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EXPERIMENTS ON THE BROODING HABITS OF THE LIZARDS *EUMECES* AND *OPHISAURUS*

By G. K. Noble and E. R. Mason

The brooding habits of *Eumeces fasciatus*, the blue-tailed skink, have been frequently described. Smith (1882), Brimley (1904), Ditmars (1904), Strecker (1908), Allard (1909), Hurter (1911), Ruthven (1911), Dunn (1920), Blanchard (1922), Brady (1927), Burt (1928), Corrington (1929), and Klots (1930) have had brooding females under their observation. Ruthven, who has given one of the most complete accounts, remarks in regard to the female and her eggs: "As is well known she remains with them until they are hatched, but for what purpose is not evident." Neither Ruthven nor the many other observers who have had brooding *Eumeces* before them have attempted experiments that might throw light on this purpose. No information is available as to the nature of the brooding response or its rôle in the economy of the species. The brooding habit is more widespread in reptiles than is usually assumed, but no one has attempted to determine whether reptiles can recognize their own eggs or even distinguish them from eggs of closely allied forms. We have studied the brooding habits of a series of *Eumeces fasciatus* and *E. laticeps* with a view to securing an answer to these questions. We have had two brooding *Ophisaurus ventralis* available for comparison and have noted various differences between the brooding of these and other reptiles.

THE EGGS OF *EUMECES*

Eumeces fasciatus has been reported to lay from 2 to 15 eggs. The smaller clutches were laid in captivity. Ditmars (1904) found that females shipped to New York deposited from 2 to 4 eggs under strips of bark. Klots (1930) describes a female as laying 2 eggs in the container where it was held captive. Strecker (1908) reports the finding in the field of several sets, each set consisting of 8 eggs, and Hurter (1911) records that a female laid 8 eggs in captivity. Corrington (1929) gives 10 to 15 as the egg-number for brooding females captured in the field in South Carolina. In western Tennessee Blanchard (1922) found a female with 9 eggs and also two females, each with a lot of 10 eggs. Ruthven

(1911) has collected several sets of eggs in Michigan and remarks in regard to the species:

"The number of eggs in the set was counted in eight instances and were as follows: 6, 6, 8, 8, 9, 11, 13, 14. An examination of the pregnant females shows that the number in each set varies with the size (age?) of the female, the smaller ones having 6 to 8 eggs, the larger ones 9 to 14."

The other records of the eggs of *E. fasciatus* fall within this range. Smith (1882) reported 9, Allard (1909) 7, Dunn (1920) 12, Burt (1928) 6, 9, 9, 9, 9, 10, and 11, and Netting (1930) 9. It is barely possible that the unusual number of 15 mentioned by Corrington may represent the laying of two females. We shall show below that if two brooding females have their nests in juxtaposition one may appropriate some of the eggs of the other.

There were only 5 eggs in the clutch described by Brimley (1904). Some of the variation in egg-number recorded above may be a consequence of abnormal conditions in captivity resulting in a reduction of the number of eggs laid, but it is also possible that the authors were considering different species. The *Eumeces fasciatus* of most authors has recently been resolved into three species (Taylor, 1932), and we have no assurance that all of the authors were describing the same form.

We have had ten females of *Eumeces* lay their eggs between damp fragments of decaying wood in the laboratory (Fig. 1). Three of these, collected in Biloxi, Mississippi, are referable to *E. laticeps*, while the others from Garnett, Anderson County, Kansas, we consider typical *E. fasciatus*. The latter average less than 10 grams in total weight, while the former group averages more than twice as much. Two of the *E. laticeps* laid 6 eggs and the other 7. Six of the *E. fasciatus* laid from 5 to 8 eggs each. This agrees well with the egg-number reported by Brimley and by Strecker. The other *E. fasciatus* deposited only 2 eggs as in the case of Klots' captive specimen. The average number of eggs laid by our series of *E. laticeps* and *E. fasciatus* is 6 for each species. The related *Eumeces anthracinus* has been reported to lay 8 eggs (Gloyd, 1928) and *E. skiltonianus*, 5 eggs (Woodbury, 1931). The American species of *Eumeces*, so far as known, do not show any constant differences in the number of eggs laid.

Our specimens of *Eumeces* were received from Kansas and Mississippi. They laid in the laboratory earlier than the Michigan specimens described by Ruthven. He writes:

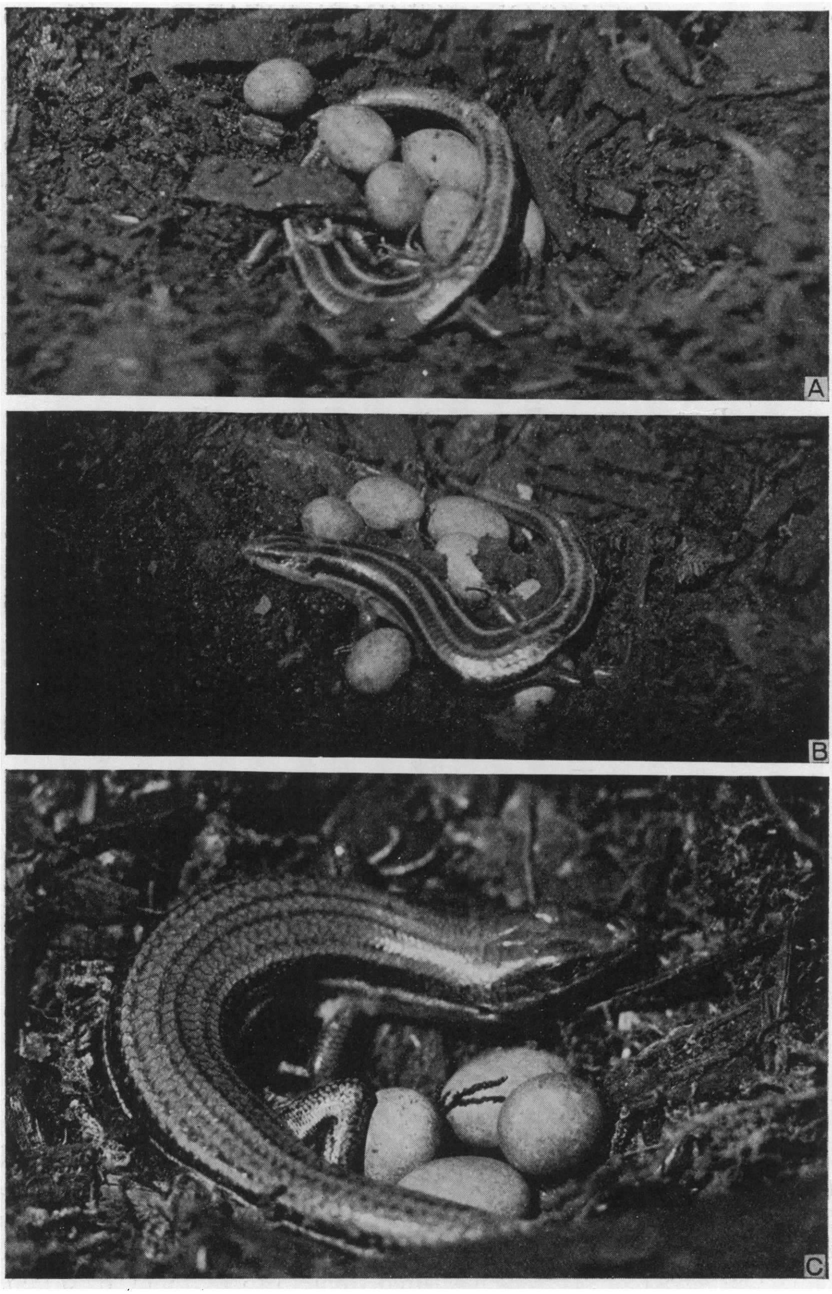

Fig. 1. Brooding postures of *Eumeces.*

A. *Eumeces fasciatus* female digging under the eggs while encircling them with her tail; B. *Eumeces fasciatus* brooding female partially assuming the S-shaped posture; C. *Eumeces laticeps* female beginning to brood her eggs.

"Females taken on June 19 were pregnant, containing large eggs apparently nearly ready to be laid. The first sets observed were on July 2, and on and after this date nests of eggs were found in numbers. Everything went to show that the eggs are mostly laid about the first of July."

Our data on the egg-laying of *Eumeces* in New York may be expressed in tabular form:

	Laid		Hatched				
	Date	Number	Date	Number	Notes	Per Cent Hatched	Incubation Time
E. fasciatus							
♀ II	May 23	5	July 9	4	1 egg died	80	47 days
♀ A	May 27	8	July 5	7	1 defective jaw	87.5	39 "
♀ III	May 31	7	July 5	6	1 died hatching	85.5	35 "
♀ C	June 6	5	July 9	5		100	33 "
♀ B 2	June 6	8	July 5	5	3 eggs died	62.5	29 "
♀ IV	June 13	6			3 shellacked; 2 lost in exp.; 1 died	....	..
♀ D	June 20	2	July 17	2		100	27 "
Average		6				86	35
E. laticeps							
♀ I	May 23	7	July 18	1	6 eggs died	14	56 days
♀ 3	May 27	6	July 5	4	2 eggs died	67	39 "
♀ E	May 28	6	July 15	4	1 shellacked; 1 died hatching	80	48 "
Average		6				54	48 "
Total Average						75	

Our eggs of *Eumeces fasciatus* measured 13 by 7 mm. when laid, and they increased in size until at the time of hatching they were from 19 to 21 mm. by 12 to 12.5 mm. Brimley (1904) records the eggs of *E. fasciatus* ready to hatch as measuring 20 by 12 mm., 20 by 15 mm., and 22 by 11 mm. Our eggs of *E. laticeps* measured from 15 to 18.5 mm. by 9 mm. when laid. They increased in size during development until they attained the size at hatching of 17 to 20 mm. by 12 mm. From these data it is clear that the eggs of *E. laticeps* are distinctly larger than those of *E. fasciatus* at the time of laying, but before hatching the eggs of the latter species have swollen to the size of the former. We endeavored to maintain the eggs under identical conditions of moisture. Hence the more rapid increase in size of the *E. fasciatus* eggs would appear to be due to a more permeable eggshell.

Although we are not concerned in this paper with the hatching or early life of these skinks, it is of interest, in passing, to note certain differences in size between the young of the two species. It might be assumed that if the eggs were the same size the young at hatching would also be the same size. This, however, was not the case. In our series the eight young *E. fasciatus* that were measured at hatching were 23, 23,

Fig. 2. Hatching of *Eumeces fasciatus*, July 9, 1932.

24, 24, 24, 24, 25, and 25 mm. long, respectively, from snout to vent. Their average length was 24 mm. The five young *E. laticeps* that were measured at hatching were 25, 25.5, 26, 27.5, and 30 mm. long from snout to vent. Their average length was 26.8 mm. At the time of hatching, the difference in head- and body-length as between *E. fasciatus* and *E. laticeps* was slightly less than 3 mm.

The hatching is accomplished by the sharp egg-tooth. This is formed of a single, elongated premaxillary tooth having its distal third bent forward nearly at a right angle to the tooth-base. The young seldom remained more than a few hours near the collapsed shells (Fig. 2), but since their nests were frequently disturbed, it is possible that they may remain together for longer periods in nature. One female in our series remained on the nest with young for over two days after they were hatched.

We supplied the young lizards with a large quantity of young larvae of the wax moth (*Galleria mellonella*) and assumed that the subsequent growth of the young skinks was normal. From our present point of view it is interesting to note that the young of *E. laticeps* grew more rapidly than did those of *E. fasciatus*. This may be considered as further evidence of distinctness of the species.

There are various differences in proportion between the young of the two species. This is expressed in tabular form on the opposite page.

Aside from the differences in proportion, there is a distinct difference in size as between the two species. The five *E. fasciatus* that were preserved within a week after hatching average 23 mm. in head- and body-length. If the young one that died in hatching be included in the series, the average is only 22.5 mm. A series of twelve young *E. fasciatus* not included in the above table averaged 24 mm. in head- and body-length when approximately a month old. The young one nearly two months old, recorded in the table, had grown to 28 mm. in head- and body-length. In contrast to these measurements, the young *E. laticeps* on hatching is approximately 3 mm. longer than is *E. fasciatus*. At one month it is approximately 4 mm. longer, and at two months, 5 mm. longer. The growth rate of *E. laticeps* is obviously greater than that of *E. fasciatus*. This probably accounts for the marked difference in size between the adults of the two species.

Taylor (1932) was aware of the fact that differences between the young of *E. fasciatus* and *E. laticeps* would probably be found on hatching. However, the youngest specimens available to him appeared to be older than he suspected. At least the measurements of our timed series would indicate that a specimen of *E. fasciatus* 26 mm. in head- and body-length was not just hatched but actually from one to two months old. Similarly we would assume a 35 mm. specimen of *E. fasciatus* was from three to four months old, and a 30 mm. specimen of *E. laticeps* was about five weeks old. It is, of course, possible that young *Eumeces* grow more rapidly in nature than in the laboratory, but we have no information on this point. Since we have given the young of both species an abundance of food, the difference in growth rate cannot be due to differential feeding.

	Eumeces fasciatus								*Eumeces laticeps*			
	7/5 ♀ A At hatching Defective jaw	7/6 ♀ III Died while hatching	7/7 2 days old	7/12 ♀ II 3 days old	7/11 B 6 days old	7/15 ♀ II 6 days old	8/1 23–27 days old	9/2 55–59 days old	7/18 ♀ E Died while hatching	8/16 29–32 days old	9/2 46–49 days old	9/6 50–53 days old
Head to Vent	23.5	20	23	23	22	22.5	23.5	28	25	28	33	33
Axilla to Groin	11	10	11	11	11	11	12	13.5	10.5	14.5	17	16.5
Width of Head	4.5	5	5	5.25	4.75	5	5	5	5.5	5.75	6.5	7
Length of Head	6	6	6	6.5	6.5	6.5	7	7	8	8	8	9
Width of Body	4	4	4.75	4.5	4	5	4	4	5.5	5	5.5	6
Hind Leg	10	9.25	8.75	8.5	9.5	11	10.5	11.5	13	12	15	16.5
Postanal Tail Width	2.5	2	2.5	2.5	2.25	2.5	2.25	2.5	3	2.5	2.75	3
Hind Foot	5.5	5	5.25	5	5.5	6	6	6.5	6	7.25	7.5	8

Measurements in millimeters.

NATURE OF THE BROODING RESPONSE

Our series of gravid *Eumeces laticeps* and of *E. fasciatus* were isolated in separate cages. The bottom of each cage was strewn with damp, decaying wood, and a number of pieces of bark were laid over this. Finally a thick covering of moss was placed over the bark. Most of the females laid their eggs in the damp wood debris beneath the bark, but a few did not avail themselves of this covering.

Once the eggs were laid, most of the females remained with them, even when the bark was gently lifted. At such times the female would be found with part of her body in contact with her eggs (Fig. 1B). There appeared to be no definite position assumed by the brooding female. There were, however, three very characteristic postures. Her body was either curved in a semicircle around the periphery of the clutch of eggs, or it formed an S-shaped figure extending between them, or it was straight and lay either over or between the eggs. Although the females remained for long periods with the eggs, we were very much interested to find that they leave them voluntarily on occasions. At certain times of the day the females were found on top of the moss. These observations, frequently repeated, clearly indicate that the female normally leaves her eggs in search of warmth or food. As we shall see later, this is of great importance in aiding the incubation of the eggs.

On returning to her nest, the female invariably touched one or more of the eggs with her tongue or thrust her snout between them and partly turned over several of them. Frequently her mouth was held slightly open during this turning process, and on two occasions, we saw a female lift an egg from the ground in her mouth and gently place it in a new position. These observations were made on partly or fully exposed nests. We have no information as to how long the adjusting process continued in a fully covered nest. Whether the nest is exposed or covered, the female invariably moves the eggs and brings them together into a compact group if they are scattered. Hence we may assume that this nosing and turning of the eggs proceeds the same way in both the covered and exposed nests.

The brooding females not only returned to their nests any of their own eggs which had been scattered, but also added to their nest nearby eggs of other *Eumeces*, both *laticeps* and *fasciatus*, whether or not the eggs were of the same size. This reaction was tested eleven times. If the eggs were merely outside the nest, they were pushed in with the snout after being tested with the tongue. If the eggs were 4 or 5 cm. away, and there were more of them, they were slowly moved by the animal's wending in and out, over and under them, moving and rolling them in the direction of the nest, as well as by pushing with the snout. Moving a number of scattered eggs into a compact group was a matter of hours, while merely returning a stray egg was in terms of minutes. We have one record of an egg's being moved back to the nest a distance of 4 cm. in less than one minute. Three eggs in a row, spaced 5 cm. apart, were rolled together in forty-six minutes. Since *E. fasciatus* reacted exactly the same toward the eggs of *E. laticeps* as it did toward the eggs of its own species, it is clear that the brooding response is not specific but may be induced by the eggs of other species of the same genus.

Ruthven (1911) noted that "there seemed to be a disposition on the part of the female to keep her set together; several times I saw a female leave her position and crawl about the eggs, and when she encountered one which I had displaced, lick it and then nose it back to the others." Our observations on exposed nests have shown that the female takes far greater care of the eggs than has been previously assumed. She not only returns stray eggs but turns over a large percentage of the eggs in the nest before settling down to brood them. Either the tongue or the snout is used to turn an egg, more frequently the latter.

Reptiles that bury their eggs naturally do not return to roll them over. Hence reptiles, as a group, differ in general from birds in that they do not turn their eggs. In fact, Halver (1931) finds that turning the eggs of *Lacerta* injures the vascular system of the embryos. This is obviously not true of *Eumeces*.

The female *Eumeces* returns at frequent intervals to her eggs. In salamanders it has been shown (Noble and Evans, 1932) that females can find their eggs even when these are placed in new localities. We were interested in testing the ability of *Eumeces* to find and identify her own eggs. Fourteen times we moved the eggs of seven females to a new locus in the cage, or to a place in a new cage in which the female had not been previously. Each time the female succeeded in finding them during the following night, if not before. We have several records of her finding them in from three to four hours. In those cases in which it was possible to observe the actions of the female, it was seen that she first returned to the old locus and investigated with her tongue and snout various objects in this place. In no case did she settle down in the old nest but invariably moved on until she found her own eggs in the new locus.

It seemed possible that we might induce *Eumeces* to brood the eggs of other genera of lizards. Both *E. fasciatus* and *E. laticeps* were tested with the eggs of *Ophisaurus* and of *Sceloporus*. As shown in the photographs, the eggs of these genera are very similar to those of *Eumeces* (Fig. 3). Nevertheless *Eumeces* responded toward them exactly as toward other foreign bodies in the nest. We performed ten experiments with the eggs of *Sceloporus u. undulatus* and five with those of *Ophisaurus ventralis*. In four of these, the foreign eggs were placed in the female's nest, and her own eggs put into a new locus in the cage, and once both sets were given new loci. When the nest was exposed, the females were seen to return, and feces indicated that they returned also to the covered nests. However, in no case did the female remain in her old nest with the foreign eggs. She was always found brooding her own eggs in their new locus. Twice the *Eumeces* eggs were entirely removed from the cage

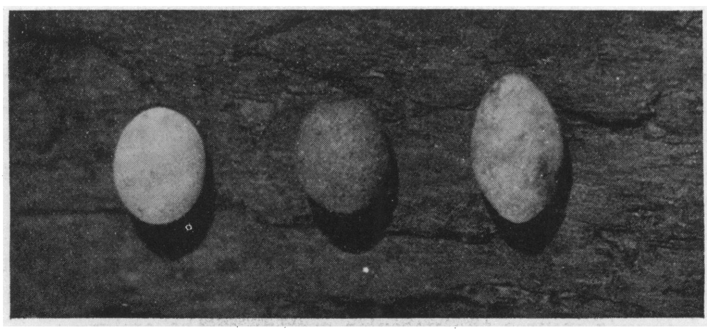

Fig. 3. Eggs of *Sceloporus undulatus* (left), *Eumeces laticeps* (center), and *Ophisaurus ventralis* (right). *Eumcees* can distinguish between these three eggs and will brood only eggs of her own genus.

and only the foreign eggs left. Even in the absence of available eggs of her own, she did not brood the other eggs, although the presence of feces showed that the female had investigated the nest. When her own eggs were returned to the nest, she brooded them.

Eight other tests made with the *Ophisaurus* and *Sceloporus* eggs, three with the former and five with the latter, consisted in attempting to have the *Eumeces* add these eggs to her nest along with scattered *Eumeces* eggs, which, as stated above, she invariably collected into her nest. The usual procedure of the female *Eumeces* with both the *Sceloporus* and *Ophisaurus* eggs was to investigate them with a single touch of the tongue and then to disregard them totally. Once when a rejected *Ophisaurus* egg was forced into an exposed nest, the *Eumeces* female bit the egg and broke the shell.

The question arose as to whether or not it was the odor that enabled the *Eumeces* to recognize their own eggs and reject others. Paraffin models of *Eumeces* eggs were made. These placed in a nest were never brooded by the females, nor were they added to the nest when placed near at hand. They were touched by the female with her tongue and discarded. Secondly, shellacked *Eumeces* eggs were tried. Half of the eggs of one female, three in number, were shellacked and put into her nest. The female did not brood them, although she did return to the nest and examine and move them. The three good eggs were placed 8 cm. from the shellacked eggs in the evening. The next morning, the female had collected them and was brooding all the eggs in the nest. The two groups were separated and moved to new loci. The female was not seen to brood either group and did not move them together again, although both had apparently been nosed and rolled. Shellacked eggs were tested on another female to see if she would add them to her nest. She always rejected them with one touch of her tongue whereas during the same tests she rolled normal eggs back into the nest. It is clear from these experiments that *Eumeces* will not brood artificial eggs made of paraffin nor usually her own eggs if they have been shellacked. Our one case of a female's brooding shellacked eggs may be accounted for by the fact that the female had previously rolled them about, for they had collected some dirt and possibly some of the shellac had been rubbed off.

The nostrils of two females were filled with stopcock grease and then with a combination of cotton and stopcock grease in an effort to eliminate the sense of smell from the finding and recognition of their eggs. Each time the plugs were inserted, they were removed by the animal by pressure from within and rubbing from without. Although some grease probably remained adherent, the results cannot be taken as conclusive. It may be noted, however, that the females did not return to their nests during this time.

The female *Eumeces* were blindfolded with adhesive tape which in turn was painted with "opaque" such as is used in photographic work. This tape eliminated the eyes as a means of locating and recognizing the eggs. This experiment was tried five times. Each time the female found and brooded her eggs, even when the eggs had been moved to a new locus. The record time for a blindfolded female's return to her nest, which had not been moved, was fifteen minutes. These experiments showed that the eyes were not necessary for the female to locate, recognize, and brood her eggs.

The end of the tongue above its forked tip was cut from the last female with unhatched eggs, who was a constant brooder. The tongue was cut in the morning. The female did not return to her eggs the rest of that day or on the next day. She did not seem disturbed but went about moving the tongue stump in and out in the usual manner. Previous records indicated that, even if the animal was disturbed one day, she would return to the nest by the following morning. Hence the failure to return after removal of the tongue tip appeared to us to be significant. This one record is by no means final, but taken together with the way the tongue was used by all the *Eumeces laticeps* and *E. fasciatus* in recognizing their own eggs and discarding artificial ones, it is evident that the tongue plays an important rôle in the location, identification, and turning of the eggs.

Although the tongue has this important rôle in brooding, it does not follow that the taste buds are the chief receptors of the stimulations received from the eggs. The recent work of Kahmann (1932) following upon that of Baumann (1929) has clearly shown that the primary function of the long forked tongue of snakes is to carry odorous substances to Jacobson's organ. Many lizards have tongues closely approximating those of snakes. Some species, such as *Varanus varius*, can find hidden food (Berg, 1913). Snakes have been known to swallow stones that had been used as nest eggs (Holt, 1919). Apparently the odor of the brooding bird clinging to the stones called forth the feeding responses. Since eliminating the nares of snakes does not prevent the normal prey-seeking habits while destruction of the Jacobson's organs does, it is clear that Jacobson's organ is the primary receptor of the chemical sense utilized in food-seeking. It was our intention to repeat Kahmann's experiments on the brooding *Eumeces*, but our material was not sufficient to permit more than the experiments outlined above. These experiments, although few, clearly show that discrimination is accomplished not by the eye but by the tongue. In view of this work and Kahmann's experiments with Jacobson's organ in snakes we may conclude that *Eumeces* depends chiefly on her Jacobson's organ in finding and identifying her eggs.

Many lizards extend their tongues toward apparent food before taking it into the mouth. Kahmann's snakes that had their Jacobson's organs destroyed did not take dead prey. Apparently Jacobson's organ has an important function in identifying food. It is also of apparent service to vipers that run down their prey after it has been struck by them and has run away to die from the effects of the poison (Baumann, 1929). Hence impulses coming from Jacobson's organ maintain a sustained interest in a particular object for long periods. The brooding response also represents a sustained interest. Responses to optic stimulations usually provoke attack or retreat, but in general the interest resulting from optical stimulations is less sustained. In this connection it may be noted that the elaboration of Jacobson's (=vomeronasal) organ in the Salientia is correlated with the development of a more advanced type of forebrain in the Amphibia. Herrick (1921, p. 274) remarks: "Though the differentiation of the vomeronasal organ peripherally was the initial point of departure for the fabrication of the amygdala, the complex, once developed, retains its individuality in the absence of the vomeronasal organ (alligator, man) and even of the entire olfactory system (dolphin)." Apparently Jacobson's organ has played an important rôle in building up the more advanced type of brain characteristic of the Mammalia. It is interesting to find that two habits of reptiles requiring sustained interest, namely, trail-following and egg-brooding, appear to be directly dependent on Jacobson's organ function.

We have shown that *Eumeces* would brood not only its own eggs but the eggs of any other female of its own or a closely related species. This fact is of interest, for it may form the basis of a peculiar habit which is probably widespread in the geckonid lizards. Noble and Klingel (1932) found that *Aristelligella*, which lays only a single egg, deposited this in contact with others that had been laid presumably by other females of the same species. Mell (1929) found in the vicinity of Canton 186 eggs of *Gekko japonicus* on a single window shutter of a convent which had from 60 to 80 similar shutters. Many reptiles lay their eggs together in the most suitable sites, but it is difficult to account for the colonial nesting habit of the geckos mentioned above without assuming that the gravid females are in some way attracted by the eggs of their own species. Possibly it is an incipient brooding habit manifest only at the time of egg-laying which brings them together in this distinctive way.

BROODING AS AN AID TO THE INCUBATION OF THE EGGS

The female *Eumeces* when brooding her eggs has more or less of her body in contact with them. This has induced Hurter (1911) to ask "whether the body heat of these so-called cold-blooded animals has any influence on the hatching of the eggs." Until the present no one has attempted to answer the question by determining the body temperature of a brooding *Eumeces*. We have secured the records of a series of brooding *E. fasciatus* and *E. laticeps* by determining their rectal temperatures with special gas-filled, seven-inch mercury thermometers constructed by the Taylor Instrument Companies. The bulb of the thermometers measured 2 mm. in diameter and 12 mm. in length, and consequently could be inserted into the cloaca without difficulty. Each thermometer registered to 0.2° C. The same thermometers were used to take nest temperatures. The nests were dampened daily and consequently were usually lower than room temperature. The lizards were gently held in thick towels while recording their rectal temperatures. This was a very necessary procedure because the heat of the hand quickly raised the body temperature of the lizard. The thermometer remained within the cloaca until the mercury level had ceased to move. This usually required between 30 and 60 seconds. The temperature of lizards taken quietly from their nest averaged 0.4° C. higher than the temperature of the nests, in both the *Eumeces laticeps* and *Eumeces fasciatus*, with a range from 0.3° C. to 0.7° C. higher. When the females struggled or when they ran from their nests before they could be taken, their temperature was higher, ranging from 0.9° C. to 2.3 C. more than that of the nest, with an average of 1.6° C.

In cages, which were not disturbed, we repeatedly observed that the female would voluntarily abandon the nest to prowl about the cage. Especially in the late afternoon the females would leave the eggs and come out on top of the moss where they would be exposed to direct sunlight. We captured six of these females and secured their rectal temperatures with a minimum amount of disturbance to the lizards. These temperatures ranged from 1.6° C. to 3.2° C. higher than that of the nest and averaged 2.7° C. higher (Fig. 4). One temperature reading of a *Eumeces laticeps* while she was out on top of the moss was 24.1° C. as compared with the nest temperature of 20.9° C. Fifteen minutes later the female was found back on the eggs, and her temperature had dropped to 22.5° C.

These temperature readings indicate that the body temperature of the brooding female varies with the environment. When the female is out on top of the moss and bark, her temperature approaches that of the room, and when she is on the nest which is damp and under bark and has a lower temperature, the female's temperature is lower. The temperature taken fifteen minutes after return to the nest shows the rapidity with which the change is made from the higher to the lower temperature.

How often the female *Eumeces* leaves her eggs in nature is not known. On returning to the nest some of her body heat must be given to the eggs by conduction. Hence the habit of voluntarily leaving the eggs and returning to them after a certain amount of exercise or sun-bathing results in supplying the eggs with a small but definite amount of heat.

In nature the importance of the mother's body heat in the incubation of the eggs probably varies greatly with the type of nesting site selected. In the case of eggs laid under the bark of standing stumps in river swamps

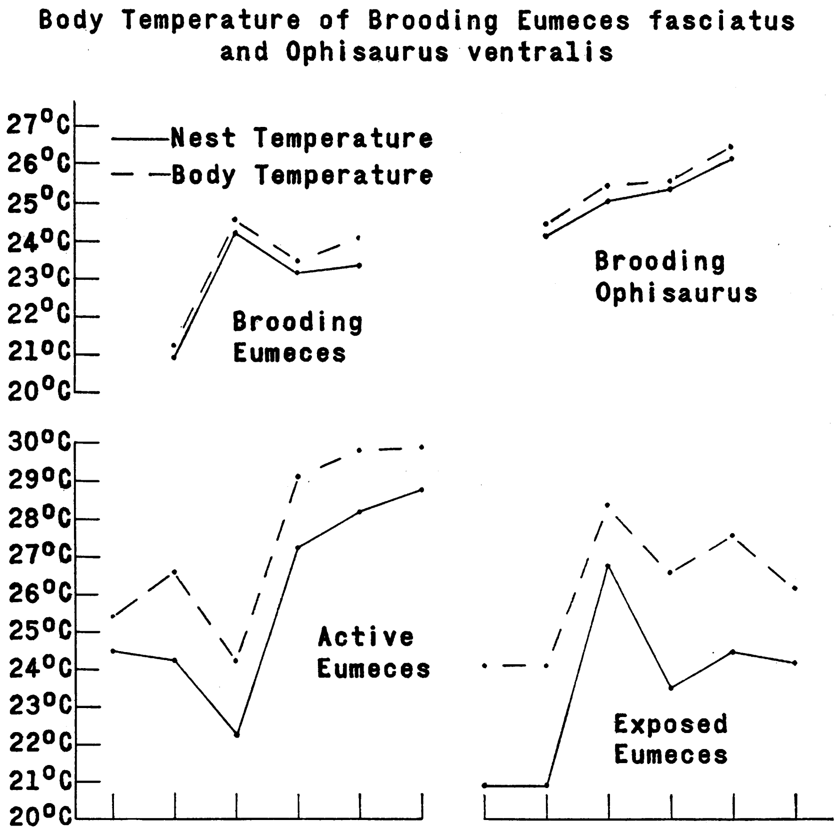

Fig. 4. Body temperature chart. The abscissa marks indicate days on which readings were taken.

such as Corrington (1929) described, or "in a hollow in a dead willow tree about fifteen feet from the ground buried in the loose, damp, rotted wood" (Blanchard, 1922), the body warmth of the female may aid the incubation considerably. On the other hand, in the case of eggs deposited under bark or wood débris exposed to the sun for long periods, it is possible that the sun aids incubation more than does the mother's body temperature. Dr. F. W. Blanchard has informed us that in northern Michigan the *Eumeces* lay their eggs in logs exposed to the sun. Since the eggs are covered merely by the outer shell of the rotting log, their temperature is presumably greatly influenced by the sun. In such situations it is possible that the female's body temperature aids incubation chiefly at night or on dull days. Unfortunately, records of the temperature both of the logs and of *Eumeces* in the field are entirely lacking. It would be interesting to compare the time required for development of a set of eggs guarded by a female with that of another set receiving no parental care.

In nature the female lizards would have a much better opportunity to sun themselves than in the laboratory. Further, while moving over the surfaces of logs warmed in the sun, they would receive heat by conduction. We found that holding quiet *E. fasciatus* two minutes in the bare hand raised the rectal temperatures on the average, 4.6° C.; five minutes, 6.9° C.; ten minutes, 8.1° C. The rectal temperature of *E. laticeps* was also raised, but to a slightly less degree, because due to the greater size of the animal a smaller area of the body was covered by the hand.

THE BROODING HABIT A PROTECTION AGAINST ENEMIES

Although many naturalists have found *Eumeces* brooding its eggs in nature, few have commented on the possible value of this habit in the economy of the species. Klots (1930) noted that the female *E. fasciatus*, which he discovered, made no attempt to defend the eggs when he disturbed her. This is apparently the experience of other observers who fail to describe a defense reaction in the brooding female. Klots' eggs were finally eaten by another specimen of *E. fasciatus* placed in the cage with the female. It would appear that *E. fasciatus* failed to protect its eggs from the attacks of even small enemies.

We have been able to confirm Klots' observation that *E. fasciatus* does not defend its eggs against man. Our experiments with small enemies, however, are totally at variance with his views. We find that both *E. fasciatus* and *E. laticeps* vigorously protect their eggs against small enemies including mice, lizards, and snakes. Mice, both adults and young, were put into the cage with brooding *Eumeces*, and each time the female bit the mouse if it approached the nest or evinced any interest in the eggs (Fig. 5). This was tried twelve times. Once when a mouse was showing interest in some *Ophisaurus* eggs, the female *Eumeces* was about to attack the mouse, but by touching the eggs with her tongue, she dis-

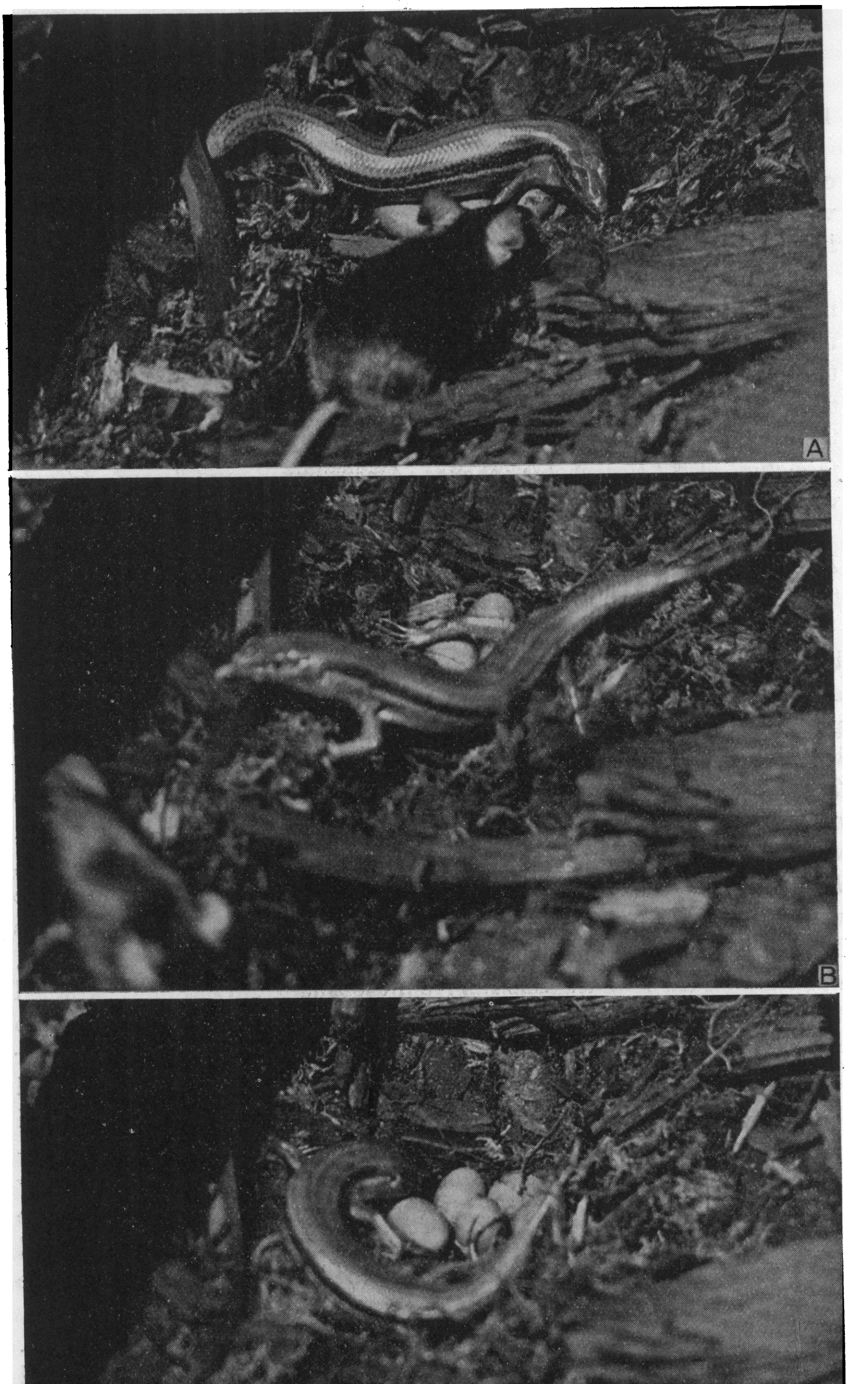

Fig. 5. Brooding *Eumeces laticeps* defending her nest.

A. The female while lying flat on her eggs watches an approaching mouse closely. B. She suddenly springs forward to bite the mouse. The latter escapes (on the left) and the female thrusts out her tongue endeavoring to pick up his scent. C. The mouse having fled from the vicinity of the nest, the female returns to her eggs and turns them over with her snout.

Photographs made during three successive trials during which the female defended her nest in essentially the same manner.

covered they were not hers, and, as a result, neglected the mouse and vented her anger on the eggs, picking one up in her mouth and retreating some distance, shaking it as she went.

Lizards were tested on the brooding females. When the lizards remained quiet, showed no interest in the eggs, and did not approach the nest, the brooding female watched them, at times touched them with her tongue, occasionally chased them, but never bit them. When, however, the lizards approached the nest and eggs, she did not hesitate to bite them and so frighten them away. Other *Eumeces laticeps* and *E. fasciatus*, also *Leiocephalus inaguae*, *Ameiva exsul*, and *Lacerta lilfordii* were used in these tests.

A gopher turtle was put into a cage with a brooding female. The *Eumeces* touched it with her tongue but did not bite it. When the turtle advanced into her nest, she retreated.

A large, striped, European snake (*Elaphe scalaris*) was tested on a brooding female, but the snake merely went into the débris and did not approach the eggs. At another time several *Thamnophis butleri* were put into a female's cage. These smaller snakes were immediately attacked by the female whenever they went in the vicinity of her nest. Larger *Thamnophis sirtalis* were tried with the same result. If the snakes were not near the nest, the female on encountering them merely touched them with her tongue, and then watched them carefully. A king snake, *Lampropeltis getulus holbrooki*, placed with a female was bitten twice without hesitation, in spite of the fact that the snake was many times larger than she. A still larger snake, a black snake, *Coluber constrictor*, was tried on the female. She ran from the snake and hid but continued to watch his movements from behind some bark and moss. She made no attempt to approach the snake, and finally when the snake started for her, it had to be removed. The king snake weighed 185.5 grams, and its total length was 84 cm. The black snake weighed 310.3 grams and measured 133 cm. Whether this 125 gram and 50 cm. difference between the snakes was the determining factor for or against an attack by the *Eumeces* female, or whether it was a matter of species cannot be concluded from these experiments. However, the black snake appeared much larger and more overpowering than the king snake, and at the time of the experiment, it seemed that size was the important factor.

Mice, lizards, and snakes were placed in cages with *E. laticeps* and *E. fasciatus* females that had not laid and with those whose eggs had all hatched. In all cases, the females disregarded all of these intruders, with the exception of the larger snakes from whom they ran when they met them face to face.

These experiments on the protection of the nests and eggs by the brooding *Eumeces* indicate that the females under normal conditions ward off enemies whether they are other lizards, snakes, or rodents. There is a size limit, but the females attack animals many times larger than themselves. These enemies are touched by the female with her tongue. If the animals do not approach the nest, they are closely watched, but if they draw near the eggs, they are immediately bitten, whereupon the intruder usually makes a rapid retreat with the female in pursuit. If given a chance within a short distance, the female frequently bites again. After the enemy has been driven away, the female returns to her nest, investigates all her eggs with her tongue, rolls them with her snout in the manner described above, and settles down again to brood them.

THE BROODING HABITS OF *OPHISAURUS VENTRALIS*

The eggs of the "glass-snake," *Ophisaurus ventralis*, have been reported by Ditmars (1904), Gloyd (1928), and Force (1930), but none of these observers have called attention to a brooding habit in this species. Apparently the brooding response is much less marked in this genus than in *Eumeces*. Pope (1929) has observed a brooding habit in the Chinese *Ophisaurus harti*. Two brooding females under his observation took flight at a slight disturbance. Since one of the nests was near a much-used foot path, this lizard had presumably left her charge only to return on many occasions. Hence we may speak of a well-defined brooding habit in this species at least.

Two of the series of *Ophisaurus ventralis* that we maintained in the laboratory during 1932 became gravid and were isolated in separate cages well provided with rotting wood and moss. One laid 15 eggs on June 2, and the other, 13 on July 13. Since both lizards came from Biloxi, Mississippi, it would seem that the breeding season in any one locality must be extensive. The first female weighed 85.1 grams and measured 235 mm. from snout to vent. She had a perfect tail 489 mm. long. The second female, the one which laid late in the season, weighed only 65.6 grams, but she measured 251 mm. from snout to vent. Her low weight was due to her short tail which had been broken and only partly regenerated and which was only 216 mm. long.

Both females brooded their eggs at intervals throughout the period of incubation (Fig. 6). Neither female was seen to bask in the sun nor even to expose much of herself to view during this time. We could secure no evidence that this species aids incubation by exercise or by sun-bathing. On June 3 and July 18 the rectal temperature of the first female, as measured by the same thermometers utilized in the *Eumeces* work, was 24.5° C. and 25.5° C., respectively, while the nest temperature was 24.2° C. and 25.1° C. This female had apparently been lying quietly with the eggs for an extended period on both occasions, and her body temperature was only 0.3° C. and 0.4° C. higher than that of the environment.

Temperature records of the second female were comparable. On August 1 and August 9 the rectal temperature was 25.6° C. and 26.5° C.,

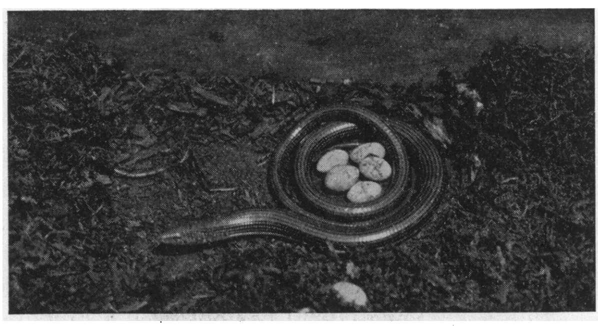

Fig. 6. *Ophisaurus ventralis* brooding.

respectively, while the nest temperature was 25.4° C. and 26.2° C. The female had been quiescent before the readings were taken. This may have been the reason why the body temperature of this female was also very low, only 0.2° C. and 0.3° C. higher than that of the environment. It is possible that in nature the brooding females are more active and raise their body temperatures by exercise if not by sunning. Our observations on the two brooding females in the laboratory gave no evidence in support of this assumption.

Ophisaurus was also found to differ from *Eumeces* in its failure to defend its eggs. *Ophisaurus* usually coils completely around the eggs which are laid in a single layer and are not gathered together in a pile as are python's eggs. The female may make one, one and a half, or two complete loops of her body about the eggs, but she makes no attempt to draw them together into a heap. We examined our brooding females frequently by gently lifting the cover of moss. If the female was disturbed, she quickly retreated into the mass of decayed wood or moss which covered the floor of the cage. We made frequent attempts to induce the female to defend her eggs. Mice and lizards, which immediately drew forth an attack from the brooding *Eumeces,* caused no such response in either *Ophisaurus.*

It was difficult to get the *Ophisaurus* to brood without a cover of moss. Whenever this was accomplished, tests were made. A two-thirds grown chocolate-brown mouse and a young mouse with hair present but eyes just barely open were placed in a brooding *Ophisaurus'* cage and the same reaction ensued. When either mouse approached the female, she withdrew, either partially or completely, into a temporary burrow. On another occasion, a small white mouse put into the cage crossed to the nest and sat on the eggs. The female saw it but made no attempt to chase it away. When the mouse finally walked on the head of the *Ophisaurus* female, she withdrew into a tunnel. On another day, an adult white female mouse, introduced into the cage at a distant corner, approached the eggs, touched them and retreated. This was repeated four times by the mouse. The *Ophisaurus* saw the action but made no attempt to bite the intruder. She merely cowered and pulled her head a little lower into the nest and moss. A female *Eumeces fasciatus* put into the cage, crossed to the nest, touched the eggs, walked on the female *Ophisaurus* and eggs, and finally stood with two feet on the eggs and two on *Ophisaurus* for a few moments. The *Eumeces* then continued her movements over the nest, and the female *Ophisaurus* partially uncoiled and slowly and quietly glided away underneath the moss, thus leaving the eggs unprotected. Usually the female did not move very far from the eggs, but did not return until the disturbing objects had been removed and the cover of moss replaced on her nest.

The brooding of *Ophisaurus* agrees with that of *Eumeces* in that if the eggs are moved into a new place in the cage or even to a new cage, the female will find them and begin to brood them again. *Ophisaurus* does not find her eggs as readily or as quickly as does *Eumeces,* but eventually the brooding is reëstablished.

As the females did not return to the eggs when they were uncovered, we were unable to determine whether or not the eggs were touched with the tip of the tongue in making the identification. However, on four occasions, the females assembled the eggs which had been scattered among the debris on the cage floor. At such times the eggs were brought together until most of them were in contact. Since such a feat meant pushing, rolling, or carrying the eggs, it is highly probable that the snout or jaws and body were used very much as in the case of *Eumeces.*

Since the life history of *Ophisaurus ventralis* is only incompletely known, it may be of interest to report further details on the two lots of eggs employed in this study. All of the eggs laid by the first female tapered more at one end than at the other. To our surprise none of the eggs in the second lot were as distinctly "egg-shaped" as those in the first. Many of the eggs in the second lot were incompletely calcified at one or both poles. The shell over these areas was formed of a yellowish membrane.

Of the 15 eggs that the first *Ophisaurus* laid, 3 hatched as follows: July 28, July 29, and August 1. The incubation varied from 56 to 60 days. The single one of the second lot that hatched was incubated 61 days. The first eggs were not measured when they were laid, but at hatching time they were 17 mm. by 13 mm.

The eggs of the second female were measured weekly throughout the incubation period. On July 30 the 9 eggs that had then been laid were measured. They averaged 18.2 mm. by 10.2 mm. The measurements of the individual eggs on August 1 will be given in detail to show the variation. The total 13 eggs were then available. On this date the eggs were:

16.5 by 10.5 mm.
16.5 by 11 mm.
17 by 10.5 mm.
17 by 10.5 mm.
17.5 by 10.5 mm.
17.5 by 11 mm.
17.5 by 12 mm.
18 by 10.5 mm.
18 by 11 mm.
18 by 12 mm.
18.5 by 10.5 mm.
19 by 10 mm.
20 by 12 mm.

The average of these is 17.8 by 10.9 mm. The following is a table of their increase in size from week to week:

Date	Number of Eggs	Number of Days Old	Average Length	Average × Width
July 30	9	0	18.2 mm.	×10.2 mm.
Aug. 1	13	2	17.8	×10.9
9	10	10	18.8	×13.3
15	10	16	19.3	×14.6
23	10	24	19.7	×14.8
29	10	30	20.0	×14.8
Sept. 6	9	38	21.1	×15.2
12	5	44	22.5	×16.5
20	4	52	23	×16.5
26	1	58	25	×19.5
29	1 egg hatched			

One egg on September 20 was 28 mm. × 18.5 mm. It died later.

A comparison of the measurements of the eggs of the second female at laying with those of the first female at hatching shows that most of the second female's eggs were as long but NOT as broad at laying as the others were at hatching. With the continuous increase of these eggs the one that survived was at hatching much larger in both dimensions than those of the first female.

The young of the first female at hatching measured 48.5 mm., 49 mm., and 50 mm., respectively, from snout to vent and had tails 65 mm. long. The one young of the second female was 46 mm. long and had an 81 mm. tail. In spite of the great difference in the size of the eggs, the body size did not differ relatively—except the tail-length. In fact, the one from the larger egg was slightly smaller than the other three. It follows from this and from the *Eumeces* work that the size of lizard eggs at hatching may be much more variable than the size of the young lizards which hatch from them.

COMPARISON WITH OTHER REPTILES

Most lizards bury their eggs and hence would not be expected to brood them. A few species of *Lacerta*, however, have been reported to take an active interest in their eggs, carrying them in their mouths or burying them in a new place when disturbed (Hilzheimer, 1910). Many geckos lay their eggs in crannies or even in exposed situations, but as the eggs are provided with resistant shells and are frequently attached to vertical surfaces at a distance from the ground, they do not require the protection necessary for more accessible layings. The eggs of *Eumeces* and *Ophisaurus* resemble those of many snakes in being provided with membranous shells. The eggs of *Eumeces* are laid in damp rotting wood. *Eumeces* evaporates considerable quantities of water through its skin (Noble and Mason, 1932), but since the eggs are presumably in contact with a damp substratum they would probably secure an adequate supply of moisture from this source instead of from the mother's body. At present we have no evidence that the eggs of *Eumeces* require more moisture than those of such snakes as *Diadophis* (Blanchard, 1926). Nevertheless the latter are not brooded by the parent.

The brooding habit is apparently widespread in the genera *Eumeces* and *Ophisaurus*. Mell (1929) lists three Asiatic species of *Eumeces* that guard their eggs. Mell states that wherever the lizards have been found with their eggs they endeavor to prevent the removal of their charges. This behavior stands in contrast to that of *Eumeces fasciatus* and *E. laticeps* which attacked only the smaller enemies introduced into their cages.

The chief value of the brooding habit would appear to be protection from enemies. It crops up in species that provide their eggs with only superficial covering. The large South American teiid, *Tupinambis nigropunctatus*, lays its eggs in termite nests and leaves them to be covered by the owners of the nest (Hagmann, 1906). The related *T. teguixin* deposits its eggs in decaying vegetation, and the mother remains to guard them (Krieg, 1925). Many snakes provide their eggs with only superficial covering, and it is perhaps not surprising to find that a variety of poisonous and harmless forms have been reported to defend them. All lizards that have been described as brooding their eggs have this in common: they depend to a large extent on their tongue in sensing the world about them. Genera, such as *Anolis* and *Sceloporus*, which depend to a greater extent upon their eyes in recognizing prey, bury their eggs or at least do not guard them. *Eumeces*, like the snakes, uses its tongue to identify objects. When deprived of vision, *Eumeces* can locate its eggs even in a foreign situation, and, as shown above, it appears to rely chiefly on the tongue to make the identification.

Since we have shown in the laboratory that the female *Eumeces* voluntarily leaves the eggs and returns to them after her body has been heated by exercise and sun bathing, the brooding habit of *Eumeces* presumably aids the incubation of the eggs. The same is very probably true of snakes. Medsger (1919) found a clutch of *Elaphe obsoleta* eggs in a cold, damp sawdust pile. Both parents sunned themselves and then returned to the eggs to incubate them. Medsger in one case found the male actually encircling the eggs and the heat of his body apparently aided their incubation. Medsger made no record of the temperature, but in a later account (1932) his description of the brooding site is very detailed and leaves no doubt that the body temperature of the brooding snake must have been markedly higher than that of the nest at the time of the snake's return to the eggs. Mell (1929) found that the temperature between the coils of a brooding *Bungarus fasciatus* was only 0.4° C. and 0.6° C. higher than that of the environment. In the case of this krait the body temperature of the female would be of little advantage to the eggs, at least at the moment her body temperature was recorded.

It is an interesting fact that in pythons, which guard their eggs continuously during the day, the brooding female is provided with a little understood mechanism for raising her body temperature. The many records of increased body temperature in brooding pythons have been critically reviewed by Benedict (1932) who has found an increase of from 3° C. to 4° C. in the body temperature of the particular female that he and his associates studied. In other species of reptiles that have been reported to leave their eggs at intervals during the day, no such mechanism for increasing the body temperature exists. Some of the latter group such as *Eumeces* and the pilot black-snake tend to make up for this deficiency by sun bathing.

Pythons with their long daytime brooding duties may be contrasted with other brooding reptiles. Not only have they developed a high body temperature in the brooding female but they are able to lay their eggs in the open (Wall, 1911). The male has no brooding duties and does not return to the vicinity of the eggs. This is also true of some intermittent brooders such as *Eumeces* but apparently not true of several snakes. Brooding pythons seem to starve themselves more than intermittent brooders, but on this point the data is very incomplete.

Unfortunately very little is known regarding the activities of most reptiles during the brooding period. Hahn (1909) found a *Heterodon contortrix* coiled around her eggs in the soft earth of a cornfield. Female *Lampropeltis triangulum* found coiled about the eggs have been assumed to be incubating them (Babcock, 1929). Wall (1907) reports a *Ptyas mucosus* with its eggs among some bricks in a rubbish heap. Mell (1929) claims that the latter species, as well as *Ptyas korros*, *Natrix piscator*, and *N. subminiata*, guard their eggs, but leave them to search for food. Mell does not, however, give the detailed evidence on which this statement is based. Pope (1929) has reported another Chinese form of *Natrix* that apparently guards its eggs. At least a female *N. percarinata* was brought to him coiled peacefully around her eggs "and beyond all doubt showed an interest in her eggs even though she would make no attempt to defend them."

It is a curious fact that some but not all of the egg-laying species of *Natrix* brood their eggs. The eggs of the common European grass snake, *N. natrix*, have been frequently found without attending parents. However, Gallwey (1932) has recently described a female as encircling her eggs and defending them for two weeks. Apparently within the genus *Natrix*, as among the varieties of domestic fowl, there may be various degrees of "broodiness."

Much more is known about the brooding habits of the cobras. Recently a pair, species not stated, bred in the zoölogical gardens in Manchester. The eggs were laid in a hollow under some sods, and both parents appeared to take turns at brooding them (Jennison, 1931). The king cobra, *Naja hannah*, lays its eggs in a heap of leaves (Wasey, 1892; Evans, 1902; Joynson, 1917; Wall, 1924; Shaw and Shebbeare, 1931). The female apparently broods the eggs, although the male is said to remain nearby. The female *Bungarus fasciatus* has been found brooding eggs nearly ready to hatch (Evans, 1905). Since she was thin and in poor condition she presumably had not left them regularly to feed. In the case of *Naja naja* it is also the female that broods (Mell, 1929). However, Green (1905) reports that in *Bungarus ceylonicus*, "Both parents were curled up in the hollow (made like a duck's nest, but not lined in any way, just scooped and hollowed out of earth), and under them were lots of eggs and little snakes." This report, taken in conjunction with that of Jennison, would indicate that both parents brood the eggs. It would be interesting to know if the male merely returns to a favorite retreat or if he is actually attracted by the eggs in the manner of the brooding *Eumeces*. Medsger (1932) twice carried a pair of *Elaphe obsoleta* a distance of approximately a hundred yards from their nest and found that in both cases the pair had returned within a day or two. Unfortunately no other experiments have been performed with any species of snake to test the nature or strength of the attraction.

In other poisonous snakes it is apparently only the female that broods the eggs. This appears to be the case in *Trimeresurus monticola* (Leigh, 1910; Pope, 1929), *Trimeresurus rhodostoma* (Smith, 1915) and *Lachesis mutus* (Mole, 1924). It is remarkable that among the sea snakes, which as a group are viviparous, a local race or at least a group of *Laticauda colubrina* should lay eggs. Further, the female guards the eggs and snaps at intruders (Smedley, 1931). Hence the brooding habit characteristic of the cobras but lost in the viviparous sea snakes reappears in one group of these snakes that has apparently redeveloped the egg-laying habit. A similar reappearance or at least parallel development is found in the salamanders. Most species that lay their eggs on land brood them, unlike a large percentage of aquatic forms. The habit has recently been analyzed in *Desmognathus fuscus*. As in the case of *Eumeces* the females will seek out and brood the eggs of any female (Noble and Evans, 1932). Since the tongue is not protruded during the search it would appear to be the olfactory and not Jacobson's organ that aids the salamanders in making the identification. This conclusion requires experimental verification because vision was not eliminated in the experiments with salamanders.

SUMMARY

1.—The eggs of *Eumeces laticeps* are larger than those of *E. fasciatus* at the time of laying. At the time of hatching both may have swollen to the same size.

2.—The young of *E. laticeps* at hatching are larger than those of *E. fasciatus*, and they grow more rapidly during the following weeks.

3.—Both *E. fasciatus* and *E. laticeps* will brood eggs of other females, and one species will brood the eggs of the other.

4.—Neither species will brood the eggs of *Sceloporus undulatus* or of *Ophisaurus ventralis*. Paraffin models of *Eumeces* eggs are rejected, and living eggs that have been shellacked are usually not attended.

5.—A blindfolded *Eumeces* will find and brood eggs even when these are placed in a foreign situation.

6.—The tip of the tongue is employed in identifying the eggs. Removing this part of the tongue prevents the female from finding the eggs.

7.—*Eumeces fasciatus* and *E. laticeps* voluntarily leave their eggs at frequent intervals to sun bathe or to seek food.

8.—Their body temperature at this time in the laboratory ranges from 1.6° C. to 3.2° C. higher than that of the eggs.

9.—This increased body temperature apparently aids the incubation of the eggs when the female returns to brood.

10.—The brooding *Eumeces fasciatus* and *E. laticeps*, but not *Ophisaurus ventralis*, will attack mice, lizards and snakes of moderate size that approach their eggs.

11.—The female *Ophisaurus ventralis* can find her eggs when these are placed in a foreign situation, but under laboratory conditions she does not increase their temperature in the manner of *Eumeces*.

12.—The eggs of *O. ventralis* may vary greatly in their increase in size during development, and yet the young on hatching from these eggs may be nearly the same size.

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