slow speed, kept the air in circulation in both compartments, although in the upper portion the movement of the air was scarcely noticeable. A Bristol Recorder was used to ascertain fluctuations in the air temperature at two-minute intervals; one terminal was inserted in a wick to record wet-bulb temperatures, while the other recorded air temperatures.

After the thermostat was set to maintain the temperature at 38° C., the chamber was operated for several hours before any animals were placed in it. When it was ready for use the temperature was found to be maintained satisfactorily. The air temperatures in the chamber varied only within the limits of 0.2° C. above or below 38° C. as indicated by the Bristol Recorder. As an additional precaution temperatures were checked frequently with thermometers calibrated by the Bureau of Standards. A closed can containing wet sand with a hole in the lid for a thermometer was placed in the upper portion of the chamber, to provide a further check. Readings from this thermometer indicated that the temperature of the sand was virtually constant at 38° C.

No attempt was made to vary the humidity during the series of experiments ex-

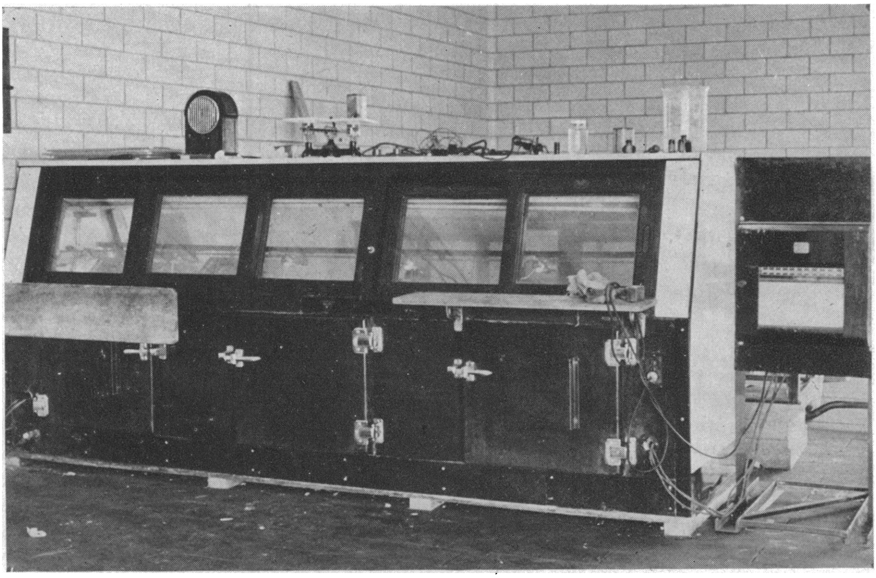

Fig. 4. The thermal chamber used in experiments, converted from a butcher's display cabinet. The apparatus at the right is a Bristol Recorder, which automatically recorded the temperatures within the chamber at two-minute intervals. The chamber was heated by means of a thermostatically controlled electrical heating element located at one end of the lower compartment, with an electric fan behind it. Temperatures of 38° C. were maintained in the chamber, with fluctuations no greater than ±0.2° C., and with the relative humidity at approximately 37 per cent.

cept once when comparisons were made of moisture loss in an alligator, and the relative humidity was raised to 46 per cent for one experiment. The relative humidity was measured by comparisons of the readings on the wet and dry terminals of the Bristol Recorder and checked with a sling psychrometer suspended in front of the fan, which was momentarily accelerated. There was very little fluctuation in the relative humidity within the chamber; it remained almost constantly at 37 per cent, with fluctuations no greater than 5 per cent, except when it was purposely increased.

A series of four wire mesh cages of suitable capacity were placed in the upper portion of the thermal chamber. After these had been in the chamber for several hours, the various reptiles used in experiments were first weighed and then placed in one of the cages. Closed cans containing wet sand were also used in some experiments in order to find out whether any loss of weight occurred when amphibians or reptiles were maintained in saturated air at 38° C.

All body temperatures were taken with gas-filled mercury thermometers made for the purpose. These instruments were designed to record temperatures within the range of 0° to 50° C. and calibrated in divisions of 0.2° C. The bulb is 2 mm. in diameter and 12.0 mm. in length so that it could easily be thrust into the cloaca of even the smallest lizards. Such thermometers reach equilibrium within 15 seconds. Temperatures of all reptiles were taken before they were removed from the chamber to be weighed.

Weights, usually determined immediately after the cloacal temperature had been recorded, were taken at intervals with a balance that was accurate to 0.1 gram. Such accuracy seemed to be adequate for our purposes, although for very small specimens a more precise instrument would be desirable. Because reptiles maintained at 38° C. in a can of wet sand, in which the air was presumably near 100 per cent in relative humidity, lost no weight it seems reasonably certain that the weight lost by reptiles in the wire mesh cages represents moisture lost by evaporation.

It may be added that Benedict (1932) found no differences between temperatures taken in the mouth of snakes and those taken in the cloaca. Skin temperatures were found by him to be somewhat lower except under unusual conditions, a fact which may possibly be attributed to the loss of moisture through the skin. Benedict also found that there was a very slight rise in a snake's temperature following ingestion of food as a result of the digestive processes. Virtually all workers who have dealt with snakes under conditions where the temperature of the environment could be spoken of with accuracy have found the body temperature slightly below that of the environment. However, a moderate amount of agitation will, according to Benedict, cause a rise in the cloacal temperature of as much as 3° C. in 19 minutes.

It is pertinent, therefore, to note that none of the specimens in the thermal chamber demonstrated any inclination to be active. All of them became almost completely quiescent within a relatively short time after being placed in the cages. Many of them voided feces or water when handled the first time they were removed to be weighed, but they rarely did so on subsequent occasions. All specimens used were freshly caught. None of the snakes showed any evidence of having eaten immediately prior to capture, although it is probable that all the lizards and some of the turtles had recently eaten.

It would have been desirable to measure the loss in weight of the reptiles studied at various temperatures and humidities, since it is known that some amphibians can survive twice as much loss if evaporation is slow then they can if it is rapid. Benedict states that there is some evidence that there may be a critical temperature for water elimination between the temperatures of 30° C. and 36° C. However, with the time at our disposal it was not feasible to determine the importance of these considerations. It was necessary to restrict the present effort to experiments permitting comparison of moisture losses with all experimental animals maintained under similar conditions of temperature and humidity.

In the following account brief notes on

the habits and habitat of each species are provided in order that some notion may be had of their ecological requirements. The species studied will be discussed in the order of their phylogenetic relationships as currently accepted.

EXPERIMENTS

The animals used in the experiments described herein have been grouped by orders and suborders to permit comparisons of the most closely related species. It should be noted, however, that because the weight of the animal, as well as the rate of water loss, varies extensively from species to species, the graphs showing actual losses in weight are constructed on different scales. An animal weighing over 2000 grams manifestly is able to lose more water than one weighing 5 or 6 grams. Water loss is possibly dependent upon several factors, not only the actual percentage of water in the tissues, but the nature and the extent of the surfaces, that is, of the lungs, skin, or intestine, through which it is lost. It is doubtful whether any entirely satisfactory means of comparing species can be devised, but rough comparisons can be made in terms of the ratio of the weight lost per hour to the original weight (see fig. 23). Whenever possible more than one specimen was used, but the results obtained with different individuals, or with repeated trials using the same individual, are sufficiently similar to show that variation is not great within the local population from which specimens were drawn.

TURTLES

On the basis of fossil evidence the turtles are the oldest surviving group of reptiles. Modern turtles are not vastly different from their earliest ancestors, reptiles that probably descended from generalized anapsids, and became incased in their bony shells by the Triassic, at least 175 million years ago. Most species are aquatic or semi-aquatic, although a few are strictly terrestrial. In general there are more species in humid than in arid regions, and relatively few of them range north of latitude 50° N. in the Northern Hemisphere.

Kinosternon subrubrum steindachneri Siebenrock

This peninsular race of the common mud turtle of eastern United States is found from central Florida northward to the upper end of the state, where it presumably intergrades with the typical race. The species, represented by the Gulf Coast race, *hippocrepis*, is found as far west as Dallas, Texas, but is replaced in the arid regions to the west by two other species. The genus is well represented in Mexico, and additional species occur in Central and South America. All of them are aquatic, although some forms live in pools or streams in desert regions, from the Colorado River eastward.

Kinosternon subrubrum steindachneri lives in streams, pools, marshes, and the smaller lakes of Florida. Carr (1940) described the species as "very aquatic; rarely seen on land." The specimens used were ploughed from the mud surrounding a small pond at the Archbold Biological Station. Three individuals weighing, respectively, 64.7, 90.0, and 117.0 grams, were used.

The two larger turtles were kept in the thermal chamber for periods of 37 and 51 hours, respectively, and showed no ill effects from this prolonged exposure to air at 38° C.; they lived for three months afterward before they were killed and preserved. When placed in the thermal chamber both turtles had cloacal temperatures of 26° C., approximately that of the laboratory sink in which they had been kept. Within the first hour the temperature of the turtles rose to 36.5°. Although the temperature of the air within the chamber was virtually constant at 38.0° C., that of the turtles was consistently lower, varying from 34.2° to 37° C., with a mean of 36.6° C.

As indicated in figure 5, there was a steady decrease in weight, with relatively slight fluctuations. The turtles at first remained with their heads protruding and the legs loosely extended, but after 12 hours the eyes were closed, and the neck and legs were withdrawn into the shell. The larger of the two turtles lost 23.6 per cent of its original weight in 51 hours, but in terms of the percentage of its original weight the rate of moisture loss was 0.46 per hour, or somewhat less than that for the smaller individual, which lost moisture at the rate of 0.61 per cent of its initial weight per hour. This smaller turtle, weighing 90 grams when placed in the chamber, lost 20 grams, or 22.2 per cent of its original weight, in 37 hours.

The smaller turtle, weighing 70 grams at the conclusion of the experiment, was placed in water five minutes after it was removed. When weighed five minutes later it had increased in weight to 76 grams, doubtless from simple ingestion of water. Fifteen minutes later it weighed 79.2 grams, and a half hour later it had further increased to 81.5 grams. The following morning, nine hours after removal from the thermal chamber, the turtle weighed 87.8 grams, and two hours later it had reached 88.8 grams, or very nearly its original weight.

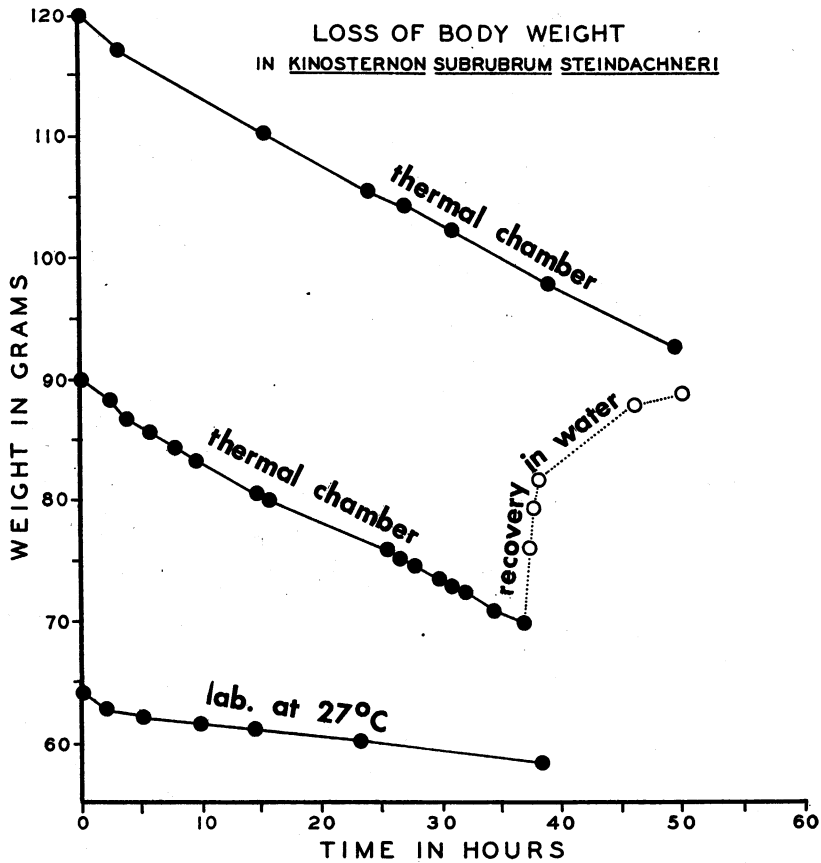

Fig. 5. The upper curves indicate fluctuations in the weight of the peninsular mud turtle, *Kinosternon subrubrum steindachneri*, in the thermal chamber (and on one, after removal). The lower curve indicates the loss in weight of a smaller turtle without access to water, in the laboratory at room temperature.

A somewhat smaller turtle, weighing 64.7 grams, was placed in wet sand in a closed container in the thermal chamber. For a period of 48 hours it remained there, invariably buried in the sand except for occasional short interruptions when it had to be removed in order to record the cloacal temperature. Although it remained at essentially the temperature of the thermal chamber, 37.9° to 38.0° C., for the 48-hour period, no weight was lost, and the turtle was in excellent condition when it was removed.

The same turtle was confined in the laboratory in a wire mesh cage without water for 37.5 hours subsequently and weighed at periodic intervals. In the laboratory the turtle's temperature was almost constantly 27° C., and whereas the humidity was probably not constant, the turtle lost weight steadily but at the relatively slow rate of 4.7 grams (6.2 per cent of the initial weight) in 38.5 hours (fig. 5).

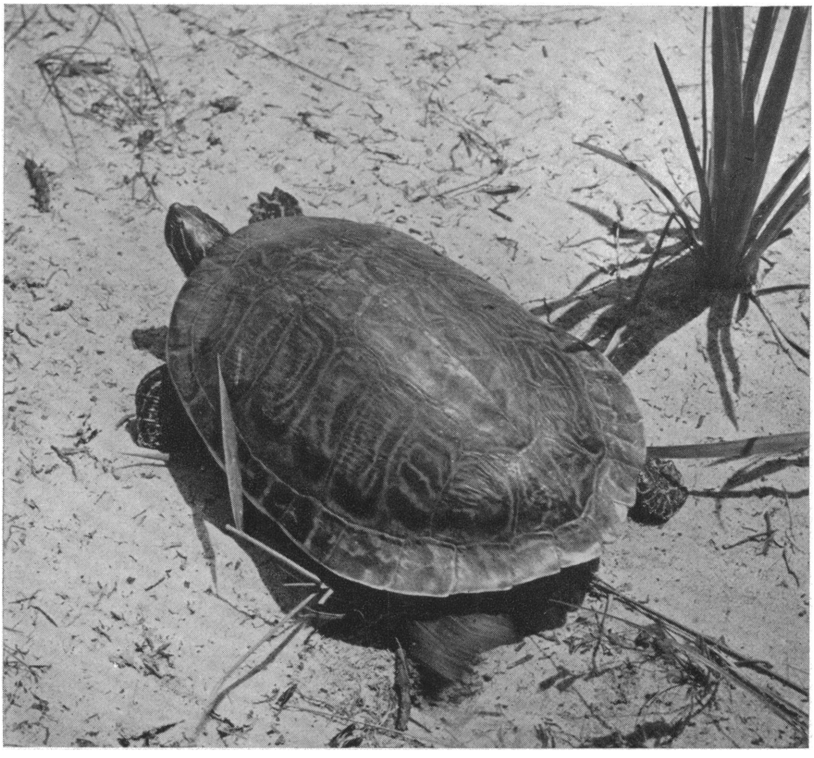

Fig. 6. The Florida "cooter," *Pseudemys floridana peninsularis*, used in experiments, an adult male weighing 2951 grams when placed in the thermal chamber.

Pseudemys floridana peninsularis Carr

This species is one of the common turtles throughout most of the southeastern portion of the United States. The subspecies (fig. 6) known as the "Florida cooter" is confined to the peninsula. The genus, however, is widespread in North America, ranging from Massachusetts southward through Mexico along both coasts to Panama. It is absent from the United States west of the continental divide, although one species occurs in southern Baja California as well as in the Rio Fuerte drainage of southern Sonora. Carr (1940, p. 103) reports that in Florida it is found in almost any aquatic situation, but it is commonest in lakes, sloughs, and the rivers of the St. John drainage. Furthermore, he notes that turtles of both sexes wander on land on warm winter days and in early spring. The specimen used was taken at the edge of the Archbold Biological Station in a relatively dry, sandy area where its wanderings had been impeded by a fence.

When placed in the thermal chamber the

turtle had an initial body weight of 2951 grams, and the body temperature was 25.5° C. Fifty minutes later the cloacal temperature had risen but 1.5°, and no loss in weight was detected. Three and a half hours after it had been placed in the chamber its temperature reached 34.5° C., and at the end of a five and a half hour period the temperature was 36.0° C., although there had been a sudden drop in weight, doubtless attributable to water voided from the bladder. The initial rapid loss (fig. 7) was followed by a generally steady but somewhat erratic reduction in weight. The body temperature was maintained between the limits of 35.0° and 36.9° C., with 36.0° as the mode. The turtle was removed at the conclusion of 49 hours in the thermal chamber, after having lost 425 grams, and placed in water. When weighed again four hours later the "cooter" had exceeded its original weight by 115 grams. Evidently, therefore, the moisture reserve of the turtle had been somewhat depleted at the time it was captured, presumably because it may have come some distance over dry land. Nevertheless it still had sufficient water in reserve to maintain itself for at least 49 hours under the extreme conditions of the thermal chamber despite the fact that it lost 14.4 per cent (425 grams) of the initial weight. This chelonian was losing moisture at the rate of only 0.29 per cent of its initial weight per hour, even though its reserve was presumably below normal at the time the experiment was begun. Obviously the "cooter" can remain out of the water at relatively high temperatures for prolonged periods with little risk of severe desiccation.

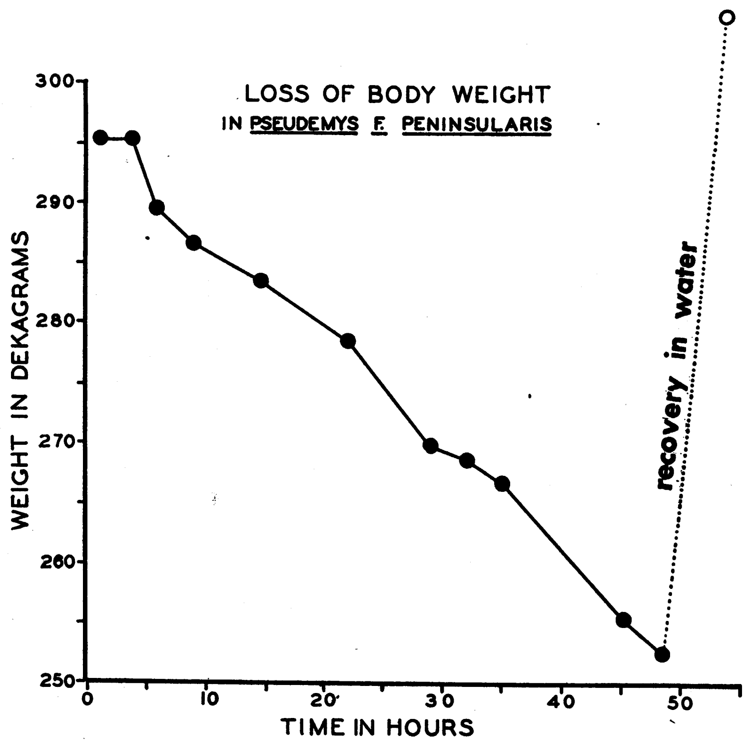

Fig. 7. Weight lost by the turtle, *Pseudemys floridana peninsularis*, during 49 hours in the thermal chamber. Dotted line indicates the recovery of water in sufficient quantity to raise its weight to a figure exceeding its original weight, after being placed in water at room temperature (usually near 27° C.) for four hours.

Terrapene carolina bauri Taylor

The Florida box turtle (fig. 8) is widely distributed on the peninsula, and according to Carr (1940, p. 100) it inhabits principally flatwoods, upland and mesophytic hammock, but occurs in high pine forests. It was of uncommon occurrence at the Archbold Biological Station where only a single individual was taken during two months' work. Box turtles of the genus *Terrapene* are largely terrestrial, but occasionally they enter the water. They occur throughout most of the United States east of the Rocky Mountains, and one species, *T. ornata*, has a range extending from the Great Plains across the continental divide into southeastern Arizona. The range of the genus extends southward to Yucatan along the east coast of Mexico, and two species occur in Sonora and Nayarit, respectively, on the Pacific slope; an additional form is known only from northern Coahuila. The genus evidently was not only much more widespread but individuals attained greater dimensions during the Pleistocene. *T. ornata* is the only species inhabiting moderately arid terrain.

The specimen used in the desiccation experiment was an adult female weighing 293.5 grams when placed in the thermal chamber. The shell could be closed so tightly with the close-fitting plastron that it was impossible to secure temperatures without damaging the turtle. Consequently no data could be recorded except the reductions in weight at periodic intervals. Moisture was not lost at a steady rate (see fig. 9), even though conditions of humidity and temperature were essentially constant in the chamber. During a 45-hour period this box turtle lost 50.8 grams, or 17.3 per cent of its original weight. The mean rate of moisture loss for the full period was 0.38 per cent of the body weight per hour, or essentially the same as that for

Fig. 8. The Florida box turtle, *Terrapene carolina bauri*, used in experiments, an adult female weighing 293.5 grams when first placed in the experimental chamber.

another terrestrial species, *Gopherus polyphemus*.

Gopherus polyphemus (Daudin)

The gopher tortoise (fig. 10) inhabits upland sandy areas throughout most of Florida, as well as the Gulf Coast. Its nearest relatives are (1) *G. berlandieri*, the species that inhabits central Texas southward into Nuevo Leon, Mexico, east of the Sierra Madre Oriental, and (2) *G. agassizii*, an inhabitant of the arid Southwest, with a range encompassing most of the Colorado and Mojave deserts, from Sonora northward to southwestern Utah. *Gopherus* is closely related and essentially congeneric with *Testudo*, a genus with species in the temperate and tropical regions in many parts of the world.

In Florida the gopher tortoise inhabits pine forests or cleared areas, where it commonly constructs burrows 30 feet or more in length. Such terrestrial chelonians are not adapted for swimming and normally shun water, aside from the moisture of the burrow. The temperatures of gopher tortoises taken immediately after capture ranged from 34° to 35° C. The individual used in the experiment was a small one, 10 cm. long or scarcely one-third the length of a full-grown specimen and considerably lighter in weight.

When placed in the thermal chamber this juvenile tortoise weighed 208.2 grams, and since it had been sunning itself in an outdoor cage the cloacal temperature was 36° C. at the beginning of its confinement. Part of the abrupt loss in weight (see fig. 11) during the first three hours resulted from the liquid expelled through the cloaca when the animal was overturned to permit insertion of the thermometer into the cloaca. Nevertheless moisture was lost at a rapid rate during the ensuing period until the twentieth hour of confinement when it abruptly began to diminish. After 40 hours in the chamber the head and feet were constantly withdrawn and the eyes were closed.

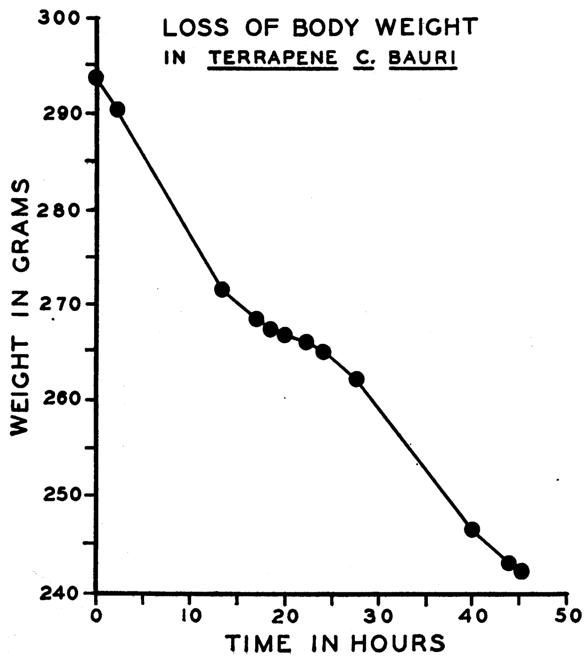

Fig. 9. Graph showing the loss of weight in an adult box turtle under experimental conditions of constant temperature and relative humidity.

Relatively little moisture was being lost after the seventieth hour, but after the seventy-fifth hour there was a marked increase before death followed 4.25 hours later.

Throughout the experiment the cloacal temperature of the tortoise, which fluctuated between 37° and 38° C., was very nearly that of the surrounding air. The difference between the means for the air and for the turtle are but 0.54° C., so that despite the loss of 63.2 grams, or 30.4 per cent of the original weight, very little lowering of the body temperature resulted. Moisture was lost at a mean rate of 0.42 per cent of the initial weight per hour for the full period of 79.25 hours.

It is probable, but uncertain, that the tortoise died as the result of desiccation rather than from the long exposure to an environmental temperature of 38° C. It is of interest to note in this connection that Miller (1932, p. 196) reports that, after drinking, the desert tortoise (*Gopherus agassizii*) increased in weight 41 to 43 per cent. If the weight lost by the gopher tortoise is calculated in terms of the percentage of the weight at the conclusion of 79.25 hours in the thermal chamber, the proportionate amount of water lost (43 per cent) is virtually the same as that ingested by the desert tortoise. It seems improbable, however, that the desert tortoise had no water in reserve at the time it was capable of drinking an amount equal to 43 per cent of its body weight, whereas the reserve in the gopher tortoise was presumably exhausted at the time the reptile died. The desert tortoise must rely upon infrequent rains before it can drink, and most of the water utilized is supposedly derived from plant material consumed. On the other hand, summer rains are frequent in the region inhabited by the gopher tortoise, and there is less need for conservation of moisture. Whether the desert tortoise can store more water than its peninsular relative remains to be determined experimentally.

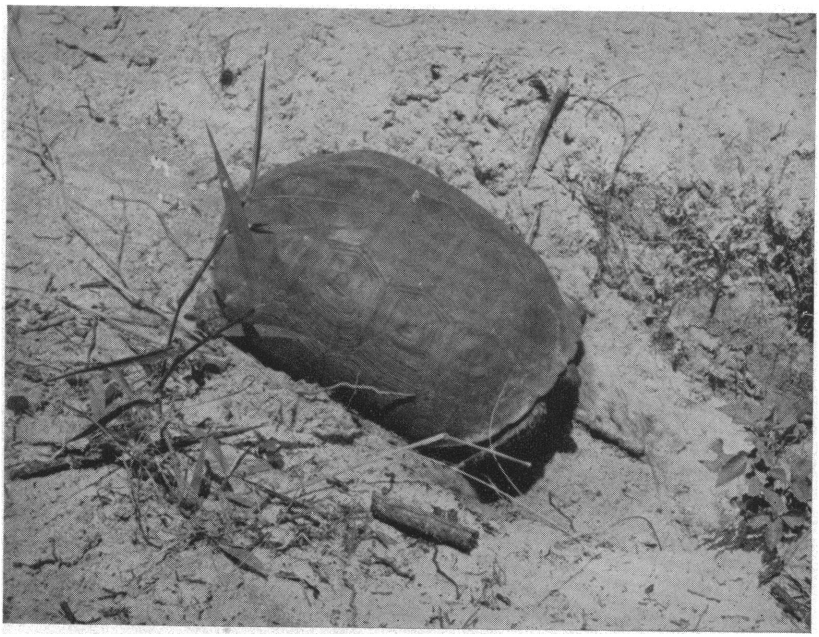

Fig. 10. The gopher tortoise, *Gopherus polyphemus*, a terrestrial chelonian of the species used in experiments. The photograph depicts an adult female, whereas a juvenile weighing 208.2 grams was used.

CROCODILIANS

The crocodilians, descendants of Triassic thecodont reptiles that also gave rise to the dinosaurs, are represented by 25 surviving species. All of them are essentially aquatic, inhabiting rivers, lakes, and estuaries, or even the oceans to a limited extent. For the most part they are confined to the tropics and subtropics, living in environments that presumably approximate those that were more widespread during the Mesozoic era. An alligator as well as a crocodile (*Crocodylus acutus*) occurs in Florida. The American alligator (*Alligator mississipiensis*), however, is more widespread and abundant in Florida. The closest living relative of the latter is the Chinese alligator (*A. sinensis*), with a restricted range in the vicinity of Shanghai, but the caimans of Central and South America are placed in the same family.

The American alligator is primarily an inhabitant of swamp-bordered streams, although it is found in virtually any aquatic situation, including brackish and even salt water. It ranges from the swamps of the Carolinas southward throughout Florida and westward along the Gulf Coast to the Rio Grande in Texas. At the Archbold Biological Station small alligators were seen in drainage ditches, roadside pools, and in small lakes, while large individuals inhabited Lake Childs, a few miles to the north.

Additional experiments of an allied nature were carried on with alligators, and these have been reported in a previous paper (Colbert, Cowles, and Bogert, 1946). For the purposes of this report only the data concerning moisture loss are presented, with additional notes not included in the previous work.

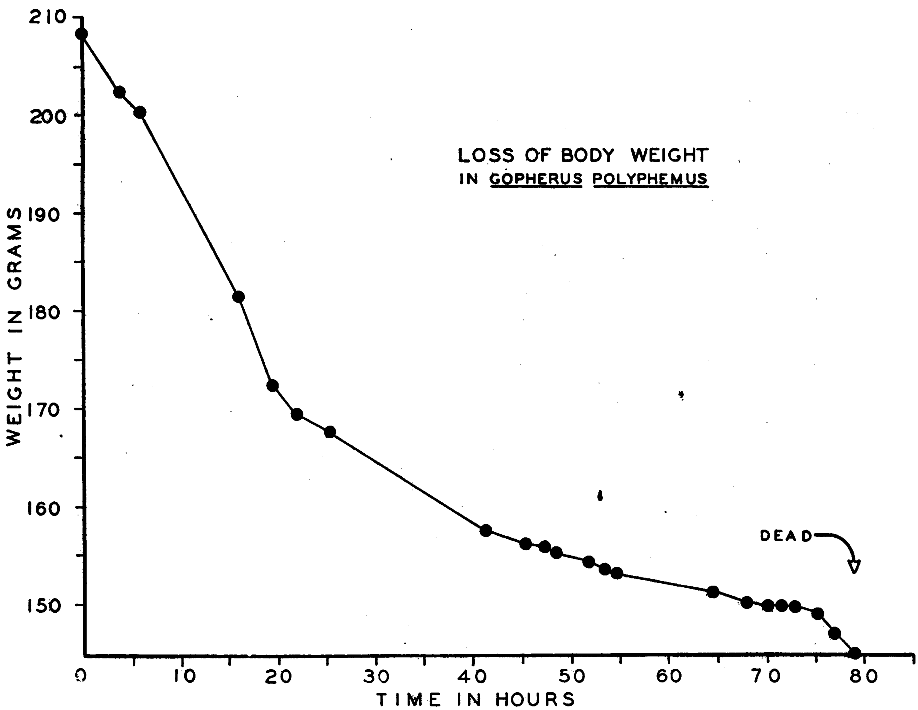

Fig. 11. Loss of weight in *Gopherus polyphemus* during 79.25 hours in the thermal chamber. Death ensued after 30.4 per cent of its initial weight had been lost.

Alligator mississipiensis (Daudin)

The alligator (fig. 12) used in these studies was a juvenile, 630 mm. in total length, that had been taken in a local drainage ditch a few days prior to its use. It was kept in the thermal chamber for two periods, first with the relative humidity in the chamber at 27 per cent, and three months later, in a second trial of shorter duration, with the relative humidity maintained at approximately 46 per cent. The temperature of the air in the chamber was the same in both instances.

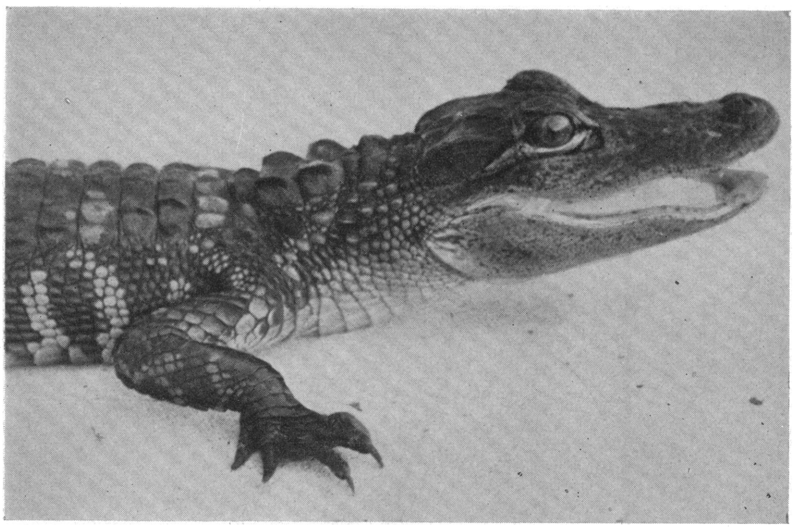

Fig. 12. American alligator, *Alligator mississipiensis*, juvenile individual used in experiments.

In the first trial the alligator weighed 668.1 grams at the beginning, but lost weight rather rapidly. The initial loss can be attributed to liquid expelled through the cloaca, but after five hours moisture was lost at a constant rate approximating 5.5 grams per hour (see fig. 13). In terms of the initial body weight the loss amounted to 0.83 per cent per hour for the 24-hour period. At the conclusion of the experiment this crocodilian had lost 133.5 grams, or 19.3 per cent of its original weight, and death undoubtedly would have resulted had the experiment been continued for many hours more. However, when removed from the chamber and placed in water, the animal ingested water immediately. Within half an hour it had taken in 28.7 grams of water, and after spending the night in a wet sink with a pan of water the weight had increased, at a somewhat slower rate, to 629.6 grams, within 40 grams of the initial weight. Three months later, when the second trial was begun, the weight had increased to 654.5 grams.

During the period that the alligator was in the chamber it remained quiescent with the mouth slightly open. Apparatus was not available to determine the respiration rate with accuracy, although it had undoubtedly increased. The body temperature fluctuated between 35.5° and 38.0° C., but remained above 37.0° after the first hour. The mean temperature for the period, exclusive of the first 15 minutes, was 37.0° C.

In the second experiment, with the relative humidity in the chamber at 46 per cent, the initial loss was not so rapid as it had been in the previous experiment, although the curve for the loss of weight (fig. 13) was similar in some respects to that for the first trial. With the increased humidity of the chamber during the second trial, however, moisture was lost somewhat less rapidly, at a mean rate of 0.52 per cent of the initial weight per hour for the 12-hour period. At the conclusion of the experiment, the alligator was removed from the chamber and placed in water, where it regained 33.2 grams during a period of 14.75 hours. It is of interest to note that the rate of recovery in water following the second trial, when the alligator was reduced in weight to only 613.2 grams, closely parallels that for the final stage of the recovery following the first trial. Evidently, therefore, the rate of moisture recovery is dependent upon the amount of desiccation.

Although in the second trial moisture evidently was lost at a somewhat slower rate, presumably because of the increased humidity in the chamber, the effect on the alligator's body temperature was relatively small. The mean temperature for the 12-hour period was 37.6° C., or 0.6° C. above the mean for the same alligator kept in the chamber when the relative humidity was 27 per cent. It may be observed that a body temperature slightly exceeding 38° C. represents the lethal for the American

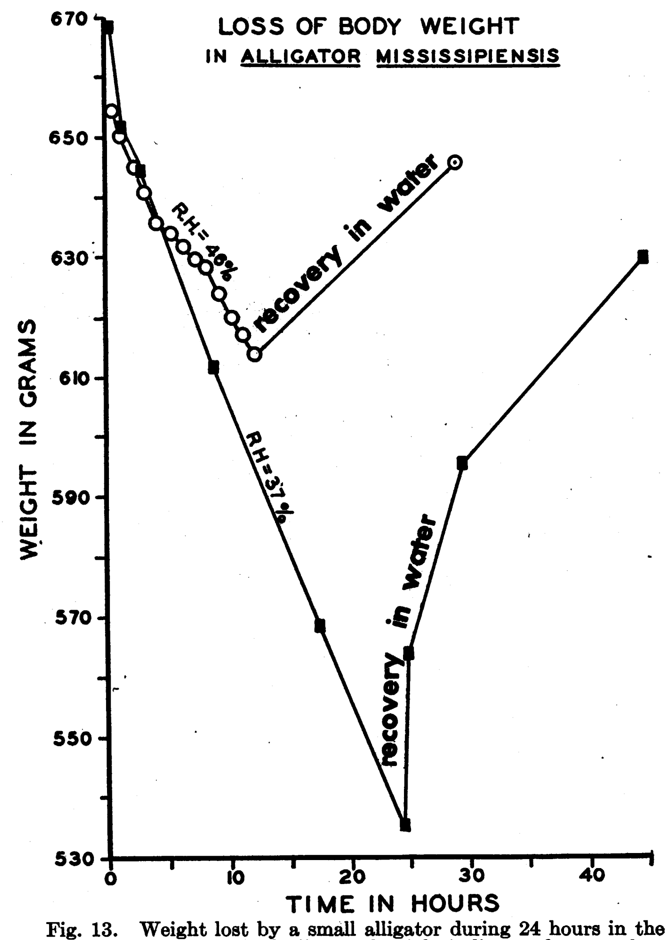

Fig. 13. Weight lost by a small alligator during 24 hours in the experimental chamber. The line at the right indicates the rate of recovery when the animal was placed in water.

alligator, so that in this instance the dissipation of body heat that accompanied the loss of moisture probably saved the animal from death. Under exceptional conditions in a natural state this margin of safety would have considerable survival value.

LIZARDS

The oldest fossils referred with certainty to the Suborder Sauria (lizards) are from the Jurassic, and most of the existing families are unknown from strata older than Cretaceous. As a group, lizards did not flourish until Tertiary times, when they began to occupy the varied habitats in which they are found today. The larger forms are confined to tropical and subtropical climates and relatively few species, most of them small, are found north of latitude 50° N. Lizards are absent from the summits of the higher mountains, except in the tropics, and whereas they occur in exceedingly moist climates they tend to be more abundant in arid or semi-arid regions.

The majority of the families include nocturnal or secretive forms, although others, notably the Iguanidae and Agamidae, are composed almost wholly of diurnal species. Arboreal, cursorial, as well as subterrestrial lizards have evolved in several family groups, and species representing intermediate states of specialization exist in many instances. All amphisbaenids are burrowing creatures, most of them limbless and with vestigial eyes. But among the Scincidae various species represent virtually every degree of specialization for a burrowing existence.

The terrestrial species, of course, were those most commonly seen at the Archbold Biological Station, but subterrestrial as well as arboreal lizards were occasionally taken.

Sceloporus woodi Stejneger

The scrub pine lizard is one of the few iguanids inhabiting Florida. The genus *Sceloporus* is more typically an inhabitant of semi-arid regions, although it enjoys a wider distribution than any North American iguanid. The *undulatus* group of the genus, to which *woodi* belongs, occupies most of the United States, although it is absent from the most arid portions of the country. *Sceloporus woodi* is an abundant cursorial species, with a range limited to the drier rosemary scrub in central and southern Florida. At the Archbold Station it was particularly common at Red Hill, nearly always on the ground at the edge of trails or cleared areas. When frightened it occasionally climbed a tree or a post, but more often it fled across the sand.

An adult male with a cloacal temperature of 36.6° C. at the time of capture had a body weight of 6.0 grams when placed in the thermal chamber. Although the cloacal temperature had risen to 37.4° C. when the animal was weighed 2.5 hours later, there

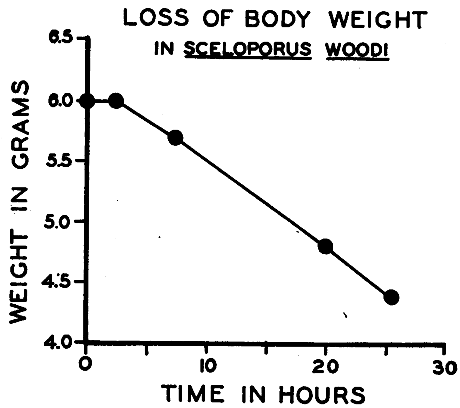

Fig. 14. Graph showing the water loss in the scrub pine lizard, *Sceloporus woodi.*

was not enough loss in weight to register on the balances used. At the time of the second weighing, 7.5 hours after the start of the experiment, the lizard had lost 0.3 grams in weight, and the body temperature had risen to 37.5° C. and remained near that figure for the duration of the experiment. Although the lizard was weighed only twice during the ensuing time that it was kept in the thermal chamber, the rate of moisture loss was apparently nearly constant at approximately 0.064 grams (or 1.06 per cent of the initial body weight) per hour. At the conclusion of 25.25 hours the lizard had lost 1.6 grams, or 26.7 per cent of its original weight. When liberated outside the laboratory, it immediately climbed the stucco wall. However, it was relatively slow in its movements and not nearly so agile as a lizard of the species that had been kept in the laboratory at room temperature for a similar period.

A smaller male weighing only 3.8 grams was placed in the thermal chamber under the same conditions, but it was removed after nine hours and ten minutes with the hind legs paralyzed, supposedly as the result of heat trauma. It died the following day. During the time it was in the thermal chamber it lost 0.4 gram in weight, or 10.53 per cent of the original weight, at a mean rate of approximately 1.14 per cent of its original weight per hour. The rate of moisture loss compares favorably with that recorded for the male weighing 6 grams.

To ascertain the effects of the same amount of heat with the humidity at a higher level, a female weighing 5.0 grams was kept in the thermal chamber. It remained inactive but could move rapidly when stimulated. Nevertheless it was dead 12 hours afterward, possibly from the effects of the temperature at which it had been maintained. *Sceloporus woodi* has been taken in the field with cloacal temperatures varying from 32.0° to 39.0° C. (the normal activity range), but the mean for 42 specimens is 36.2 ± 0.79° C. Undoubtedly the lizard can tolerate temperatures of 39° C. for short periods of time, and when heated rapidly death does not ensue until a cloacal temperature slightly exceeding 44° C. is reached. Nevertheless, prolonged exposure to body temperatures nearly 2° C. above the mean for the normal activity range may be sufficiently deleterious to cause death.

Eumeces inexpectatus Taylor

The Scincidae are virtually cosmopolitan in distribution, but far more abundant in the Old World, particularly in the Australian region, than they are in the Americas. Most skinks are terrestrial and secretive in habits, although many of them are burrowers. In general they are restricted to moist situations, and in the Americas they are absent from the deserts. Skinks are more abundant in eastern United States where the mean annual rainfall in most areas exceeds that for most of the region west of the Rocky Mountains. More than twice as many species of the family Scincidae are found east of the continental divide than occur in the territory to the west. In fact seven scincids occur in Florida, in contrast to six found in the entire Pacific drainage of the United States.

The common skink at the Archbold Biological Station was *Eumeces inexpecta-*

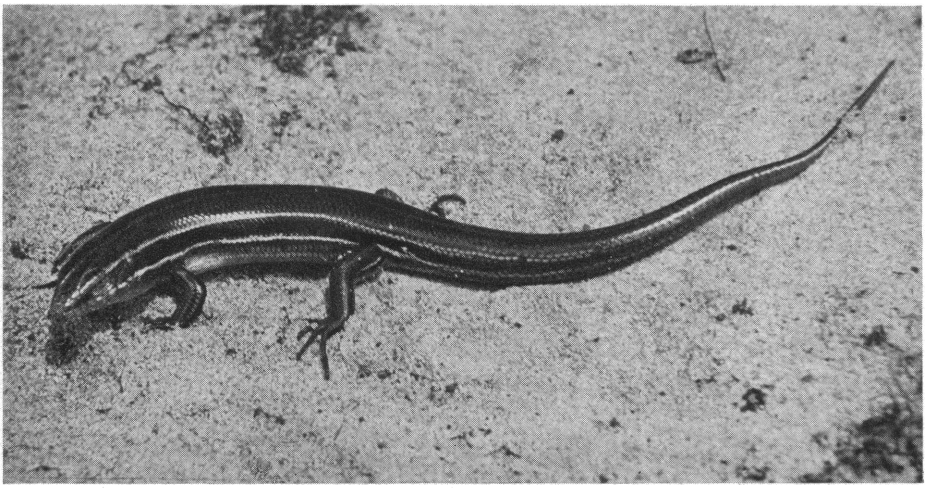

Fig. 15. The Gulf Coast skink, *Eumeces inexpectatus*, used in experiments.

tus, although it was neither abundant nor easily caught. Most individuals taken were found under boards, logs, or debris where there was plenty of moisture. These skinks were rarely seen abroad, although the largest individual obtained (weight 14.3 grams) was found while basking at periodic intervals at the entrance to a shed in a plant nursery located in Bear Hollow, a few miles southeast of the Archbold Biological Station. When captured this individual had a body temperature of 33.2° C. It was placed in the direct sunlight on a warm pavement where it reached the critical maximum (as defined by Cowles and Bogert, 1944) at 41.6° C. in five minutes, and subsequently recovered.

A skink weighing 4.5 grams was placed in the thermal chamber in an open container with the initial body temperature at 34° C. Thirty minutes later its temperature had risen to 37.0° C., but no loss of weight could be detected. After an additional hour the temperature and the weight were the same. When examined following 2.5 hours in the chamber the weight still had not dropped below 4.5 grams, but at the end of 3.5 hours the weight had decreased to 4.0 grams. The lizard was still alive when examined after 5.5 hours in the chamber, with the body temperature at 37° C. and a body weight of 3.7 grams. Sometime within the next 3.75 hours the animal died, although the weight was the same as when tested at the conclusion of the 5.5-hour period. The body temperature of the dead lizard had risen, however, to 38.0° C., that of the air and the container in the thermal chamber.

The curve for the loss of body weight in this specimen is peculiar, and it is unfortunate that no specimens were available to carry out additional experiments under similar conditions of temperature and humidity. Why weight was not lost during the initial 2.5 hours in the thermal chamber, but suddenly began to drop at the rapid rate of 0.5 gram per hour cannot be explained. The diminishing rate of moisture loss to a mean of 0.065 gram per hour for the next two hours can be attributed to the fact that relatively little moisture remained in the body, more especially since there was no further loss during the ensuing 3.75 hours during which the animal died.

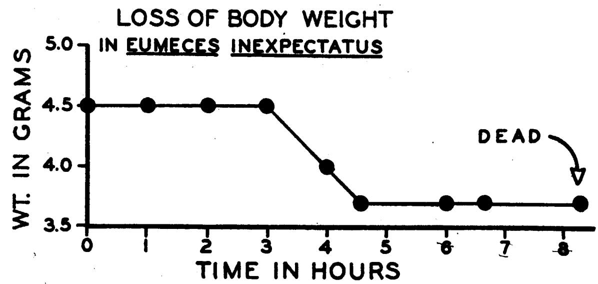

Fig. 16. Weight lost by the skink, *Eumeces*, under experimental conditions, with the environment maintained at approximately 38° C., and the relative humidity at 37 per cent.

Even though the data leave much to be desired, it is relatively certain that this skink loses moisture rapidly. For the purposes of comparison with other species, the total loss of 0.8 gram (17.5 per cent of the initial body weight) during the entire period of 8.25 hours in the thermal chamber indicates a mean loss of 2.1 per cent of the initial weight per hour under the conditions in which it was kept. Despite the fact that moisture was not lost at the beginning or at the end of the experiment, it is evident that this skink lost moisture at a more rapid rate than any reptile tested. The inability of most skinks to survive in containers when no moisture is readily available can be accounted for on this basis, and presumably the absence of skinks in truly arid environments or habitats can be attributed to their inability to retain water under such conditions.

In a second experiment a skink weighing 8.3 grams was kept in the thermal chamber in a can of wet sand. At the conclusion of 40 minutes its temperatures had risen to 37.5° C. and the weight had increased to 8.4 grams. After 1.5 hours the weight had dropped to 8.2 grams and the temperature had subsided to 37.2° C. However, an hour later it had risen again to 37.8° C., and when the lizard died after only 5.5 hours in the thermal chamber the body was still 37.8° C. and the weight had returned to the original figure of 8.3 grams.

It is of interest to note that the larger skink, under conditions where the humidity approached saturation, survived for a slightly shorter period than the smaller one in an atmosphere where the relative humidity was 37 per cent. Quite possibly the difference is the result of the lower body temperature that could be maintained by the lizard in the drier atmosphere. In the closed container the skink probably died from overheating, but in the open container high temperatures as well as desiccation were responsible. As noted above, this species can survive exposure to body temperatures as high as 41.6° C. for a brief interval, but body temperatures of 37° C. are undoubtedly above the normal activity range.

The fluctuations in the weight of the skink in the moist atmosphere suggest that moisture is absorbed or lost in some obscure fashion, even when the relative humidity approaches 100 per cent. The physiological aspects of the problem remain to be investigated.

Rhineura floridana (Baird)

The Florida worm lizard, as are the majority of the Amphisbaenidae, is completely fossorial. Ordinarily it is found when accidentally dug from the ground, although according to Carr (1940, p. 77) occasionally it is discovered beneath logs or leaf mold. Some of the larger South American amphisbaenids occasionally move about on the surface, and in Africa, at least, floods sometimes force them to abandon their subterranean habitats; if the water rises sufficiently high they drown in fair numbers. All members of the family are vermiform and, with the exception of three species (in a single genus known from western Mexico and the extreme southern portion of Baja California) that retain vestiges of the fore legs, they are limbless.

The four species in North America are clearly relicts, with ranges restricted to what Schmidt (1943) has termed "paleopeninsulae." Fossils from the Oligocene of South Dakota have been referred to *Rhineura*, although the genus is restricted

Fig. 17. The Florida worm lizard, *Rhineura floridana*. These lizards lose moisture rapidly when placed in dry sand, but absorb water when returned to moist sand, their normal habitat.

to the northern half of the peninsula of Florida at present. Representatives of the family reach their greatest abundance in Africa and South America, and most of them seem to prefer a relatively moist, tropical or semi-tropical climate. Presumably they are absent from southern Florida because of the periodical floods and the inadequate drainage that characterized the region prior to man's activities.

Carr (*supra cit.*) describes the habitat as "upland and mesophytic hammock; high pine; usually in dry soil." Contrary to Carr's impression, it seems likely that the characteristic habitat is moist soil, more often of sand where there is adequate drainage so that the surface may be dry. Land subject to periodic inundation is almost certainly an unsuitable habitat for such lizards; under laboratory conditions they do not survive in dry sand.

Only two specimens were secured at the Archbold Biological Station. Both of these were found when yams were being dug from very moist sandy soil near the summit of Red Hill. The day these were taken an adjacent plot of land was being plowed, and although a careful search of the furrows over two or three acres was made by following the plow, no *Rhineura* was discovered. The soil was slightly moist below the surface, but owing to the absence of larger plants there were no exceptionally moist pockets of earth in the plowed plot, whereas the yams in the adjacent garden apparently held more moisture in their root systems where the specimens were found. The tubers were but a few centimeters below the surface, and both lizards were dug from a depth, as nearly as could be estimated, between 10 and 15 cm. where the soil at that time of year (September 13) had a temperature approximating 32.5° C. The surface temperature slightly exceeded 60° C., and gradually diminished to 29° C. at a depth of 30 cm. Below that, at least to a depth of 70 cm., it remained virtually constant at 29.5° C., with a rise of 0.5° C. between the depths of 40 and 50 cm. Thus, by burrowing in the sand, the *Rhineura* could choose between environmental temperatures ranging from 29° to at least 50° C., although it is probable that temperatures much exceeding 35° C. were avoided.

Equipment to determine the weight with the accuracy required was not available at the Biological Station, so the two *Rhineura* were taken alive to New York City. Here one was placed in moist sand and the other in dry sand at room temperatures. The individual in dry sand was dead within 24 hours, evidently shrunken and desiccated. The other was kept in a large glass jar where there was some opportunity to observe its movements. The jar was filled two-thirds with sand sufficiently moist that the particles tended to adhere; the upper layer was dry sand. Although the lizard occasionally burrowed in the dry sand, there was no evidence that it ever came to the surface. More often it remained at the bottom of the jar at a depth of 20 cm., making a network of burrows in the moist sand.

The lizard was kept alive for a year, during which time it was observed to be active at temperatures between 20° and 38° C. It was fed on a diet of termites, and was observed feeding at temperatures between 18° and 35° C. At higher temperatures it remained inactive at the bottom of the jar, and finally died when the temperature of the moist sand rose to 41.5° C., even though it survived at this temperature for two days.

It was not feasible to experiment with the *Rhineura* under conditions where a constant temperature could be maintained, but the animal appeared to be ideal for the purpose of ascertaining whether moisture could be absorbed through the skin. The lizard was weighed on an analytical balance sensitive to $^1/_{20}$ of a milligram, and found to have a weight of 3.42 grams, when placed in a jar of dry sand at a temperature of 27° C. Two hours later the lizard was removed and weighed immediately. The weight had dropped to 3.29 grams, indicating a loss of 0.13 gram for the two-hour period. Fifteen minutes after removal from the dry sand the lizard was restored to moist sand at the same temperature as the dry sand. The following day, after 24 hours in the moist sand, the weight of the *Rhineura* had increased to 3.47 grams, slightly more than when first removed from the jar of moist sand. When the experiment was repeated on subsequent occasions very nearly the same results were obtained.

Under the same conditions of the experiment it is improbable that sufficient moisture was available in the sand to permit the lizard to ingest water by way of the mouth. Other lizards with forked tongues lap water with the tongue, but *Rhineura* appears to use the tongue solely for the purpose of picking up odorous particles to be carried to the organ of Jacobson. Following each thrust of the head, as the lizard forced its way through the soil, the head was raised and slightly withdrawn to permit the tongue to be used. Whether directed by olfactory or auditory cues, the lizard, with amazing accuracy, managed to direct itself to the clusters of termites that had tunneled into the sand from the surface. When water was poured in a burrow, however, the *Rhineura* invariably retreated, and demonstrated no desire to drink. Hence there is reason to assume that the increase in weight following desiccation in dry sand can be attributed to the absorption of moisture through the skin.

The results of this experiment are, of course, not comparable to those derived from keeping lizards in the thermal chamber at constant, higher temperatures. *Rhineura* was omitted from figure 23 for this reason. Nevertheless it is instructive to note that in dry sand at temperatures approximating 27° C. the worm lizard lost moisture at the rate of 0.065 gram per hour. The reptile was not kept in dry sand for periods exceeding two hours, but if moisture had been lost at a steady rate, the original weight would have been decreased 35 per cent within a 24-hour period. The lizard presumably would have perished as a result.

At the same time that *Rhineura* was being tested in dry sand a specimen of the California limbless lizard, *Anniella pulchra*, was made available through the kindness of Mr. Charles M. Miller. During 24 hours in dry sand the original weight of this lizard decreased but 6.5 per cent. In moist sand the weight increased from 4.415 to 4.435 grams after 24 hours. Thus moisture appears to be lost or absorbed through the skin of *Anniella*, but not so rapidly as in *Rhineura*. Presumably these differences are reflected in the nature of the habitats in which the lizards live. *Anniella* is most commonly found in relatively moist situations in a semi-arid, mesothermal climate with a summer deficiency in rainfall, whereas the range of *Rhineura* is restricted to regions having a sub-humid, mesothermal climate, with a rainfall distributed throughout the year, and a total rainfall about thrice that of coastal southern California where *Anniella* is most abundant.

SNAKES

Snakes are essentially specialized lizards that evolved from the same platynotid stock that gave rise to the modern Varanidae. It is not impossible that some of the families independently evolved from other saurian stocks. There are few fossils to trace the ancestry of the families currently included in the Suborder Serpentes, and with only recent material from which to draw conclusions the relationships of some of the groups are uncertain. Although snakes are derived from saurian ancestors, the evolution of snakes and lizards evidently was almost coetaneous, since fossil serpents begin to appear in the late Mesozoic, whereas those belonging to modern progressive stocks do not appear until the Oligocene.

Except for a few islands, snakes occur in most parts of the world where the subsoil is not permanently frozen. Evidence thus far assembled indicates that snakes, on the whole, prefer somewhat lower body temperatures than lizards. In temperate climates, as well as in the tropics, many species tend to be nocturnal or crepuscular in habits.

About 20 kinds of snakes are known to inhabit the land surrounding the Archbold Biological Station, but only a few of the diurnal species were at all abundant. The three found in sufficient quantity to permit their use in experiments all belong to the family Colubridae, and the species used are not distantly related.

Drymarchon corais couperi (Holbrook)

The indigo snake inhabiting Florida is one of several races belonging to a species with a range extending from southeastern United States into South America. In the United States the indigo snake is restricted to the Atlantic Coastal Plain, from the Carolinas southward throughout Florida, and westward along the Gulf Coast to Texas. *Drymarchon* is absent from the Mexican Plateau, but its range extends along both coasts of Mexico, into Texas on the east, and into the moist barrancas of southern Sonora on the Pacific coast. It may occur in some of the barrancas north of the Rio Fuerte drainage in southern Sonora, but without doubt it is absent from the arid coasts of the state in the Colorado Desert.

In Florida *D. c. couperi* inhabits several types of terrain, but Carr (1940, p. 83) reports that it is most abundant south of Lake Okeechobee near the lower end of the peninsula, where it is often plowed from the damp soil of truck fields. The indigo snake is rarely encountered at the Archbold Biological Station, although it is not uncommon along the borders of Lake Childs a few miles to the north. It is one of the largest snakes inhabiting the United States, sometimes attaining an over-all length in excess of 7 feet.

A rather small specimen weighing 368.5 grams was placed in the thermal chamber where its initial body temperature of 26.9° C. rose to 37.5° C. within two hours, but occasionally dropped to as low as 36.0° C. before the snake was removed at the conclusion of 9.5 hours. During this period of time the snake lost weight at an exceedingly rapid, but slowly diminishing rate, losing moisture to the extent of 46.2 grams at a mean rate of nearly 5 grams (1.3 per cent of the original weight) per hour. When removed from the thermal chamber and placed in a laboratory cage, the snake was abnormally sluggish in its movements, and it died within seven hours.

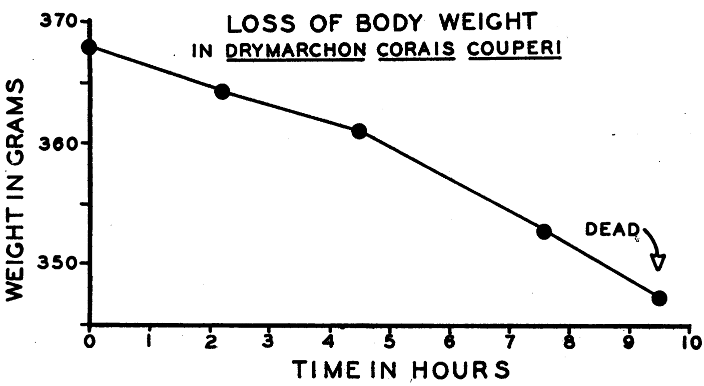

Fig. 18. Graph showing the rapid rate of moisture loss in the indigo snake, *Drymarchon corais couperi*, under experimental conditions. The snake died a few hours after its removal from the thermal chamber after 9.5 hours of exposure to virtually constant environmental temperatures of 38° C., with the relative humidity at approximately 37 per cent.

A larger snake, weighing 1247.4 grams was placed in the thermal chamber, even, though it was obviously about to shed its skin. This specimen survived slightly more than five hours and weighed but 1036 grams when removed after death. The shorter period of survival undoubtedly resulted from the rapid loss of moisture under such circumstances, and the experiment tends to confirm the observations of Benedict (cited in the Introduction) who noted the increased rate of moisture loss prior to ecdysis. A few days before sloughing, captive snakes commonly seek water, and in a natural state they are usually found in some moist sanctum during similar periods.

Keepers in zoological gardens are well aware of the snake's requirements under such conditions, and it is a common practice to cover large pythons with moist towels at such times. Whereas keepers usually regard the process as one of "soaking the skin loose," it is obvious that snakes must resort to some means of avoiding the rapid desiccation to which they are subject during ecdysis. Manifestly a snake can prevent the loss of moisture through the skin by immersing its body, or by seeking a moist environment.

The snake in normal condition that survived for 9.5 hours in the thermal chamber presumably died as the result of desiccation, even though it lived nearly twice as long as the larger individual about to cast its epidermal covering. A snake weighing 388 grams, with an over-all length of 1145 mm., was placed in direct sunlight on a substratum with a temperature approximating 45° C. Within 10 minutes it became uncoördinated in its movements when its cloacal temperature reached 42.2° C. However, this individual recovered, so it is apparent that body temperatures somewhat higher than those reached in the thermal chamber can be withstood for periods of short duration.

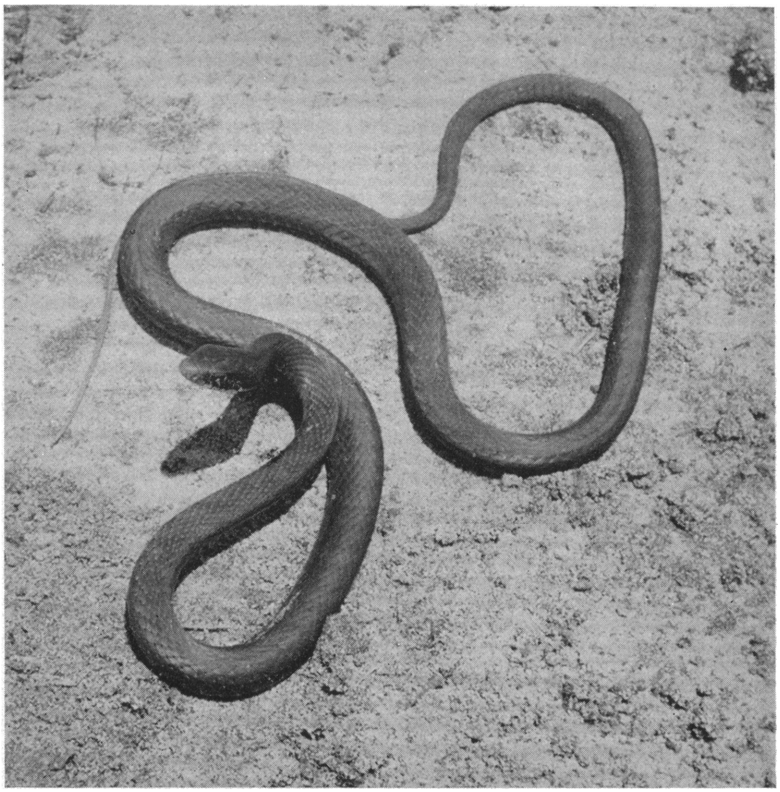

Fig. 19. The common black snake of Florida, *Coluber constrictor priapus*, one of the few reptiles that occurs in nearly every habitat in the state.

Coluber constrictor priapus Dunn and Wood

The common black snake found at the Biological Station is the peninsular race of a wide-ranging species found throughout most of the United States, although it is absent from the higher mountains as well as the deserts. In the extreme Southwest it is confined to an area on the Pacific slope where it occurs in scattered localities, principally in relatively moist valleys. An old record for the species from Fort Buchanan in a relatively arid portion of Arizona is undoubtedly erroneous despite its acceptance by Ortenberger (1928, p. 219).

The black snake was the most abundant serpent in the vicinity of the Archbold Biological Station, and specimens were seen or taken in virtually every habitat represented. Specimens used in preliminary experiments were found to be exceedingly hardy, unless they were approaching ecdysis. Only one healthy specimen in normal condition was kept in the thermal chamber until death ensued, although others were kept there for shorter periods. In terms of the percentage of the original weight lost per hour there was relatively little variation in several specimens tested, and for the purpose of this report the details of one experiment will suffice.

A large adult male weighing 535.9 grams was placed in the thermal chamber with an initial body temperature of 27.2° C. The temperature of the snake had reached 37.4° C. within an hour, and for the ensuing period during the experiment the recordings indicated extremes in body temperature of 37.5° to 38.0° C. The snake was found to be dead at the conclusion of 99.5 hours after having lost 57.1 grams, or 24.7 per cent of its initial body weight. As may be seen in figure 20, the weight of the snake declined at a nearly constant rate of 0.56 gram (0.25 per cent of the original body weight) per hour, and yet managed to survive for over four days.

When placed in direct sunlight on a warm day, four of these snakes reached the critical maximum at temperatures of 43, 44, 44, and 44.5° C., respectively, and all of them subsequently recovered. Evidently, therefore, the black snake can withstand slightly higher temperatures than the indigo snake. Moreover the latter loses moisture five times as rapidly as the black snake under conditions as extreme as those maintained in the thermal chamber. The advantage this gives to the black snake is apparent from the fact that it survived 10 times as long as the indigo snake under laboratory conditions, with the relative humidity at 37 per cent, and the air as well as the cage at 38° C.

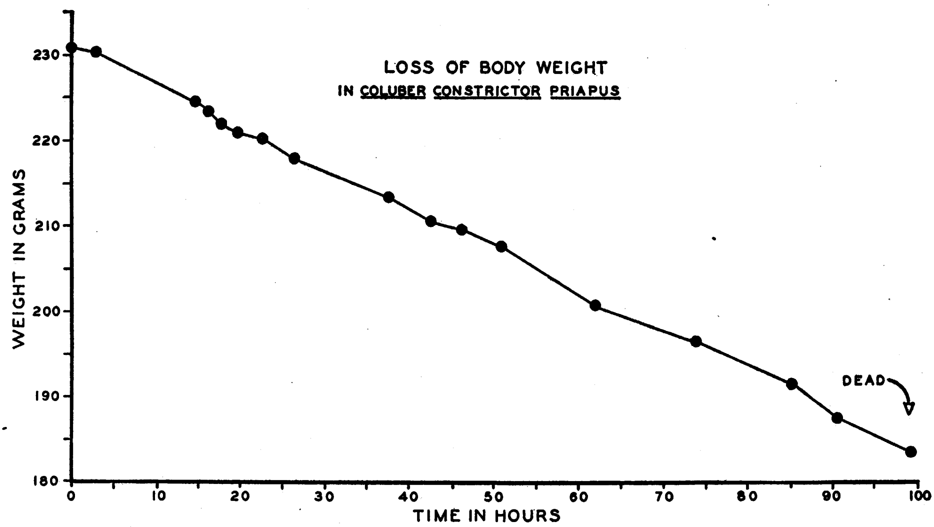

Fig. 20. Graph showing the relatively slow rate of moisture loss in the black snake, *Coluber constrictor priapus.*

Coluber flagellum flagellum (Shaw)

The coachwhip snake of Florida is a member of a species that ranges from the Atlantic to the Pacific in middle North America, occupying the valleys throughout most of the area between latitude 40° N. and the Tropic of Cancer. The eastern race, *C. f. flagellum*, is found from the Carolinas to southern Florida, and westward to the ninety-seventh meridian where it is replaced by *C. f. testaceus* in the less humid plateau region of central United States and northern Mexico. The southwestern race, *C. f. piceus*, is found in coastal as well as desert regions.

In Florida the coachwhip snake is less abundant than the black snake, and seemingly prefers somewhat more arid habitats, "high pine, rosemary scrub and dry flatwoods," according to Carr (1940, p. 81). Two specimens captured at the Biological Station were available for experiments, one taken in the spring and the other near the end of the summer. Both specimens were extremely resistant to desiccation, as the following notes will indicate.

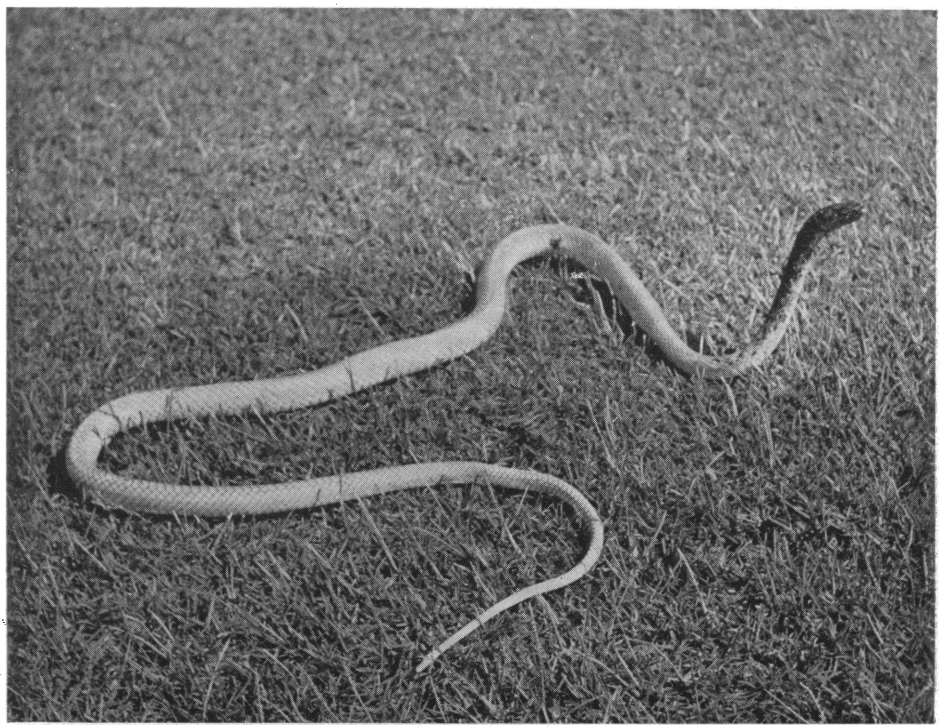

Fig. 21. The eastern coachwhip snake, *Coluber flagellum flagellum*, a snake that prefers dry habitats. This adult male was the hardiest of 10 reptiles subjected to the extreme conditions of the thermal chamber. It was alive after 99.5 hours of exposure to an environmental temperature of 38° C., with the relative humidity at 37 per cent.

The first specimen was captured with a body temperature of 32.6° C. When placed in the thermal chamber the snake weighed 535.9 grams, and its body temperature was 33.4° C. Forty-five minutes later its temperature had risen to 38° C., that of the thermal chamber. During the ensuing 46.25 hours the snake was weighed 10 times, and the cloacal temperature was obtained 12 times. Weight was lost steadily but slowly (see fig. 22) as compared with other reptiles tested, at a mean rate of 0.74 gram (only 0.14 per cent of the initial body weight) per hour.

The second specimen tested (no. 2 on fig. 22) was an adult male that weighed 655.0 grams at the beginning of the experiment. As did the previous specimen, it lost weight slowly but steadily, with a temporary decrease in the rate between the fortieth and forty-fifth hours, and a second drop in the rate after the ninetieth hour. The snake was still alive when removed at the conclusion of 99.5 hours, but the body was rigid and the snake had difficulty crawling when it was liberated.

After being subjected to 99.5 hours in the chamber, with the relative humidity at 37 per cent and the air, as well as the cage, at 38° C., the snake had lost only 73.8 grams (11.3 per cent of the initial body weight). Throughout the experiment only minor fluctuations in the cloacal temperature were detected. The temperature of the animal reached 38.0° C. within three hours, and remained there most of the time, rarely dropping (four occasions out of 14 that the cloacal temperature was recorded) to temperatures between 37.5° and 37.9° C.

It is significant that the relatively slow rate of desiccation was reflected in the higher body temperatures, even though these were but a few tenths of a degree Centigrade above other reptiles tested. The coachwhip snake was the most resistant to desiccation of the reptiles maintained in the thermal chamber, and it is unfortunate that no records of the critical maximum were obtained. A few data are available for the desert subspecies, *Coluber f.*

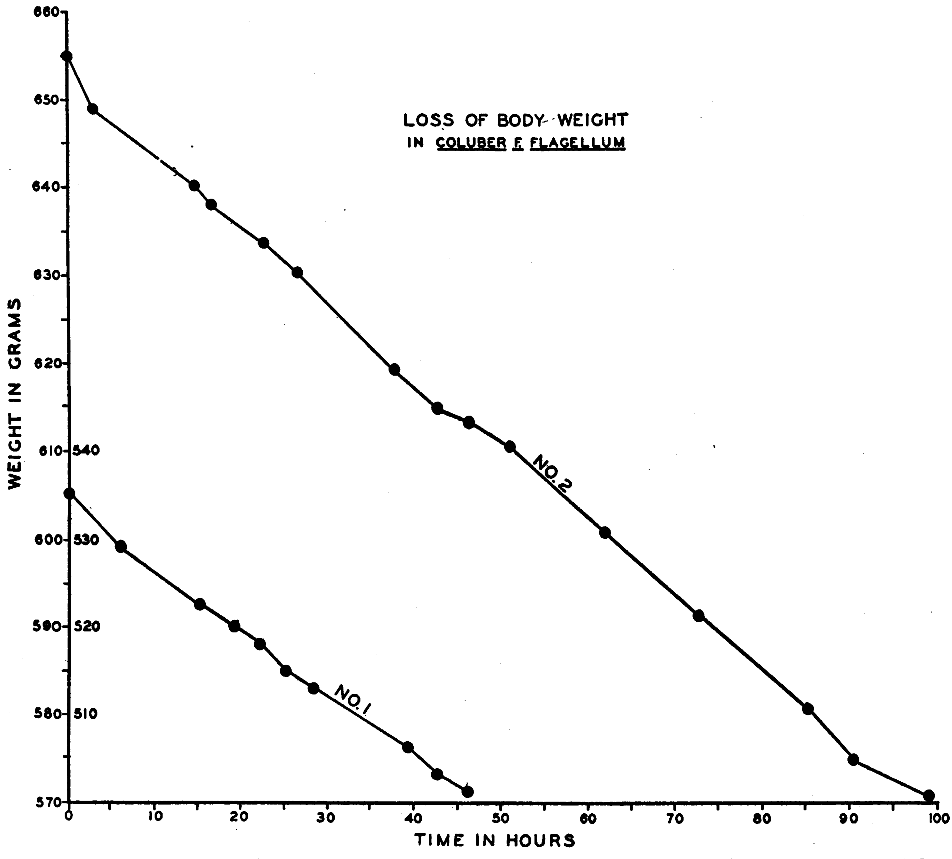

Fig. 22. Graph showing the remarkably slow loss of weight by two coachwhip snakes, *Coluber flagellum flagellum*, subjected to the extreme environmental conditions of the thermal chamber.

piceus, body temperatures of which reach 46° C. or even 47° C. before the reptile dies. Few other snakes tested thus far are able to survive when the cloacal temperature reaches 44° C., and many are killed when the body temperature reaches 40° C. Therefore, there is some indication that *Coluber flagellum* is better adapted in this respect for a hot, dry environment than are other serpents. More data are needed to demonstrate satisfactorily that the species is better equipped for survival in arid regions than are other diurnal terrestrial snakes, but the information available is suggestive.

Rapid locomotion is an element of importance in the existence of snakes living in deserts, since they are able to move from one source of shade to another before body temperatures reach the critical maximum. Rodent burrows, rock crevices, or shrubs provide protection from solar radiation, as well as a cooler substratum. If the snake can move from one retreat to another with sufficient rapidity, it is possible for it to be abroad during the day in desert regions where shelter is relatively sparse. In the Colorado and Mojave deserts *Coluber f. piceus* is the only snake ordinarily seen in daytime during the summer months. Other serpents inhabiting the same region are forced to estivate, adopt a subterranean existence, or become either crepuscular or nocturnal in habits during the warmer months.

Whether the subspecies of *Coluber flagellum* that occurs in the southwestern deserts is better able to resist desiccation than the eastern race remains to be determined. In desert regions snakes must rely almost entirely upon the moisture content of their prey, in lieu of water, inasmuch as rains are infrequent and highly irregular throughout the deserts. Hence it is of utmost importance that a diurnal terrestrial animal be able to conserve moisture, and it is apparent that *Coluber flagellum* is better equipped to do so than other snakes that have been tested.

DISCUSSION

It is generally recognized that animal life is not equally distributed, and that various habitats or biotopes can be distinguished, each with its characteristic soil, climatic conditions, vegetation, and its animal community. Moreover, it has become apparent that some animals are restricted to one sort of biotope, whereas others are not so exactly adapted and may occur in divers environments. Carr (1940), in his extremely useful paper on the herpetology of Florida, recognizes over a score of habitats in his analysis of distributions in the state. Each of these habitats, Carr shows, has its characteristic species, but others occur therein either frequently or occasionally. One animal may be abundant in one habitat and uncommon or absent in another. Thus the scrub pine lizard, *Sceloporus woodi*, is "confined to the earliest stages in dune succession—rosemary scrub or treeless dunes," and its distribution is necessarily discontinuous. The indigo snake, *Drymarchon corais couperi*, occurs throughout Florida, in a variety of biotopes, but is most abundant south of Lake Okeechobee where the substratum is more often moist. Finally, a few species are virtually ubiquitous; such reptiles as *Coluber constrictor priapus* are so widely distributed that it is difficult to say where they are most abundant.

It is evident, therefore, that there are varying degrees of restriction to one or more habitats. In most instances it is possible to do little more than speculate concerning the factors that limit individual species in their choice of biotopes, unless they are confined to caves, to sand dunes, or to other highly specialized environments. Even in such exceptional cases the nature of the restraining factors is not always apparent. An animal living in desert sand dunes may be quite unable to survive in dunes along the ocean because the sand in the latter is not sufficiently fine, or because the thermal requirements of the animal cannot be met. Another animal may live in caves, but it may be restricted to limestone caves, or a flowing stream and a moist atmosphere, coupled with air temperatures of definite extremes, might be additional requirements.

In some instances animals seemingly have become so specialized in their feeding habits that their existence in a given habitat may be dependent upon the presence of suitable prey. Carr (*supra cit.*) reports that only crayfish (*Cambarus fallax*) were found in the stomachs of over a hundred specimens of the mud snake, *Liodytes alleni*, that he examined. It does not follow that *Liodytes* is restricted to marshes, bogs, and sloughs where the crayfish is found, but evidence might be assembled to demonstrate such a limitation.

One factor or another may limit the choices of habitat open to an animal, and it is probable that more often the selection is dependent upon several elements of the environment. As a corollary, the distribution of an animal in turn is dependent upon historical factors as well as the vagility of the species, that is, upon its ability to overcome barriers, whether these be physiographic in a strict sense, or climatological barriers that in many instances are associated with topographical features. Some of the endemics in the peninsulas of Florida, Mexico, and Baja California perhaps are confined to these southern extensions of the North American continent because they cannot tolerate the cold winters of the mainland to the north. Regions with low rainfall are obstacles to the dispersal of some species; distributional data for reptiles and amphibians suggest that many amphibians and reptiles are restricted in their east-west dispersals by the southwestern deserts.

Climatic conditions on each side of the Gulf of California are similar, yet less than half of the species found in Sonora are known to occur in Baja California. Those common to the two regions are principally species that have been able to invade the intervening deserts north of the Gulf. Approximately one-fifth of the amphibians and reptiles found in Sonora are tropical forms. These appear to be confined to the moist barrancas in the southern portion of the state. Seemingly they have failed to penetrate Arizona because of the relatively arid conditions that prevail in the lowlands in northern Sonora and southern Arizona. High temperatures as well as low humidity may be the inhibiting factors in some instances.

By means of controlled experiments it is possible to gain some notion of the validity of such speculations. The experiments carried out at the Archbold Biological Station were designed to measure the amount of moisture lost under conditions that would permit comparisons of the species tested. Undoubtedly the artificial environment maintained in the thermal chamber was more extreme than that ordinarily encountered by Floridian reptiles. Air temperatures of 38° C., with the humidity at 37 per cent, are often encountered in arid regions, however, and commonly the surface of the substratum exceeds 50° C. in deserts as well as in Florida. Reptiles living under such environmental conditions, of course, are not normally subjected to such extremes for prolonged periods. It has been pointed out elsewhere (Cowles and Bogert, 1944) that through their activities, their behavior, and posture, reptiles are able to control the body temperatures and to maintain them within relatively narrow limits. Only under extenuating circumstances are reptiles unable to seek the necessary shade of burrows, rock crevices, or other places of refuge where temperatures tend to be lower and the humidity is likely to be higher. Reptiles inhabiting regions with scanty vegetation and no outcrops of rock may be forced to burrow into the soil to attain the same ends. On the other hand, species living in aquatic situations supposedly are rarely subjected to high temperatures owing to the thermal capacity of water. Only in times of drought would they find it difficult to maintain sufficiently low body temperatures.

Few aquatic reptiles are strictly confined to water. Indeed some of them can make journeys of some length over dry land, even though such travel more often is carried on during or following heavy rains. Terrestrial species, however, supposedly would find it less difficult to undertake migrations, since land habitats are continuous, whereas aquatic situations, whether they be streams, ponds, lakes, or marshes, are invariably disjunct. Reptiles able to endure the high body temperatures that result when the temperatures of the substratum as well as that of the air are high, and when water is not available, would be expected to be less inhibited in their migrations and their dispersals than other reptiles. Consequently it is of interest to ascertain whether any correlations exist between a species' ability to survive the high temperatures and the low humidity of the thermal chamber, and the choice of habitat. Any correlations that exist supposedly would be reflected in the ranges of the species.

If extreme cases are considered there appears to be a measure of truth in this supposition. It is noteworthy that the one skink (*Eumeces*) tested lost moisture at an extremely rapid rate and survived for the shortest period of any animal tested. Lizards of the genus *Eumeces* are notably absent from the more arid regions of the United States. In contrast, the coachwhip snake, *Coluber f. flagellum*, which survived longest in the thermal chamber and lost moisture at the slowest rate, is the Floridian race of a species that ranges throughout the southern portion of the United States, inhabiting deserts as well as less arid terrain. In such regions as the Gulf Coast the coachwhip snake seemingly prefers the drier habitats, avoiding dense woods and moist situations. Moreover, *Coluber flagellum* is one of the few reptiles that ranges from coast to coast in the United States. Relatively minor morphological differences serve to separate the subspecies, but it is conceivable that there are more pronounced physiological differences; the subspecies *C. f. piceus*, inhabiting the deserts, may be even more resistant to dehydration than its Floridian relative.

It is evident, nonetheless, that *C. flagellum* has encountered few barriers in its east-west dispersal. The range of *Coluber constrictor* is less readily interpreted upon the basis of the results obtained in the experimental chamber. Whereas this snake was not quite so resistant to desiccation as *C. f. flagellum*, it was capable of surviving the extreme conditions of the thermal chamber for a prolonged period. Its hardiness is reflected in its wide distribution in Florida, but in the western portion of the United States the species does not occur in the truly arid regions. It is found as far north as Canada, while *C. flagellum* is restricted to the southern half of the United States, ranging barely north of latitude 40° in Nevada. The distributional data suggest a somewhat lower temperature preference for *Coluber constrictor*, which would explain its absence from the deserts despite its ability to resist desiccation. *Coluber flagellum* is normally active only when its body temperature lies between 27° and 35° C., and it will voluntarily tolerate 37° C. on occasion (Cowles and Bogert, 1944, p. 284), but there are no data available concerning the activity range of *Coluber constrictor*.

The third species of snake tested, *Drymarchon corais*, survived the extreme conditions of the experimental chamber for a relatively brief period and lost weight at an extremely rapid rate. These results offer some explanation for the abundance of the indigo snake in moist habitats, and because such habitats are more abundant in coastal plains, the restriction of the range of the species to the coastal plains of the United States can be attributed, in part at least, to the physiological requirements of the species. Thermal factors supposedly prevent the indigo snake from ranging north of the Carolinas, and the temperature extremes, as well as the aridity of the Mexican Plateau, may be responsible for the restricted range of *Drymarchon* in Mexico. The aridity of the land bordering the Colorado River in the Southwest presumably antedated the western dispersal of the species; had *D. corais* succeeded in reaching California or Baja California it is probable that colonies would have survived in some of the moist localities.

Regardless of historical factors, however, there is evidently a rough correlation between the preferred habitats of the three snakes tested and the ability of each to withstand the extreme conditions of the experimental chamber. *Drymarchon*, with a marked preference for a moist substratum, survived the shortest period and lost weight rapidly. The ubiquitous *Coluber constrictor* was relatively hardy, but not so well able to resist desiccation as *Coluber flagellum,* a species that prefers the most arid habitats available to it in Florida.

In terms of their moisture requirements one snake can apparently be compared with another. But it is doubtful whether the reptiles of one group can be compared with those in other groups. It is manifest, easily be detected by histological examination, and Noble and Mason do not state how they arrived at their conclusion.

The results of the experiments described above demonstrate that when the rate of loss is expressed as a percentage of the body weight, some snakes lose water much more slowly than any of the four turtles tested. The horny layer of the epidermis of chelonians, particularly of *Gopherus,* is thicker than it is on any of the snakes used in ex-

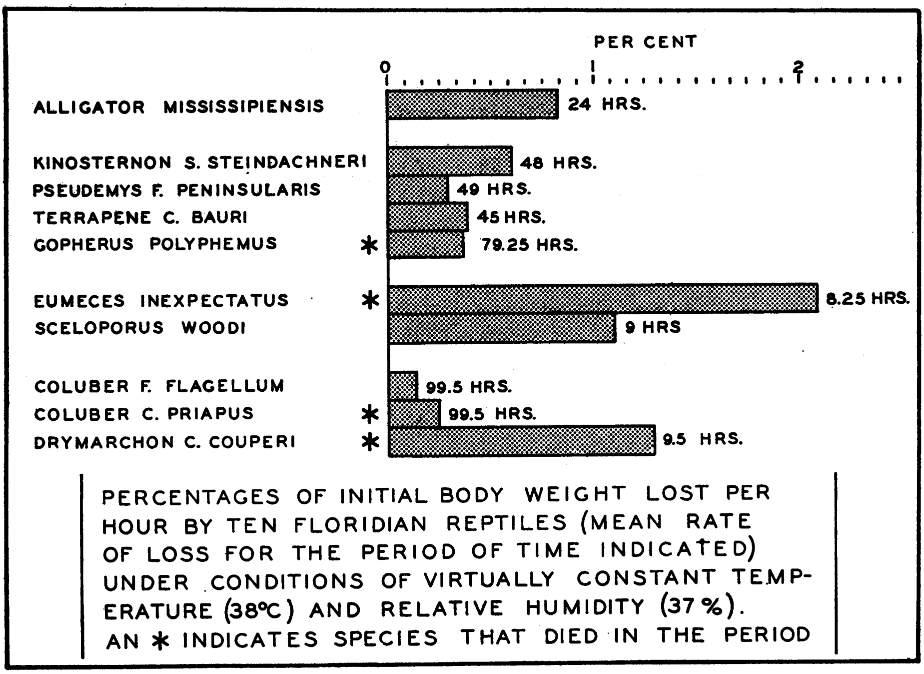

Fig. 23. Comparisons in the rate of moisture loss (in terms of the percentage of the initial body weight lost) of 10 species of Floridian reptiles used in experiments.

for example, that the surface area per unit weight is much less in turtles than it is in snakes. Moreover, since moisture is lost through the lungs as well as through the skin, the extent of the area of the lung surface would have to be taken into account. Noble and Mason (1932) report that there is little correlation between water loss and skin structure, except that the most impervious skins are provided with the thickest horny layer. It is doubtful, of course, whether physiological differences could periments. Since the surface-volume ratio is considerably higher for snakes than it is for tortoises, it is a fair assumption that, as far as the lungs or the skin is concerned, there are physiological differences between the two types of reptiles. Because the relationships between moisture loss and habitat selection involve such factors it seems preferable to confine comparisons to species in one order or suborder. Even though the two lizards used in experiments were taken in the same habitat (they sometimes occur side by side), the skink (*Eumeces*) is not ordinarily seen moving about except in heavily shaded areas. Usually it is found in moist places under logs, boards, or decaying plant material, whereas the scrub pine lizard (*Sceloporus*) is abroad in open areas throughout the day. The amphisbaenid (*Rhineura*) was not tested under similar conditions, but its seeming inability to venture to the surface and its restriction to moist sand are quite in keeping with the fact that it died within a few hours when kept in dry sand at room temperature.

Turning now to the turtles it is instructive to note that the species (*Kinosternon subrubrum*) that lost water most rapidly is among the most aquatic of Floridian turtles, and that it is rarely seen on land. It lost moisture in the experimental chamber much more rapidly than the terrestrial *Gopherus*, and *Terrapene*. Not so easy to explain is the hardiness of the *Pseudemys*. The "cooter" is essentially an aquatic turtle, even though it often wanders about on the land. This ability to remain on land for prolonged periods may account for the wide dispersal of the genus. Few groups of chelonians are quite as widespread in North America, although *Pseudemys* is surpassed in a few respects by *Kinosternon*, some species of which are also given to semi-terrestrial habits. *Gopherus* in Florida has recourse to its moist burrows, and *Terrapene* commonly buries itself in humus or beneath the roots or overhanging branches of shrubs during its inactive periods. *Pseudemys* apparently relies upon its ability to reach water before seeking protection from desiccation.

As a group, turtles are probably resistant to dehydration in spite of the fact that relatively few species are completely terrestrial. The persistence of turtles since the Mesozoic, despite their conservative evolution, may perhaps be attributed to their structural peculiarities; their compact bodies and their cornified exteriors may have evolved in response to other requirements, but thus equipped the turtle was able to survive climatic changes that led to the extinction of the dinosaurs and decimated the crocodilians.

The American alligator is the only member of its group that could be tested, but it is readily apparent that an animal of such proportions must have frequent recourse to water if it is to survive. A creature that within 24 hours loses 20 per cent of its body weight under conditions maintained in the thermal chamber is manifestly not suited for conditions that prevail in arid regions. Permanent water and shade and an adequate food supply are conditions that could readily be met only in a moist, semi-tropical region. Only along the Gulf Coast in the United States do such conditions prevail. The arid regions in western Texas with little cover and high summer temperatures are doubtless an insuperable barrier to crocodilians.

Audova (1929) suggests that during the transition from the Paleozoic to the Mesozoic reptiles may have suffered from increasing dryness. Nopcsa (1924) before him had indicated that increasingly arid climatic conditions had been a major factor in the extinction of the dinosaurs. However, both Nopcsa and Audova, as well as the majority of the paleontologists, have attributed widespread extinctions to a general lowering of the temperature. Cowles (1939, 1940, and 1945) disagrees, pointing out the susceptibility of present-day reptiles to high temperatures.

Audova intimates that primitive reptiles were more thermophilic than modern reptiles, but this statement is not borne out by recent investigations. Contrary to widespread notions the highest environmental temperatures are not encountered in the tropics, but in the so-called temperate zone. The reptiles inhabiting moist tropical climates are less able to withstand high temperatures than those of the arid regions; the few data available indicate that lower temperatures are preferred by reptiles living in the tropics. Noteworthy in this respect is the restriction of existing giant reptiles to tropical or insular environments where they are not subjected to extremes of temperature. The tuatera (*Sphenodon*), a relict of an ancient group, survives only in the islands around the Bay of Plenty off the coast of New Zealand in a relatively cool but moist climate.

Thus increasing aridity coupled with greater extremes of temperature seems to have driven the more primitive reptiles into moist habitats, either in the tropical or semi-tropical regions, or to insular habitats where the climate is tempered by the thermal capacity of the surrounding water. Crocodilians and marine turtles, the largest reptiles in existence, must have survived when other gigantic reptiles became extinct because their moisture and thermal requirements were more readily met in an aquatic environment. Bulk evidently is disadvantageous to ectothermic terrestrial animals subjected to extremes in temperature, if for no other reason than the difficulties that a large animal encounters when it must seek shelter.

Although the body temperature of reptiles is depressed somewhat as a result of water loss, it is doubtful whether the cooling from evaporation is of great ecological importance under ordinary conditions. Under extenuating circumstances respiratory cooling undoubtedly has survival value. But the relatively slow rate of dehydration characteristic of terrestrial and arboreal reptiles under field conditions must be of far greater importance in that it enables them to survive periods of deficient rainfall. Similarly the reptile's ability to absorb moisture through its skin obviates the necessity for drinking during periods when water is otherwise inaccessible. The forms that live in dry environments are able to do so, not because they can absorb water, but because they do not lose it rapidly.

SUMMARY

Ten species of Floridian reptiles were subjected to nearly constant environmental temperatures of 38° C. in an experimental chamber in which the relative humidity was maintained at a level approximating 37 per cent. An additional species, a subterrestrial lizard, was subjected to wet and dry sand at room temperatures. The experimental animals were weighed at periodic intervals during their exposure to such extreme environmental conditions, and those that survived were returned to a moist environment and weighed again. A few reptiles maintained in the thermal chamber in closed containers with wet sand in the bottom lost no weight so that it could be relatively certain that loss in weight represented a loss of moisture.

CONCLUSIONS

1. Under similar environmental conditions there are marked differences between various species of reptiles in their ability to resist desiccation.

2. Aquatic reptiles or those that habitually live in damp sites lose moisture at a more rapid rate (in terms of the percentage of their original body weight) than those commonly found in dry habitats. There is therefore a definite correlation between habitat selection and the ability to resist desiccation.

3. Although the Floridian race of each wide-ranging species was the only one tested, a rough correlation was found to exist between the ability of representatives of the species to resist desiccation and the vagility of the species, particularly when comparisons are restricted to species belonging to one major group.

4. The reptiles tested with reference to the phenomenon are able to absorb moisture through their skins when in moist sand, and lose moisture when in dry sand. Immediately prior to ecdysis the rate of moisture loss in snakes is greatly accelerated; death results if they are subjected for relatively brief periods to environmental temperatures of 38° C., with the relative humidity at 37 per cent.

5. The evolutionary implications of moisture loss in relation to habitat selection are discussed, and it is suggested that increasingly arid climatic conditions during

the transition from the Paleozoic to the Mesozoic may have been a factor of importance in the extinction of the dinosaurs. However, distributions of the largest existing reptiles imply that increasingly high (rather than low) temperatures can more readily account for such extinctions, despite the beliefs of competent paleontologists. The most primitive existing reptiles tend to prefer moist environments where moderately low temperatures without great extremes prevail.

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