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MATERNAL BEHAVIOR OF THE RED-BACKED SALAMANDER, PLETHODON CINEREUS

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree of
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INTRODUCTION

Plethodon cinereus is a slender terrestrial salamander found in several types of wooded habitats, such as northern hardwoods, oak-hickory , pine barrens and birch-mixed forests (Cochran, 1911; Burger, 1935; Test, 1952 and 1955; Test and Bingham, 1942; Test and Heatwole, 1962). Eggs of this completely terrestrial amphibian are laid in cavities and crevices within decaying logs and under logs and stones. The literature (Piersol, 1910; Cochran, 1911; Bishop, 1941; and others) includes numerous references to eggs found in the field which were attended by a female. From these observations, it has been assumed that these females are the ones which laid the eggs, that they remain with them from oviposition to hatching, and that their presence enhances the survival of the eggs. It is the purpose of this study to test these hypotheses by observing individuals with their eggs and young in laboratory nest cavities during both pre-hatching and post-hatching periods.

More specifically, I hoped to learn: a) the length of the nesting season, b) whether the female remains with the eggs continuously, c) the physical relationship of the female to the eggs, d) whether the female defends her eggs against members of her own species and against predators, e) whether she can recognize her own eggs and, if so, what factors are important in such recognition, f) her

attraction and responses to eggs which she did not lay, g) her reaction to her own and to strange young, h) the tendency of a displaced female to return to her eggs, and i) responses of the young to the attendant female.

LITERATURE REVIEW

Individuals of Plethodon cinereus may be either uniformly grey dorsally or may have a wide dorsal stripe of a variable reddish color. At one time these two color types were considered to be separate species. However, Burger (1935) found that both types can occur in the same egg clutch and they are now recognized to be genetic variations of the same species. The inheritance of these color types has been studied by Highton (1959 and 1960) and their distribution discussed by Test (1952 and 1955), Reed (1955) and others.

Although these animals have not, to my knowledge, been bred successfully in captivity, their courtship has been partially observed (Noble and Brady, 1930) and generally follows the pattern found for other members of the family Plethodontidae. The typical plethodontid courtship consists of a series of complex responses by which the female is induced to pick up the spermatophore. Courtship has been described for Plethodon jordani, P. welleri and P. glutinosus by Organ (1958, 1960a, 1960b), Plethodon metcalfi by Green and Richmond (1944), and Ensatina eschscholtzii by Stebbins (1949a).

Breeding of *E. cinereus* occurs in the fall and spring and the eggs are deposited in June of the following spring (Blanchard, 1928). Egg laying by a captive female was first described by Piersol (1914). Dates given in the literature for the time of egg laying vary from early June through July. Cochran (1911) mentions finding eggs for the first time on July 5th in 1910. Piersol (1910) mentions June 16 as the earliest date and July 3 the latest date on which he found a recently oviposited clutch. Bishop (1941) reports June 17 as his earliest recorded date. However, Cochran (1911) makes the statement that eggs are laid during July and August. Newly oviposited eggs were found on August 2, 1959, by Davidson and Nestwole (1960), who suggest the existence of two distinct periods of oviposition during the summer. They consider it likely (as did Bishop, 1941) that a particular female lays only once each year.

The eggs are usually attached by a mucous strand to the roof or side of the nest cavity in a grape-like cluster. The number of eggs has been found to range from five to thirteen (Blanchard, 1928). The embryos go through their larval stages while still within the egg membranes and lose their gills around the time of hatching (Piersol, 1910), which ordinarily occurs in the early part of August (Davidson and Nestwole, 1960; Highton and Savage, 1961; and others).

The types of food eaten by this species have been

studied by Murphy (1913), Smallwood (1928), Hamilton (1932), Jameson (1944) and others and were found to consist of various small invertebrates. Heatwole and Test (1961) suggest that these salamanders probably eat any small animals which are sufficiently active to attract their attention. Oophagy occurs in this species (Piersol, 1914; Highton and Savage, 1961), as well as cannibalism (Heatwole and Test, 1961).

Studies of the distribution and movements of P. cinereus within the soil have been conducted by Heatwole (1960 and 1962) and by Taub (1961). Taub's studies of movements of individuals suggest a limited activity range. The existence of activity ranges and homing tendencies has been reported for a number of other amphibians (Hartof, 1953a, Rana clamitans; Noble, 1921, Rana catesbeiana; Carpenter, 1954, Bufo boreas and Rana pretiosa; Pearson, 1955, Scaphiopus h. holbrooki; Grant, 1955, Eurycea bislineata and Hemidactylium scutatum; Gordon, 1961, Ambides aeneus; Twitty, 1959, and Packer, 1962, Taricha rivularis; and Hendrickson, 1954, and Cunningham, 1960, in the genus Batrachoseps.

Heatwole (1962) states that P. cinereus, although occurring in the leaf litter and under logs during periods of sufficient moisture, moves down into the soil during periods of excessive dryness. He (1960) also found them able to burrow in some substrates, in addition to following existing crevices into the soil. Vernberg (1953) studied the hibernation of these animals in the soil and their

survival in relation to depth and also found them able to burrow under some conditions.

P. cinereus is also noted for its ability to leap using its tail. This is considered by Murphy (1917) to be related to its feeding habits. The ability to throw off the tip of its tail (autotomy) is another well known characteristic of this animal. These and other aspects of the ecology of this species have been well summarized by Dunn (1926).

Aside from inferences based upon a few observations, there is a noticeable gap in the literature concerning brooding behavior. The only report of laboratory observations on this phase of the ecology of P. cinereus is by Highton and Savage (1961) who induced oviposition in the laboratory, noting that the presence of the female increased in some way the chances of survival of the embryo, and that one female, at least, defended her eggs against other salamanders.

Although studies of brooding behavior in other vertebrates (notably birds) have been numerous, there have not been many reported for salamanders. Gordon (1952, 1961) investigated the behavior of attendant females of the Green Salamander, Aneides aeneus; he noted that they made aggressive lunges at inserted objects and returned to the nesting crevice when displaced. Thorn (1962) found that captive males of Hynobius nebulosus guarded the eggs and would bite repeatedly at an

inserted lead pencil. Organ (1960b), in studying the life history of Plethodon welleri, discussed the behavior of attendant females before and after hatching of the eggs. Females were curled around the eggs and maintained contact with them. After hatching, both female and young remained close to the empty egg capsules. Stebbins (1954) found that females of Ensatina maintained physical contact with their eggs.

Gorman (1956) referred to attendant females with clutches of the eggs of Hydromantes shastae, but obtained no information regarding details of their behavior. In many other species of salamanders, particularly plethodontids, eggs are laid in nests or depressions (Bishop, 1941; Stebbins, 1951); however, detailed studies of brooding behavior have not been made.

Although the attendant female P. cinereus has been referred to often as guarding her eggs, it was not until 1961 when Highton and Savage described the defense of eggs by a single female that the literature contained any actual evidence of defensive activity. The only species of plethodontid in which the female has been shown to exhibit defensive behavior is Aneides aeneus (Gordon and Smith, 1949, found all clutches of eggs accompanied by a "guarding" female); however (Gordon, 1952), it responded only to objects and not to other individuals.

Aggressive behavior has been reported for many vertebrates (reviewed by Collias, 1944, and also by Smith and

Ross, 1952); however, reports of such activities occurring among amphibians have been few until relatively recently. However, males or females of several species of anurans and urodeles are known to attend or "guard" their eggs.

Aggressive encounters between males during the breeding season have been observed in several plethodontid salamanders, including Plethodon welleri (Organ, 1960b), P. glutinosus (Organ, 1960a), and P. jordani (Hutchinson, 1959). Grant (1955) reported aggressiveness and territoriality in Eurycea bislineata. However, as late as 1960, Cunningham (1960) states that territoriality has not been clearly demonstrated for amphibians.

Aggressive behavior in other amphibians was found by Fost (1954), and later discussed further by Sexton (1960), among females of the Venezuelan frog, Prosthcrapis trinitatis, which actually fought with and drove away intruders of the same species. Sexton (1962) also reports aggressive behavior among breeding males of Leptodactylus insularum, which were calling from depressions in foam nests. Lutz (1960) found that males of the tree frog, Hyla faber, make rounded nest pans in shallow pools and defend these against the invasion of other males. Martof (1953a) found that males of the Green Frog, Rana clamitans, spaced themselves into primitive territories and suggested that the males tested one another early in the season. Breder, et. al. (1927), working with the same species, found it capable of returning to a given area and thus suggested

territoriality. Stebbins and Hendrickson (1959) found that males of *Phyllobates subpunctatus* guarded the eggs.

DESCRIPTION OF NESTS AND NESTING PLACES

Collecting Methods

The individuals of Plethodon cinereus used in the experimental parts of this study were collected from several wooded areas near Pellston, Michigan. Since the purpose in collecting the animals was simply to obtain enough individuals for the experiments and not to secure information for population analysis, systematic sampling was not attempted. Collecting, therefore, was limited to the areas which were considered habitats according to previous collecting experience. Nesting females and their egg clutches were mostly obtained from large, decaying logs, which were carefully and slowly broken apart. Other individuals were found in the same logs or by rolling over others of various sizes lying on the forest floor.

When a nesting female was located, she was caught by hand and placed in a small plastic bag (approximately 4 by 8 inches). The wood to which the eggs were attached was cut or broken from the log whenever possible and placed in the bag with the female. Each bag was labeled, and data on the physical nature of the nest and nest site as well as the behavior of the female were recorded. For those logs in which nests occurred, temperature (telethermometer), relative humidity (hand-aspirated psychrometer) and moisture content (oven drying of log samples) were

determined. The disturbance of the bags was held to a minimum in transport back to the laboratory.

Description of Collecting Areas

The experimental animals were collected from the following forest areas: (1) Colonial Point (Burt Lake), Cheboygan County, Michigan; (2) Carp Lake, Emmet County, Michigan; (3) Two miles west of Pellston, Emmet County, Michigan. These served as both collecting and study areas from which some behavioral observations and physical data were obtained. All are mature stands of northern hardwoods with sugar maple (Acer saccharum), beech (Fagus grandifolia), and hemlock (Tsuga canadensis) as the dominant trees. Although logging was being done in the Colonial Point area at this time, the other two stands were relatively undisturbed. In no area had the large fallen logs been removed, so there were numerous suitable nesting sites within each stand. The hemlock logs, which are commonly used as nesting sites, were not distributed uniformly throughout the stands due to the tendency of the species to grow on knolls or in groves.

Characteristics of Logs Used as Nesting Sites

In some preliminary studies all decayed logs in certain parts of the above areas in which collecting was done were searched for nesting females. In one such survey

one nest was under a board, one in a beech log, one in a birch log, another was under a hemlock log, and 17 were found in hemlock logs. Subsequent collections were therefore restricted to hemlock logs. Test and Heatwole (1962) state that in this area nests of P. cinereus are most commonly found in decaying hemlock logs containing "...a network of cracks". Heatwole (1962) has classified these hemlock logs into three main types, based on their state of decay: chunky, fibrous and powdery; of the animals collected by him in hemlock, 88% had nested in the chunky logs. These logs break up into blocks along radial and annular cleavage planes. Perhaps the many crevices between blocks made these logs more easily accessible to the salamanders than the other types. Heatwole (1962) suggests another possibility, that the water could move down these cracks and thus not be uniform within the log, explaining the fact that most of the animals were found in the cleavage planes and not in smaller cracks within the separate blocks.

The moisture content of these chunky logs was exceedingly high. The values obtained from samples from the parts of logs from which females with eggs were collected ranged from 87 - 381% of dry weight. Actually, most of these logs had so much water in them that one could squeeze it out by hand. During 1959, the average moisture content value for June 21-30 was 290% of dry weight (five logs), for July, 186% of dry weight (eight logs) and for August 2-3, 244% of dry weight (five logs). Samples taken from

four logs in June 19-30, 1960, had an average of 363.5% of dry weight.

Average temperatures found within hemlock logs in June and July of 1960, at depths of 5, 10 and 15 cm were: 17.0 ± 1.6 C, 16.5 ± 1.4 C, and 15.7 ± 1.6 C (± refers to standard deviation; sample size was 9, 10 and 11 respectively). It is apparent from these values that temperatures did not vary greatly either between or within logs. The logs are thus good insulators and protect the female from rapid and extensive temperature fluctuations.

Samples of wood from logs in which nesting salamanders were found were tested for pH with a Beckman meter. Similar samples were taken from chunky logs without nests. The pH values for both ranged from 4.0 to 4.2 and differences between them were not significant. By way of comparison, a sample of the fibrous type had a pH of 3.9 and the powdery a pH of 3.2.

Location of Nests Within Logs

In logs having both chunky and fibrous sections, nests were usually found only in the former, located either in cracks or in insect tunnels.

Some nests were depressions or cavities just large enough to accommodate the female and her eggs; others were found in a cleavage plane and there was no other cavity. Egg clutches usually were secured to one wall of the surrounding wood by a mucous thread. A few were

found unattached and lying on the floor of the cavity.

Logs in which part of the length was not in contact with the forest floor contained no nesting females in such parts, but only within the sections which either touched or were embedded in the ground. However, in most logs nest sites were not confined to areas near the ends of the log. Many of the nests were just under the bark or well decayed outer section of the log when it was present (Fig. 1). Of 74 nests collected in 1958-60 for this study, 50 were less than 10 cm beneath the top surface. Only 17 of the 74 were in logs smaller than 50 cm in diameter and 12 of these were deeper than 10 cm below the log surface. From this sampling, it can be said that nests were almost never found in the interior of large logs (sections were always searched throughout except for solid parts). However, they were more uniformly distributed within suitable sections of smaller logs.

Relation of Nests to Other Inhabitants of Logs

Social interaction among individuals of the same species, and particularly brooding females, depends in part upon the abundance of individuals in an area or space and the proximity of the nesting sites. Therefore, it becomes important to know if nests are close enough for behavior patterns observed in the laboratory to occur also in the field.

On July 24, 1950, a section 2 m long midway between the ends of a large hemlock log (9 m long, 110 cm wide and 50 cm deep) was searched thoroughly for salamanders and other easily visible animals. The log, in the chunky condition, with the upper 10 cm well broken up and invaded by numerous small roots of beech (Fagus grandifolia) and sugar maple (Acer saccharum) seedlings, was located in a beech-maple forest two miles west of Pellston, Michigan. Relative humidity 10 cm from the top of the log surface was 93%, while temperatures varied from 20°C at a depth of 5 cm to 17° C at 25 cm.

The locations of nests and individuals are shown in Fig. 1. A total of 12 salamanders and 9 nests were found. Five of the females were attending eggs; one other female was found which might have been disturbed from one of the unattended nests; the remainder were males and juveniles. If the single female came from one of the nests, and if each nest had a brooding female before disturbance, the total number of salamanders in that section was 15. With the volume of the log section calculated to be 0.84 m^3, the average density of salamanders in that section was 18/m^3. In the side view of Fig. 1, it is seen that most of the nests and individuals were clustered in a section 50 cm^2. The end view shows most of them to be concentrated in the left half of the diagram. The volume of this portion of the log was 0.105 m^3, and the average density of salamanders was 76.2/m^3 and of nests 47.6/m^3.

FIGURE 1. Locations of salamanders in a section of a decayed hemlock log (9 m long, 110 cm wide and 50 cm deep). The nests are represented by the letters A - I, while the numbers 1 - 7 indicate the locations of non-brooding individuals. View A is from the end and B from the side of the log. Portion of log above dashed line was well decayed and invaded by small roots.

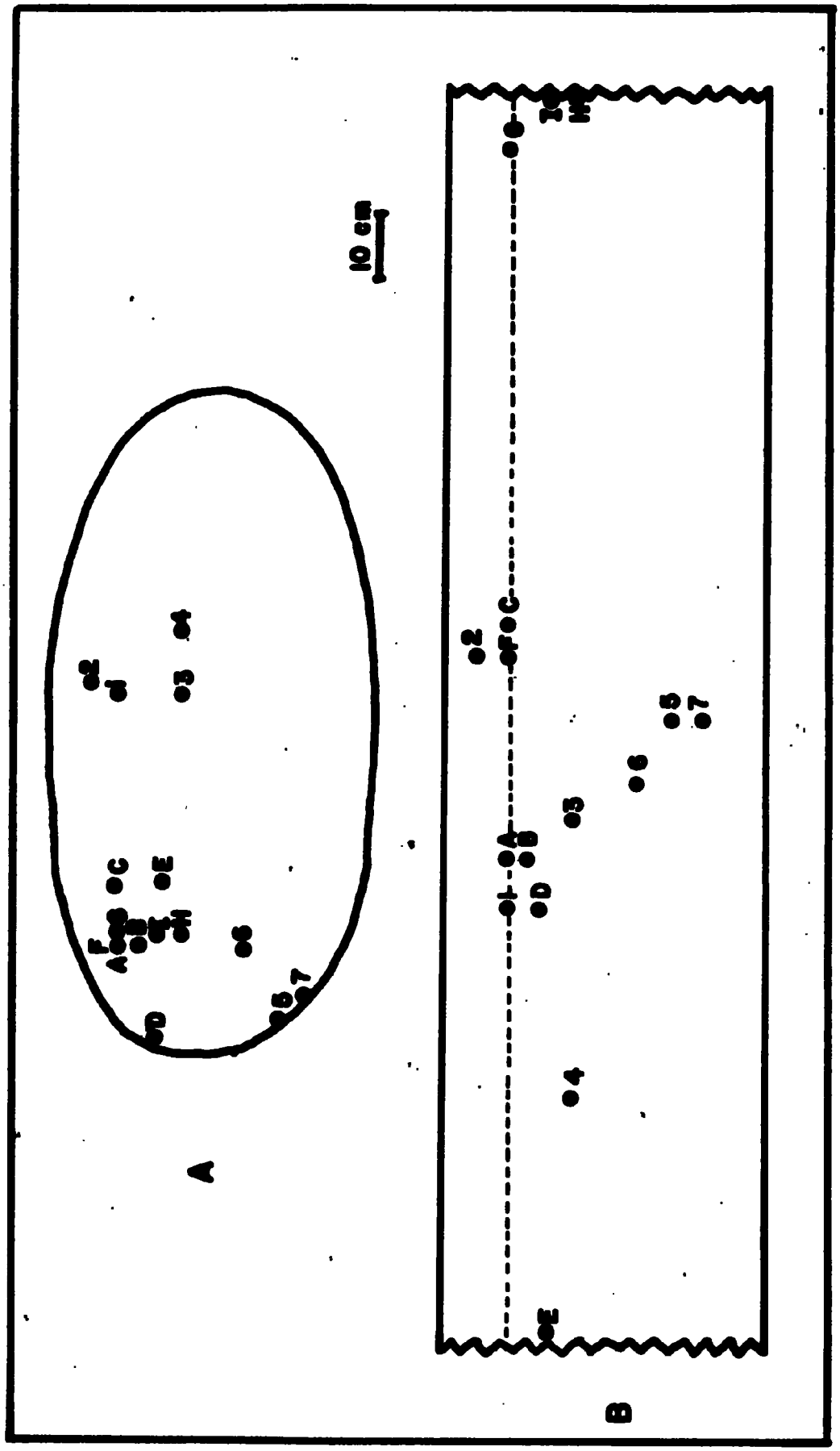


FIGURE 1

Shortest direct distances between two nests were 3 cm for one pair, 4 cm for another, with a third pair (A and F) on the same cleavage plane 30 cm apart. However, around those nests which were in or above this cleavage plane (dotted line on Fig. 1) and thus in the zone of roots and humus, movement was less obstructed than below. It is also probable that the females entered the log and traveled along this crevice before ovipositing. Since most of the nests and individuals were on the left, or uphill side of the log, it is suggested that the ecological conditions, such as moisture content, were more suitable or that entry was easier from that side.

Other organisms found in the log were: three different species of spiders (Araneae), two individuals of one species of diplopod, three individuals of two species of chilopod, one dipteran larva (Tabanidae), one larval and one pupal lepidopteran, three coleopteran larvae and one slug (Mollusca). No vertebrates other than P. cinereus were present. It is clear from this list that the log was not rich in macrofauna, many of which are probably too large for food but not large enough to be predators.

BEHAVIOR PATTERNS OF BROODING FEMALES

Nesting females of the Red-backed Salamander have been found with eggs and young at all stages from oviposition through hatching. It is usually assumed that the female remains with them throughout this time, providing some kind of care, and that her presence has some beneficial effects. Prevention of molding of the eggs (Piersol, 1910; Noble, 1931; and others), retention of moisture (Heatwole, 1961) and protection from predation (Piersol, 1910; Highton and Savage, 1961) have been suggested as possible beneficial effects.

In order to determine the amount and kind of parental care provided by the attendant female and the importance of any beneficial effects, it is desirable to have extended observations of individual females which would provide the following information regarding their behavior: 1) the amount of activity, 2) extent of feeding and/or foraging, 3) whether their behavior changes through the season in any predictable manner, 4) their physical relationship to the eggs and 5) their reaction to disturbance. As it is quite difficult to obtain this information by field studies, observations were carried on during the nesting season in the laboratory. To gain an overall picture of the behavioral patterns throughout this time, an idea of the

range of individual variation and a description of average behavior were major objectives. Although a few observations were made during collecting trips, information on these behavior patterns was derived mostly from laboratory studies.

Field Observations

When the experimental animals were collected, it was sometimes possible to break open the log and expose a cavity without disturbing the female. In these instances the female was always in contact with the eggs. Some had their bodies curled around the eggs with the back or side of the head against them; others were stretched out next to the eggs with some part of the body touching them.

If the nest depression was destroyed when the log was broken open, one of several things occurred: 1) the female immediately began to crawl away, 2) she fell into an open crack, or 3) she remained with the eggs in spite of the disturbance. In addition, some nests were found with no female in the immediate vicinity. Perhaps she had left during the time required to break open the log.

Some of the females were extremely sluggish and could be picked up without difficulty; often they did not move at all for nearly a minute, even retaining the same curled position in the palm of my hand. Others, leaving the nest as it was exposed, required a quick response on my part to capture them. None of the females ever showed any

aggressive response (e.g. biting) when picked up. The frequency of attempts to escape immediately decreased later in the nesting season. An exception to this was a female, collected in August while in the process of oviposition (Davidson and Heatwole, 1960), which was much more active when disturbed than other females collected the same day. Decreased activity may be a function of the length of time she has been with eggs.

Three individuals found in June in the process of oviposition were also very active. Although additional eggs were visible through their body walls, they were never laid after the females were brought into the laboratory. None of these females remained with her eggs in the laboratory nest cavities and one of them ate the two eggs she had laid.

Laboratory Observations

A small basement room was chosen for observation of the brooding females to maintain darkness, high humidity and relatively low temperatures, both to insure the survival of the experimental animals and to approximate field conditions.

Terraria were 60 x 30 x 30 cm, of wood with sliding covers and two glass sides. The bottom of each terrarium was covered to a depth of 4 cm with bog humus, which retained moisture over an extended period of time and could be packed solidly enough to prevent the animals from

burrowing. The humus was kept moist by adding a half pint of water every two weeks.

Eight nest cavities, 6 x 2 cm and 2 cm deep, were constructed in each terrarium, four along each long side. Therefore, the glass at the side of the terrarium was also one side of each cavity. These cavities were lined with small pieces of decayed hemlock log, and a cover of the same wood was placed on each. Small spaces were left under the cover at the ends of each cavity to allow salamanders to enter and leave at will when the cover was placed loosely on top. I found that cavity linings and covers could be used only one year. When I attempted to use them a second time, the eggs had a greater tendency to mold.

The density of the nest cavities was 88 nests/m^3, which was in the general range of those found in the field in a large hemlock log (76.2 salamanders/m^3 and 47.6 nests/m^3). It should be pointed out, however, that the laboratory nest cavities were essentially on one plane, while those in the log were in three dimensions with free movement restricted to cleavage planes and insect tunnels.

The terraria were arranged so observations could be made through the glass sides; however, mirrors were used behind two of the terraria when limited space prevented direct observation of one side.

Four nesting females with their eggs were introduced into alternate cavities in each terrarium. Whenever possible, the animal was brought from the field and put

into a nest cavity within two or three days, although some remained in the plastic bags up to two weeks (in the same room with the terraria) until needed. Eggs still attached to a piece of hemlock from the original nest were placed in a hanging position. Unattached eggs were placed by hand in the center of the cavity. The female was picked up by hand from the plastic bag, gently put beside her eggs and the cover placed over the cavity. The female was prevented from leaving the cavity upon release by holding the cavity cover down for a few minutes, after which the top was replaced on the terrarium and observations begun.

For many experiments in this study, the salamander or the eggs were moved from the nest cavity. Although this could have been done by mechanical means, I found my fingers were apparently least disturbing to the animals, with less danger of injury. Eggs were moved either with a small spoon or by hand. If the eggs were attached to the cavity cover or to a smaller piece of wood, the wood was picked up and the moving accomplished without touching the eggs.

Hygrothermograph records of relative humidity and temperature were kept during the summer of 1959. These showed the relative humidity in the laboratory to be fairly constant throughout the summer, fluctuating usually between 80 and 90%. Psychrometer readings in the summer of 1960 also fell within that range. Readings inside the terraria (obtained with a hand-aspirated psychrometer) were 85-95%

and were very similar to those obtained within logs from which some of the animals were collected.

At the end of each summer, the moisture content of the cavity linings and cover for each cavity was determined by oven drying. Average per cent of dry weight for these cavity linings and covers was 307 in 1959 and 254 in 1960, well above the absorption threshold (65-75) found by Heatwole (1960) for P. cinereus. Average values for each terrarium ranged from 209 to 277 in 1960 and from 252 to 347 in 1959. Samples of the humus from each terrarium averaged 142% of dry weight.

Laboratory temperatures during the summer of 1959 varied from 15.5 to 21.6° C, averaging 18.3° C. For 1960, temperatures went from a minimum of 19.3° C to a maximum of 22.2° C. Temperatures recorded in the field within logs varied from 13.5 to 20.0° C in both 1959 and 1960.

The laboratory was kept dark, with colored light bulbs used only for observation. In 1958, red bulbs (25 watt) were placed in the overhead and side light sockets and a flashlight with red cellophane covering the end was used for close observation. However, because the animals responded to this light, these were all changed to green light in 1959. Although no response by the animals to the overhead green lights was observed, a direct beam from the green flashlight had to be avoided, as the females either turned their heads in the direction of the light or began to move around.

In the first part of this study, records were written at the time of observation. As this limited the records which I could make during an extended observation, a portable Dictet tape recorder was used during the summer of 1960. This enabled me to see the animals and record simultaneously. Following each observation period, the tape was replayed and written records made.

Behavior of Females When First Placed in Nest

Since transfer to a laboratory is obviously an extreme disturbance to the brooding female, her initial behavior after being placed in the terrarium should be indicative of her reaction to disturbing factors in the field. Therefore, observations of such females, collected at various times throughout the summer, should provide a relative measure of the degree to which outside influences will disrupt the brooding behavior and of how this is related to the length of time she has been attending the eggs.

Upon being placed in a laboratory nest cavity with her eggs the female usually was active for 5 or 10 minutes, either crawling around within the cavity or, if her body remained stationary, moving her head in several directions. Following this initial activity, most females quickly assumed a position in contact with the eggs and sometimes curled around them. Others did not remain within the cavity but began crawling in and out of other cavities. Some explored only one or two other cavities before

returning; others explored all of the other cavities before returning, and some never returned. Those which did not return were observed in cavities without eggs for one to three days, after which they usually were found between the cover of one of the empty cavities and the humus on which it rested. If I then placed them in a cavity with eggs, they showed no apparent interest and did not remain.

If females were in contact with the eggs in the collecting bag while waiting for transfer to the laboratory nest cavities, they were more likely to continue to attend the eggs after transfer. Of the nine known to be in contact in the bags, all remained with their eggs after transfer. On the other hand, of five not in contact in the bags, three remained and two did not. Also, I found in a previous study that it was especially important that the female remain in the cavity for at least the first few minutes. Those females which left the cavity immediately upon release never returned. Therefore, after placing each female in a cavity, I imprisoned her for five minutes by holding the cover down.

The response of the female to being moved to a laboratory nest cavity was greatly dependent upon how early in the nesting season this was done. Some females transferred in the middle of June did not attend their eggs in the laboratory, whereas after the 6th of July, all females continued to attend their eggs after transfer to the laboratory. (Fig. 2). Females collected or transferred late in

FIGURE 2. Relation of time to continuance of brooding by females after their transfer with eggs from the field to laboratory nest cavities during the 1959 and 1960 nesting season.

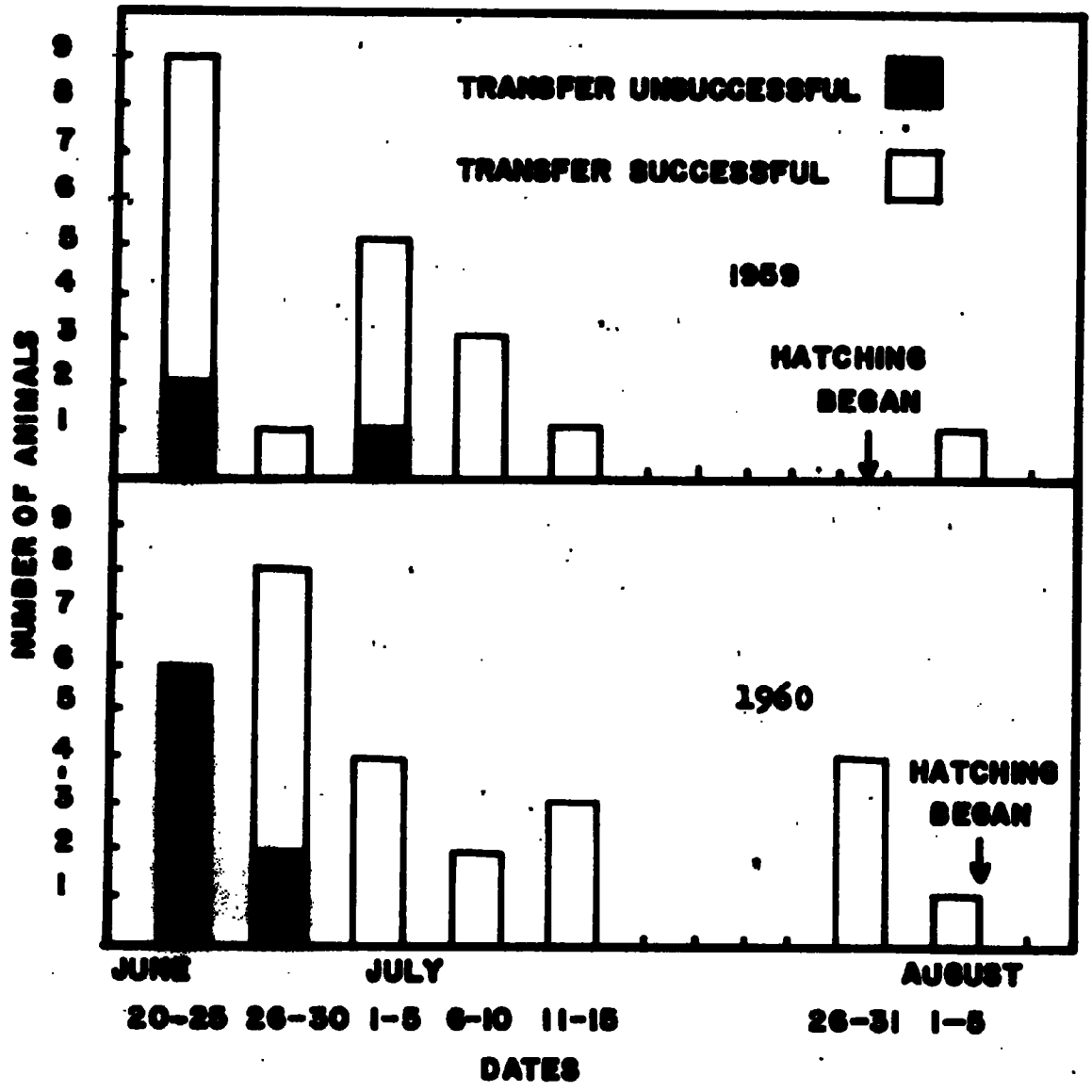

TRANSFER UNSUCCESSFUL
TRANSFER SUCCESSFUL
1959
HATCHING BEGAN
1960
HATCHING BEGAN
NUMBER OF ANIMALS
JUNE
JULY
AUGUST
20-25 26-30 1-5 6-10 11-15 26-31 1-5
DATES

FIGURE 2

the season and placed into cavities generally moved into contact with their eggs rather rapidly, usually curling around them. These females rarely wandered from their cavities; even if I moved them away, they returned.

This difference in behavior is related to the length of time which elapsed since the female began attending the eggs, rather than to any specific calendar date. For example, two females were collected on June 29, 1960, which had not laid all of their eggs, as evidenced by the presence of large eggs in the abdomen. After transfer to the laboratory, one female ate her eggs and the other left the cavity and did not return. Also, a single female found in the midst of oviposition in early August (when other eggs were hatching) exhibited behavior similar to females in June. She left the cavity as soon as she could escape and cared for the eggs only when I moved them to the cavity in which she finally settled.

Thus, the greater the length of time that has elapsed since a female began attending the eggs, the less likely she is to leave them if she is disturbed; therefore, disturbances early in the nesting season are more likely to cause the female to desert her eggs.

Behavior of Established Females

Position in nest in relation to eggs and cavity. Soon after they were placed in the nest cavity, those females which did not leave brought some part of the body in contact with or at least close to the eggs. They usually assumed

a position with the long axis of the body along the length of the cavity regardless of the part of the body touching the eggs. When the eggs were hanging in the nest cavity, the female often pushed her head underneath them and remained with them on her neck and back. However, in most cavities the egg clutch was lying on the center of the cavity floor and, although females sometimes were observed with such eggs on their neck or back, they were more often against or around the eggs (Fig. 3). These females remained in the cavity proper with the eggs rather than between the cavity cover and the humus at the edge of the cover as did nonbrooding females and other individuals. Females attending eggs always appeared alert, keeping the head off the cavity floor and at an angle above the body if not against the eggs.

Throughout most of the nesting season, the majority of brooding females maintained physical contact with their eggs (Tables 1 and 2). Although as much as 32% of the observations in some early periods of the nesting season were of females not in contact with eggs, later this was usually less than 5%. The head, either alone or in addition to other parts of the body, was most often in contact. The part of the head used was somewhat related to the position of the eggs, whether they were hanging from the roof of the cavity or unattached. For example, hanging eggs were usually touched by the back of the head or neck, others by the side of the head or chin. Often

FIGURE 3. Variations in physical contact with eggs by brooding females. A. Eggs on head and neck. B. Side of head against eggs. C. Curled around eggs. D. Chin on eggs. Sketches made from observations of specific females.

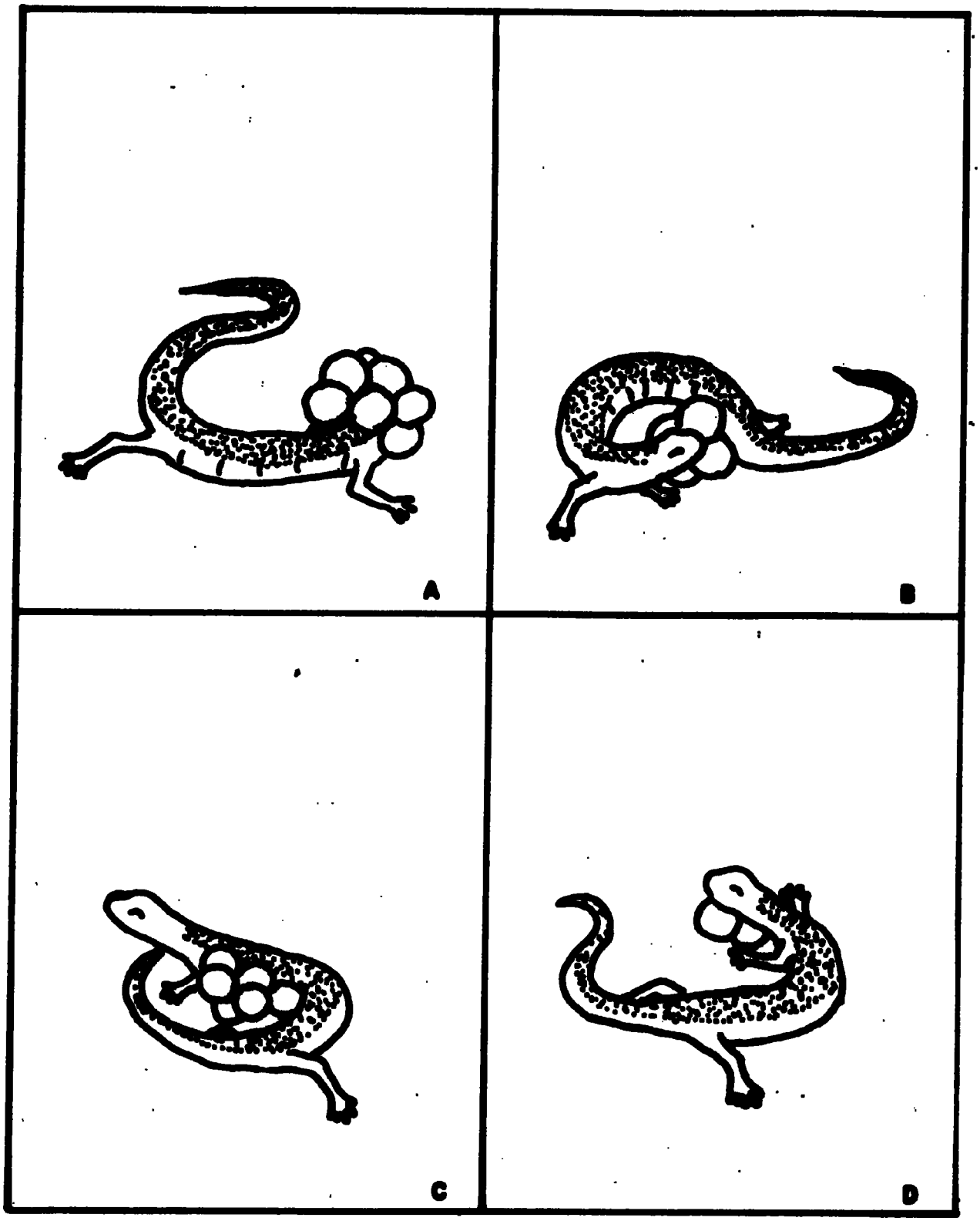


FIGURE 3

TABLE 1. Laboratory observations on contact of brooding females with eggs during the 1959 nesting season.

Dates	Part of body in contact with eggs									
	Head alone		Head & Body, with or without tail		Body, with or without tail		Tail alone		None	
	No.	%	No.	%	No.	%	No.	%	No.	%
June 20 - 25	7	39	1	6	4	22	2	11	4	22
June 26 - 30	31	46	2	3	8	12	5	7	21	32
July 1 - 5	55	65	3	4	12	14	1	1	13	15
July 6 - 10	125	58	22	10	40	19	6	28	23	11
July 11 - 15	111	47	48	20	64	27	9	4	2	1
July 16 - 20	63	45	55	37	18	13	4	3	1	1
July 21 - 25	102	43	103	43	27	11	1	1	5	2
July 26 - 31	75	37	87	43	31	15	4	2	6	3
Aug. 1 - 5	41	32	61	48	21	17	3	2	1	1
Aug. 6 - 10	22	43	21	41	7	14	1	2	0	0
Aug. 11 - 15	7	28	10	40	5	20	2	8	1	4
Aug. 16 - 20	1	17	1	17	4	66	0	0	0	0

TABLE 2. Laboratory observations on contact of brooding females with eggs during the 1960 nesting season.

Dates	Part of body in contact with eggs									
	Head alone		Head & Body, with or without tail		Body, with or without tail		Tail alone		None	
	No.	%	No.	%	No.	%	No.	%	No.	%
June 20 - 25	no data		-	-	-	-	-	-	-	-
June 26 - 30	11	44	2	8	5	20	6	24	1	4
July 1 - 5	40	49	20	24	8	10	5	6	9	11
July 6 - 10	29	44	16	24	18	27	2	3	1	2
July 11 - 15	11	21	27	52	14	27	0	0	0	0
July 16 - 20	5	17	21	72	3	10	0	0	0	0
July 21 - 25	1	7	8	53	3	20	2	13	1	7
July 26 - 31	14	33	21	48	8	19	0	0	0	0
Aug. 1 - 5	26	27	54	56	15	16	0	0	1	1
Aug. 6 - 10	22	28	33	42	19	24	3	4	2	3
Aug. 11 - 15	11	22	20	40	10	20	3	6	6	12

the female curled around the eggs. For the different time periods, the frequency of curling ranged from 32-91%. Females which were curled around the eggs generally had their heads in contact.

The strength of the female's tendency to maintain physical contact with her eggs was shown by one which followed an insect moving through her cavity until only her tail touched the eggs. Although the insect was almost within reach, she did not continue but turned back into the cavity and curled around her eggs.

Change of position through the nesting season. When the position of the brooding female in relationship to her eggs is analyzed on the basis of time throughout the nesting period, differences appear in the tendency to keep specific parts of the body against the eggs.

Although most females kept the head against the eggs, this tendency did not remain the same throughout the nesting period. The number of observations of this contact rose from less than 50% in the first ten days to nearly 90% in the middle of July and began to drop a few days before hatching (Fig. 4). This trend toward increased head contact is further supported by the close correlation which exists between results for the two separate nesting seasons.

If these results are further separated according to whether contact is by the head alone or by head and body, another change becomes apparent. In the first five days of observations in 1959, 39% of the females kept only the

FIGURE 4. Variation through the nesting seasons of 1959 and 1960 in frequency of observations of females having head contact with their eggs. Sample sizes for each five day period are the same as those given in Figs. 5 and 6.

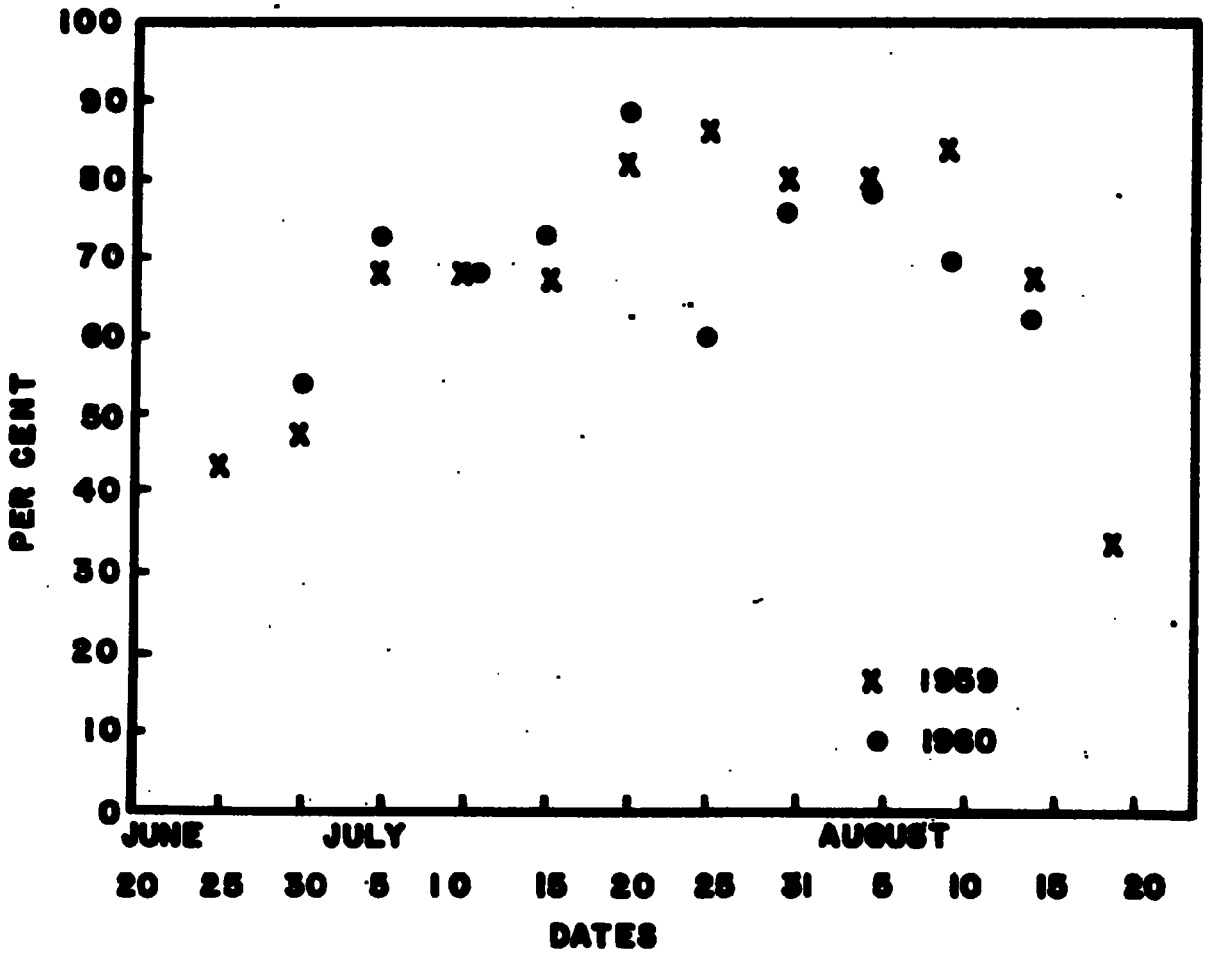

100
90
80
70
60
50
40
30
20
10
0
PER CENT
1959
1960
JUNE
JULY
AUGUST
20 25 30 5 10 15 20 25 31 5 10 15 20
DATES

FIGURE 4

head against the eggs, while 5% used the body as well. Similar results were found for June in both 1959 and 1960. However, by the middle of July the relationship had reversed, as more animals had head and body in contact and fewer had only the head touching (Figs. 5 and 6). These results show a closer physical relationship of the brooding female with her eggs as the nesting season progresses and more of the body comes in contact.

This same trend through time from head alone to head and body contact also appears when records of specific individuals are analyzed.

From the close agreement which exists between results for the two summers and between average and individual data, it seems probable that the strong attraction to eggs exhibited by brooding females develops as a function of the time she attends the eggs.

In addition to the amount of contact with eggs, observational records from the summers of 1959 and 1960 were analyzed to see if the degree to which the female curled around her eggs was dependent upon time. Any tendency of the female to flex her body around the eggs was designated as curling. This was further subdivided into three categories: 1) loosely curled, 2) moderately curled, and 3) tightly curled. Individuals which had only the anterior or posterior half of the body around the eggs were designated as loosely curled, those with most of the body around the eggs as moderately curled, and individuals

FIGURE 5. Observations of physical contact with eggs by brooding females during the 1959 nesting season. Along the curve are given the total number of observations for each five day period.

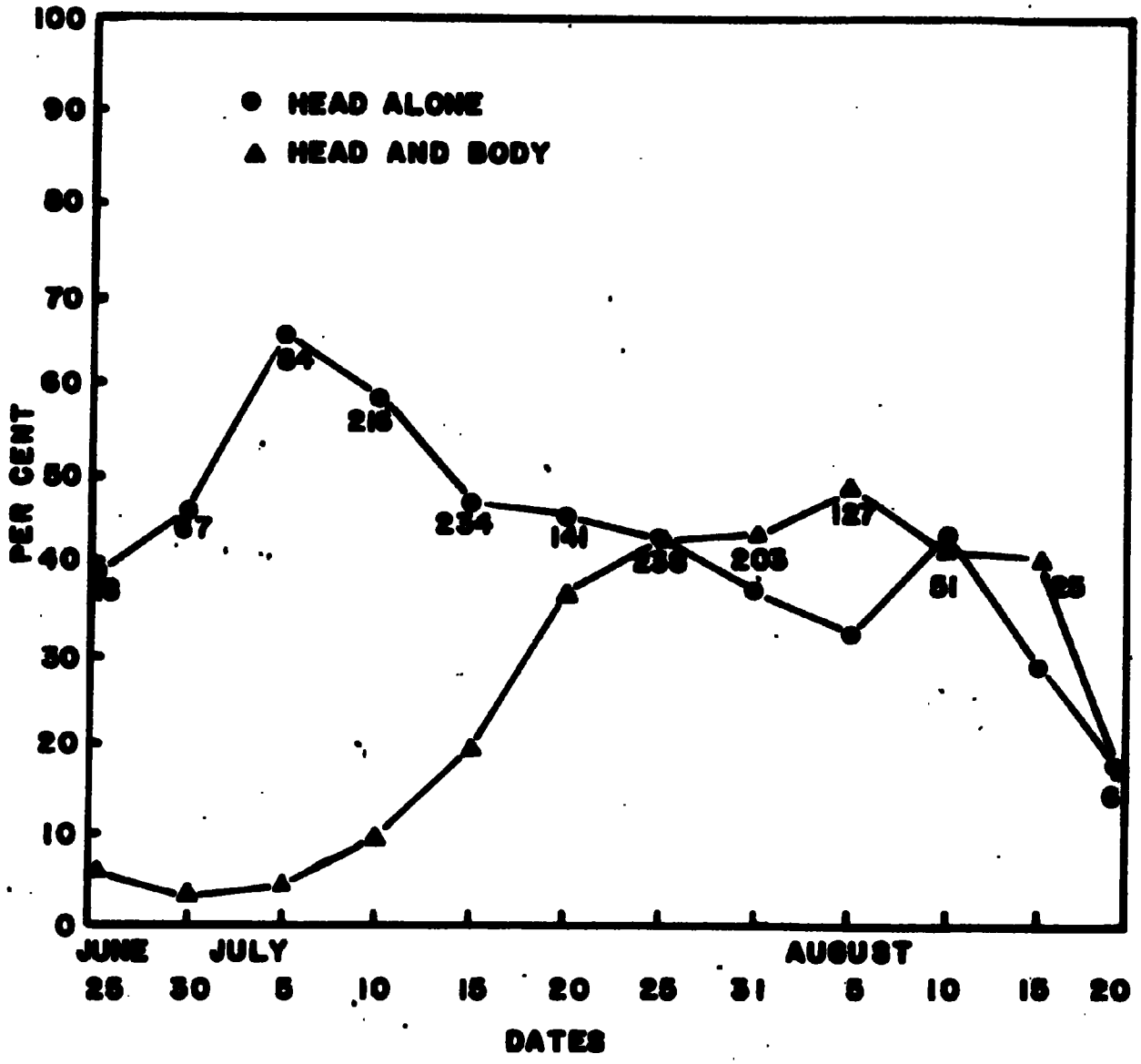

HEAD ALONE
HEAD AND BODY
PER CENT
100
90
80
70
60
50
40
30
20
10
0
64
215
234
141
127
51
JUNE
JULY
AUGUST
25
30
5
10
15
20
25
31
5
10
15
20
DATES

FIGURE 5.

FIGURE 6. Observations of physical contact with eggs by brooding females during the 1960 nesting season. Along the curve are given the total number of observations for each five day period.

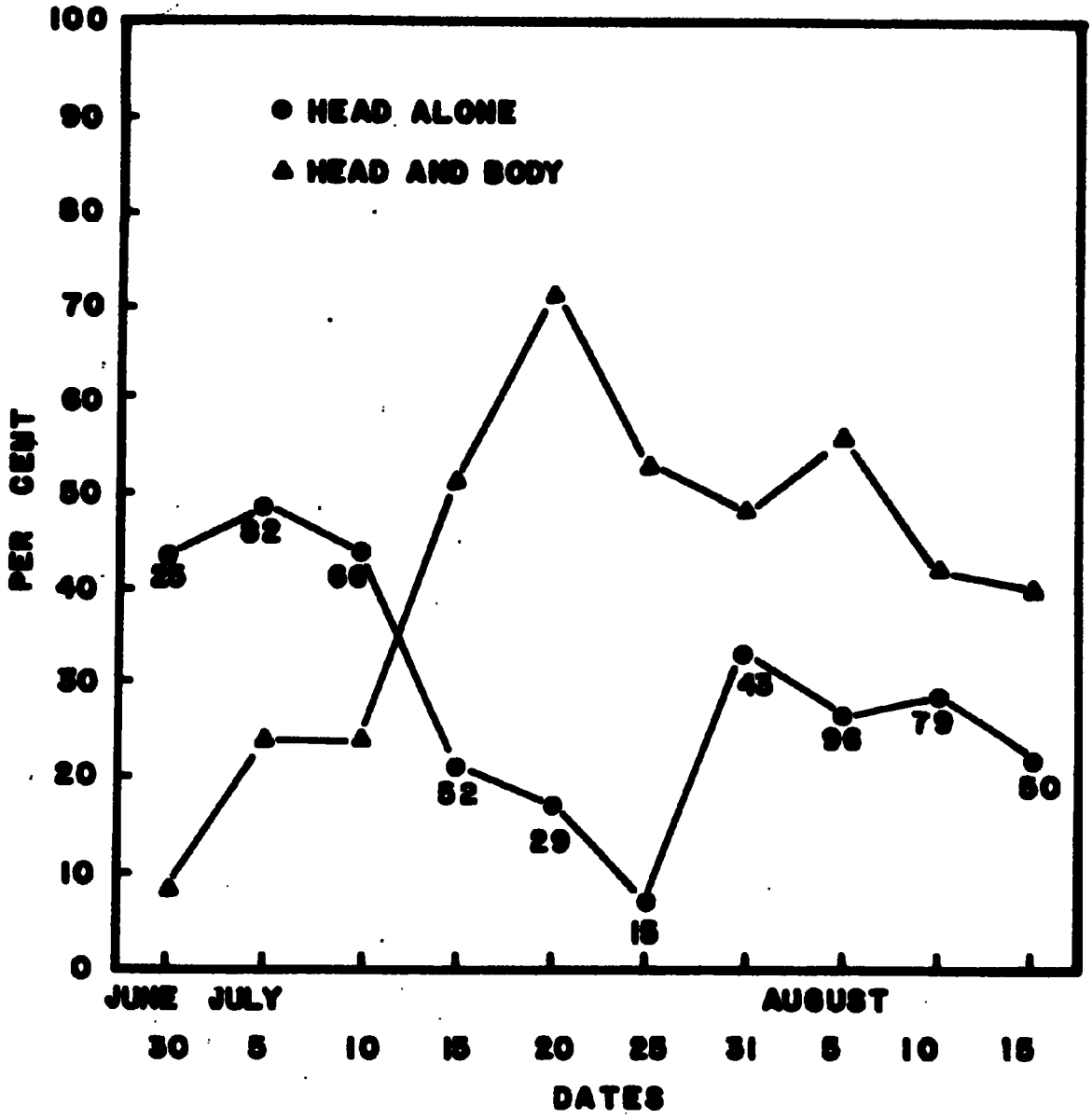

100
90
80
70
60
50
40
30
20
10
0
PER CENT
● HEAD ALONE
▲ HEAD AND BODY
43
52
44
21
16
33
26
28
21
JUNE
JULY
AUGUST
30
5
10
15
20
25
31
5
10
15
DATES

FIGURE 6.

with the whole body around the eggs, the head and tail sometimes overlapping, as tightly curled. While the first two categories usually but not always involved body contact, the third always included close contact.

Figures 7 and 8 show the degree of curling for five-day intervals during the 1959 and 1960 nesting seasons. Whereas less than 30% of the females showed any degree of curling around their eggs during the beginning of the experimental period, by the middle of July, 85-92% of them were curled. Most of these latter individuals were either moderately or tightly curled. The percentage of curling began to decrease after July 25 as the time of hatching approached. Although the percentages of those tightly curled show the same fluctuations, the moderately curled rose from 4-5% in June to 60-75% by the middle of July, then dropped to 30-32% by August 15.

When the three categories of curling are combined and graphed comparatively for 1959 and 1960 (Fig. 9), the resulting curves are quite similar. Comparable results for 1960 appear to be approximately five days behind those for 1959, suggesting a lag of almost a week in the 1960 nesting season. The possibility of such a lag in 1960 is supported also by other laboratory and collecting data. In 1960, two females were collected on June 29 which had not finished ovipositing, whereas all individuals collected in 1959 (beginning June 18) had already oviposited. In addition, no females transferred to the laboratory in

FIGURE 7. Degree of curling around eggs by brooding females during the 1959 nesting season. Data are plotted for five day periods.

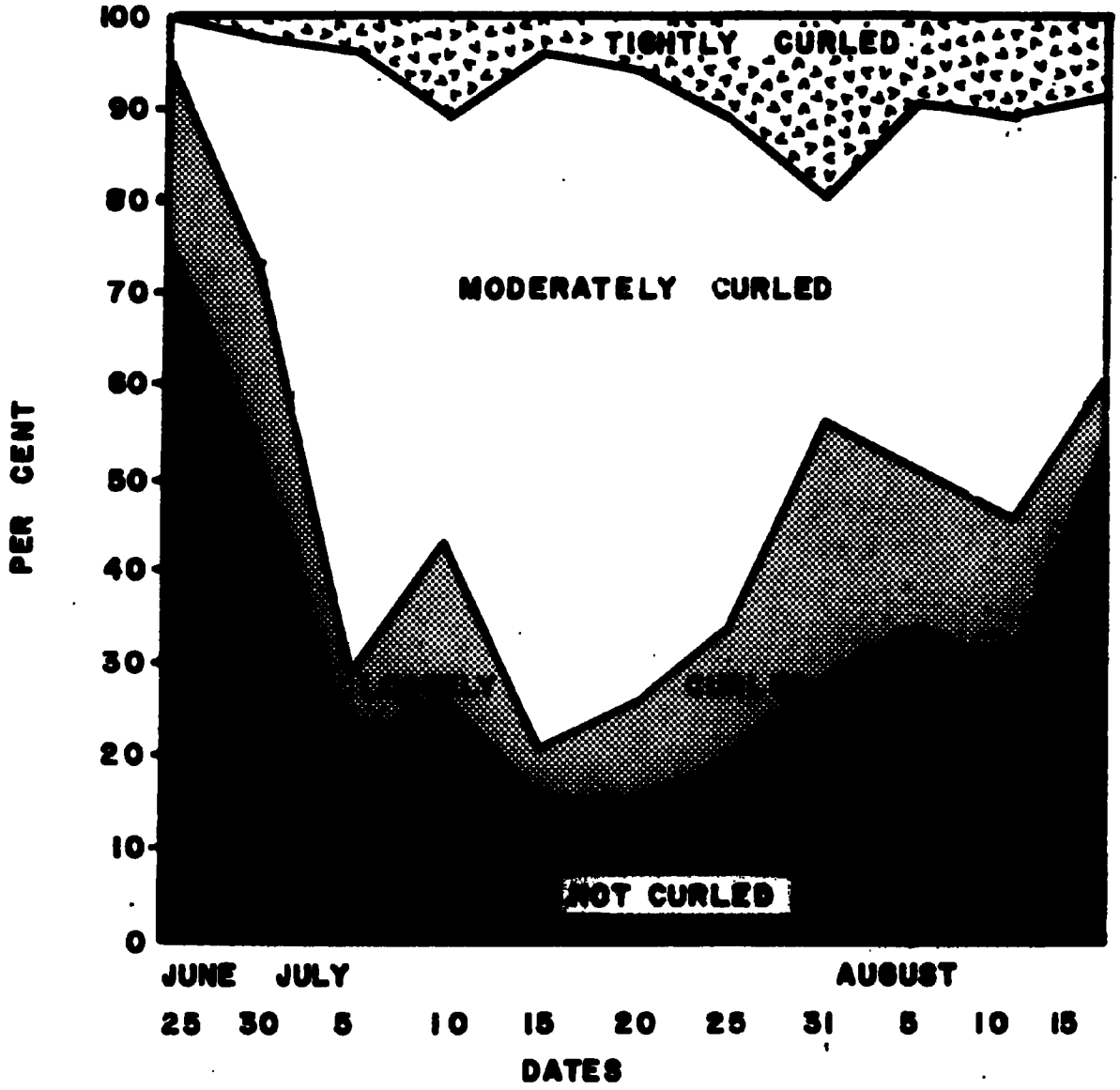

100
90
80
70
60
50
40
30
20
10
0
PER CENT
TIGHTLY CURLED
MODERATELY CURLED
NOT CURLED
JUNE
JULY
AUGUST
25
30
5
10
15
20
25
31
5
10
15
DATES

FIGURE 7.

FIGURE 8. Degree of curling around eggs by brooding females during the 1960 nesting season. Data are plotted for five day periods.

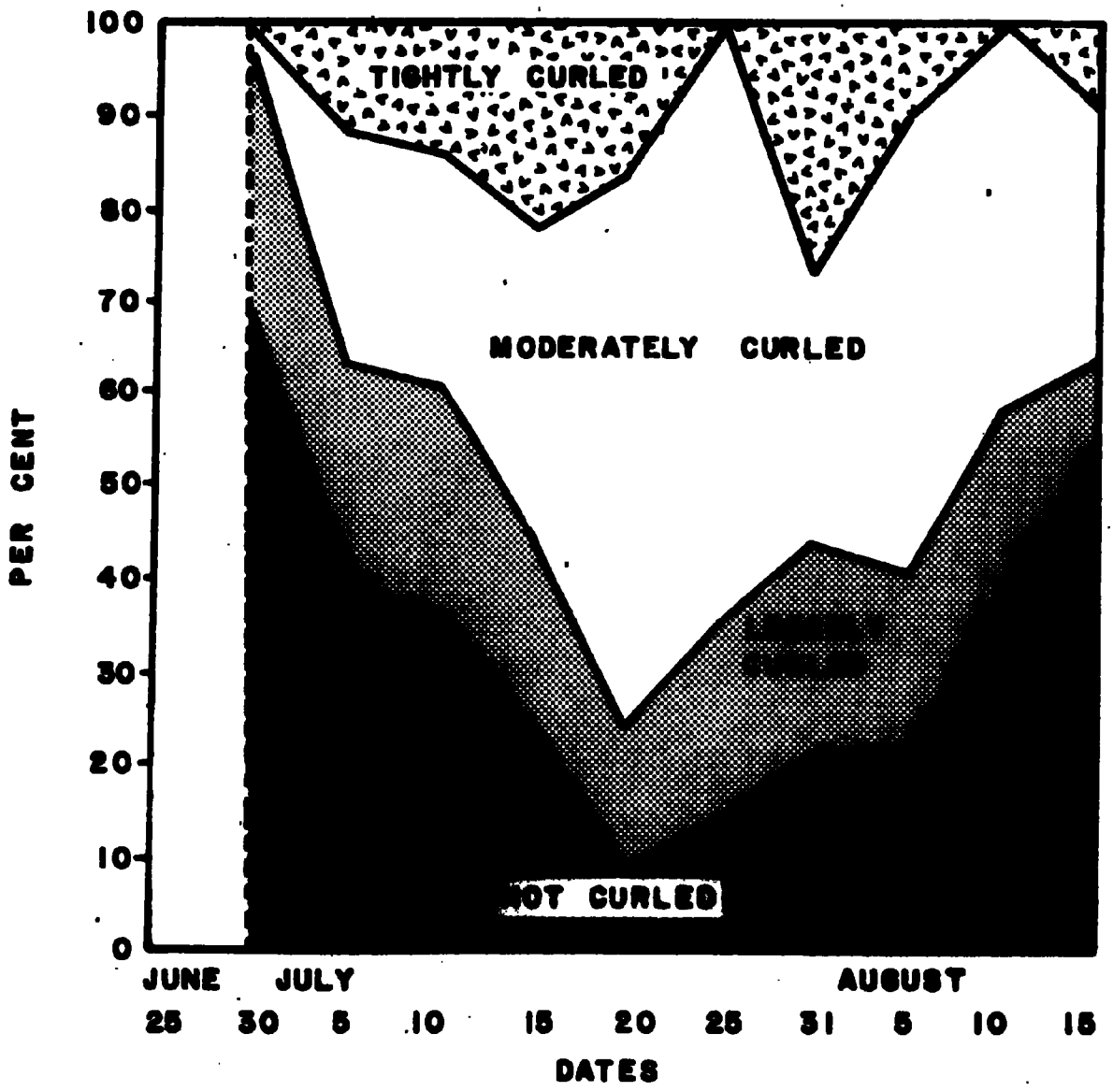

100
90
80
70
60
50
40
30
20
10
0
PER CENT
TIGHTLY CURLED
MODERATELY CURLED
NOT CURLED
JUNE
JULY
AUGUST
25
30
5
10
15
20
25
31
5
10
15
DATES

FIGURE 8.

FIGURE 9. Variation in proportion of observations of females curled around their eggs through the nesting seasons of 1959 and 1960. Total numbers of observations for each five day period are the same as those given for Figs. 5 and 6.

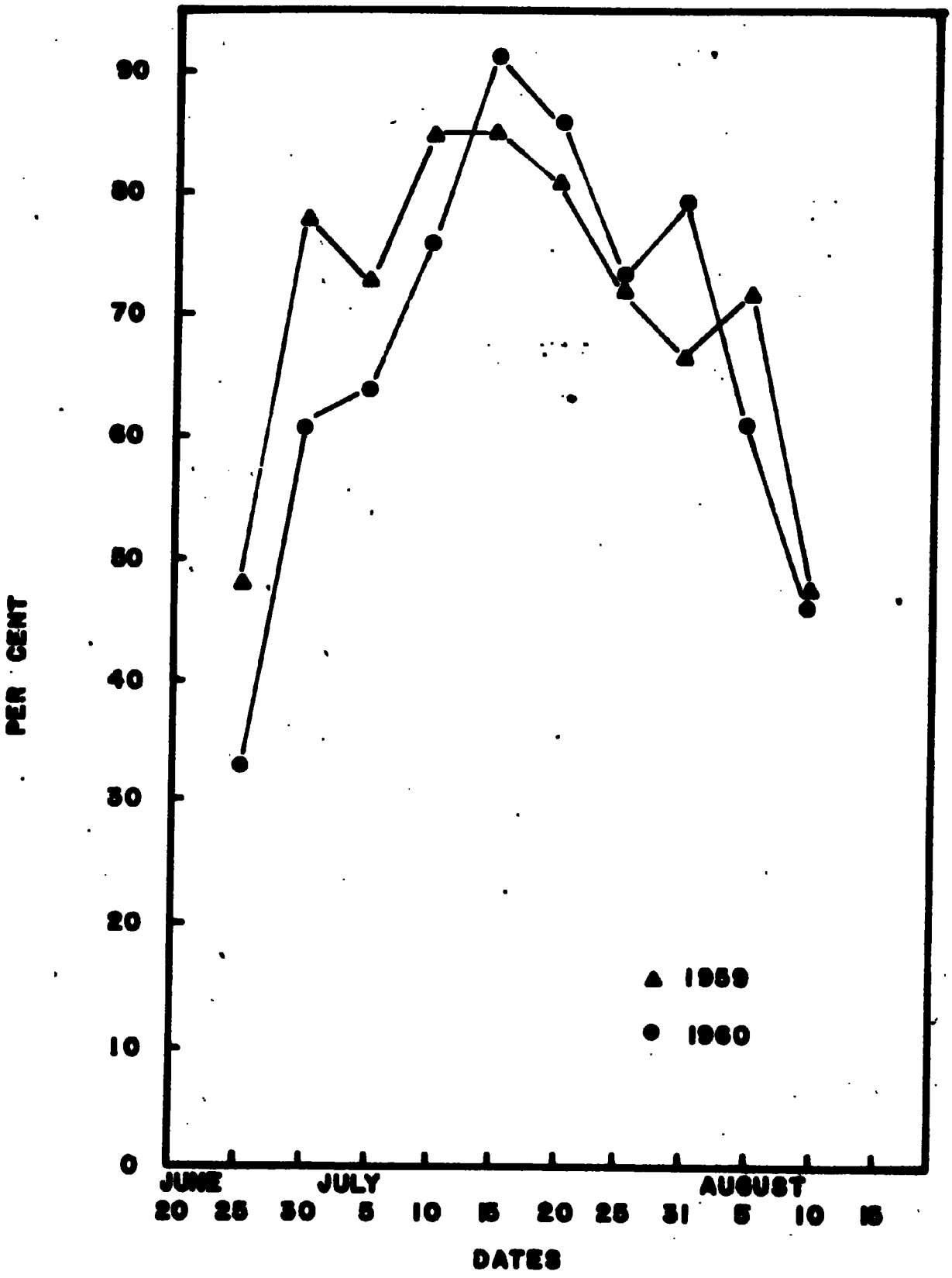

90
80
70
60
50
40
30
20
10
0
PER CENT
JUNE
JULY
AUGUST
20 25 30 5 10 15 20 25 31 5 10 15
DATES
▲ 1959
● 1960

FIGURE 9.

June 20-25, 1960, remained with their eggs in contrast to seven out of nine which did in 1959 (Fig. 2).

The tendency of brooding females to curl around their eggs probably represents a form of maternal care. Since a curled position generally involves a greater degree of body contact than other positions, any beneficial effects of such contact will be maximized.

The literature contains numerous references to attendant females maintaining body contact with their eggs. Piersol (1910), for example, mentions observing females in the field which were holding the dorsal surface of the head and neck against the eggs. However, none of these observations provides any information on whether these females remained relatively immobile while attending the eggs or moved around within the nest cavity.

My observations of nesting females, made one to several times daily over a period of two months, include records of the position of the females in relation to the eggs at each observation. Any change in the recorded position indicates at least one movement by the female in the intervening time. Obviously, the female may have assumed several different positions in the meantime, and even possibly have reassumed the original position; therefore, recorded changes of position must be regarded as minimal.

Position records from June through August were analyzed for each of seven animals selected at random. The close

agreement of results made further analyses seem unnecessary. The percentage of times when the female had moved varied from 61 to 75 (average of 67) for the seven females, with 30 to 42 records for each.

It can be concluded, then, that attendant females do not maintain the same position in relation to the eggs for any length of time and probably change position one or more times a day. As observations were taken no closer than five hours, the actual amount of intracavity movement is probably greater than the data indicate.

Extracavity Movement of Brooding Females. The question of whether the female remains in the nest cavity continuously or occasionally leaves (perhaps to forage for food as suggested by Burger, 1935) is of interest for several reasons. The existence of such movements would provide opportunities for interaction with other brooding as well as nonbrooding individuals, increase the possibility of encountering organisms suitable as food, and increase the chances of egg injury or predation by other organisms in the absence of the female. Since Highton and Savage (1961) found that unattended clutches of eggs were less likely to hatch, it is possible that inconstant attendance would reduce egg survival.

From my records on 15 brooding females from June 25 to August 7, 1960, I determined the percentage of times that each was found outside of the cavity. These ranged from 3 to 91% with an average of 21%. However, if those females

in terrarium B are omitted, the range narrows to 3-18% and the average drops to 10%. (Table 3).

Of the salamanders in terrarium B, B1 attended her eggs regularly. On observed occasions when she left them, she was found entering other cavities which were inhabited by brooding females. A few days after she was placed in the cavity, B3 deserted her eggs and remained under various cavity covers throughout the remainder of the summer. B6 became less and less regular in attendance and also remained under cavity covers. B8 alternated in the early part of the season between the eggs of B3 and her own, eventually abandoning her own eggs, which then molded. Why the females in this terrarium were so much less regular than others in attending their eggs is a matter for conjecture. It is possible that the presence of one or two restless individuals affects the others. It cannot be due to experimental disturbances alone, for the animals in terrarium D, though disturbed for experiment most often, were among the most regular attendants.

Those salamanders which were not in their cavities at the time of observation were most often in another cavity rather than under covers or on the exposed humus. On the occasions when they were seen entering other inhabited cavities, they did not stay long; usually within a few minutes they crawled out again. There was one notable exception to this. At the beginning of the nesting season B1 and B8 were both found in the cavity of B3 several times

TABLE 3. Extracavity movement of brooding females and its relationship to egg survival (17 - 41 observations for each female in the summer of 1960.) Late embryos includes those which hatched by the end of the experiment.

Animal	Estab. in lab. cavity	Frequency of disturb.	% of observations out of cav.	No. orig. eggs	No. Late embry.	No. molded in lab
D1	6/28	Often	8%	7	6	0
D2	6/28	Often	10	7	3	0
D3	6/28	Often	3	10	4	0
C3	6/28	Often	11	7	7	0
B1	6/30	Occas.	17	5	5	0
B3*	6/30	None	91	6	6	0
B6	6/30	None	52	6	2	4
B8**	6/30	Rarely	48	5	0	5
G2	7/4	Occas.	7	5	5	0
G4	7/4	Occas.	17	2	2	0
G8	7/4	None	8	7	7	0
F2	7/4	Occas.	10	6	6	0
C1	7/11	None	12	4	4	0
C6	7/11	None	6	5	5	0
C7	7/11	None	18	4	4	0
Average			21			
Average when terrarium B is not included			10			

* Deserted eggs two days after placement in cavity.
**Cared for eggs of B3 also and finally deserted her own on July 13.

in succession. Females which were frequently found under the cavity covers were only those which were irregular attendants or which had deserted their eggs.

These data indicate that the extracavity movement of nesting females is probably not great. How much of this movement actually does exist under field conditions is not known and would only be revealed by further study. However, between 1958 and 1960, an attendant female was present in 74 (86%) of 86 nests found. Furthermore, the females not found were probably disturbed by the collecting procedure. Therefore, opportunities for social interaction with other individuals are possible, but limited.

In the two clutches of eggs deserted, and not attended by any other female, there was a high incidence of molding and poor survival of the embryos. On the other hand, within the normal range of extracavity movement (3-18%), there was no apparent reduction in survival.

In terrarium D, where the animals were often disturbed by the experimenter, 11 of the original 24 eggs could not be accounted for at the end of the experiment (Table 3). In the absence of predators their disappearance was almost certainly caused by oophagy. Egg disappearance also occurred among females collected during the early part of the nesting season, when it was difficult to get them to remain with their eggs in the laboratory nest cavities. Highton and Savage (1961) also state that oophagy occurred during the first 10 days following induced

oviposition.

Reaction to Disturbance. The tendency of P. cinereus in northern Michigan to nest in cavities and crevices within decaying hemlock logs has been discussed previously. Within these logs the animal normally finds a high relative humidity and is protected from the drying effects of solar radiation and air movements. The importance of moisture to this terrestrial amphibian has been well shown by Heatwole (1960) in his studies on desiccation. Because of their location, these nests are in continual darkness and also are relatively protected from sudden sounds or vibrations. Thus, the combined effects of a positive response to moisture (Heatwole, 1960) and a negative response to light (Test, 1946) are important factors in the selection of suitable nest sites. In the relatively stable environment of nest cavities within logs, any change in such factors as light, sound or vibration may elicit behavioral responses by the brooding female.

In laboratory studies of behavior, such factors, as well as those resulting from the presence of the experimeter, may act as disturbing factors and thus become added variables. Observations of the responses of the experimental animals to a disturbing factor allowed the experimenter to minimize it and at least to recognize the extent to which it influenced the animal's behavior.

Responses by brooding females to different types of light were: 1) a movement of the head, first toward the

light for several seconds to minutes and then away from the source, and 2) if the light was not removed, movement of the whole body away from the light and out of the cavity. Light from an unfiltered incandescent bulb, either diffuse or concentrated, caused both responses 1 and 2; therefore, it was not used in this study. A direct and bright light, such as from a flashlight, usually brought a quick retreat by the animal. Red light, unless weak, such as from a 25 watt bulb 3 or 4 feet away from the terrarium, elicited response 1. Since it was not possible for me to observe the animals adequately under light weak enough to elicit no response, red light was discontinued. Green light evoked both responses if a flashlight was shone directly at a female, but no responses were observed with the overhead 25 watt bulb or when the outer margin of the flashlight beam was used. Vernberg (1955) also found that P. cinereus responded less to green than to red light.

There was no observable response to the experimenter's voice, even during continued periods of dictation, or to any laboratory vibrations which did not directly contact the terrarium. However, if care was not taken in removing or replacing the terrarium cover, the females would leave the nest cavity. On the occasions when one or more females were observed to leave after such disturbances, they were usually in the cavities again within five or ten minutes.

At no time did any of the experimental animals exhibit

any aggressive responses toward the experimenter. Fingers placed into the cavity caused the female to retreat. Upon being picked up, the female generally attempted to escape. As mentioned previously, the effect of disturbance upon the nesting female was greater at the beginning of the nesting season. For example, the reaction of the animal to being picked up was much more violent during the early part of the nesting season.

Feeding During the Nesting Season. Organisms eaten by P. cinereus have been listed by several authors (for example, Murphy, 1918; Smallwood, 1928; Hamilton, 1932; and Brandt, 1946), based on analyses of stomach contents. From this type of work the diet is indicated to be composed mostly of small insects and other invertebrates. Since nesting females are attending their eggs during two months of the time when such food is abundant, it becomes important to know whether they feed during this period. Although Burger (1935) believed that females did actively forage for food, it is generally assumed that brooding plethodontid females do not obtain much food during the nesting season. Organ (1960b) described females of P. welleri with young hatched as"....very much emaciated". Gordon (1952) found stomachs and intestines of Aneides aeneus empty and observed that brooding females were thinner than males at the end of the brooding season. Smallwood (1928) found no mature females of P. cinereus near the surface of the ground during the nesting season and stated that they fed when

they came up late in the summer. Six brooding females which I dissected during July and early August had empty stomachs and intestines.

Food organisms were offered to 16 brooding females during the summers of 1959 and 1960 to determine whether females accept food while attending eggs, if they leave their eggs in pursuit of food, and whether they actually forage for food. Although no attempt was made to cover the range of acceptable food organisms, several kinds and sizes were used. Results of these feeding experiments are given in Table 4.

The food organisms were placed in the nest cavity by slightly opening the cavity cover and dropping them from the tip of a spoon. When fruit flies (Drosophila melanogaster) were used, they were first anaesthetized. The amount of time between introduction and ingestion of the food organism includes the time required for the flies to recover from the anaesthetic.

All of the females showed a definite interest in at least some of the offered food organisms, and when fruit flies were used only one did not eat. Of 186 flies placed in cavities, 47% (88) were eaten while observations were being made. It is not known how many of the remainder were eaten at a later time. From 2 to 16 flies were placed in a cavity at one time; females were observed eating 1 to 12 of these flies. Females often were seen moving around within the cavity with their snouts close to the floor,

TABLE 4. Reaction of brooding females to potential food organisms inside and outside of nest cavities. Time includes up to 20 minutes required for flies to recover from anaesthetic (salamanders ate only active flies). (-) indicates flies were eaten outside cavity. "Interest shown" refers to orientation by female toward food organism.

Animal	Date 1959	Organism	No.	Interest shown	No. eaten	Time in minutes	♀ left cavity	Remarks
A3	7/11	Drosophila	6	yes	?	30	no	None eaten in 30 min.
Ter. A	7/12	Drosophila	12	no	0		no	Flies on humus outside cavities
A3	7/15	Drosophila	8	yes	2	10	no	
A1*	7/24	Drosophila	3	yes	3	32	no	Flies - 20 min. to begin moving
A3	7/24	Drosophila	3	yes	3	14	no	
Ter. A	7/25	Drosophila	12	no	0		no	Flies on humus outside cavities
A8*	7/29	Drosophila	8	yes	1	13	yes	
A6*	7/29	Drosophila	8	yes	0		no	
A8	7/29	Drosophila	8	yes	1	2	no	
A6	7/29	Drosophila	8	yes	3	21	no	
A1	8/5	Drosophila	12	yes	12	30	no	
A3	8/5	Drosophila	12	yes	11	30	no	

TABLE 4. (Continued)

Animal	Date	Organism	No.	Interest shown	No. eaten	Time in minutes	♀ left cavity	Remarks
	1960							
Ter. D	7/18	Drosophila	16	yes	(5)		yes	Two females left cavities for flies
D2	7/18	Drosophila	14	yes	4(2)	45	yes	
D2	7/18	Drosophila	10	yes	3	16	no	
D8*	7/20	Earthworm 3 cm	1	yes	½cm	5	no	Held on until worm broke, ate the piece
C3	7/20	Earthworm 4 cm	1	yes	0	15	no	Bit worm 4 times, then held on 2 minutes
C1*	7/20	Earthworm 4 cm	1	no	0		no	Female backed up under cavity cover
C8*	7/20	Earthworm 3 cm	1	yes	0		no	Snapped once at worm
G6	7/28	Drosophila	12	yes	6(1)	19	yes	Climbed glass after fly
G6	7/28	Earthworm 2 cm	1	yes	0	2	no	Snapped and followed worm to edge of cavity
C3	7/28	Drosophila	10 (6)	yes	10(4)	24	yes	Crawled across humus
C1	7/28	Drosophila	16	yes	9	20	no	Trail of flies from cavity to humus
C1	8/1	Earthworm 1½ cm	1	yes	0		no	Snapped at worm and pushed it from eggs
C3	8/1	Earthworm 1½ cm	1	yes	0		no	Snapped once at worm
B8	8/1	Tenebrio larva 5mm	1	yes	1	2½	no	
C3	8/1	Tenebrio larva 15 mm	1	yes	0	2	yes	Bit it twice and followed to next cavity

TABLE 4. (Continued)

Animal	Date	Organism	No.	Interest shown	No. eaten	Time in minutes	♀ left cavity	Remarks
	1960							
C3	8/1	Earthworm 9 cm	1	yes	1cm	7	yes	Held on until piece of worm broke, ate it
B8**	8/1	Tenebrio larva	2	yes	2	1	no	
B1	8/4	Drosophila	36	yes	1	50	yes	24 of the 36 flies were between cavities
B2	8/4	between cavities 1,2,&3		yes	3	6	no	
B3	8/4	and 4 in each cavity		yes	4(15)	45	yes	
C3	8/4	Drosophila	10	yes	(10)	15	yes	Flies on humus
A3*	8/5	Millipede 3 cm	1	yes	0	1	no	Followed millipede to edge of cavity
F2	8/8	Drosophila	12	yes	4	5	no	
D3	8/8	Drosophila	12	yes	2	10	no	Young also interested
D3	8/8	Drosophila	24	yes	6	25	no	Young also interested

* Animals disturbed experimentally for the first time.
** Attending eggs of B3.

apparently searching for more flies after those offered had been eaten or had crawled away. After all parts of the cavity had been covered, the female resumed attendance of the eggs.

Females exhibited interest in the food by first moving the head in the direction of it, then placing the snout a few millimeters away from the animal. When the insect moved, the female quickly opened her mouth, extended her tongue and ate the fly. If the fly was crawling, the female often kept her snout close to it for several seconds before snapping it up. The typical eating procedure can be described as a slow approach to the food organism followed by a quick flick of the tongue and snap of the mouth. The tongue was not employed in obtaining a larger animal such as an earthworm. Females ate only those organisms which moved and quickly lost interest when movement ceased.

Food organisms were placed on the humus (using the same procedure described above) in several locations: 1) 1-6 cm from the edge of the cavity, 2) in a continuous trail from within a cavity, 3) on the humus near the center of the terrarium.

Of 82 flies on the humus, 40% (33) were eaten; however, 25 of these 33 were eaten by two salamanders. In 8 of the 31 trials, females left the nest cavity to follow food or to reach for food which they apparently could see. One female (B1), after eating flies in her cavity, went to

another nest cavity and ate flies there. Another female followed crawling flies across the terrarium. In contrast, one remained in her cavity and watched flies 3 cm away on the humus, yet made no attempt to get them. A female in terrarium C followed a large beetle larva from her cavity into the next one, snapped at it and returned to her cavity only after the larva crawled out of sight.

Drosophila were employed in most of these experiments and were accepted readily by the females. All of the types of organisms used elicited interest from the females. Beetle larvae and parts of earthworms also were eaten.

The data in Table 4 show that brooding females, while readily eating food organisms which are within the nest cavity, were more reluctant to leave in pursuit of or in search of food. Probably an individual female in the field acquires little food during the time she is attending her eggs.

Return of Displaced Females to Laboratory Nest Cavities

Since brooding females of P. cinereus occasionally left their laboratory nest cavities and returned to them, the next step was to determine whether they would return after being displaced. Although the distances involved in displacement of the females were small (10-30 cm), the results of such trials would indicate the extent of their tendency to return and the ability to recognize a specific cavity and/or eggs.

The animals used for these experiments were kept in the laboratory under the same physical conditions as previously described for this study. Again, the terraria contained eight cavities and four females with eggs. I found that my fingers were best for picking up the females from their nests. In most instances it was possible to move the females with a minimum of disturbance, especially during the last month of the nesting season, when they were more sluggish. Females were placed in the center of the terrarium humus (10-30 cm from their cavities), covered with a petri dish for a few seconds until they faced the desired direction, then released. Timing was begun upon release and observational records, whenever possible, were kept of their subsequent movements until they returned to the cavity.

Upon being released, most of the females turned their heads in several different directions for as long as three minutes before moving away. In traveling from one part of the terrarium to another, nearly all of them followed the edge of a cavity cover and often crawled under a cover, not entering the cavity. Most females did not move continuously but stopped under cavity covers and in cavities, sometimes for several minutes. One female turned her head in all directions after being released, crawled directly to her cavity and entered to curl around her eggs within two minutes.

During the summers of 1959 and 1960, 17 brooding

females were tested in 31 trials for their tendency to return to their laboratory nest cavities. Results of these trials are given in Tables 5 and 6. Every individual except one returned, after being displaced, to its original nest cavity. In the instance where the female did not return, newly hatched young, but no eggs, were in the cavity. Four of the eight cavities in each terrarium were unoccupied by brooding females, and in several trials there were unattended egg clutches present; therefore, the return of the female to the original cavity was not because it contained the only available eggs. The known time required for the return ranged from 2 to 297 minutes. The median return time was 13 minutes, as was the mean when the two trials where the time was unknown and the two longest trials are eliminated.

The direction in which the female was facing at the beginning of the trial was recorded. A comparison of return times for those headed toward the nest cavity and those headed away from it yields median times of 12.3 and 13 minutes respectively (If again the two unknowns and the two longest times are eliminated, the means are 12 and 13 minutes). From these results it is obvious that the direction the female faces upon release has no effect on the time required to return.

Displaced females entered as many as four cavities before arriving at their own nests, but most entered only one or two. Some females entered and re-entered the same

TABLE 5. Time required for displaced brooding females to return to their nest cavities in relation to starting position and number of other cavities entered (summer of 1959). Direction headed refers to whether females placed on humus facing toward or away from their cavities.

Animal	Date	Direction headed	Return time - min.	Other cavities entered: Occupied	Other cavities entered: Unoccupied
C3	7/11	-	31-285*	1	1
C6	7/15	Toward	30	0	1
C6	7/25	-	35-175*	1	1
C6**	7/30	Away	37	0	1
C1	7/15	Away	11	1	1
C1	7/24	Toward	25	0	1
C1	7/25	Away	20	1	1
C8	7/18	Toward	8	1	0
C8	7/24	Away	7	0	0
C8	7/25	-	19	0	1
E1	7/31	-	14	2	2
LBc**	8/1	-	8	1	0

* Female returned in interval between observation periods. Nos. of cavities refer only to observation time and are therefore minimal.

**Eggs in cavity not laid by this female.

TABLE 6. Time required for displaced brooding females to return to their nest cavities in relation to starting position and number of other cavities entered (summer of 1960). Direction headed refers to whether female placed on humus facing toward or away from her cavity.

Animal	Date	Direction headed	Return time-min.	Other cavities entered	
				occupied	unoccupied
C3	7/8	Away	10	0	0
C3	7/20	Toward	12	0	1
C3[c]	8/11	Toward	4	0	0
D1	7/8	Away	297	1*	2*
D1	7/9	Toward	2	0	0
D2	7/11	Away	8	0	0
D2	7/13	Away	10	0	0
D2	7/20	Away	13	0	1
B8[b]	7/13	Away	10-395[a]	1*	0*
B8	7/20	Away	252	1*	0*
WP5	7/25	Toward	15	1	0
B1	7/30	Toward	13	0	1
B1	8/1	Toward	2	0	0
F6	8/2	Away	3	0	0
F6	8/3	Toward	25-425[a]	1*	0*
F2[b]	8/3	Away	28	0	0
D3	8/4	Away	13	0	0
D3[c]	8/12	Away	21	0	0
G8[c]	8/12	-	never	1	1

a Female returned in interval between observation periods. Cavities entered refers only to observation time and and therefore minimal.*
b Eggs in cavity not laid by this female.
c Young and eggs with D3, young but no eggs with G8.

occupied cavity consecutively; however, these re-entries are not included in the data in Tables 5 and 6 (but can be found in Table 13). Most females crawled along the edge of the cover of at least one cavity before returning. Of the eight females which did not enter any other cavities in eleven trials, only four moved directly to their own.

No difference is evident between average times required to return for different parts of the nesting season. However, since no experiments were run in June when the animals have been shown to be most easily disturbed, such a conclusion necessarily applies only to July and the prehatching part of August.

On July 9, 26 and 27, experiments were run in which the eggs were removed to a different cavity after a female was displaced to the center of the humus. Each of the three females returned to her original cavity but did not remain, one finding her eggs in 40 minutes, another in 42 minutes, the other in several hours. They remained with their eggs until the following day when I returned females and eggs to the original cavities.

The data obtained in these experiments show that a displaced brooding female can and will return to her own eggs, either in her original cavity or to another if they have been moved. Moreover, these females apparently located their original cavities by trial and error. Although females moved directly to their own cavities in four trials, this is exactly the proportion which would be expected on

the basis of chance alone (since the terraria contained eight cavities).

ATTRACTION OF INDIVIDUALS TO EGGS

Although it has been known for many years that the nesting females of P. cinereus attend their eggs during the nesting season, it has not been shown whether the female found with the eggs was the individual which laid them. Both Cochran (1911) and Piersol (1910) mention finding two individuals, a female and a male, with one set of eggs. However, no real investigation of the extent to which other individuals might be attracted to and perhaps remain with eggs of their own species has been made.

A wooden box, one meter square and 30 cm deep, was divided by wooden partitions into quarters. Data for four types of individuals, brooding females, nonbrooding females, males and juveniles, with one type in each quarter, were thus obtained under very similar physical conditions. Bog humus was added to the box to a depth of 5 cm, leveled, and packed tightly to prevent burrowing. The partitions were set in place by sinking them into the humus until the tops of the partitions just touched the sliding glass cover of the box, preventing the animals from escaping to other quarters.

Eight nest cavities were constructed in each quarter of the box. The cavities (6 x 2 cm and 2 cm deep) were sunk into the humus approximately 5 cm apart in a diamond

pattern and lined with pieces of decayed hemlock in the same manner as those in the experimental terraria previously described. A cover of the same kind of wood was placed on top of each cavity. These cavities were so constructed that observations could not be made from the side as in the other terraria, but only from the top by lifting the cover of the cavity.

The box was kept under the same physical conditions as the terraria used in the other sections of this study. Clutches of eggs, collected from a different area than the experimental animals, were placed in alternate cavities. In this way, four cavities contained eggs and four did not. The 16 animals were collected during the week preceding the experiment and kept in separate plastic bags until they were introduced into the terrarium. The four striped brooding females were collected near Gaylord, Michigan. Three striped and one black female were collected from under small logs and were considered to be nonbrooding as they were without eggs. That these probably were nonbrooding females is based on two premises. First, females in this collecting area do not usually nest under logs, as evidenced by the fact that no nests were found in such locations on either 1959 or 1960 collecting trips (Test and Heatwole, 1962, also mention that, in this area, nests are most commonly found within logs). Second, females with eggs seldom leave them. Of 86 nests found in 1958-1960, only 12 were not attended when collected (86% attended).

These nonbrooding females, four striped males, and two striped and two black juveniles were collected near Pellston, Michigan. Adults were all between 36 and 42 mm and juveniles between 26 and 30 mm (snout-hind leg length).

The four individuals of each group were placed together in the center of a different quarter of the box and allowed to move freely. Their locations were recorded then and four times daily (at approximately 8 a.m., 12 noon, 5 p.m., and 9 p.m.) by gently raising the hemlock cover of each cavity. The individual's position and relation to any eggs present were recorded and the animal allowed to remain where it was. Two or more animals were considered to be aggregated when the distance between them was less than one body length. From the size of the cavities, it can be seen that two animals lying on the floor of the same cavity were necessarily aggregated.

A total of 28 observations on each animal was made from July 27 to August 3, 1959. These results are given in Tables 7 and 8.

Extent of Attraction for Various Types of Individuals

The four brooding females were definitely attracted to the eggs, even though they were not their own. They were in cavities with eggs 106 times and in cavities where no eggs were present only six times. Two females remained with the eggs to which they had gone on the first day of the experimental period. Of the other two females, one

TABLE 7. Attraction to eggs for different types of individuals as indicated by observations of their occurrence in cavities with eggs and body contact with them (based on 28 observations of each of 4 animals in each group, July 27 to August 3, 1959).

Observations	Brooding Females	Nonbrooding Females	Males	Juveniles
Total	112	112	112	112
Salamanders in cavities with eggs	106	17	28	22
Salamanders in cavities without eggs	6	95	55	74
Salamanders not in cavities	0	0	29	16
Salamanders in contact with eggs	100	4	11	6
Part of animal in contact				
Head only	60	2	1	0
Body only	14	0	7	5
Tail only	6	2	3	1
Head, body and tail	13	0	0	0
Salamanders curled around eggs	32	1	1	1

TABLE 8. Observations showing the tendency of different types of individuals to aggregate in relation to the presence or absence of eggs (based on 28 observations of each of 4 animals of each group, July 27 - August 3, 1959).

	Breeding Females	Nonbreeding Females	Males	Juveniles
No. of records of animals found singly				
Eggs present	98	9	20	23
Eggs absent	6	7	51	22
No. of records of animals found aggregated*				
Two together				
Eggs present	4	4	4	0
Eggs absent	0	6	9	14
Three together				
Eggs present	0	0	0	0
Eggs absent	0	12	5	5
Four together				
Eggs present	0	0	0	0
Eggs absent	0	10	0	2

* One record represents the two, three or four animals in each aggregation.

immediately entered a cavity with eggs upon being released, the other a cavity which did not contain eggs. Within a few minutes, the latter entered the cavity occupied by the other female. Between July 27 and 29, one or the other of these two females occupied the cavity, except for four occasions when both were around the eggs (in three of these four instances, both were touching the eggs). No aggressive behavior was observed between these females. On July 29, one of the females found the unattended fourth set of eggs and remained with them.

When in contact with the eggs, brooding females were curled around them in one-third of the observations. In more than half, the head was the only part of the body in contact.

Nonbrooding females were found in cavities with eggs only 17 times. In the four observations of contact with eggs, no salamander had her entire body in contact, although one was curled around them once. A high degree of aggregation is shown by 96 observations of individuals in cavities in groups of two, three and four. These comprise 32 aggregations, all except four of which were in cavities where there were no eggs. It is also of interest that in most observations these nonbrooding females were under the wooden cover of the cavity where it extended onto the humus, rather than in the cavity itself. The black female was found in a cavity with eggs in nine of the observations, whereas the three striped females were observed with eggs

only a total of eight times.

Males were in cavities with eggs 28 times and in contact in only 11. They were rarely curled around the eggs and their heads were seldom in contact. Males showed a greater tendency to wander around the terrarium than those of other types; in 29 observations of locations outside cavities, males were found burrowed into the humus, in another quarter of the box (which involved climbing over a partition), crawling on the humus, and on the sides of the terrarium. There was some tendency to aggregate, mostly in cavities where no eggs were present.

Of the 22 records of juveniles in cavities with eggs, only six were in contact. This contact was mostly with the side of the body, never with the head. In nearly half of the observations, two or more salamanders were found together; however, there was never any aggregation in cavities with eggs. In contrast to the many larger aggregations occurring among nonbrooding females, the majority of aggregations among juveniles involved only two individuals. There was no significant difference between black and striped individuals in tendency to aggregate; however, the black juveniles wandered more than the striped ones and were found outside the cavities 13 times in comparison to three for the striped.

When results are compared for the different types of individuals, it is evident that only the brooding females show a strong attraction to eggs. Other types of

individuals were observed in cavities with eggs far fewer times than should occur on the basis of chance alone (χ^2 tests on each were significant at the 5% level); therefore, these individuals exhibited an avoidance of cavities with eggs. Salamanders found in the field with eggs, then, are most probably brooding females. However, as these experimental brooding females were attracted so strongly to eggs laid by another, one can not be sure that a female attending eggs in the field is the one which laid the eggs.

Although brooding females possess strong attraction even to eggs they did not lay, the question arises whether females in the field would leave their eggs in the first place. Both laboratory and field observations have shown that the attraction of brooding females to their own eggs is less at the beginning of the nesting season; therefore, these data obtained late in the season probably illustrate maximal attraction. It would not be surprising if this experiment would show less attraction to foreign eggs if conducted early in the season, particularly since it was difficult to get females to remain with their own eggs in June. It seems conceivable that, early in the season, some females might wander from the cavities or leave as a result of some disturbance, come upon another, unattended, set of eggs, and remain.

In these experiments nonbrooding females showed a greater tendency to aggregate than did the brooding females.

Although the few aggregations among the brooding females occurred only in the presence of eggs, nearly all of the aggregating groups of nonbrooding females were away from eggs. Therefore, nonbrooding females, as well as males and juveniles, tended to be attracted to cavities in which at least one other individual was present, and eggs were absent. This is supported by the many groups of three and four among nonbrooding females. Perhaps this avoidance of cavities with eggs where another salamander was present might be a learned response, a result of previous encounters with brooding females attending eggs (in the field).

Factors Important in Egg Recognition

The brooding female P. cinereus has been shown to have a strong attraction toward eggs, whether her own or those laid by another individual, and will return to such eggs after being moved or disturbed. On several occasions I observed females, whose eggs had been removed, traveling continuously through many nesting cavities, even crossing a wooden partition (over which they did not attempt to escape when eggs were present) until they located another set of eggs. The following experiments were designed to give some indication of the means by which females recognized these objects as eggs. Some possible factors which might be involved in such recognition are visual clues, such as size, shape, color, and pattern; olfactory clues; and tactile clues, such as texture, resiliency and moisture.

For these experiments, two kinds of artificial eggs, which resembled the natural eggs in several ways, were used. Berries from the herbaceous plant, Maianthemum canadensis, which are approximately the same size, spherical and have a "whitish" background color, were used first. Berries with the size and color most resembling eggs were tied together in grape-like clusters of five to seven by their stems. These were tested on the same brooding females in one quarter of the meter square box as described in the preceding section. The four females were moved to the center of the humus and the berries substituted for the eggs in their absence. They were allowed to move freely and their location and relation to the berries was recorded four times during the next 24 hours (a total of 16 observations on August 3-4, 1959). Only once in this time did a female have her head in contact. Three of the females crossed the wooden partition which divided the box and were found curled around eggs in nest cavities on the other side (and were placed back in the center of the humus again). Tail contact was seen twice and in the other observations females were in cavities without berries.

Plastic beads (imitation pearls) were used next to simulate eggs. These "eggs" were thus white, spherical, smooth, and could be made easily into clusters because of the hole through the center. These were substituted for the eggs of females in the small terraria described at the

beginning of this paper.

Between July 9 and 27, 1960, clusters of six beads were added to the cavities of four females in their absence and left for one to three days. The eggs of these females had been moved to another cavity. Upon their return, two of the females turned to look at the beads, touched them lightly with their snouts and left within 10 minutes, while the others ignored them. None maintained contact with the beads or appeared to accept them by remaining longer than 10 minutes. Although these beads were in the cavities during some of the displacement experiments, such cavities were not even entered by the wandering females.

In two other trials (July 29 and August 3, 1960) the beads were rubbed against the eggs for which they were substituted. In both instances, the female approached the beads with her snout, touched them, remained near them for several minutes, then deserted the cavity and located her own eggs in 45 minutes and in 3 hours.

In one trial (July 26, 1960), one real egg was placed among the beads which replaced the eggs of D2 while she was away from the cavity. The clutch was placed so that the egg could not be seen by the female as she entered the cavity. She returned to the cavity, headed toward the cluster of artificial eggs, pushed them with her snout, pulled them by the string with her mouth, rolled them over and immediately placed her chin on the one real egg. She remained with these beads until the next day (her chin

still on the one egg) when I returned her own eggs to the cavity and removed the artificial ones.

Since the preceding experiment demonstrated the female's ability to locate an egg which was out of sight and therefore suggested that odor was an important factor in the recognition of eggs, the next step was to cover the eggs so that the only means by which the female could be attracted was odor. The eggs were wrapped in "Saran Wrap" which, when crinkled, reflected the light and the eggs were not visible to me. The wrap was left open at the top. These were added after moving B1 to the center of the terrarium on July 30, 1960. When next observed (1.5 hours later), the female was inside the wrap, curled around the eggs. She remained there until the following day, when I removed her again. She soon was back inside the wrap and curled around the eggs. In this instance, the female presumably could not see the eggs and could not touch them before crawling in through the top of the wrapper to get to them; therefore, it seems that the odor of the eggs is the primary attractive factor. However, since the females were so often observed pushing eggs with their snouts and even rolling the clutches over, perhaps recognition of them as eggs is then confirmed by one or more physical features of eggs discernible by touch.

Although females in these laboratory experiments had sufficient light to see eggs and other individuals during the times when I was observing them, the remainder of the

time their activities were carried on in darkness. Under field conditions the female could not rely on sight if she had nested inside the large hemlock logs or under stones. Therefore, and on the basis of the few preliminary experiments described here, it is probable that females rely on odor followed by touch for egg recognition, although they are no doubt able to see them when light is available.

Recognition of Specific Eggs by Females

Preceding experiments have suggested that females recognize an object as an egg primarily by the sense of smell and probably confirm this by tactile contact with the eggs. If this is true, then it is likely that a female might be able to recognize a particular odor and thus a specific set of eggs. A definite tendency to return to their eggs and nest cavities was also shown for brooding females in the laboratory. Since one or more unattended clutches were sometimes present in trials where the female was displaced, the females must have been able to differentiate between the eggs of other females and their own.

A number of experiments in which eggs and/or females were moved were carried out to investigate this ability more completely, and also to differentiate between the female's attraction to the eggs and to the nesting site itself. Females and eggs, when moved, were picked up by hand. Often the eggs were still attached to the piece of hemlock wood from the original nesting site and were easily

moved. In some trials the female was in the cavity at the time the eggs were moved, in others she had been displaced to the center of the humus and the eggs removed during her absence. One to three extra clutches of eggs were always present in the terrarium.

When the eggs of four females were moved while they were in their cavities (between July 9 and 21, 1960), three became restless within a few minutes and left the cavity; the fourth remained in the cavity with a clutch of strange eggs which I had substituted for her own. When the strange eggs were removed, she left her cavity immediately and was found with her own eggs 30 hours later. The other three females found their eggs in 1 hour, 10 minutes; 3 hours; and 5 hours, 40 minutes. These females did not go directly to the cavity containing their eggs, but found them by trial and error, wandering through several cavities first.

The eggs of two females were exchanged on July 30, 1959. One female (A8) showed no apparent reaction to the switch of eggs, and did not even change her position. The eggs were attached to a piece of hemlock wood and the exchange was very easy. The other female (A6) became restless immediately and, within a few minutes, left the cavity and went directly to the one containing her eggs. As she began to enter, the attendant (A8) became immediately alert and the other backed away, returned to her cavity, and curled around the new eggs. She repeated this three

times and also moved about restlessly within the cavity. The eggs were changed back the next day with A8 again showing no response. A6 immediately curled tightly around her own eggs. Eggs were exchanged between another pair of females on July 20, 1959. Although one became slightly more alert, neither moved from the cavity and each was still in its own cavity the following day.

Three females, whose eggs were moved to other cavities in their absence (July 9-27, 1960) found their eggs in 20, 25 and 42 minutes. Three other females were moved between July 9 and 25, 1960 and strange eggs placed in their cavities. One returned, pushed and prodded the strange eggs, left, and found her own eggs in two hours. Another female, moved on July 25, 1960, found her own eggs in 15 minutes. The third female, after returning and finding strange eggs present, left, wandered through several other cavities, found her own eggs, but did not remain. She then returned to her original cavity and the strange eggs. The following day (21 hours later) she was found curled around her own eggs in the other cavity.

On two occasions a female was placed in a terrarium in which she had never been before. On July 30, 1959, the eggs of P-9 were placed in a cavity with another female. She found her eggs within 5 minutes after being placed in the terrarium and attempted to curl around them, but was driven out by the attendent. She made three more attempts to re-enter the cavity, after which I

removed her from the terrarium. On July 23, 1959, WP5 was placed in a terrarium containing three unattended clutches of eggs, one of which was her own. She pushed and prodded the first two she encountered and found her own in 2.5 hours.

When a female, either after being displaced or after leaving the cavity, encountered a set of eggs which was new to her, her behavior was distinctly different from that observed when the eggs were her own. In nearly every instance, the female pushed and prodded the eggs with her snout, often rolling them over and over (if they were not attached) for 10 or 15 minutes. One female in investigating a set of eggs lifted them off the substrate with her snout. As she pushed them around the cavity, it appeared as if she was attempting to rub something on or off them. Two other females bit at and grabbed eggs in their mouths, but there was no apparent damage to the eggs. When a female pushed and rubbed a set of eggs, then left and returned again, she did less pushing and prodding and sometimes remained with them two or three hours. It is possible that the female recognizes her own odor on the eggs left from previous contact with them (or may become familiar with their odor).

From these experiments it can be concluded that brooding females (at least during the middle of the nesting season) can recognize their own eggs and show a preference for their own by following them if they are moved, even

though another clutch of eggs is present. It is also evident that females usually reacted differently to strange eggs (pushing and rolling them over) than to their own. Although females touched their own eggs with their snouts after being away from them, they never pushed or rolled them around in the cavities.

Acceptance of Other Eggs by Females

During 1959 and 1960, three females each accepted and attended a clutch of eggs in addition to her own. On July 30, 1959, C6, after being displaced to the center of the terrarium, returned to find two clutches of eggs in her cavity, her own and one which I had placed there. After touching her snout to both substrate and eggs, she curled around both clutches of eggs. On July 13, after being moved, D2 returned to find two clutches of eggs 2 cm apart in her cavity (the new clutch in the place previously occupied by hers); she immediately went to her own eggs and curled around them. Several minutes later she investigated the new clutch with her snout and attempted to curl around them both. On July 28, 1960, after finding a clutch of eggs which I had left on the humus of the terrarium approximately 10 cm from her cavity, C3 alternated between this clutch and her own over a period of nine days. On several occasions she was seen pushing the eggs (twice in the direction of her own cavity). She moved them as close as 1 cm from the cover of her cavity, but they were several centimeters away from the cavity

the next day. When I placed her own eggs on the humus and the new ones in the cavity, she still alternated between them. At one observation she was curled around one clutch, at the next around the other. When both clutches were placed on the humus and later together in the cavity, she curled around both at the same time. They were left in the cavity and attended by C3 during the hatching period, which began August 9, until the experiment was terminated on August 13.

On July 6, 1959, one brooding female (E7) escaped from the terrarium and another (E1) began to attend the deserted eggs. When I placed another brooding female (P-10) near the cavity of E1, she entered and remained with the eggs. Thus, both females attended eggs which they did not lay and remained with them until after the eggs had hatched.

It is evident from these observations that brooding females will accept eggs in place of or in addition to their own and will remain with them, attending them as if they were their own.

DEFENSE OF EGGS AND NEST CAVITY

Prior to 1959, no aggressive behavior had been seen in Plethodon cinereus, either in captivity or in the field. However, during the 1959 experiments I observed a brooding female defending her eggs and nest cavity against another brooding female. On the assumption that this behavior is common among nesting females, a series of experiments was designed to test their tendency to defend their eggs and/or nest cavities against members of their own species, predators and objects inserted into the cavities. Since then, Highton and Savage (1961) have reported observing a single brooding female defend her eggs against another female, and Taub (1961) has suggested territoriality for this species on the basis of a possible home range.

Brooding females used for the following experiments were kept in the same terraria and under the same physical conditions as described in the first section on methods. Again, four of the eight nest cavities in a terrarium were occupied by brooding females. When females were moved, they were placed in the center of the terrarium following the same procedure used for the displacement experiments. In fact, many of the encounters resulted from displacement trials, since returning females often entered cavities occupied by other females. Other encounters

resulted from voluntary wanderings of the brooding females or the introduction of females from other terraria.

Nonbrooding individuals used in these trials were placed either in the center of the terrarium, as the brooding females were, or within a few centimeters of a particular cavity, and allowed to wander during the observation period. The animal was then removed from the terrarium. Juveniles were placed near the edge of a cavity occupied by a brooding female and hatchlings just within such a cavity.

Each encounter was recorded as completely as possible and the actions of the animals were classified into several types. Responses made by attendant females in these encounters were: watch without moving or move only the head, move toward the intruder slowly, lunge at the intruder, push the intruder with head or body, snap, bite, bite and retain the hold, and follow or chase the intruder from the cavity. Reactions of the intruder were: leave quickly, push against the attendant or toward the eggs, remain in spite of the attendant's actions, snap, and bite. In some encounters the intruder made several, often determined, efforts at re-entry.

Reaction of Attendant Females to Intruding Brooding Females

In contrast to the more deliberate actions involved in feeding, brooding females faced with an intruder often reacted quickly with a lunge, snap or bite. In their efforts

to chase the intruder from the cavity, they often retained holds on the intruder's head or body and the two rolled over and over.

During the summers of 1959 and 1960, 23 brooding females were observed or tested in trials involving 58 encounters with other brooding females. Some of the 25 brooding females which were the intruders in these encounters inhabited nest cavities in the same terrarium and others were either from another terrarium or recently brought in from the field. Observations of these encounters are summarized in Table 9.

In 53 of the 58 encounters, the attendant showed a definite aggressive or defensive response to the intruder, reacting in one or more ways to eject her from the nest cavity or prevent her from approaching or touching the eggs. In four of the encounters (involving four different females), there was no observable response; however, the intruders left the cavity within two minutes. (Two of these females responded defensively in other trials.) In another encounter the attendant backed up as the intruder passed through the cavity.

Both the attendants and the intruders varied greatly in the intensity of their responses. Some attendants were immediately aggressive to the intruder, others were slower or less definite in their responses. Some very aggressive individuals lunged at and bit the intruders before they had any opportunity to get near the eggs. Others remained

TABLE 9. Responses of brooding females to the intrusion of other brooding females into laboratory nest cavities during the 1959 and 1960 nesting seasons. A refers to attendent, I to intruder, Time to length of encounter. No opp. indicates that A responded before I had opportunity to show interest in eggs.

A	I	Date	Time in min.	Previous Activity of intrus. A	Previous Activity of intrus. I	I when A responded	Responses Attendent	Responses Intruder	Interest in eggs	Remarks
		1959								
C1	C6	7/25	-	0	0	Pushed against A and eggs	Snapped and bit I	Pushed toward eggs and left	yes	
C1	P9	8/6	5	1	0	Entering cavity	Arched neck, snapped, bit	Tried to enter 3 times, left	no opp.	A followed 6 cm from cavity
C3	C8	7/18	1	0	1	-	None	Backed away and left when 1 cm from A	yes	
C28	C29	8/2	5	0	0	Curled around eggs	Re-entered cav. bit I	Left cavity	yes	A left cav. returned soon
C6	C8	7/12	25	0	0	Moved toward eggs	Pushed, bit, snapped at I	Pushed and rubbed snout on eggs	yes	A left cav. briefly
C6	C3	7/18	1	1	1	-	None	Moved to 1 cm of A and left	no	
C6	P10	7/30	10	2	2	Curled around eggs	Bit, chased I from cav. 4 times	Tried to curl around eggs	yes	I's eggs also in cavity
E1	P10	7/29	2	0	0	Entered cavity	Moved forward, snapped at head of I	Left quickly	no opp.	

TABLE 9 Continued

A	I	Date	Time in min.	Previous Activity of intrus. A	Previous Activity of intrus. I	I when A responded	Responses Attendant	Responses Intruder	Interest in eggs	Remarks
		1959								
E1	P9	8/6	1	1	2	Entered cavity	Bit I	Left immed-istely	no opp.	
E3	P10	7/29	3	0	1	Moving to-ward cav. (1 cm away)	Ran forward, bit I on tail	Jumped and ran	no opp.	A returned to eggs
E3	E1	7/31	10	1	0	Touched snout of A (out of cav.)	Snapped	Left cavity	no opp.	A came on cav. cover
E3	E1	7/31	1	2	0	Moved past A and eggs	Bit I on head, tail	Jumped and left	no	
E3	p9	8/6	1	3	1	Entered cav. (1 cm from A)	Bit I	Left cavity	no opp.	
E3	P9	8/6	1	4	3	Entered cav.	Bit I	Left quickly	no opp.	
		1960								
B1	B3	7/20	5	0	0	Entered cavity	Backed up, very alert	Passed through cavity	no	
B1	B3	7/20	1	1	1	-	None	Touched eggs with snout, left	yes	
B2	B8	8/3	19	0	0	Entering cavity	Pushed I from eggs, snapped, bit	Snapped and bit A, touched eggs	yes	A left before I

TABLE 9. Continued

A	I	Date 1960	Time in min.	Previous Activity of Intrus. A	Previous Activity of Intrus. I	I when A responded	Responses Attendent	Responses Intruder	Interest in eggs	Remarks
B2	B3	8/3	7	1	1	Entered cavity	Put head near eggs	Bit A and held on	yes	A left cavity
B8*	B4	7/13	5	0	0	Leaving cavity	Bit I on head	Left cavity	no	
C1	C8	7/21	3	0	1	Moved within ½ cm of eggs	Repeatedly bit I	Pushed toward eggs	yes	I curled in cav. 2 min. then left
C1	C8	7/21	2	1	3	Entering cavity	Moved toward I	Backed away	no opp.	
C1	C8	7/21	2	2	6	Touched snout of A	Bit and chased I out	Returned twice then left cav.	yes	A chased I out 3 times
C1	WFG	8/4	2	3	0	Put snout on eggs	Snapped and bit I	Left cavity	yes	
C3	C8	7/21	5	0	0	Entering cavity	Bit I and chased her out	Tried repeatedly to enter, left cavity	yes	Eggs of C8 also in cav.
C3	C8	7/21	7	1	2	Entering cavity	Bit her repeatedly	Left cavity	yes	Eggs of C8 also in cav.
C3	C8	7/21	2	2	4	Entered cav. (1 cm from A)	Bit I	Left cavity	yes	A followed to cav. edge
C3	C8	7/21	3	3	5	Entering cavity	Bit I	Returned once then left cav.	yes	A&I "thrashed around"

TABLE 9. Continued

A	I	Date	Time in min.	Previous Activity of Intrus. A	Previous Activity of Intrus. I	I when A responded	Responses Attendant	Responses Intruder	Interest in eggs	Remarks
		1960								
C3**C6		7/28	5	4	2	Moved toward eggs outside cavity	Ran forward 9 cm, bit I	Ran into unoccupied cav.	yes	A followed her to cav., returned
C3**WPG		8/5	16	5	2	Around eggs outside cav.	Snapped and bit I	Snapped and bit A, then left	yes	C3 then curled around all eggs
C3**C7		8/7	20	6	0	Moved under cav. cover	Put snout near I	Left cavity	no opp.	
C7	WPG	8/4	1	0	1	Put head in to cavity	Bit I immediately	Left cavity	no opp.	
C8	C3	7/20	2	0	0	Moved onto cav. cover	Jumped up, snapped	Left cover	no opp.	A put head out of cav.
D1	D3	7/13	3	0	0	Entered cavity	Bit I on body for 3 min.	Pushed under and around eggs	yes	I left cav.
D1	C6	7/20	1	1	2	Entered cavity	Bit I on body	Flipped out of cavity, left	no opp.	A left, not following I
D2	D1	7/9	1	0	1	Moved under cav. cover	Bit I immediately	Left immed.	no opp.	
D2	D1	7/9	1	1	2	Entered cavity	Bit I on head	Left cavity	no opp.	

TABLE 9. Continued

A	I	Date 1960	Time in min.	Previous Activity of Intrus. A	Previous Activity of Intrus. I	I when A responded	Responses Attendant	Responses Intruder	Interest in eggs	Remarks
D2	D3	7/23	2	3.	1	-	Did not move	Entered cav., turned and left	no	
D2	D1	7/23	5	4	4	Touched eggs	Bit I on head	Left cavity	yes	
D2	C6	7/19	2	2	0	Entered cavity	Snapped quick-ly, bit I on head	Backed away and left cav.	no	
D2	D7	8/7	1	5	0	Entered cavity	Moved for-ward	Left cavity	no?	Could not see more
D2	WPH	8/7	1	6	1	Entered cavity	Snapped immediately	Left cavity	no opp.	
D3	D1	7/8	1	0	0	Put head into cavity	Lunged and bit I	Left cavity immediately	no opp.	
D3	C6	7/19	2	1	1	Moved past eggs	Bit I on tail	Left cavity	no	
D3	D1	7/20	2	2	3	Moving toward cav.(2 cm away)	Opened mouth twice at I	Backed away and left	no opp.	
D3	D7	8/2	5	3	0	Entered cavity	Bit I, held on 20 sec.	Thrashed about, left when released	no	
D3	WPH	8/7	1	4	0	Put head into cavity	Snapped immed-iately	Left cavity	no opp.	

TABLE 9. Continued

A	I	Date 1960	Time in min.	Previous Activity of intrus. A	Previous Activity of intrus. I	I when A responded	Responses Attendant	Responses Intruder	Interest in eggs	Remarks
D3	CVI	5/12	2	5	1	Entered cav. (1 cm from A and young	Snapped "viciously"	Jumped, left cavity	yes	
D7	CVI	3/2	2	0	0	Entered cav. (1 cm from A)	Snapped	Left cavity	no	
D8	D3	7/23	5	0	2	Entered cav.	Snapped	Curled near eggs, left cav.	yes	
F2	WP5	7/23	7	0	0	Touched snout of A	Bit I, pushed between I and eggs	Pushed under A, left cav. in 7 minutes	yes	
F2	WP5	7/23	5	1	1	Touched eggs, began leaving	Snapped at I repeatedly	Left cavity	yes	A followed I halfway out of cavity
G2	G6	7/20	2	0	0	Curled around eggs (A gone)	Returned, moved to eggs	Left cavity	yes	
G2&	G4	7/22	10	1	0	Entered cav. (A & I)	G4 bit G2, G2 pushed and grabbed eggs in mouth. Both left cav.		yes	Eggs of A & I moved to cav. 3 by me
G4	G6	7/20	1	0	1	Entered cav.	Turned toward I, snapped	Left cavity	no	
G6	G4	7/27	14	0	1	Touched eggs	Snapped, came between I, eggs	Grabbed eggs, snapped	yes	A & I in cav. at end of 14 min.

TABLE 9. Continued

A	I	Date 1960	Time in min.	Previous Activity of intrus. A	Previous Activity of intrus. I	I when A responded	Responses Attendant	Responses Intruder	Interest in eggs	Remarks
G8	G4	7/27	2	0	0	Entering cavity	Snapped as I tried to enter	Left, tried to re-enter	no opp.	
G8	WPH	8/6	1	1	2	Put head into cavity	Snapped immediately	Left cavity	no opp.	

* Attending eggs she did not lay.
** Attending two clutches of eggs simultaneously.
*** Eggs of both females placed in another cavity where encounter occurred. G2 entered cavity first and is therefore designated as A.

passive until the intruders began to push past them toward the eggs before they reacted by pushing with their heads or by snapping and biting. Some intruders showed a very definite interest in the eggs and returned several times after being chased from the cavity, while others showed no apparent interest. For example, D3 continued to push around the attendant and against the eggs, even though she was being snapped at and bitten by the attendant. Another intruder (33) supplemented the usual pushing by the intruder by snapping at and biting the attendant, finally causing the latter to desert her cavity temporarily.

However, a typical encounter usually involved different actions on the parts of the attendant and the intruder. The intruder, upon entering, was met by the attendant, who, snapping and biting, kept herself between the intruder and the eggs. If the intruder persisted, she pushed against the attendant with her head, but did not snap back, and moved toward the eggs. Such persistence resulted in repeated bites from the attendant, until the intruder left the cavity. The difference in responses between attendant and intruder is apparent when the same animal is an attendant in one encounter and an intruder in another. For example, D3 was observed to bite and snap in five of six encounters when she was the attendant, but not in the three encounters as an intruder.

In four encounters, the intruder rubbed her snout against the eggs. One of these intruders also grabbed the

egg clutch in her mouth (with no apparent damage to the eggs) in spite of the pushing and snapping of the attendant female.

There were no demonstrated differences in the responses of either attendants or intruders during different parts of the nesting season. However, due to the difficulty of inducing females to remain with their eggs during the first two weeks of the season, no trials were run (and no encounters due to wandering observed) during that time. Since there is a real difference in the behavior of brooding females during these two weeks, it is probable that attendants might be less inclined to defend their eggs and that intruders might exhibit little interest in them. The few trials run during the post-hatching period (Table 9) indicate that females are as aggressive in the presence of their young (at least during the first few days after hatching) as they are when only the eggs are present.

Effect of Distance

Since it was important to determine whether the female was defending only the eggs, or a particular area consisting of the nest cavity itself, or the nest cavity plus some surrounding area, records were kept of the distance of the intruder from the eggs when the first response of the attendant was observed.

Of the 49 encounters where the attendant responded aggressively, 9 intruders had not yet entered the cavity, were on the cavity cover, or had only their heads inside.

In 22 encounters, the intruder had entered the cavity, but was more than one centimeter away from the attendant and eggs; and in 13 encounters she was closer than one centimeter from the attendant. Seven of the 13 had come into contact with the attendant or eggs before the attendant responded.

These results indicate that the females were reacting to the invasion of the cavity and thus were defending more than the eggs themselves.

Effect of Intruder's Interest in Eggs

The data above show that the females in approximately three fifths of the encounters responded aggressively before the intruder exhibited definite interest in the eggs. However, the variability of the attendant's response could be related to the actions of the intruder. In 26 of the total encounters, the intruder indicated an obvious interest; i.e. pushing against the eggs or rubbing them with her snout. Twelve intruders showed no observable interest, the rest had no opportunity as they were attacked immediately. In 22 (38%) of the 26 encounters where definite interest was exhibited, the attendant responded by snapping and biting. Where there was no obvious interest, the intruder was bitten in only 58% (7) of the 12 encounters.

More violent and aggressive behavior was exhibited by females when the intruder showed a definite interest in the eggs. Probably the intruder which made a greater effort to approach the eggs provided greater stimulus than one

which left the cavity at the first aggressive action of the attendant. Of the 22 intruders showing interest in the eggs, 17 made repeated attempts to get close to or curl around the eggs. The remaining five left quickly after being snapped at or bitten. Females which showed no interest left quickly when bitten.

The effect of interest in the eggs is well illustrated by a rather unusual encounter which involved two clutches of eggs, two females, and no cavity. On August 5, 1960, two striped females, designated as C3 and WPG, were curled around two clutches of eggs on the humus in the center of terrarium C, approximately 5 cm from their own cavities and 3 cm apart. Interest by C3 in an unattended set of eggs, left by me on the humus on July 28, had caused her to alternate between attending them and her own eggs in her cavity during the ensuing time. I had placed WPG in a cavity with only one of her five eggs and had removed the other four from the terrarium. At the beginning of the observation period, both females were alert and WPG moved forward and bit C3. Both began to snap and bite and rolled over and over as they pushed each other from the eggs. After five minutes of wildly biting and rolling around on the humus (during which time the eggs were knocked closer together by the action of their bodies), they suddenly separated and returned to the edges of their cavities. They then turned and ran back to the clutch of eggs around which they had been curled at the beginning of my observation.

After C3 had touched her eggs and WPG had rubbed her snout on the others, they began to bite and snap again. After another five minutes, C3 chased WPG back to her cavity and returned to the eggs. She then curled around both clutches. This encounter is an excellent example of the effect of interest, as both females were intent upon curling around the eggs and there was no apparent difference in their aggressive actions. Contrary to encounters where one female was attending one clutch of eggs, both females were aggressive and engaged in snapping and biting.

Another good example of the effect of interest in eggs on the responses of both females occurred in the summer of 1960. A female (D3) wandered into the cavity of D1 and was bitten as she entered. Although she was bitten rather continuously on head, neck, and tail for nearly 2 minutes, D3 continued to push under and around the eggs and finally left at the end of 3 minutes. Table 9 summarizes other encounters which illustrate the effects of little or no interest as well as great interest.

The length of time taken by each encounter was usually between 1 and 3 minutes. The longer encounters of 10-25 minutes (including those which involved the intruder's own eggs) usually involved an intruder which showed great interest in the eggs. In these longer encounters the intruder was usually quite persistent, despite aggressive responses by the attendant. Such intruders either repeatedly tried to re-enter after being driven from a cavity

or continued to push toward the eggs regardless of the attendent's actions.

Effect of Previous Intrusions

Since specific attendants and intruders sometimes were involved in several encounters, the possibility was considered that they might become either more or less aggressive with each succeeding encounter.

Table 9 lists the encounters of individual females in the order of their occurrence. Reference to several females which had four or more encounters shows no trend in their behavior with time. For example, in 1959, E3 had five encounters, in which she always bit and snapped, giving four of the intruders no time to show interest in the eggs. In 1960, D3, in six encounters, bit and snapped at five intruders, opened her mouth at the sixth, and caused all six to leave. Although D2 had seven encounters with five females, there was no trend either in the length of time of each encounter or the strength of aggressiveness. In 1960, C3 bit and snapped in six encounters and kept the seventh intruder from entering the cavity. Four of these intrusions were by the same female. Each time she was bitten and chased out, but the last two encounters required 2 and 3 minutes, while the first two required 5 and 7. The intruder exhibited interest in the eggs in all four encounters. However, in 1960, D2 had three encounters with D1 in which the first two lasted only 1 minute and the third (two weeks later) lasted 5 minutes.

The above examples indicate that the attendant does not react differently after several intrusions. However, in one series of encounters the intruder left sooner and was somewhat less persistent in attempts to approach the eggs. This was also true of encounters where the intruder returned several times after first entering and being driven out by the attendant. One female (CVI), after being involved as an intruder in several trials, would not enter an occupied cavity, even when I moved her nearby. She turned around in my hand and attempted to run in the opposite direction. In contrast to this, other individuals moved toward a cavity when placed near its opening.

Extracavity Movement of Attendants During Encounters

In 8 of 58 encounters, the attendant followed the intruder out to the edge of the cavity or farther. This ranged from simply following the intruder under the cavity cover (G8) to chasing the intruder 25 cm across the humus(C3) to her own cavity, then returning to her eggs. In six encounters the attendant left the cavity following an intrusion, but was not chasing the intruder. One of these females (B2) was chased from her own cavity twice in the same day by B8, who had left by the following day. At that time, B2 was also back in the cavity with her own eggs. Attendants in the other four encounters left at about the same time as the intruder did and all returned within 24 hours.

It is apparent from these results that attendants do

not usually leave the cavity when defending the eggs, but confine their aggressive actions to the vicinity of the eggs.

Effect of Feeding on Aggressive Behavior

Only four of the encounters occurred within 24 hours of the time an attendant had been fed. Since other females in the same terrarium could have eaten food organisms (Drosophila) which had escaped into the terrarium, after the first addition of flies there is no way of knowing if and when other females used in 1960 had eaten. However, no food was ever offered to females in the terraria in which these trials occurred during 1959. The dates on which the first fruit flies were introduced into terraria in 1960 are given in Table 4 (p.58).

The only direct effect of feeding on the responses of the animals involved was on August 3, 1960. Both B2 and B8 (in cavity of B1) had been offered and had eaten flies. After eating the flies which were in the cavity in which she was attending eggs, B8 crawled out on the humus and over to the adjoining cavity occupied by B2. After entering the cavity, B8 snapped at the attendant, ignored the eggs, and began moving around the cavity with her snout to the substrate where the flies had been. The attendant snapped and bit B8 as she entered the cavity. After moving around the cavity, B8 turned and touched the eggs. She also began to bite, retaining one hold on B2 for 1.5 minutes, and continued to push toward the eggs. The attendant then left the cavity. After 15 minutes, B8 returned to the adjoining

cavity. She re-entered the cavity of B2 the same day. Both females engaged in snapping and biting and B2 again retained a grip with her jaws on the attendant, who again left the cavity at the end of the encounter.

Although it is possible that B3 was just a very aggressive individual, it seems more likely that the extreme aggressiveness was initiated by the presence of food and remained at the same level when her interest was transferred to the eggs. She was not observed as an intruder at any other time, so there can be no comparison with her behavior when food was not a factor. However, in an encounter on July 13, 1960, she was not unusually aggressive as an attendant.

One other encounter occurred which might have been influenced by food. While attending eggs in her own cavity on July 28, 1960, C3 had been offered flies and had eaten 14 of 16 offered, following some of them out of the cavity. She then remained on the humus, attending a clutch of eggs which I had placed there earlier. At this time, C6 left her cavity and, perhaps attracted by the flies, crawled toward C3. The aggressive reaction of C3 probably was influenced by the presence of the flies. Before C6 was closer than 9 cm to the eggs, C3 moved toward her rapidly, bit her and chased her to a cavity. In previous encounters, C3 had been aggressive, but she had not left the cavity or followed an intruder.

Defense of Eggs Not Laid by Attendant

In several instances, a female attending eggs which she did not lay was observed defending these eggs against intruders. In one encounter on July 13, 1960, B8, attending eggs in another cavity, bit B4 and caused her to leave. (She also responded aggressively to a juvenile and a hatchling while attending the same eggs.) The defense of a clutch of eggs on the humus by C3 has already been mentioned. When the eggs which C8 had been attending were placed in the cavity of C3 in addition to her own, C3 repeatedly attacked and chased the intruding C8 from the cavity. In another instance, B1 defended a clutch of moldy eggs (which I had previously put in place of her own) against a juvenile intruder.

In an encounter on July 20, 1960, G6, curled around the eggs of another female, left immediately when the attendant returned to her cavity.

From the examples cited above, it is clear that nesting females will defend eggs which they did not lay. The last example indicates that this may not be true when the intruder is the one which laid the eggs.

Reaction of Attendant Females to
Intruding Nonbrooding Individuals

It has already been shown that brooding females defend their eggs and cavities against intruding brooding females by various types of aggressive actions, usually including biting and snapping. Since it has also been

shown that brooding females have a definite interest in eggs, it is of interest to know whether the same defensive actions occur in response to the intrusion of nonbrooding individuals, which generally showed little interest in eggs.

During the summers of 1959 and 1960, 30 encounters involving 15 nonbrooding individuals with 16 brooding females were observed. These observations are summarized in tables 10, 11, and 12. Three of these trials involved the same male, eight were with three different nonbrooding adult females, ten with two different juveniles, and nine involved one each of nine hatchlings up to four days of age.

The same adult male was allowed to enter the cavity of a brooding female three times. He was bitten in the last two of these encounters, threatened by the female in the first, and always left in less than two minutes. He showed no observable interest in the eggs and began to leave the cavity at the first aggressive action of the female.

The attendant responded aggressively to each intrusion of a nonbrooding adult female. One intruder left the cavity after the attendant (C3) pushed her away from the eggs. Snapping and biting occurred in the other encounters and all intruders eventually left the cavities. In six of these the intruder had entered the cavity but was not within a centimeter of the eggs or female when the attendant

TABLE 10. Responses of brooding females to the intrusion of adult males and nonbrooding females into laboratory nest cavities during the 1959 and 1960 nesting seasons. A refers to attendant, I to intruder. Time indicates length of encounter.

A	I	Date	Time min.	Responses Attendant	Intruder	Interest in eggs -I
		1959				
E3	Male	8/1	1	Moved toward I	Left cavity	no
E1	Male	8/1	2	Snapped, bit, chased I to edge of cav.	Left cavity	no
E1	Male	8/1	1	Bit I	Left cavity	no
		1960				
C8	Female a	7/21	3	Pushed I from eggs	Moved to eggs, left	yes
D1*	Female b	7/25	2	Snapped once at I	Remained in cavity	-
D2	Female c	7/22	1	Bit I, held on to tail	Left cavity	no
C1	Female c	7/31	?	Snapped, bit I	Left cavity slowly	no
C3	Female c	7/31	5	Bit I as she entered cav.	Tried to enter twice, then left	no
C3	Female c	7/31	10	Snapped at I, followed onto humus	Left cav- slowly	no
G4	Female c	7/31	5	Snapped at I, followed under cav. cover	Head near eggs, left	yes
G8	Female c	7/31	3	Snapped, moved under cover	Head on eggs 2 min. left	yes

* D1, a brooding female, encountered nonbrooding female in another nest cavity.

TABLE 11. Responses of brooding females to the intrusion of juveniles into nests during the 1960 nesting season. A refers to attendant, I to intruder. Length is shout-hind leg. Time = length of encounter.

A	Length of I	Date	Time min.	Responses Attendent	Intruder	Interest in eggs
G2	17 mm	7/29	1	Watched I, did not snap	Moved under female and eggs, left cavity	no
G4	17 mm	7/29	2	Bit I, broke tail, bit again	Left cavity when released	no
B1*	17 mm	7/31	?	Stood over 1 egg, watched I	Left cavity	no
B2	20 mm	8/11	.5	Moved forward	Left cavity	no
B8	17 mm	7/31	?	Snapped at I	Left cavity	no
B8	20 mm	8/11	1	Snapped at I	Left cavity	no
D3**	17 mm	8/7	?	Bit off end ate tail, then rest of juv.	--	--
C3	20 mm	8/8	4	Turned head toward I	Moved past on humus	no
C3	20 mm	8/11	5	Snapped at I 3 times	Moved through cavity, left	no
F6	20 mm	8/8	1	Fed two hatchlings turned toward I	Moved through cavity, left	no

* Her eggs previously replaced by moldy eggs
** All eggs hatched, young present
Attending eggs on humus.

TABLE 12. Responses of brooding females to strange young up to four days old placed in the nesting cavities during the 1960 nesting season.

A	Age of young	Date	Responses Attendant	Intruder	Young of A
G8	24-48 hrs.	8/8	Touched it then snapped, 35 min. later hatchling with other young	Remained still, then began to move among young	Crawled over to it, one touched it.
B2	24-48 hrs.	8/9	Snapped, bit and held on to hatchling for 3 min.	Turned toward A then rolled over on its side. Moved under cover when released by A	No young present
B8*	24-48 hrs.	8/9	After 1 min. snapped at hatchling, then ate it, left		No young present
B8*	4 days	8/11	Touched it with snout, arched neck as it came to edge of cavity cover	Moved away and out of cavity	No young present
C3	4 days	8/10	Touched hatchling, bit and held on. Did not follow when it left cavity	Left cavity when released by A	No interest in hatchling shown
F2*	24-48 hrs.	8/9	Turned toward it, touched it with snout. 10 min. later ignoring it	Remained inactive. 7 hrs later it was on eggs	No young present
B8*	2-4 days	8/12	When placed in cav. it fell on neck of A. A raised head, moved to another cav.	Remained on neck of A. 4½ hrs. later, hatchling on eggs, A curled around them	No young present

TABLE 12. Continued

A	Age of young	Date	Responses Attendant	Intruder	Young of A
G2	0-7 hrs.	8/12	Ignored it	Remained inactive. Against A 10 min. later	No interest in hatchling shown
D1	2 days	8/12	Returned to cav., touched it and substrate, then A's own young. A then turned away	Remained inactive, stayed in cavity	One turned away when hatchling approached it later

* Attending eggs laid by another female.

responded. Female 33 did not respond actively until the intruder was close enough to be pushed away from the eggs.

No eggs were involved in another encounter, in which D1 wandered into a cavity and, finding another individual, snapped at her once and left two minutes later.

In three of the encounters, the intruder exhibited apparent interest in the eggs by pushing toward or against them. In one instance, an attendant left the cavity after snapping at the intruder, which remained in the cavity for two minutes.

None of these nonbrooding individuals exhibited any aggressive responses toward the attendents. Female c, a large (44 mm snout-hind leg length) slowly moving individual, never moved quickly, even when being bitten, passively resisted leaving the cavity, and in one instance attempted to re-enter the cavity. She was removed from the terrarium after each trial.

A juvenile (17 and 20 mm snout-hind leg length) was placed near the edge of a cavity and allowed to enter. Each time, the female was immediately responsive to its presence and turned her head in its direction. Definite aggressive responses by the attendant occurred in half of these encounters. In another encounter, 31 moved over to stand with forelimbs around one of the eggs and faced the juvenile. In the other four encounters, the attendant either moved toward the juvenile or simply stood still. One encounter resulted in cannibalism. After biting and

breaking the tail, D3 ate first the tail, then the rest of the juvenile. Her own young showed no response to this action. The following day, the regurgitated remains of the juvenile were found in a corner of the cavity. In all encounters the juvenile attempted to leave as quickly as possible. Although one crawled over the eggs in its attempt to leave the cavity, no definite interest in the eggs was observed.

From these few encounters, it is apparent that the appearance of a juvenile intruder can, but does not necessarily, incite a defensive response from the attendant. It seems probable that the size of these animals, coupled with their lack of interest in either the eggs or in remaining in the cavity, may account for the less aggressive response.

In August of 1960, nine individuals between 7 hours and 4 days of age were placed by hand in the nest cavities of females, some of which had young present. Newly-hatched young are approximately 10 cm snout-hind leg length. Four of the young were snapped at by the brooding females and one was eaten. Two days later, a 4 day old hatchling was placed near the cavity of the female which had eaten a hatchling in a previous test. She moved over to it, arched her neck, and the hatchling moved away. No aggressive responses were observed in the other four trials.

Three of the young left the cavities in which they had been placed, the other five remained in the cavities

and were removed several days later when the experiment was terminated.

It is apparent that these attendent females did not always react in a defensive manner to the intrusion of strange young. Since newly-hatched young are within the size range of possible food organisms, a feeding response was also involved.

Reaction of Attendent Females to Two Species of Snakes and to Inanimate Objects

In the preceding sections, it has been shown that the brooding females responded aggressively to the intrusion of members of their own species and defended their eggs. The next step was to determine whether such females would respond in a defensive manner to possible predators and to inanimate objects thrust into the cavity by me.

Two snakes, one (Diadophis punctatis - 25 cm, snout-anus) known to feed on F. cinereus and the other (Opheodrys vernalis - 45 cm, snout-anus length) which does not, were introduced into the nest cavities of four females. Since the snakes were large enough to damage the nest cavities and also would interfere with other nesting females in the terrarium if turned loose, each was held in my hand and only the anterior third of the body allowed to enter the cavity. While not affecting the response of the female, this allowed greater control of the snake. In one of the five trials (Table 13) the attendent remained with the eggs

TABLE 13. Responses of brooding females to the intrusion of inanimate objects and two species of snakes into the nest cavities during the 1959 and 1960 nesting seasons. Time is length of trial. A refers to attendant.

A	Object or snake	Date	Time in minutes	Responses of Attendant
		1959		
C1	Broomstraw	7/30	1	Opened mouth, then backed up
C3	Broomstraw	7/30	1	No response
C3	Broomstraw	7/30	1	Backed up. No further response even when touched with straw
C6	Thin twig	7/30	1	Snapped as if feeding when twig wiggled 1 cm from snout
C6	Broomstraw	7/30	1	Backed up, turned head aside
C8	Broomstraw	7/30	1	Snapped as if feeding when straw touched snout
		1960		
D2	Broomstraw	7/15	1	Snapped at straw
D2	Broomstraw	7/15	7	Snapped at it when touched. Continued to snap as it was moved. Followed straw out of cavity (4 cm)
D2	Diadophis punctatis 25 cm	7/16	7	Snapped as head of snake entered cavity. Snake retreated, then put head near eggs. A snapped twice more. Snake snapped back (removed)
D2	Broomstraw	7/19	3	Moved toward it, snapped, followed it out of cavity. Same response when procedure repeated.
D2	Opheodrys vernalis 45 cm	7/29	1	Female left immediately as head of snake entered cavity. Snake showed no interest in eggs

TABLE 13. Continued

A	Object or snake	Date	Time in minutes	Responses of Attendant
D3	Diadophis punctatis	7/18	2	Snake moved head toward A and A left cavity
D3	Broomstraw	7/19	2	Snapped at it, using tongue when it was .5 cm from snout. Followed it 1 cm out of cavity
D1	Opheodrys vernalis	7/29	1	Remained inactive until head of snake almost touched her, then A moved up onto glass.
CV1*	Broomstraw	7/18	2	No response
CV1**	Diadophis punctatis	7/18	1	Left cavity when snake began to enter

* Straw rubbed against D. punctatis

** In another cavity with eggs of another female. Deserted her own the first week in the laboratory

and attempted to defend them. As the snake (D. punctatis) entered the cavity (4 cm from the female), the attendant snapped, then repeated this as the snake came closer. When the snake snapped, it was removed from the cavity. When the Green Snake (O. vernalis) was introduced into the cavity of the same female thirteen days later, she left as soon as the snake's head entered the cavity. In the other three trials with these snakes, the females left the nest cavity with no attempt to defend the eggs.

Table 13 records the results of several attempts to incite defensive behavior in brooding females with a broomstraw and a very small twig. The object was inserted into the cavity, close to the female, then wiggled just above the substrate. In two of the eleven attempts the females made no definite response; in three instances they backed up or turned their heads aside. In three attempts they snapped at the object. The snapping seemed to be more of a feeding reaction and in one of these observations the tongue was used. The snapping was light and quick, with no apparent attempt to actually bite the straw or twig, and no mouth contact was made. Some females followed the straw out of the cavity as I wiggled it and withdrew it slowly from the cavity.

BEHAVIOR OF BROODING FEMALES TOWARD YOUNG

Patterns of Behavior

Although the brooding female of Plethodon cinereus has been found attending hatched young as well as embryos, her behavior during this hatching and post-hatching period and her relationship to the young have not been investigated. Simply being present constitutes some degree of parental care. Mersol (1910) and later Heatwole (1960) and Test and Heatwole (1962) have suggested that the presence of the attendant female is an aid in the retention of moisture. Organ (1960b) found that newly-hatched young of Plethodon welleri remained in contact with the old egg membranes and the female and presumed that they were obtaining moisture from both sources. The defense of the eggs by the female of P. cinereus against members of her own species and against a possible predator (shown in the preceding section) has obvious survival value and thus such care is highly important. Whether the female continues this care after the eggs have hatched and therefore enhances the chances of the young surviving a period when they are relatively weak is also important. Observations discussed in this section were made in order to determine whether the female continues such care as was given the eggs, how long she and the young remain in the nest, her physical relationship to the young, her reaction to her

own young and young from other nest cavities, and whether she feeds during this period.

Hatching of the Young

Although a few clutches of eggs molded and did not develop further (previously discussed), the remaining embryos in the terraria continued to develop successfully during the nesting seasons of 1959 and 1960.

When the experiments were terminated on August 18 for 1959, there were 119 young and 5 unhatched embryos from 21 clutches of eggs. By August 13 of the summer of 1960, 54 young and 48 unhatched embryos were present from 24 clutches of eggs. Although I observed the entire hatching process only twice, I had numerous opportunities to see young ones still struggling to free themselves from the membranes. Young from a particular clutch did not all hatch at one time, but over a period of 2-4 days.

Hatching began on July 29 in 1959 and on August 16 all clutches had at least begun to hatch. In 1960, hatching began on August 5 and slightly over half had hatched by August 13, when the experiments were terminated. Tables 14 and 15 present the dates of hatching for egg clutches of females used in the preceding experiments. Since the eggs were laid on some unknown date before collection, the time interval between collection and hatching represents the minimum length of the hatching period. The maximum value was 55 days, with an average of 48 days when including only those collected prior to June 20. Thus, a probable

TABLE 14. Dates of collection and hatching in the laboratory of egg clutches in the 1959 nesting season. Date refers to beginning of hatching.

Female with eggs	Date of collection	Date of hatching	Days from collection to hatching
A1	June 21	August 5	45
A3	June 21	August 5	45
A6	June 18	August 5	48
A8	June 18	August 6	49
B1	June 25	August 2	39
C1	June 19	August 4	47
C3	June 18	July 29	41
C6	June 18	August 1	44
C8	June 19	August 6	48
D1	June 29	July 30	31
D3	June 29	August 7	37
D6	June 29	August 2	32
D8	June 29	August 4	34
E1	June 25	August 9	45
E3	June 29	August 2	34
E6	June 18	August 12	55

TABLE 15. Dates of collection and hatching in the laboratory of egg clutches in the 1960 nesting season. Date refers to beginning of hatching.

Female with eggs	Date of collection	Date of hatching	Days from collection to hatching
D1	June 19	August 8	50
D2	June 23	*	*
D3	June 23	August 8	46
C1	June 29	*	*
C3	June 23	August 9	47
C6	June 29	*	*
C7	June 29	August 9	41
C8	July 24	August 8	15
F2	June 19	August 7	49
F6	June 29	August 13	45
G2	June 29	*	*
G4	June 29	August 12	44
G6	July 24	*	*
G8	June 29	August 6	38
B1	June 29	August 13	45
B2	June 23	*	*
B3	June 29	August 12	44
B6	June 29	*	*
B8	June 29	*	*

* Clutches had not begun to hatch when experiments were terminated on August 13; however, live embryos were present in each.

estimate of the minimum number of days required for hatching is 48 days. A clutch was collected at the time of oviposition in August, 1959, near Pellston, Michigan (Davidson and Heatwole, 1960) and, kept under similar conditions, hatched 43 days later.

When cumulative curves of the number of clutches which had begun to hatch on successive dates are plotted for 1959 and 1960 (Fig. 10), it can be seen that the curve for 1960 is approximately 7 days behind that for 1959. This aggrees with data found for the tendency of females to curl around the eggs in the laboratory (Fig. 9) and collecting and laboratory data, further supporting my conclusion that the nesting season in 1960 began about one week later than it did in 1959.

When hatching began, the young salamander flexed and straightened repeatedly with several minutes of inactivity between. When the membrane broke, the head emerged and the hatchling lay motionless for five or ten minutes. It then slowly emerged from the membrane by a series of flexions. On two occasions I saw the female place her snout on an egg. The embryo flexed suddenly and in one of these the membrane then broke. Although this was not observed again and may have been coincidental, it is possible that the touch of the mother caused the embryo to flex quickly and hastened the breaking of the membrane. Stebbins (1949b) observed a similar incident with a brooding female of Batrachoseps wrighti. This female moved among the eggs

FIGURE 10. Cumulative number of clutches of eggs which had begun to hatch in the laboratory on successive dates during the 1959 and 1960 nesting seasons.

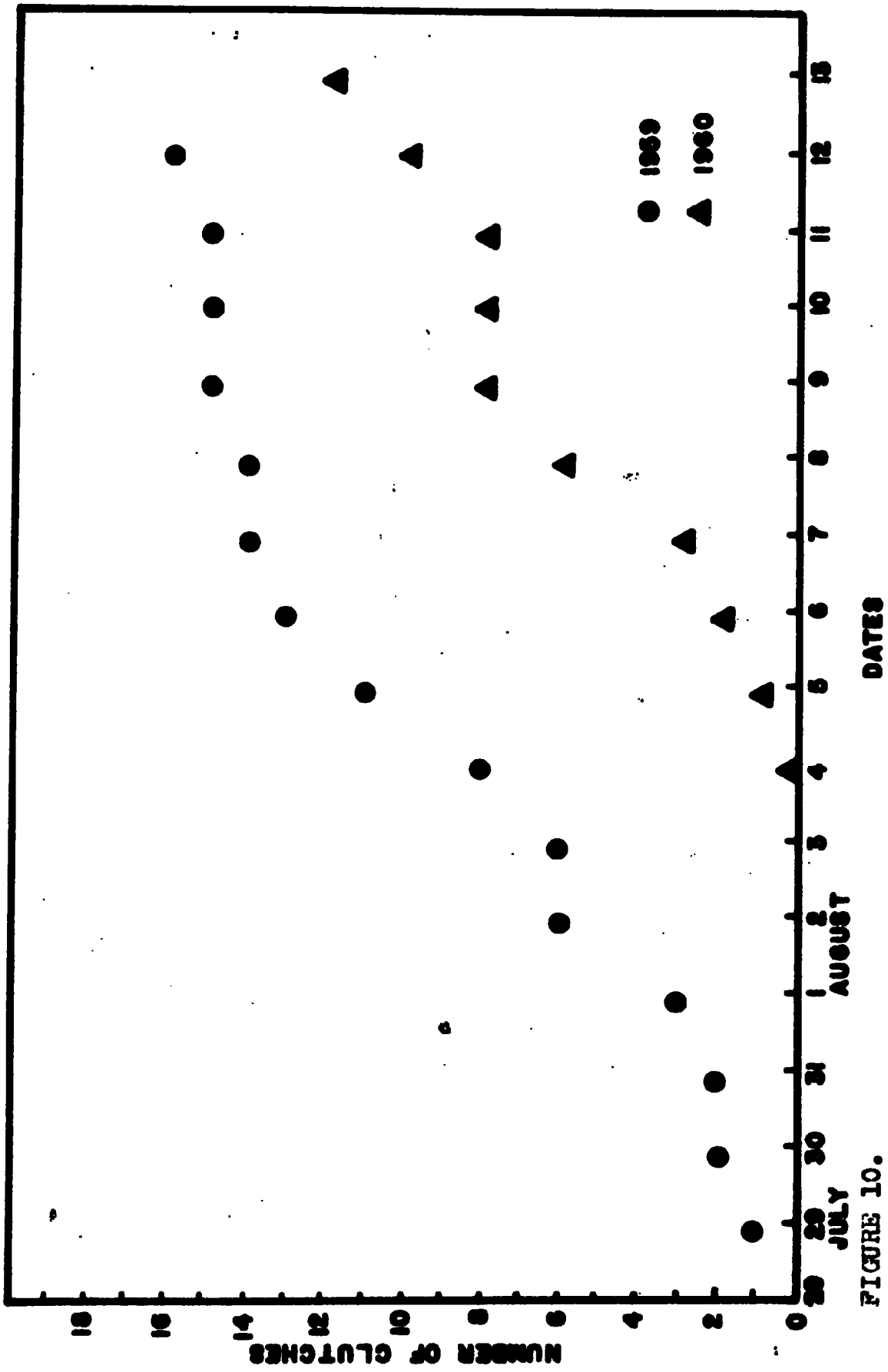

1959
1960
NUMBER OF CLUTCHES
0
2
4
6
8
10
12
14
16
18
20
JULY
30
AUGUST
2
3
4
5
6
7
8
9
10
11
12
13
DATES

FIGURE 10.

and twice nosed emerging young. Although he considered it to be probably accidental as it was observed only once, this female aided hatching by pushing the egg membrane off the back of an emerging young by sliding her chin along its body. Evans (1959) found that emerging young of the skink, Eumeces obsoletus, moved spasmodically when touched by the mother and indicated that this is a definite aid to hatching in this animal.

At the time of hatching, the young are approximately 10 mm long (snout-hind leg length) and have a large abdominal bulge, since the yolk sac does not disappear until 2 or 3 days after hatching.

Contact Between Female and Young

Newly-hatched young usually remained relatively inactive for approximately 24 hours after emerging from the egg membranes, then slowly moved closer to the female or, if they had dropped off the egg clutch while hatching, closer to the young and eggs. Their movements were slowed considerably by the protruding still present yolk sac and were jerky at first. The brooding female always stayed close to the eggs which had not yet hatched (stretched against or curled around them) or to the old egg membranes when all young had hatched. The young either remained on the clutch or slowly climbed on the egg mass or the mother. It was quite common to see several young ones on the neck, body or tail of the female and others on the remaining eggs or egg membranes (Fig. 11).

FIGURE 11. Relationship of brooding females and young during the post-hatching period of the 1960 nesting season. A. F2 with strange eggs and one young and her own one young, August 11. B. G8 with her six young and egg membranes, August 10. C3 with her eggs and six young and strange eggs which had not yet hatched, August 10. D. D3 with six young, August 11.

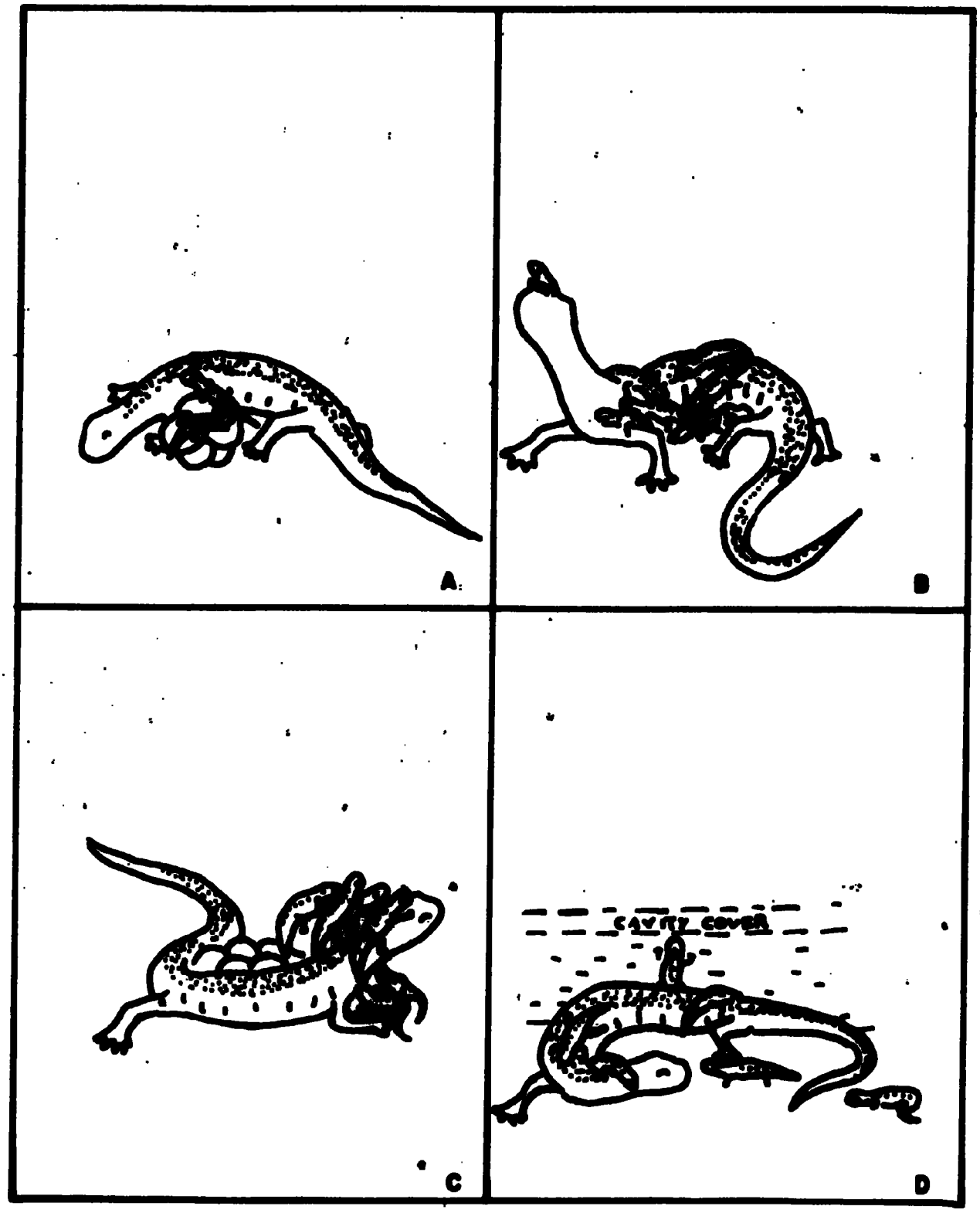


FIGURE 11.

The female was not observed to make any attempt to maintain contact with the young. She remained stretched out next to the old egg membranes, perhaps touching them with one side of her body, but made no head contact with them once all young had hatched. After 2 to 4 days, the young were more active and were often seen on the sides of the cavity or moving around near the female.

Care of Young

During the post-hatching period, the female remained quiet and usually showed no outward interest in the presence of the young. Although they crawled on and over her, and even climbed on her head, with one exception she was not observed to make any response other than to touch them occasionally with her snout. In the exception an active hatchling had moved close to the edge of the cavity, and at the same time another female attempted to enter and put her snout down to touch the young. The attendant moved between them, pushed the hatchling back into the cavity with her snout and remained stationary until the intruder moved away. The undisturbed female cares for her young mainly by remaining with them, but also protects them against intruders. The young were not restricted within the nest cavity and left at will.

Feeding During the Post-hatching Period

Food was offered to several nesting females during the post-hatching period. Methods of feeding are discussed in

a previous section and feeding observations summbrized in Teble 4. Females A1 and A3 on August 5, 1969, and D3 and F2 in 1960 were offered fruit flies after some of their eggs had hatched. All of these females ate some of the flies. Young in one cavity revealed a definite interest in the flies by moving toward them with their snouts close to the floor of the cavity, but did not eat any. None of the females left the cavity or followed in pursuit of the flies.

There is no evidence that the presence of the newly-hatched young altered the reaction of nesting females to food. They ate what was easily available and probably do not often follow food or leave to forage for it. The young did not eat, but perhaps the food organisms offered were not of the right size, as they did appear interested. Also, their interest in food is probably slight as long as the yolk remains.

Duration of Time Young and Female Remain in Nest

Contrary to an early hypothesis by Piersol (1910), who thought that the female and young left the nest together or perhaps that she led them from the cavity, I found that, in the nests where observations were carried on until hatching was complete, every female remained as long as young were present.

Two to four days after hatching, the young began to move around within the cavity. The range of their movements increased on succeeding days as they spread out

within the nest and began to climb on the sides and under the cavity covers. By the end of two weeks, the young were out of the cavity and, in some instances, had crossed over to other cavities. As the young became more active and ceased to remain together and against the female, she became increasingly restless and alert. By the end of the second week after the young had moved out of the cavity, she began to move around within the cavity and often kept her head at the edge or up near the cover. One to two days later she moved under the cover and began to wander to other parts of the terrarium. This is a shorter time period than Gordon (1952) found for the brooding female Green Salamander (Aneides aeneus), which was observed in crevices with the young for one to two months.

Behavior of Brooding Females Toward Strange Young

In order to observe the attending female's reaction to strange hatchlings, recently hatched young were placed in the cavity among the eggs and/or young. The young salamanders were moved by hand. Results are summarized in Table 12.

On August 9, 1960, one newly-hatched salamander was added to each of two cavities occupied by a female with eggs but no young. In one cavity when a hatchling was placed on the floor, the female (B3) moved immediately toward it and touched it with her snout. The hatchling did not move, but the female snapped at it, held on and

then swallowed it. The second female (B2) also put her snout on the hatchling, grabbed it with her jaws and held on for five minutes before releasing it. The hatchling then climbed under the cover and the female did not follow. One four-day-old hatchling was added to another cavity with a female and eggs. The female (B8) quickly placed her snout near the young and it immediately moved away and left the cavity. The female did not follow.

Single hatchlings were added also to four cavities, each occupied by a female with eggs and young. The first female (G8) snapped quickly at it, then kept her snout near its body. The hatchling remained motionless. Both of the attendant's young were interested in the stranger; one touched it with its snout and the other crawled closer. Thirty-five minutes later it was over against the female with the other young. The stranger was apparently accepted by the female, as she subsequently showed no interest in it and it was left in the cavity. Another female (G2), after turning her head toward the hatchling added to her cavity, paid no further attention. It moved among the other young and was apparently accepted.

One female (C3) had been attending two sets of eggs. Her own seven eggs had hatched and the other clutch had not. When a strange hatchling was placed near the edge of her cavity, she moved her snout to touch it, grabbed it in her mouth, then released it. It moved under the cavity cover with no further attention from the female.

Three minutes later I placed one of her own young, which had wandered out onto the humus, in the cavity. She put her snout on it then turned away, whereupon it crawled over among the others, which were all together near the old egg membranes and other eggs (Fig. 10).

A newly-hatched young was placed just inside a cavity after the attendant (D1) was removed. When she returned minutes later and entered the cavity, she moved over and touched the stranger, then put her snout among her own young, next on the floor of the cavity where I had first placed the hatchling, and finally back to touch it again. She then turned away and moved close to her eggs and young. The stranger moved over with the others.

One cavity was occupied by a female (F2) whose own eggs had been replaced four days earlier by another clutch, which had not yet begun to hatch. When I placed a hatchling from her own clutch into the cavity, she touched it quickly, then turned away; the young one crawled up onto the egg clutch and remained. The stranger was not removed from the cavity until the experiment was terminated on August 13 (Fig. 10).

These experiments are too few to permit any general conclusions. However, the results do show several things. When newly-hatched strange young were added to cavities where the eggs had not yet hatched and the female had had no recent contact with young, the hatchling was either driven away or, in one instance, eaten. The only female

to accept the stranger under this condition was really its mother, although she had not been present when it hatched. Tinbergen (1956) mentions that breeding herring gulls will not accept strange young until after their own eggs have hatched. He suggests that internal changes resulting from the external stimuli from hatching are required before she can accept other young. With one exception, all young placed in cavities where young had already hatched were finally accepted by the female and allowed to remain. All of the females apparently recognized the addition of a stranger; all except G2 touched it with their snouts. Their actions, especially in the instance where the female touched the stranger, her own young and the place where I had originally placed the hatchling, indicate that such differentiation is based on odor.

The reaction of attendant females to the addition of older young (juveniles) was much quicker and more like their response to intruding adults. The juveniles showed no tendency to remain in the cavities and left quickly.

DISCUSSION

One of the major hypotheses of this study was that females of the Red-backed Salamander, Plethodon cinereus, provide parental care for eggs and young, thereby enhancing their survival, throughout the nesting season. On the basis of the preceding results, it is my conclusion that this hypothesis is correct.

There is wide variation in the degree of parental care provided by vertebrates, from the simple release of eggs into the water by many fishes and amphibians to the complex care commonly found among birds and mammals. In discussing the various stages in the development of parental care in birds, Kendeigh (1952) considers the first stage as being the choice of a particular site for oviposition, instead of laying eggs randomly; this is followed by the acts of building and guarding the nest as the second stage. His third stage involved attending the eggs and the transfer of heat. Although females of P. cinereus do not actually build or construct a nest, they do apparently choose suitable sites, then remain with and guard their eggs. Females in this study were found to remain with their eggs in the laboratory approximately 90% of the time. Thus, while they left the cavity occasionally, the major portion of the nesting season was spent attending

eggs and young.

While these salamanders are ectothermic and therefore cannot transfer heat and so qualify for the third and most complex stage of parental care, there is an analogy which can be drawn here. Heatwole (1961) has shown that the eggs of this species can lose and absorb moisture and that the females lose moisture through the skin in a dry environment. The physical contact with the eggs maintained by females during the nesting season is probably sufficient to permit transfer of moisture from one to the other.

Most field observations mention finding the attendant female in contact with the eggs. Piersol (1910) says that she will be found with the dorsal part of her head against the eggs. Montgomery (1901) and Piersol (1914) also mention finding her curled around the eggs in the field. Both types of contact have been observed by later workers also (i.e. Bishop, 1941). This same type of physical contact has been observed in other plethodontid salamanders. Organ (1960b) refers to such contact among females and eggs of Plethodon welleri as typical plethodontid brooding behavior.

The above field observations are well substantiated by the behavior of the laboratory females in this study. These females showed a very strong tendency to maintain physical contact with the eggs and the majority of observations found some part of the body, usually the head, against the eggs. In addition they were usually curled

around the eggs, a position which permitted greater physical contact. During one five day period, more than 90% of the observations indicated some degree of curling.

Numerous references have been made in the literature to the beneficial aspects of the attendance of the female. For example, Pierrol (1910), Noble (1931), and Heatwole (1961) refer to the beneficial value to the eggs of the moisture from the female. Heatwole (1961) supports this possibility by demonstrating that the eggs can absorb water from a moist substrate and thus the eggs could also absorb moisture from the female. Stebbins (1951) suggests that the attending adult Aneides lugubris helps keep the eggs moist by body fluids, either through the skin or the bladder.

It has also been suggested that the presence of the female in some way prevents mold from killing the embryo (Noble, 1931). Highton and Savage (1961) found that mold grew only on dead embryos and concluded that any inhibitor could come only from the embryo. However, I found that eggs deserted by the female became moldy often within a week and never molded when attended regularly by a female. In addition, one clutch of eggs, which became moldy during experiments when it was not attended by a female, yielded one hatchling, even though that egg had been completely covered with whitish mold hyphae. Thus, it seems likely to me that there is an inhibition of mold growth when the female attends the eggs, but further work would be

required to reveal whether there is a true antibiotic effect.

The degree of physical contact was found to increase as the nesting season progressed. Head contact was observed to increase until about the middle of the nesting season and then to drop off somewhat. However, the tendency to maintain contact with the head alone decreased as the tendency to keep both head and body against the eggs and to curl around them increased. In fact, the strength of attraction to eggs as shown by the percentage of observations in which curling occurred seems to be related to the length of time since the female began attending the eggs. Comparison of curves plotted from such observations indicate a lag of about a week in the 1960 nesting season behind 1959 (Fig. 9). This is supported by collecting data, behavior of the females when brought into the laboratory, and by a comparison of the dates of hatching in the laboratory for the two years (Fig. 10).

The presence of the female with the eggs during a relatively long period of time has caused investigators to consider whether she occasionally leaves to forage for food. Although Burger (1935) thought that she did leave the nest to forage for food, it has been assumed generally that she does not feed to any great degree during that time. Organ (1960b) believes that Plethodon welleri, like most plethodontids, does not forage during the brooding season. I found that females in the laboratory would

accept food but seldom left the cavities to search for it. Thus, the only food which a brooding female would obtain in the field would be if any suitable organisms entered the nest cavity. An analysis of a section of a large hemlock log occupied by nesting females indicated that such logs are not rich in suitable food organisms. Thus, it probably would not be unusual if they did not feed at all during this time. Also, it has been found in many species of animals that parental behavior is resistant to food deprivation (Collias, 1944).

In addition to a nest site in the form of a cavity or crevice for the eggs and young, another form of parental care, that of the defense of eggs and young, is provided by the female. The possibility that she protects the eggs from insects was suggested early by Piersol (1910) and apparently assumed by other writers, as indicated by the use of the word "guarding" in reference to the brooding female (Bishop, 1941).

Laboratory females in the present study defended their eggs and young against the invasion of other members of their species. Thus this protective function of the attending female (referred to as a guarding female by Piersol, 1910, and others), which ceased to be only an assumption with Savage's (Hinton and Savage, 1961) observation of defense in a single female, has now been shown to occur regularly in the laboratory in a large number of brooding females and against several types of individuals

of the same species. Also, they are exhibiting what Kendeigh (1952) considers one of the ultimate objectives in parental care, that of the protection of young until they are independent.

Although earlier workers (especially Altum, 1867) had observed and reported that male birds occupy areas or territories which they defend against others of their species, Howard in 1920 "...established the concept of territoriality among those interested in the broad fields of animal behavior." with his book Territory in Bird Life (Carpenter, 1953). Since then, investigators have described territorial behavior in other groups of vertebrates (Carpenter, 1953; Scott, 1953; and others).

Since territoriality was first studied in birds by Altum and by Howard, the use of the word has changed somewhat (Nice, 1941). There are now considered to be a number of types of territories. Allee, et al. (1949) lists five types, based upon work with birds. Birds may defend their mating, nesting and feeding areas; mating and nesting areas; mating areas only; nesting areas only or nonbreeding territories. In addition, such defense need not be permanent, but may occur only during a particular part of the year, such as the nesting season. Territoriality seems to be mostly a vertebrate characteristic and is based on the combination of a positive reaction to a particular place and a negative reaction to other individuals (Nice, 1941). In other words, it is

"...chiefly a matter of defense." (Mice, 1941).

Since the brooding females of P. cinereus usually responded before an intruder (of the same species) actually reached the eggs, it appears that they were defending a limited area around the eggs and /or young as well as the eggs and young themselves; therefore, they were possibly exhibiting territoriality.

While the intrusion of other brooding females elicited the most intense and prolonged defensive actions, the same kinds of behavioral responses were obtained when using other adults. Introduction or intrusion of females interested in the eggs resulted in the most aggressive responses from the attendant. In addition to preventing another salamander from pushing her away from her own eggs, defense behavior by the attendant female enhances the survival of eggs and young by preventing oophagy (found to occur in this species by Highton and Savage, 1961, and Test and Heatwole, 1962) and cannibalism (Test and Heatwole, 1962).

The most common defensive response was biting or snapping at the intruder. This was often accompanied by use of the body to push the intruder away from the eggs. The intruder usually did not bite in these encounters, but often was persistent and attempted to push toward the eggs. In Savage's (Highton and Savage, 1961) observations, the intruder retreated and did not defend itself. In my observations of an intruder biting in return, all except

one encounter occurred when two clutches of eggs were present. The other involved the presence of food, which might account for the unusual aggressiveness of the female.

In defending her eggs against others of her species, the attendant female succeeded in the majority of encounters in driving out the intruder. This is a characteristic of territorial behavior. The individual is dominant in his own nesting territory and is defeated in that of another individual (Nice, 1941). While the results of my study do not show any effect of winning upon the behavior of the female, there was some evidence that those which lost became less determined after several such encounters.

The intrusion of juveniles and hatchlings into the nest cavities resulted in aggressive actions by the attendants which were somewhat different from those elicited by the intrusion of adults. The attendant responded to adults more quickly and was more likely to snap at or bite the intruder. Biting occurred only one fifth of the time when juveniles were introduced and one third of the time when hatchlings were involved. Cannibalism was observed twice, once with a juvenile and once with a hatchling. Some of the introduced hatchlings were allowed by the female to remain in the cavity and appeared to be accepted by her and by any young present.

The brooding female exhibited aggressive behavior toward a possible predator (Diadophis punctatus) and in response to inanimate objects inserted into the nest cavities.

A response to introduced inanimate objects was also found by Gordon (1952) in the Green Salamander, Aneides aeneus. A brooding female made aggressive lunges and bites at an inserted wire while nesting in a crevice in the field. Although the response to the snake by the attendant P. cinereus which I observed occurred only once, it does show that this type of defense exists. Perhaps, had smaller predators been used more defensive behavior would have occurred. The female's reaction to inserted objects was more like a feeding reaction in some instances and aggression in others.

Males, females and juveniles were kept together with no observed aggressive behavior. When nonbrooding individuals came in contact with one another, each ordinarily ignored the other; however, they sometimes remained aggregated. It was not unusual for two salamanders to crawl over or under one another when they met and to continue on with no further notice.

The existence of aggressive behavior between the brooding females in the laboratory leads next to the question of whether such encounters actually occur in the field. When the distribution and density of nests within the logs selected for nesting sites was studied, it was noted that a number of nests often occurred relatively near one another in the same log. A two meter section of a large hemlock log was broken apart and found to contain 9 nests and 12 salamanders. Nests were as close as 3 cm.

In another log two nests were 5 cm apart in the same cleavage plane. Thus, while such encounters might not be frequent, both brooding and nonbrooding individuals occur close enough to one another for social interaction to be possible.

Although cannibalism was never found when a female was attending her own young, two strange young were eaten by two different females. Collins (1944) referred to infant cannibalism in amphibians, even though other types of aggression had not been reported, at that time, to occur in this group. Since no females were found to be cannibalistic in the laboratory toward their own young in two years of observations (226 young hatched from 45 clutches of eggs), it is doubtful whether this occurs very commonly in the field. Cophagy appears to be related to "unnatural conditions in the laboratory"(Hinton and Savage, 1961) and it is probable that cannibalism might increase under such conditions. Heatwole and Test (1962) found two instances of this in dissections of animals collected in the field, but they believe their instance of adult cannibalism to be due to crowded laboratory conditions.

During the post-hatching period, the newly-hatched young were found against and on the female and the old egg membranes. Probably they are able, in these positions, to absorb moisture from the body of the female and perhaps the egg membranes. Organ (1960b) found that newly-hatched Plethodon welleri also stayed close to the female and egg

membranes and suggested the absorption of moisture. I found the female P. cinereus usually appeared indifferent to the presence of the young. However, on one occasion a female pushed a hatchling away from the edge of a cavity when an intruder attempted to enter. This usual indifference was also found in P. wilderi by Organ (1960b).

In addition to providing moisture and protection for the young, it is possible that the female may assist them to hatch. The sudden flexion of the young which I observed following a touch of the embryo by the female's snout might have been coincidence, or it might have been actual assistance. Stebbins (1949b) observed one instance of assistance in hatching by an attendant female Batrachoseps wrighti but considered it probably accidental.

Investigators in the past have had difficulty in getting females of this species to lay eggs in the laboratory and then to attend them until they hatch. Certain types of studies, such as those dealing with inheritance, have had to rely on data obtained from field collections based on the assumption that the female found with the eggs or young is the mother. While recent success in inducing oviposition (Highton and Savage, 1961) has somewhat solved this problem, I believe there is something to be gained from considering this question in the light of results from this study.

Probably the first question is what might cause the female, after laying her eggs, to desert them. That she

does leave the eggs under some circumstances is evident from collecting observations. Although most nests contained both female and eggs, a small percentage of clutches were found unattended (probably as a result of collecting disturbances). Females in the laboratory were found to stay with their eggs 90% of the time, indicating a certain degree of wandering. In addition, they also left their cavities as a result of vibrations from the movement of the terrarium cover.

With the exception of the first two weeks of the nesting season, females exhibited a strong attraction to their eggs and, when moved, would return in a relatively short time. Also, those females which wandered voluntarily from their cavities usually returned in a few minutes to a few hours. However, in comparison to the length of time these females were observed, voluntary extracavity movements were not common.

In addition to returning to their nests after being displaced, breeding females were able to recognize their own eggs. When other eggs were substituted for her own in her absence, the displaced female would return, then leave, and was able to locate her own, when they had been placed in another cavity. She was also able to distinguish between her own and a second set placed in her cavity while she was absent.

In experiments with artificial eggs (using berries of Melanthemum canadensis and beads) odor reinforced by touch

appears to be the primary factor enabling brooding females to recognize an object as an egg. Although females are without doubt able to see the eggs, the location of their nest sites inside logs and therefore in complete darkness precludes the possibility that egg recognition is based on visual clues. A number of experiments on egg recognition in the Herring Gull (Larus argentatus) have been conducted by Tinbergen (1953) and by Baerends (1959). They found, using wooden models of eggs, that recognition of an object as an egg in the gull is chiefly by sight. Baerends (1959) states that they react to models or to the eggs "...on the basis of the summation of sign stimuli." In other words they reacted to the combination of separate characteristics of the model rather than to its general appearance. More specifically, he found that the speckling and the size of the egg were more important than the color or the shape. Tinbergen (1953) also mentioned that the gulls "preferred" larger than normal egg models and clutches with more eggs than they had been attending when tested with two choices. Although I did not try any oversize artificial eggs, I did remove four of five eggs a female was attending and found that she did not remain with the one egg in her cavity.

When brooding females encountered a strange clutch of eggs, they pushed and prodded it with their snouts and often rolled it over and over for perhaps half an hour. They were never observed to react in this manner to their

own eggs, regardless of where the eggs were.

Although only a small number of experimental trials were run, it is apparent that females are able to recognize a specific clutch of eggs chiefly by odor, possibly reinforced by tactile stimuli.

Also, it is possible that predators might cause the female to desert the nest; however, it seems likely that she would return and that, at least in the hemlock logs commonly used as nesting sites in northern Michigan, chances of encountering predators of any size are few. (However, it is possible that a wandering female could encounter the snake, Diadophis punctatus, which lives in logs and is known to prey upon P. cinereus.)

Therefore, it is not likely that the brooding female often deserts her eggs under normal field conditions. If she does leave, it is quite probable that she has not gone far and will return. Since females can be collected in the field, transported in a plastic bag and be placed in a terrarium and yet remain with the eggs through the remainder of the nesting season, it seems that they will tolerate a fair amount of disturbance before permanently deserting their eggs.

However, if a female did wander from her cavity (or if her eggs had been destroyed) and came upon an unattended clutch of eggs, she would probably attempt to remain with them. Brooding females have been shown to be definitely attracted to eggs, including those they did not lay. This

attraction is so strong that they will accept two sets of eggs simultaneously and attempt to curl around them both. Therefore, although it is not probable that the female often deserts her eggs or that a clutch is left unattended for long, it is possible that this could happen and that the female collected with the eggs was not the one which laid them.

On the other hand, the question of whether the young found in a particular cavity are those which hatched from the eggs laid by that female is another matter. Females in the laboratory would accept young from other clutches once their own had hatched. Also, once the young had become active and began to disperse, they were found in the laboratory to have moved as much as 10 cm. Since nests in the field were as close as 3 cm, it is possible for the young to wander into another nest. Thus, although the young probably belong to the clutch laid by a particular female, there is no guarantee that this is always true.

SUMMARY

During the nesting season, eggs of Plethodon cinereus have been found attended by a female. From this it was assumed that attendant females are the ones which laid the eggs, that they remain with them from oviposition to hatching and that their presence enhances the survival of the eggs. The purpose of this study was to test these hypotheses by observing females with their eggs in the laboratory. From these observations it was hoped that specific information could be obtained regarding the behavioral patterns of these animals during the nesting period and the type and degree of maternal care, if any, received by the eggs and young.

Brooding females and their eggs were collected from forest areas near Pellston, Michigan during the summers of 1958-1960. During these collections, data were obtained on the characteristics and locations of nests, commonly found in large, decaying hemlock logs. Temperature, relative humidity, moisture content and pH also were obtained for the logs in which nests had been found.

Females with their eggs were brought back to the laboratory and placed in artificial nest cavities within terraria. They were kept in the dark, except for a green light used during periods of observation, and under conditions of temperature and relative humidity which were

relatively constant.

Successful transfer of these animals to the laboratory nest cavities, resulting in continuing attendance of the eggs by the female, was partly dependent upon the length of time the female had been attending the eggs.

Females usually maintained physical contact with the eggs. Closeness of such contact and the tendency to curl around the eggs (which involves greater physical contact) increased as the nesting season progressed, then began to drop off about the time hatching began.

While attending the eggs, the female did not maintain the same position for any extended period, changing it at least once a day. However, only limited extracavity movement was observed, as the females were found outside the cavity only 3-18% of the time. Probably the female attending eggs in the field does not often leave them.

The constancy of attendance was not affected by the amount of experimental disturbance; however, the number of eggs which survived was decreased, probably due to oophagy. Unattended or irregularly attended eggs molded, but a small amount of extracavity movement had no effect on the survival of the eggs.

When offered suitable food organisms, attendant females fed within the cavity, but seldom left it to follow or search for food. This indicated that females in the field probably do not forage for food during the nesting season, eat only those organisms which wander into the

cavity, and therefore obtain very little food during that time.

Displaced females returned to their eggs in a relatively short time and were able to locate them if they had been moved to another cavity in their absence. They apparently located the cavity containing their eggs (10-30 cm away) by trial and error and seldom returned directly to them.

Brooding females were strongly attracted to eggs, their own and those laid by another female. Nonbrooding individuals, however, avoided the cavities containing eggs and tended to aggregate.

Limited experiments with berries and beads as artificial eggs indicate that, although females were doubtless able to see when light is available, egg recognition is primarily by odor, supplemented by touch.

Females accepted and attended eggs in place of or in addition to their own. When they encountered strange eggs, they pushed and prodded them with their snouts, often rolling the clutch around the cavity; however, this was never observed when the eggs were their own.

Brooding females defended eggs, young and perhaps a limited area around eggs and/or young against intruders of their own species. Defensive actions usually included biting and snapping, although the presence of the attendant was sometimes sufficient to cause the intruder to leave. Females usually responded aggressively when the intruder

entered the cavity and did not wait until it displayed an interest in the eggs. However, the most aggressive actions of the attendant were in response to an intruder with interest in the eggs and which persisted in its attempts to approach them. The intruder did not generally bite in return, but simply pushed against the attendant or toward the eggs.

Females responded aggressively (or snapped as if feeding) to small straws and twigs inserted into their cavities. One female snapped aggressively at an intruding snake, Diadophis punctatus. In other trials the female left the cavity when the snake began to enter and did not attempt to defend the eggs. Nonbrooding individuals were never observed to display any aggressive actions toward one another.

Records of hatching in the laboratory suggest a minimum period from oviposition to hatching of 48 days. Eggs in a single clutch hatched over a period of 3 or 4 days rather than all at once. In 1959, 18 days elapsed after the beginning of hatching before the last clutch had begun to hatch.

The brooding female did not maintain contact with the young, although they remained against or on her body or the old egg membranes for several days after hatching. Strange young placed into cavities of females whose eggs had not yet begun to hatch were driven out or, in one instance, eaten. Females with young present accepted

additional young.

It can be concluded that the female found with eggs in the field is probably, but not necessarily, the one which laid the eggs, and that she remains throughout the nesting season, leaving the cavity permanently only after the young have left the cavity (about two weeks). Her presence reduces the tendency of the eggs to mold, helps eggs and young retain moisture and provides protection from predators of both eggs and young.

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