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Water Relations of Cockroach Oöthecae¹

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The eggs of the cockroaches *Blattella germanica* (L.) (Patten 1884), *Blaberus craniifer* Burm. (Nutting 1953), and *Diploptera dytiscoides* (Serv.) (Hagan 1951) increase in size during embryonic development. It is well known that the eggs of some insects (e.g., grasshoppers) absorb water from the environment (Buxton 1932, Wigglesworth 1950). However, the water relations of cockroach eggs have not been studied in detail although the importance of water in the development of the eggs of the German cockroach has been indicated (Ross 1929, Parker & Campbell 1940). We are studying the water relations of the oöthecae of several species of cockroaches, and herein present data from four representative species with three different types of ovipositional habits.

OVIPOSITIONAL TYPE 1.—The oötheca is carried by the female for only a short time after formation, frequently being deposited and abandoned within 24 hours.

Blatta orientalis L.—During embryonic development about fifteen per cent of the initial weight of the oötheca may be lost. The proportion of water in the oötheca remains fairly constant throughout development (Figure 1), as both water and solids are lost at about the same rate, but the water content of the eggs actually increases during development (Table 1). During the early stages of embryonic development the outside of the eggs and the inside of the oötheca are very moist. As development proceeds these surfaces become progressively drier, but the inner surface of the chorion and the embryo itself remain moist. Evidently during development water is absorbed by the egg from the inner surface of the oötheca. At the time of its formation, the oötheca is obviously moist. The water which is later picked up by the eggs is undoubtedly the water which was initially present in the oötheca outside the eggs.

The oötheca of *Blatta orientalis* is covered with a material which retards the loss of water. So effective is this

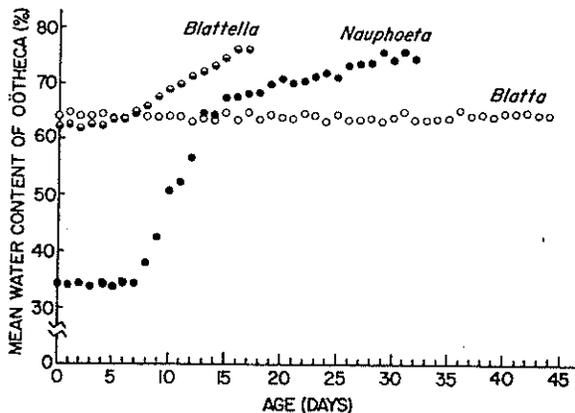


FIG. 1.—Water content of the oöthecae of 3 species of cockroaches. (Temperature, 27° to 29° C.)
 ○ = *Blatta orientalis* (343 oöthecae).
 ● = *Nauphoeta cinerea* (348 oöthecae).
 ⊙ = *Blattella germanica* (385 oöthecae).

Table 1.—Variation with age in water content of eggs of *Blatta orientalis*.^a

AGE OF EGGS (DAYS)	MEAN WEIGHT (MG.)		MEAN WATER CONTENT ± S.E. ^b (PER CENT OF WET WEIGHT)	NUMBER USED	
	Wet	Dry		Eggs	Oöthecae
12	6.80	2.50	62.9 ± 0.34	22	13
18	7.00	2.43	65.2 ± 0.34	19	10
21	7.15	2.34	67.2 ± 0.26	31	22
26	7.28	2.29	68.5 ± 0.14	24	17
33	7.45	2.14	71.4 ± 0.42	9	5

^a One or more eggs were dissected out of an oötheca, cleaned, weighed and then dried. We did not succeed in dissecting out eggs which were younger than 11 days because the chorion adhered to the inner walls of the oötheca; eggs older than 33 days were difficult to remove without rupturing the chorion which had become dry and brittle.
^b S.E. = standard error.

substance that eggs hatched about 46 days later from oöthecae which had been kept in an atmosphere of 0 per cent relative humidity from the age of less than 1 day. The rates of weight loss of oöthecae subjected to abrasion or rinsing in water and drying are compared with the rate of loss from untreated oöthecae in figure 2. The respiratory ducts in the keel of the oötheca, because of their small connections with the outer air, allow a minimum of water to be lost from the eggs. It is likely that most of what little water is normally lost by untreated oöthecae escapes through the respiratory ducts, rather than through the wall of the oötheca. According to Pryor (1940) the oötheca of *B. orientalis* is covered with an oily secretion probably derived from the cuticle of the mother. The cuticular wax on the body of the cockroach seems to be secreted in a solvent which evaporates slowly keeping the wax greasy (Beament 1951). The cuticular grease retards water loss from the cockroach at normal temperatures; when the insect is exposed to slightly higher temperatures (e.g., *Periplaneta americana* at 35° C.), there is an abrupt rise in the loss of water following a change in the physical properties of the grease (Ramsay 1935). The effect of temperature on the weight loss of the oöthecae of *B. orientalis* is shown in figure 3. This temperature experiment indicates that the water proofing material on the oötheca is not the same as the mobile grease on the body of the cockroach; otherwise, one would expect a sudden increase in water loss at temperatures lower than 60° C. Beament (1945) found that the critical temperature of the cuticular grease of *B. orientalis* is about 30° C. *in vitro*.

Periplaneta americana (L.).—In laboratory colonies the American cockroach frequently eats part or all of the keels of recently deposited oöthecae. Almost invariably the eggs in these damaged egg cases fail to hatch and usually fail to develop into recognizable embryos because of the rapid loss of water. The effect of removing

¹ Accepted for publication September 16, 1954. Throughout this paper use of the term oötheca implies both the egg case and its enclosed eggs.

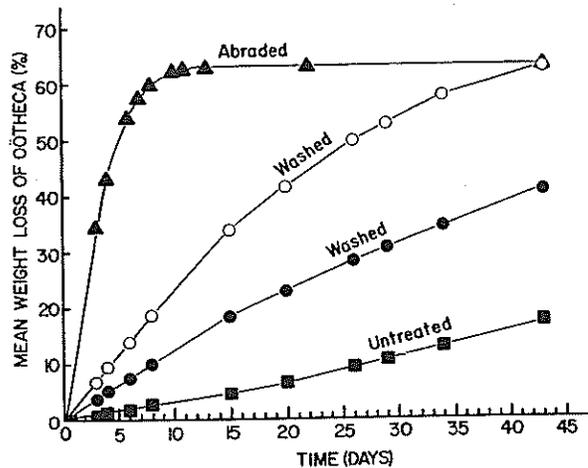


FIG. 2.—Effect of abrasion and rinsing the oöthecae of *Blatta orientalis* on weight loss.

- = 8 untreated oöthecae (eggs hatched).
- = 4 oöthecae that were dipped in distilled water and wiped dry (87 to 100% of the eggs in the oöthecae completed development but did not hatch).
- = 10 oöthecae that were dipped in distilled water and wiped dry (none of the eggs completed development).
- ▲ = 20 oöthecae that were gently abraded on No. 2/0 Crystal Bay Emery cloth (none of the eggs developed).

All oöthecae were less than one day old at the time of treatment. Temperature, 27° to 28° C.; Relative Humidity, 30 to 35%. The difference between the 2 groups of oöthecae that were dipped and wiped dry (solid and open circles) may have resulted from variation in the extent to which the oöthecae were rubbed dry; the 4 oöthecae in which eggs developed were undoubtedly least damaged by wiping.

the keels on the hatching of eggs in oöthecae kept at a low or high humidity is shown in table 2. The loss in weight of oöthecae lacking keels is compared with that of intact egg cases in figure 4. The membranes of the recently-laid egg retard water loss poorly, and one of the principal functions of the oötheca in this species, as in *B. orientalis*, is protection of the eggs from drying.

OVIPOSITIONAL TYPE 2.—The oötheca is carried externally by the female until or shortly before the eggs hatch.

Table 2.—Effect of removing the keels from oöthecae on hatching of the eggs of *Periplaneta americana*.

CONDITION OF OÖTHECAE	AGE (DAYS) AT TIME OF TREATMENT	NUMBER OF OÖTHECAE USED	NUMBER OF OÖTHECAE IN WHICH EGGS:		PER CENT EGGS PER OÖTHECA WHICH HATCHED*
			Hatched	Developed but Did Not Develop	
<i>Oöthecae kept at 16% relative humidity</i>					
Normal	<1	16	14	1	92
Keels removed	<1	20	0	20	—
Normal	14	20	13	3	93
Keels removed	14	20	0	20	—
<i>Oöthecae kept at 90% relative humidity</i>					
Keels removed	<1	20	1	15	—
Normal	3-6	24	22	1	97
Keels removed	3-6	18	10	3	87
Normal	16	20	20	0	90
Keels removed	16	20	18	2	99

* Based only on oöthecae from which eggs hatched.

Table 3.—Weight loss of detached oöthecae^a of *Blattella germanica*.

CONDITION OF OÖTHECAE	NUMBER USED	WEIGHT LOSS (%) ± S.E. ^b AFTER 24 HOURS
Normal	8	30.5 ± 1.96
Sealed with beeswax		
Posterior half	10	28.9 ± 0.86
Anterior half	10	1.8 ± 0.34

^a All oöthecae were 5 days old when detached from the females and were kept at 28° C. and 17 to 30% R. H.
^b S.E. = standard error.

One end of the oötheca is in close contact with the female for the duration of embryonic development.

Blattella germanica (L.).—The variation with age in the amount of water in oöthecae of the German cockroach is shown in figure 1. During embryonic development the oötheca acquires additional water from the body of the female. Ross (1929) and Parker & Campbell (1940) predicated that the wall of the oötheca in contact with the female's genital pouch must be permeable to water. The anterior end of the oötheca, held by the female, is lighter in color and not as sclerotized as the posterior part. We demonstrated a difference in permeability of the two regions of the oötheca by sealing, with beeswax, the anterior or posterior halves of manually detached oöthecae and measuring weight loss. The results are shown in table 3. Further proof that the two ends of the oötheca vary in permeability was shown by keeping either the anterior or posterior ends of detached oöthecae on filter paper wet with distilled water. After 15 hours, 15 oöthecae that had had their anterior ends in contact with the water had gained 8.3 ± 0.86 per cent in weight; 14 oöthecae that had had their posterior ends touching the water had lost 6.1 ± 0.61 per cent in weight. The humidity was high in the covered petri dish in which

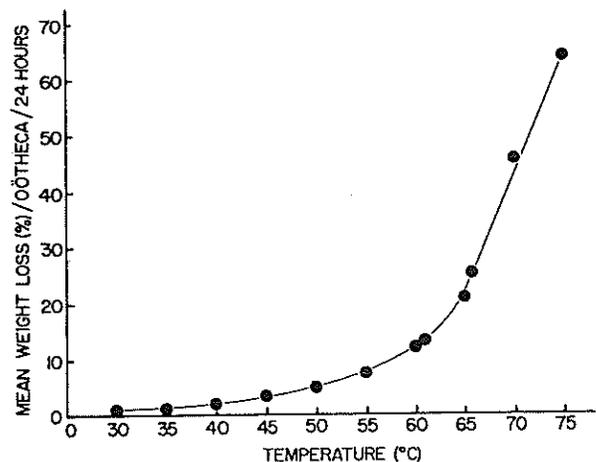


FIG. 3.—Weight loss of oöthecae of *Blatta orientalis* as a function of temperature. Oöthecae less than a day old were placed individually in tubes containing pellets of CaSO₄ (Drierite); the tubes were immersed for 24 hours in constant temperature water baths. Plotted points are means of data from 10 to 15 oöthecae (total for all tests 170).

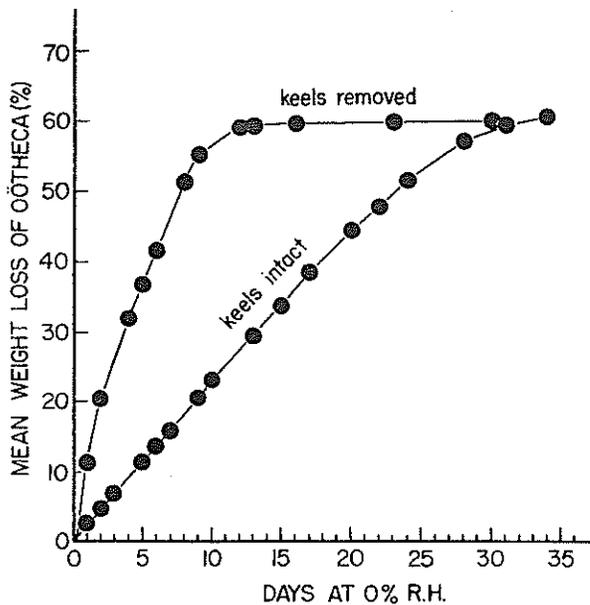


FIG. 4.—Effect, on weight loss, of removing the keels from oötheca of *Periplaneta americana*. Fifteen treated and 10 untreated oötheca, less than 1-day old, were used. Temperature 27° to 28° C. None of the eggs developed.

these oötheca were kept; yet in spite of this, oötheca with their anterior ends not in contact with water lost weight.

OVIPOSITIONAL TYPE 3.—The completed oötheca is retracted into a brood sac, inside the female's body, where the eggs are incubated until hatching (Chopard 1950, Roth & Willis 1954).

Nauphoeta cinerea (Oliv.).—The initial water content of the oötheca and eggs of this species is low compared to that of *Blatta* or *Blattella*. The water content remains constant at about 34 per cent. for 7 days, increases markedly for a week, and then rises more gradually until at hatching time the oötheca may contain about 75 per cent water (Figure 1). There was no indication of any gain in solids; the amount of dry matter in the eggs decreased gradually with embryonic development.

WATER LOSS THROUGH OÖTHECAE.—The oötheca of the above cockroaches differ as markedly as the three types of ovipositional behavior. The egg cases of *Blatta orientalis* and *Periplaneta americana* are hard and normally impermeable. The anterior end of the egg case of *Blattella germanica*, which is in contact with the oöthecal cavity of the female, is relatively soft and permeable to water. The oötheca of *Nauphoeta cinerea* is very soft, thin, may not cover the eggs completely, and presumably is permeable. The comparative losses in weight of oötheca and eggs kept in a dry atmosphere are shown in figure 5. The eggs of *Nauphoeta*, the ovoviviparous species, lost practically all of their water within 2 days; the eggs of *Blatta* lost water most slowly, taking about 5 weeks to dry; *Blattella* eggs lost water at a rate intermediate between the other species. The three types of oötheca differ in their ability to prevent desiccation of the eggs; the difference is correlated with oöthecal structure.

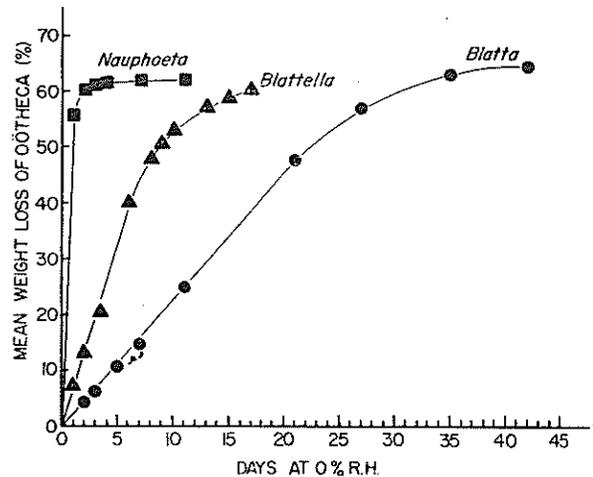


FIG. 5.—Weight loss of the oötheca of 3 species of cockroaches.

● = 10 oötheca of *Blatta orientalis* less than 1 day old.
 ▲ = 10 oötheca of *Blattella germanica*, 1 to 2 days old when detached from the females.
 ■ = 4 oötheca of *Nauphoeta cinerea*, about 2 weeks old when removed from the females.
 All oötheca kept at 0% relative humidity and 27 to 28° C. None of the eggs completed development.

Data on the water relations of the eggs of other cockroaches, viz., *Supella supellecillum* (Serv.), *Blattella vaga* Heb., *Pycnoscelus surinamensis* (L.), *Leucophaea maderae* (F.), and additional data on the eggs of *Periplaneta americana* will be reported elsewhere.

SUMMARY.—Some of the water relations of the oötheca and eggs of the following species of cockroaches have been studied:

Blatta orientalis (which does not carry its egg case during embryonic development): The oötheca loses water and solids at about the same rate. During embryonic development, however, the eggs actually pick up water from the moist inner surface of the oötheca. The oötheca is covered with a water proofing material which differs from the mobile grease on the body of the insect.

Periplaneta americana (which does not carry its egg case): Eggs frequently fail to develop in oötheca with damaged keels because of the rapid loss of water. However, eggs 3 or more days old in oötheca with damaged keels had a high hatching rate when kept at 90 per cent relative humidity but at 15 per cent none hatched.

Blattella germanica (which carries its egg case externally): During embryonic development the eggs acquire additional water from the body of the female. The anterior end of the oötheca which is in contact with the female is permeable to water, whereas the posterior end is not.

Nauphoeta cinerea (which carries its egg case internally): The water content of the eggs increases rapidly after the first week of embryonic development. By hatching time the water content has more than doubled. Dry matter decreased during embryonic development.

Differences in the oötheca of the above cockroaches are consonant with the insects' ovipositional behavior.

Oöthecae of *B. orientalis* and *P. americana* are hard and normally impermeable. The anterior end of the oötheca of *B. germanica* is soft and permeable. The oötheca of *N. cinerea* is soft, thin, and presumably permeable. The three types of oöthecae differ widely in their ability to prevent desiccation of the eggs.

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