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WATER CONTENT OF COCKROACH EGGS DURING EMBRYOGENESIS IN RELATION TO OVIPOSITION BEHAVIOR

LOUIS M. ROTH AND EDWIN R. WILLIS
Pioneering Research Division
U. S. Army Quartermaster Research and Development Center
Natick, Massachusetts

NINE FIGURES

In a brief note we ('55) have pointed out that the water content of cockroach eggs varies with age and may differ among different species according to their oviposition behavior. In this paper we report the water relationships of the eggs of several species of cockroaches. Additional detailed material is included on the four species treated in the earlier paper.

The following 10 species of cockroaches were used: *Blatta orientalis* Linnaeus, *Blattella germanica* (Linnaeus), *Blattella vaga* Hebard, *Eurycotis floridana* (Walker), *Periplaneta americana* (Linnaeus), *Periplaneta australasiae* (Fabricius), *Leucophaea maderae* (Fabricius), *Nauphoeta cinerea* (Olivier), *Pycnoscelus surinamensis* (Linnaeus), and *Supella supellectilium* (Serville).

Pycnoscelus was reared and maintained on lettuce; all of the other species were fed Purina dog chow checkers. Oöthecae[1] of the oviparous species were collected once a day; the females of the ovoviviparous species were isolated as they formed their oöthecae. At various times after oötheca formation these ovoviviparous females were anesthetized with CO_2, and the oöthecae were ejected from the

[1] Unless otherwise indicated, use of the term oötheca implies both the egg case and its enclosed eggs.

uterus by finger pressure on the base of the abdomen. If the uterus was everted as a result of this manipulation, it was pushed back into position with a pair of forceps. *Blattella germanica* and *B. vaga* were also anesthetized with CO_2 while their attached oöthecae were removed. All weights were determined on torsion balances which were sensitive to 0.02 mg, 0.01 mg, or 0.05 mg; in a few instances, some of the heavier oöthecae (e.g., those of *Eurycotis* and *Leucophaea*) had to be weighed on an analytical balance. The oöthecae were air-oven dried at about 80°C. to constant weight. Higher temperatures such as 100°C. were not used, as they caused some of the young oöthecae to become greasy.

There are at least 5 possible types of known ovipositional behavior among cockroaches. These are arranged, below, to show a progressive tendency toward retention of the eggs within the body of the female until hatching (Roth and Willis, '54).

Oviposition type 1. Oötheca extruded and carried by the female for only a short time, then deposited and abandoned: oviparous cockroaches (see table 1 for examples).

Oviposition type 2. Oötheca extruded and carried by the female for a longer period than type 1, but eventually dropped long before the eggs hatch: oviparous cockroaches [*Ectobius panzeri* Stephens (Brown, '52); *Ectobius livens* (Turton) carries her oötheca up to 16 days and perhaps longer before she deposits it (personal communication from Mr. Paul Rolander through Dr. Harvey Sweetman, University of Massachusetts)].

Oviposition type 3. Oötheca extruded and carried externally by the female until, or shortly before, the eggs hatch: oviparous cockroaches (see table 1 for examples).

Oviposition type 4. Oötheca extruded (fig. 1A, B) then subsequently retracted into a brood sac where the embryos develop until, or shortly before, hatching. Although we have previously considered cockroaches (see table 1 for examples) with this kind of behavior ovoviviparous, we have also questioned the validity of this classification (Roth and Willis, '54,

'55b). Hagan ('54) agreed that "... the process of extruding oöthecae is truly oviposition..." and later retraction into the female's brood sac does not make the embryos viviparous when they are born. We suggest that this type of reproduc-

TABLE 1

Initial water content of oöthecae and enclosed eggs of several species of cockroaches

Note: Based on oöthecae which were 24 hours old or less. The oöthecae of the false ovoviviparous cockroaches (4, below) were removed from the female either prior to their complete retraction into the brood sac or just after they had been retracted.

SPECIES AND TYPE OF OVIPOSITIONAL BEHAVIOR	WATER CONTENT (%) ± S.E.[1] OF OÖTHECAE AND EGGS	N[2]
1. Species which deposit and abandon the oötheca shortly after its formation:		
(1) *Periplaneta americana*	59.8 ± 0.23	27
(2) *Periplaneta australasiae*	62.7 ± 0.50	10
(3) *Eurycotis floridana*	62.0 ± 0.36	10
(4) *Blatta orientalis*	64.1 ± 0.38	20
(5) *Supella supellectilium*	64.3 ± 0.28	15
3. Species which carry the oötheca externally until or shortly before the eggs hatch:		
(1) *Blattella germanica*	62.2 ± 0.20	20
(2) *Blattella vaga*	59.5 ± 0.53	10
4. Species which extrude then retract the oötheca and carry it internally until the eggs complete development:		
(1) *Nauphoeta cinerea*	34.2 ± 0.71	10
(2) *Pycnoscelus surinamensis*	39.4 ± 0.44	7
(3) *Leucophaea maderae*	37.1	1

[1] S.E. = standard error.
[2] N = number of oöthecae.

tive behavior be called false ovoviviparity, or possibly pseudo-oözootoky. True ovoviviparity would encompass those animals in which eggs, with enough yolk to allow the embryos to complete development, are retained within the female's body from formation until hatching. We know of no truly ovo-viviparous cockroaches at this time.

Oviposition type 5. Oötheca probably not extruded, the egg case being directed from the vestibule into the brood sac where the eggs remain until hatching: viviparous cockroaches [*Diploptera dytiscoides* (Serville)].

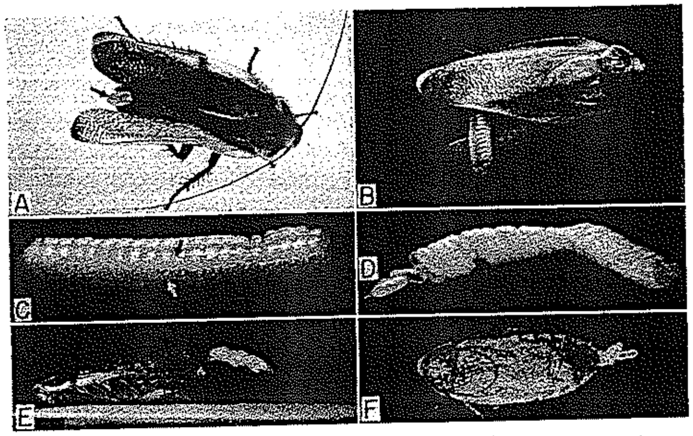

Fig. 1 A–D.—*Leucophaea maderae.* A. Oötheca (arrow) beginning to form. × 0.7. B. Same female shown in A with oötheca almost fully formed and ready to be retracted. It is uncommon for the oötheca to protrude between the wings as happened with this specimen; frequently the egg case is extruded toward the rear, not upward, and lies under the wings. × 0.7. C. Normal oötheca (cephalic view). Note the limits of the oötheca (arrows) which does not cover the eggs completely. The small circular areas on the bottom row of eggs are the micropylar regions. × 2.3. D. Abnormal oötheca which contained a double and single row of eggs. × 1.7.
E–F.—Two females producing abnormal oöthecae. Approximately × 1.7.

The species used in this study represent behavioral types 1, 3, and 4; nothing is known of the water relationships of the eggs of cockroaches which belong to type 2. A study of *Diploptera* (type 5) will be reported elsewhere (Roth and Willis, '55b).

The percentages of water in the oöthecae of several species of cockroaches, arranged according to oviposition behavior, are shown in table 1. Initially, the eggs of the species which carry their oöthecae internally contain a smaller percentage of water than the eggs of either those species which drop the oötheca shortly after its formation or species like *Blattella* which carry their oöthecae externally until the young hatch. In *Diplotera* the newly formed oötheca contains about 34% water (Roth and Willis, '55b).

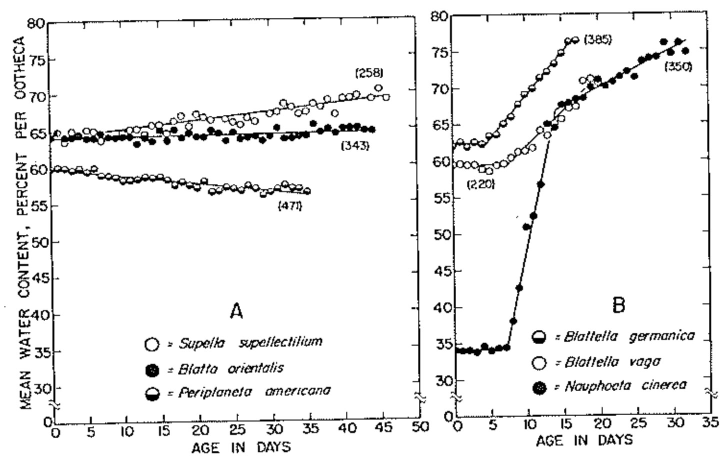

Fig. 2 Water content of the oöthecae of 6 species of cockroaches. Temperature, 27°–29°C. The oöthecae used to obtain the curves for A were kept at about 30% relative humidity; all three species were run concurrently. The oöthecae used in B were obtained from females which had continuous access to drinking water. The values in parentheses indicate the total number of oöthecae used for each curve.

With embryonic development the water content of the eggs changes. These changes were followed daily and will be discussed separately, according to the oviposition behavior of the females.

Oviposition type 1. The water content of the oöthecae of *B. orientalis*, *P. americana*, and *S. supellectilium* is shown in figure 2A. The proportion of water in the oötheca of *B. orientalis* remains fairly constant throughout development.

In *P. americana* the proportion of water drops with time, and in *S. supellectilium* the proportion of water increases during embryonic development. The differences between these three species are due to differences in rates of water loss

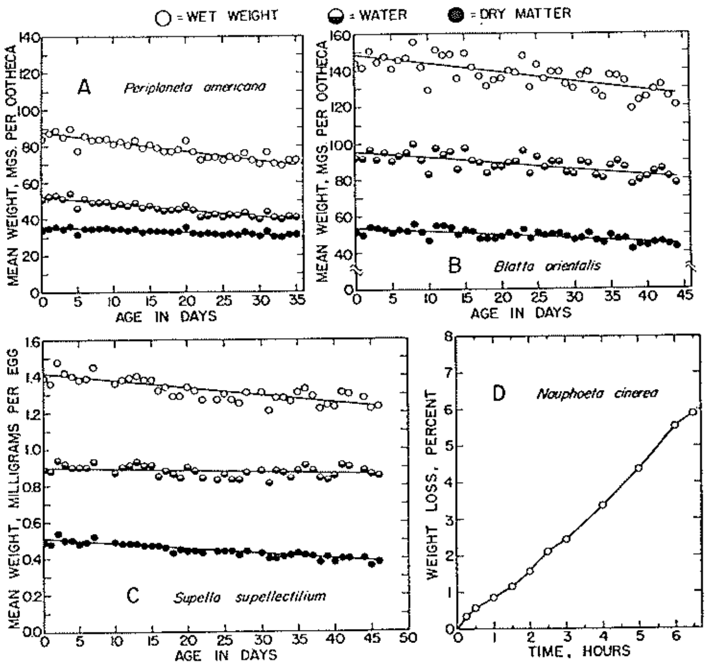

Fig. 3 A–C. Changes, with age, in water and dry matter content of three species of oviparous cockroaches. Data obtained from the same oöthecae used in figure 2A. In A and B, no egg counts were made for each oötheca, so that the means are calculated on a per-oötheca basis. In C, counts were made of the number of eggs in each oötheca and the calculations were made on a per-egg basis; however, these mean values include the weight of the oötheca inasmuch as the eggs were not removed from the egg cases. D. Weight loss of a single oötheca (containing 36 eggs) of *Nauphoeta cinerea*. The oötheca was almost completely retracted into the brood sac at the time of its removal from the female. The oötheca remained on the torsion balance during the entire experiment and the weight changes were noted at the indicated time intervals; relative humidity about 32% and temperature about 26°C.; at the end of 22 hours, the oötheca had lost 16% of its weight.

relative to loss in dry matter (fig. 3A-C). In *B. orientalis* both water and solids are lost at about the same rate (fig. 3B); in *P. americana* (fig. 3A) water is lost at a greater rate than dry matter; in *S. supellectilium* dry matter is lost at a greater rate than water (fig. 3C).

In *B. orientalis* the water content of the eggs actually increases during embryogenesis (fig. 4). During the early stages of development, the oötheca is very moist inside; after the

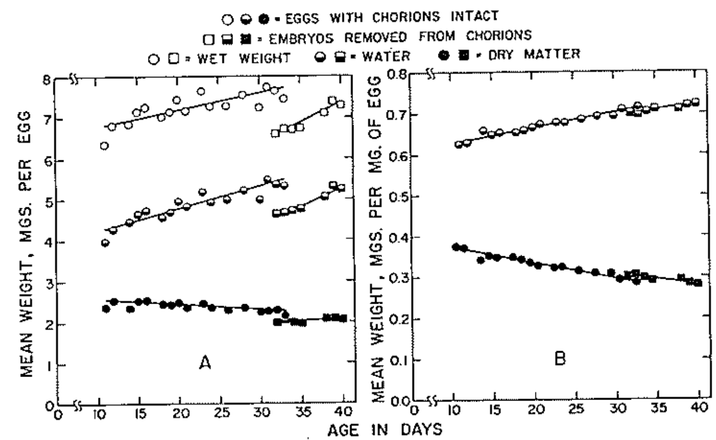

Fig. 4 Changes, with age, in water and dry matter content of eggs of *Blatta orientalis*. All eggs were removed from the oöthecae. A total of 284 eggs taken from 186 different oöthecae was used to obtain data for these curves.

eleventh day of development, which was the earliest we could remove the eggs from the oötheca, the inner surface of the oötheca and the outer surface of the chorion are very moist. As development proceeds, these surfaces become progressively drier. After about a month, the chorion is so brittle that it is difficult to remove the eggs without having the well-developed embryos rupture through the chorions. The inner surface of the chorion and the outer surface of the embryo itself, however, are still quite moist at this time. Undoubtedly during development water is absorbed by the egg from the spongy inner surface of the oötheca (Roth and Willis, '55). According to Pryor ('40), the fluid surrounding the eggs in the newly deposited oötheca of the oriental cockroach contains a dihydroxyphenol, subsequently identified as protocatechuic acid (Pryor et al., '46). Presumably this compound, which tans and hardens the oötheca, is present as a dilute solution in the moisture surrounding

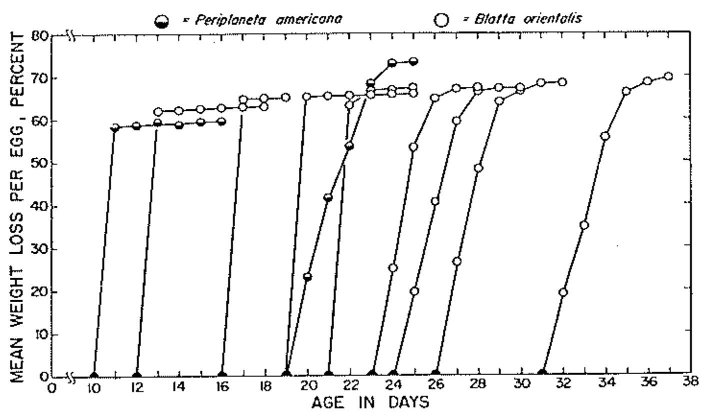

Fig. 5 Weight loss of different aged eggs, removed from the oöthecae of *Blatta orientalis* and *Periplaneta americana*. Each curve starts (black semicircle) at the age of the egg when it was dissected from the oötheca. The eggs of *Blatta* were kept at 28° ±1°C. and about 30% relative humidity. A total of 110 eggs was used to obtain the mean values for the 8 different aged groups. The eggs of *Periplaneta* were kept at room temperature and 0% relative humidity; 4 eggs for each of the two age groups were used.

the eggs. The inner surface of the oötheca remains moist for some time after the egg case has assumed its final dark coloration.

During embryological development, certain changes in the eggs of *B. orientalis* result in a greater ability of the egg itself (without oöthecal protection) to withstand desiccation. This is shown in figure 5; eggs that were 12 to 21 days old lost practically all of their water within 24 hours, whereas eggs that were 23 days old or older required two or more

days to dry out. The same apparently is true of the eggs of *P. americana,* 10-day-old eggs losing water much more rapidly than 19-day-old eggs (fig. 5); the eggs of this species can also, apparently, pick up water from the oötheca since the 19-day-old eggs contained more water than the 10-day-old.

Oviposition type 3. In *Blattella* one end of the oötheca which is permeable to water (Roth and Willis, '55) is in contact with the female for the duration of embryonic development. In *B. germanica* the percentage of water remained constant at about 62% for 4 days and then increased steadily

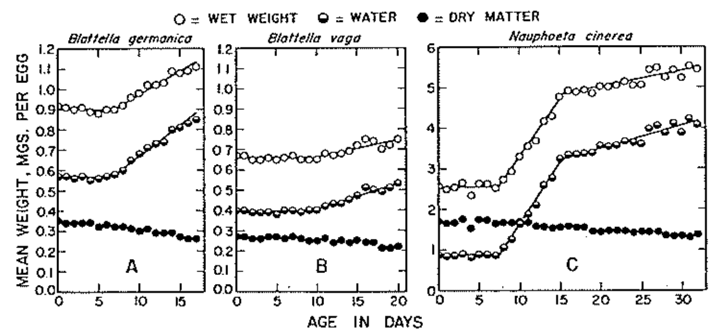

Fig. 6 Changes, with age, in water and dry matter content of the oöthecae of three species of cockroaches. Data obtained from the same oöthecae used in figure 2B. Calculations were made on a per egg basis but include the weight of the oöthecae since the eggs were not dissected from the egg cases.

to about 76% by the time hatching occurred (fig. 2B). Results with *B. vaga* (fig. 2B) were similar, except that the initial water content of about 60% remained constant for 7 days and then increased to about 70% by time of hatching. The percentage increase in water content of the oöthecae of these two species of *Blattella* is due to both loss in dry matter and uptake of water from the female. In both species, dry matter is lost slowly (fig. 6A, B). When calculated on a per-egg basis, the wet weight of the oötheca of *B. germanica* (fig. 6A) drops slightly during the first 5 or 6 days of development; this may be explained by the fact that though dry weight is being lost, the eggs are apparently not yet absorbing any water. After the 6th day the wet weight begins to increase because water is being absorbed from the female. *B. vaga* (fig. 6B) differs from *B. germanica* in that the amount of water present in the eggs initially is less,

TABLE 2

Changes in length, wet weight, water, and dry matter of eggs of Pycnoscelus surinamensis during embryogenesis

Note: The values for 0 days are the means of 7 oöthecae; all other values are based on one oötheca for each age represented. Computations include the weight of the oötheca. Females were kept at 27°–28°C., at which temperature the eggs hatch in 31 to 35 days.

AGE	LENGTH	WET WEIGHT PER EGG	DRY MATTER PER EGG	WATER PER EGG
days	*mm*	*mg*	*mg*	*mg*
0	2.62	1.887	1.140	0.747
1	2.55	2.009	1.219	0.791
3	2.84	2.026	1.233	0.793
5	2.74	2.155	1.310	0.845
6	2.79	2.127	1.325	0.802
7	2.40	2.158	1.242	0.917
8	2.55	1.862	1.106	0.756
9	2.94	2.522	1.450	1.072
10	2.94	2.258	1.175	1.083
12	3.58	2.976	1.131	1.845
13	3.58	2.935	1.159	1.776
14	3.43	3.324	1.174	2.150
15	3.53	3.310	1.158	2.152
16	3.53	3.345	1.133	2.212
17	3.82	3.653	1.194	2.459
18	3.58	3.209	1.056	2.153
19	3.87	3.489	1.115	2.374
20	3.58	3.500	1.125	2.375
21	3.77	3.204	1.082	2.122
22	3.77	3.929	1.446	2.483
23	3.63	3.695	1.205	2.490
24	3.53	3.533	1.161	2.372
25	3.58	3.208	1.090	2.118
26	3.92	3.728	1.244	2.483
27	3.58	3.297	1.110	2.187
29	3.72	3.280	1.039	2.241
32	3.92	3.800	1.184	2.616

water begins to be absorbed later (after about 11 days), and less water is absorbed during development.

Oviposition type 4. The water in the oöthecae and eggs of false ovoviviparous *Nauphoeta cinerea* (fig. 2B) remains at about 34% for the first 7 days of development, increases markedly for a week, and then rises more slowly until at hatching time the oötheca may contain about 75% water. There is a marked increase in the size of the eggs during development (figs. 7A–D, 8A,B); the increase in length may amount to as much as 80% by the time hatching occurs.

TABLE 3

Changes in length, wet weight, water, and dry matter of eggs of Leucophaea maderae during embryogenesis

Note: All values are based on one oötheca each for each of the 4 ages represented. Females were kept at 27°–28°C., at which temperature the eggs hatch in about 62 days. Weight of the oötheca is included in the computations.

AGE	LENGTH	WET WEIGHT PER EGG	DRY MATTER PER EGG	WATER PER EGG
days	*mm*	*mg*	*mg*	*mg*
0	4.80	7.661	4.818	2.843
18	5.24	8.885	4.279	4.606
28	7.25	12.738	4.462	8.276
41	7.35	15.689	4.353	11.336

The eggs increase slightly in length shortly after the female retracts the oötheca, but this increase is not correlated with an uptake of water. It is possible that internal body pressure lengthens the eggs by altering their shape just after they have been retracted into the uterus. The weight and length of the eggs increased during development as the eggs absorbed water (figs. 6C, 8A); solids were lost slowly during embryogenesis (fig. 6C).

Water determinations and egg-length measurements were made on a small number of oöthecae of the false ovoviviparous cockroaches *Pycnoscelus* and *Leucophaea*. The results (tables 2 and 3) show that these eggs also absorb water and increase in length. The data for *Pycnoscelus*, when plotted, gave curves similar to those for *Nauphoeta* (fig. 6C), although the curves were not as smooth because of the smaller number of specimens used.

Abnormal oöthecae. The arrangement of the eggs within the oötheca is usually the same in all cockroaches, the eggs

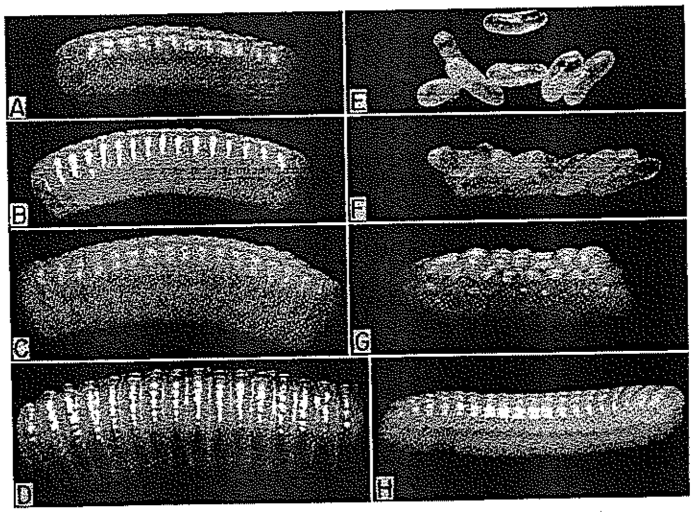

Fig. 7 Eggs and oöthecae of *Nauphoeta cinerea.* A–D. Four oöthecae of different ages showing increase in size of the eggs with embryonic development. A. 1-day-old oötheca; there are fewer eggs in this than in the following oöthecae. B. 11 days. C. 15 days. D. 30 days. E–G. Aberrant oöthecae. E. From female shown in figure 1F. F. From female shown in figure 1E. G. Oötheca (caudal view) with 3 rows of eggs (cf. with H). H. Normal 14-day-old oötheca (caudal view) with two rows of eggs. × 3.3.

being placed in a double row (figs. 1C, 7H). Sometimes the false ovoviviparous species form abnormal oöthecae; the eggs may be arranged in a single row (fig. 1D), or in a triple row (fig. 7G). Squeezing the abdomen of *Nauphoeta* in order to remove the oötheca sometimes caused subsequent formation of abnormal oöthecae (figs. 1E, F; 7E, F); the females usually cannot retract these abnormal oöthecae into the brood sac.

However, many of these squeezed females produced oöthecae from which eggs hatched normally.

Water loss from oöthecae. The oöthecae of cockroaches differ in their ability to prevent desiccation of the eggs. The oötheca of false ovoviviparous cockroaches is soft and

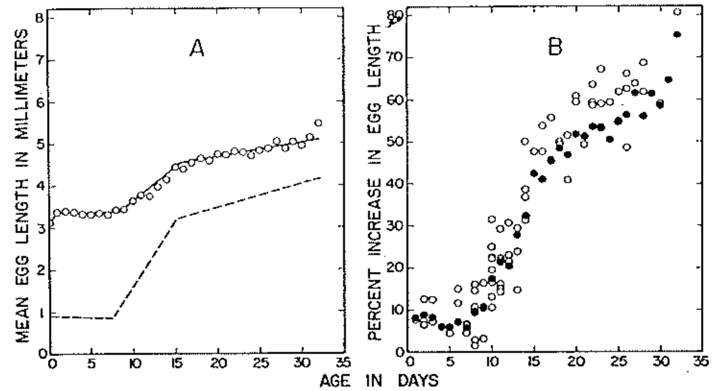

Fig. 8 Increase in length of eggs of *Nauphoeta cinerea* during embryonic development. The length of the eggs at one end of the oötheca was measured with an ocular micrometer. A. Comparison of egg length with water content. Open circles = egg length; eggs from 93 oöthecae were used to determine the 0-day value, and eggs from 347 oöthecae were used to obtain the other values. Dashed line = mean water content, milligrams per egg, from figure 6C. B. Solid circles = theoretical mean percent increases calculated from the values used in figure A. Open circles = actual observed values, each circle representing one determination (or more if the values superimposed; total of 86 determinations). These data were obtained by first measuring the length of the eggs at the time the oötheca was being formed (and had been rotated), and then measuring again at a known age after the oötheca was manually extruded from the brood sac.

pliable, in contrast to the hard, rigid oötheca of oviparous forms like *Blatta* and *Periplaneta*. The eggs of *Nauphoeta* lose water most rapidly, those of *Blatta orientalis* most slowly, and those of *Blattella germanica* lose water at a rate intermediate between the other two species (Roth and Willis, '55). Additional data obtained with oöthecae of *Supella*, *Pycnoscelus*, and *P. americana* (fig. 9) confirm the earlier findings. Eggs which failed to complete development lost water much more rapidly than those which did develop. Changes in weight of a recently formed oötheca of *Nauphoeta* over a period of 6.5 hours are shown in figure 3D; the eggs in this oötheca lost water, when exposed to the atmosphere, much more rapidly than those of the oviparous species studied.

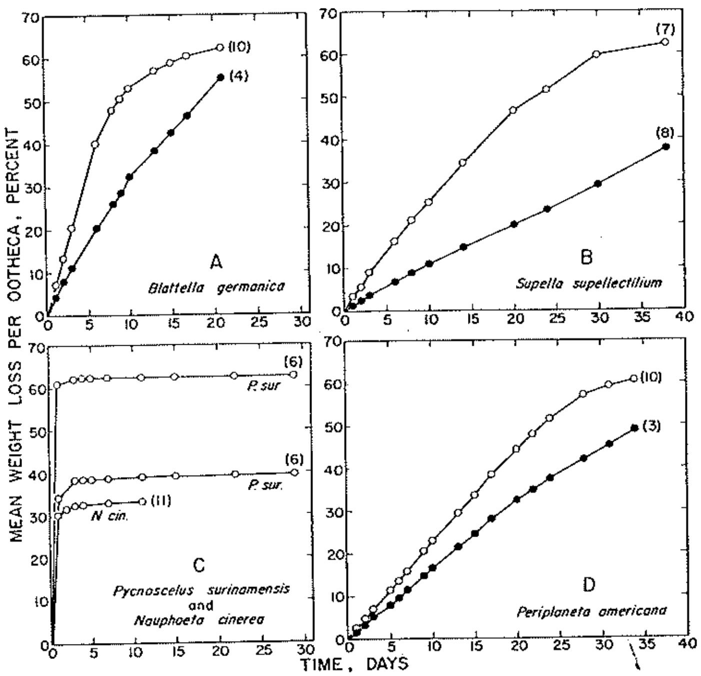

Fig. 9 Weight loss of oöthecae of 5 species of cockroaches. Oöthecae kept at 0% relative humidity and 27° to 28°C. The values in parentheses indicate the number of oöthecae used to obtain each curve. Solid circles = some eggs in the oöthecae developed. Open circles = none of the eggs developed. A. *Blattella germanica* oöthecae 1 to 2 days old when removed from the female. B. *Supella supellectilium* oöthecae less than one day old. C. *Nauphoeta* oöthecae one to 7 days old; *Pycnoscelus* oöthecae 14 days old (upper curve) and one to 7 days old (lower curve). D. *Periplaneta americana* oöthecae less than one day old.

DISCUSSION

Common to the embryogeny of cockroaches is the absorption of water by the eggs sometime during development. In the oviparous species that drop their oöthecae (*Blatta, Periplaneta*), water is obtained from the moist inner surface of the egg case; this moisture, present in the oötheca at the time of its formation, is supplied by the female all at one time. In *Blattella* additional water enters the eggs, from the female, through the permeable portion of the oötheca which is in continuous contact with the female's oöthecal cavity (Roth and Willis, '55). In the false ovoviviparous species (*Nauphoeta, Pycnoscelus,* and *Leucophaea*), water must pass from the female's body, through the uterus or brood sac, to enter the eggs. In all of the species studied, including the false ovoviviparous forms, solids were lost during development. Only in viviparous *Diploptera dytiscoides* is there a gain in both water and solids during embryogenesis (Roth and Willis, '55b). The port of entry of water, whether through a localized area or through the entire surface of the egg, is unknown. Undoubtedly the time at which water uptake occurs depends upon definite stages in development and probably on the formation of embryonic membranes; unfortunately, little is known about cockroach egg membranes.

It is apparent that in the three types of ovipositional behavior presented in this study, the species of *Blattella* fall between the oviparous species that drop their oöthecae and the false ovoviviparous forms. Though the oötheca is not retracted into the body of the German cockroach, the eggs gain water from the female during the later stages of development; in this respect, *Blattella* is closer in habit to *Nauphoeta* than to *Blatta*. Yet the initial water content of the oötheca of *Blattella* is high and more nearly like that of *Blatta* or *Periplaneta* than that of the false ovoviviparous species. Actually there is sufficient water, initially, in the eggs of *B. germanica* to permit, under ideal conditions, development and hatching without the additional water provided by the female; however, when removed from the female, the oötheca of

Blattella is not capable of preventing excessive water loss from the eggs at ordinary room humidities (Roth and Willis, '55a).

The uptake of water increases the size of the eggs. This is quite apparent in the false ovoviviparous species, but less discernible in the other species. However, Patten (1884) has mentioned the increase in size of the eggs of *B. germanica;* apparently, the oötheca of this species is sufficiently soft to allow some stretching by the growing eggs. The eggs of *Blatta* and *Periplaneta* also increase in size, even though they are encased in a hard oötheca. This is possible because the inner layer of the oötheca is spongy, allowing the eggs to expand as they absorb water. On the other hand, the egg case of *Ectobius livens,* which appears to be hard like that of *Blatta,* visibly increases in size as hatching time approaches (Mr. Paul Rolander, personal communication, and our own observations).

As far as we know, the eggs of cockroaches are enclosed in some type of oötheca, which may be more or less developed depending upon ovipositional behavior and species. Imms ('25) stated that some blattids do not construct an oötheca at all; unfortunately, Imms did not specify the species. It is possible that he was referring to statements by Shelford ('12) and Riley (1890). Shelford ('12) made this sweeping statement "... I can state with confidence that about one-third of the genera form no ootheca at all, or only a most imperfect one ..."; however, he cited no examples in which the oötheca was entirely lacking. Riley (1890) claimed that the oötheca of *Panchlora viridis* was lacking; however, in 1891 Riley found that these eggs were surrounded by a thin membranous sheath which covered about half of the egg mass. Riley's description of the *Panchlora* oötheca indicates that in this species the egg case is less extensive than in *Blaberus, Pycnoscelus, Leucophaea,* or *Nauphoeta,* and approaches that of *Diploptera.*

Present-day cockroaches descended from insects that lived more than 250,000,000 years ago. Fossils from the Upper Carboniferous show that among the earliest insects were cockroaches with at least two different oviposition habits: those with elongated ovipositors, which apparently laid single eggs not enclosed in an egg case, and species that deposited oöthecae in the manner of the oviparous forms found today (Laurentiaux, '51). We do not know whether there were species that incubated their eggs internally coexisting in early geologic times with oviparous species. Internally developed eggs, not enclosed in a sclerotized egg case, might presumably escape fossilization.

Hagan ('51, p. 433) gave several reasons for believing that viviparity is of more recent origin than oviparity among insects. Although examples of present-day cockroaches may be arranged in a series progressing toward viviparity, this series is not necessarily evolutionary (Hagan, '51; Roth and Willis, '54). If there has been an evolutionary trend toward viviparity in cockroaches, it is interesting to speculate on the possible changes that may have occurred, particularly in the light of present knowledge of ovipositional behavior and water relations of the egg. Hagan ('51) stated that in the evolutionary trend toward viviparity in cockroaches, "... the preliminary necessary step appears to be the reduction or elimination of the oötheca ...". The oöthecae of viviparous and false ovoviviparous cockroaches do show varying degrees of reduction, although this may be a result, rather than a prerequisite, of viviparity.

A rationale for the evolution of viviparity might follow these steps: the preliminary step, from the oviparous habit of dropping the oötheca, would seem to have been for the female to retain the oötheca, clasped in the oöthecal chamber, for longer and longer periods of time. Gradually the oötheca came to be retained for the entire period of embryonic development. Concurrently or subsequently, the oötheca was shifted anteriorly into the female's body until it was completely contained. During this process, a relatively impermeable oötheca would be essential to prevent excessive loss of water from the eggs. Lack of such protection, which would occur if the oötheca were reduced before provision had been made for depositing the oötheca entirely within the female's body, would result in death of the eggs which is not consonant with continued evolution. Once the egg case had become located within a protecting brood sac, degeneration of the oötheca could occur without impairing development of the embryos through loss of water. Supply of additional water from the female to the developing eggs apparently evolved before the oötheca was completely contained within the female's body. Ultimate viviparity appeared with the provision of solid nutriment as well as water to very small eggs enclosed in a greatly reduced oötheca.

We do not know the forces involved in the trend toward viviparity, but Laurentiaux ('51) suggests that the oötheca appeared as an "adaptive reaction" to climatic and hygrometric changes. Internal incubation of the eggs also affords definite benefits to those species with this type of behavior. There are two principal dangers which beset cockroach eggs. One is desiccation and the other insect egg parasites. The hard oötheca of some oviparous cockroaches like *Periplaneta, Blatta,* and *Eurycotis* does not protect the eggs from being destroyed by parasitic wasps which can penetrate the oötheca with their ovipositors; however, the oötheca of these species does protect the eggs from desiccation. As far as we know, the eggs of false ovoviviparous and viviparous cockroaches are not attacked by insect parasites because the eggs are protected within the female's body (Roth and Willis, '54); however, the poorly developed oötheca of these species would not prevent desiccation if the egg case were deposited outside of the female's body. We ('54) have pointed out the fact that the time required for the false ovoviviparous female to form and retract her oötheca is much less than that required by the oviparous female to form and drop her oötheca. This speed is vital to the false ovoviviparous species because the eggs will lose water while exposed to the atmosphere during oötheca formation. The eggs of false ovoviviparous and viviparous species, being deposited inside the female's body, are protected from both desiccation and insect parasites.

Accompanying the variation in ovipositional behavior were certain other important alterations. A change in the amount of water initially present in the eggs, a reduction in the amount of yolk (in *Diploptera,* Hagan, '51), and a modification in the structure of the oötheca, making it more pliable and permeable to water; differences in the oötheca imply changes in the chemical nature of the secretions of the colleterial glands which produce the oöthecal substance.

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SUMMARY

The water relationships of the eggs of several species of cockroaches have been studied in relation to the ovipositional behavior of the female. Species belonging to three of 5 possible ovipositional types were available for study.

Oviposition type 1. Species in which the female drops the oötheca shortly after its formation. The proportion of water in the oötheca of *Blatta orientalis* remains fairly constant throughout embryonic development, whereas it drops with time in that of *Periplaneta americana* and increases in the oötheca of *Supella supellectilium.* These differences in the proportions of water result from differences in the rates at which water and dry matter are lost during embryogenesis. The actual water content of the oöthecae of all three species drops with time. However, the water content of the eggs of *B. orientalis* and *P. americana* increases during embryogenesis as the eggs absorb water from the interior of the oötheca. Changes during development enable older eggs, isolated from the oöthecae of *B. orientalis* and *P. americana,* to withstand desiccation better than younger eggs.

Oviposition type 3. Species in which the female carries the oötheca externally during embryonic development. The percentage and amount of water in the oötheca of *Blattella germanica* increase during embryogenesis. The percentage

increase in water results from both loss of dry matter and uptake of water from the female. Similar results were obtained with *Blattella vaga*. However, the egg of *B. vaga* differs from that of *B. germanica* in having less water initially, in starting to absorb water later, and in absorbing less water during development.

Oviposition type 4. Species in which the female extrudes the oötheca outside the body and then retracts it into the uterus where the eggs complete their development; we have called this type of behavior false ovoviviparity. Water in the oötheca and eggs of *Nauphoeta cinerea* remains constant for the first week, increases markedly for another week, and then rises more slowly. Embryogenesis is accompanied by a marked increase in the length of the egg; this increase is caused by absorption of water from the female as solids are lost during development. The eggs of *Pycnoscelus surinamensis* and *Leucophaea maderae* also absorb water from the female with a corresponding increase in length.

Oöthecae of cockroaches differ in ability to prevent desiccation of the contained eggs. Hard, relatively impermeable oöthecae of oviparous cockroaches *(B. orientalis, P. americana, S. supellectilium)* lose water most slowly. Soft, thin oöthecae of false ovoviviparous species *(N. cinerea, P. surinamensis)* lose water rapidly when exposed to the atmosphere. Partially permeable oöthecae carried externally by the female *(B. germanica)* lose water at an intermediate rate.

Two principal dangers beset cockroach eggs: desiccation and insect egg parasites. The hard oöthecae of oviparous species do not protect the eggs from destruction by parasites, but do protect eggs from desiccation. Eggs of false ovoviviparous cockroaches are protected from both insect parasites and desiccation by being carried within the female's body.

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