Journal of the Lepidopterists' Society
43(3), 1989, 167–177

REPRODUCTIVE ENHANCEMENT BY ADULT FEEDING: EFFECTS OF HONEYDEW IN IMBIBED WATER ON SPRUCE BUDWORM

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ABSTRACT. Captive budworm adults obtained as wild pupae were divided into two groups, and each group was offered liquids to imbibe once daily. One group received plain water, the other water containing honeydew of hemispherical scale, *Saissetia coffeae* (Walker), at concentrations averaging 6.5%. Two such experiments were conducted, a preliminary one with 28 fertile pairs, and the main one with 34 fertile pairs. In both experiments, honeydew prolonged female lifespan, egg maturation, and oviposition, the latter two causing redistributions within apparently fixed oocyte complements. Honeydew effects interacted with female body size, large females laying relatively more eggs than small females. In the main experiment, imbibing did not begin until the third day of adulthood. Thereafter, fertile females imbibed more often than infertile ones, the frequency among the former peaking at 97% of their number during the seventh and eighth days of adulthood. Amount imbibed per individual per day averaged 4.5 mg as determined by weighing females before and after imbibing. In fertile females of average lifespan, expected lifetime honeydew-water intake was 31.6 mg of liquid containing 2.05 mg dry weight of honeydew, the latter corresponding to 3.5% of female average initial live weight. Enhanced reproductive effects did not appear until late in adulthood.

Additional key words: *Choristoneura fumiferana*, Tortricidae, Tortricinae, fecundity, *Saissetia coffeae*.

That tortricine adults are capable of imbibing has long been known (Powell 1965:26), but only recently was reproduction in a tortricine rigorously shown to be enhanced by imbibing. Thus, the spruce budworm, *Choristoneura fumiferana* (Clemens) (Tortricidae), matured more oocytes and laid more eggs when females received water containing 15% bee honey than when they received plain water (Miller 1987). Imbibing habits of the adults are still obscure, however.

Honeydews might be available to spruce budworm adults in nature. Precipitated water is often present, and such water is doubtless sweetened at times by honeydews of co-occurring insects such as the balsam twig aphid, *Mindarus abietinus* Koch (Aphididae). While bee honey consists mostly of fructose and glucose (White 1975), honeydews may contain these sugars as well as sucrose, other sugars, and nitrogenous compounds (Auclair 1963).

Here, for captive budworm females given plain water or water containing honeydew, I report several aspects of reproduction as well as imbibing frequencies and amounts imbibed. Reproductive attributes measured were lifespan, oviposition period, number of eggs laid daily, egg viability, number of mature and immature oocytes in ovaries after death, and attributes derived from these. The honeydew source was hemispherical scale, *Saissetia coffeae* (Walker) (Coccidae).

MATERIALS AND METHODS

Two experiments were conducted, a preliminary one followed by the main one. In both experiments, one group of moths received honeydew solution for imbibing, and a second group received plain water. The main experiment differed from the preliminary one chiefly in that pupae and emergent adults were not cold-stored before use, female imbibing was recorded, the different imbibing liquids were dispensed in exactly the same way, and reproductive attributes were measured in greater detail.

For both experiments, wild pupae reachable from the ground were collected from 25 or more large trees of balsam fir, *Abies balsamea* (L.) Mill. (Pinaceae), growing in one area of 0.1 ha or less. Pupal collections were timed to coincide with incipient adult emergence. In the preliminary experiment, pupae came from 12 km E of Meadowlands, St. Louis Co., Minnesota, and in the main experiment, from 8 km W of Grand Marais, Cook Co., Minnesota. In the preliminary experiment, pupae and emergent moths were stored within 36 h of collection at 8°C and held for two weeks during a start-up delay. In the main experiment, pupae and emergent moths were in use within 36 h of collection.

The first step in both experiments was to sex pupae (Jennings & Houseweart 1978) and emergent adults. Some females were freeze-killed within 2 h of eclosion for ovarial study. Male-female pairs for imbibing experiments were placed in 1-pint (0.48 l) cardboard ice cream containers capped with Petri dish lids, one pair per container. A shoot of balsam fir ca. 8 cm long was placed in each container as a substrate for oviposition; in the preliminary experiment, the shoot also served as an imbibing substrate for plain water. Containers were numbered and assigned by equal and odd numbers to the two imbibing treatments.

Moth containers in both experiments were held in a temperature-controlled room maintained at 23°C during the preliminary experiment, and at 25°C during the main experiment. In the former, moths received natural July light through a large N-facing window; in the latter, they received fluorescent light on a 12L:12D schedule. Containers were examined daily near mid-day, at which time imbibing liquids were introduced and reproductive data were gathered.

The honeydew-providing colony of hemispherical scale infested a 2-m tall indoor-growing spineless yucca, *Yucca elephantipes* Regel (Liliaceae). Upper surfaces of the plant's leaves were nearly completely coated with honeydew. In both experiments, segments ca. 6 cm^2 were cut from the honeydew-laden leaves, misted with water just short of runoff to form honeydew-water solution, and placed in moth containers

for imbibing. Segments were misted every day and replaced every second or third day. Plain water for imbibing was provided in the preliminary experiment by misting the balsam fir shoot, and in the main experiment by misting yucca leaf segments also ca. 6 cm^2 from which honeydew had been washed. All misting was done outside containers with a hand-powered household sprayer containing distilled water.

Misted yucca leaf segments remained wet in moth containers for 1.2–1.5 h before drying naturally. Whether or not females imbibed was determined by monitoring main-experiment individuals during this interval on arbitrarily chosen days. Imbibing moths were spotted by their characteristic preimbibing head movements, and by proboscises extending to the wet yucca leaf segments.

Liquid intake was measured as the difference between pre- and postimbibing weights of individual females preweighed just before they were routinely offered liquids. Sample females were selected arbitrarily for this purpose, and weights were recorded to the nearest 0.1 mg. Imbibing occurred rapidly enough so that pre- and postimbibing weighings were seldom separated by more than 25 min. To verify that weight differences truly represented intake, two females that walked and rested on misted yucca leaf segments for 5 min without imbibing were weighed in the same manner as imbibing females. These nonimbibers underwent no weight gain, thus indicating that imbibing liquids were not absorbed by body parts coming in contact with wet surfaces.

Eggs were spotted by examining shoots and container walls under a 2× reading magnifier. Shoots were removed from containers for this examination. Deposited eggs were counted under stereomicroscope magnifications up to 25×. In the preliminary experiment, female fertility and egg viability were determined by observing 21–112 deposited eggs per female for a week or until larval heads showed through chorions. In the main experiment, fertility and viability were determined by observing all deposited eggs until hatching or imminent hatching.

Oocytes in excised ovaries were identified as mature or immature by size and stainability after 2–4 min exposure to ca. 0.2% aqueous methylene blue. Chorionated (mature) eggs take up such stains less readily than nonchorionated (immature) ones (Jennings 1974). Immature oocytes were counted at stereomicroscope magnifications up to 45×. Length of one forewing measured to the nearest 0.5 or 0.2 mm in the preliminary and main experiments, respectively, was used as a female body size index (Thomas et al. 1980, Results section of present paper).

For chemical analyses of hemispherical scale honeydew, several honeydew-laden yucca leaves were sprayed with distilled water, and 75

TABLE 1. Performance of spruce budworm females imbibing plain water and honeydew-water in the preliminary experiment. SD preceded by ±, range in parentheses.

Attribute	Mean		Departure from plain-water group (%)
	Plain water [19 pairs]	Honeydew-water [9 pairs]	
Oviposition span, days[1]	8.8 ± 1.8 (6–12)	10.3 ± 4.1 (5—17)	17[a]
No. eggs and oocytes			
Total	326 ± 46 (243–395)	339 ± 75 (204–446)	4
Matured	200 ± 46 (134–291)	245 ± 71 (109–350)	22[b]
Laid	197 ± 46 (130–289)	235 ± 76 (98–348)	19
Change in no. laid (L) as function of fore-wing length (W)	28.2	102.8	264[c]
Unlaid immature	127 ± 28 (88–176)	94 ± 58 (0–184)	−26[a]
Egg viability, %	75 ± 20 (28–97)	81 ± 15 (50–94)	8

[1] Defined as time from first oviposition to death, usually one day longer than oviposition period.
[a] $P < 0.01$, 1-tailed Wilcoxon 2-sample test.
[b] $P < 0.05$, 1-tailed Student t-test.
[c] $P < 0.01$, F-test. Values are slope coefficients from the regressions $L = 28.2W - 126$ ($r = 0.40$) and $L = 102.8W - 930$ ($r = 0.75$).

ml of runoff were collected. One aliquot was analyzed for sugars by high-pressure liquid chromatography, one for total nitrogen by a high-sensitivity Kjeldahl method, and one was oven-dried at 70°C to nominally constant weight for dry-weight conversions.

Honeydew concentration of imbibed honeydew-water was determined from weighings as follows. Honeydew-laden 25–50 cm^2 yucca leaf segments were weighed (weight x), misted as for imbibing, reweighed (weight y), thoroughly washed, towel-dried, and again reweighed (weight z). These weightings were completed within 15 min, and were to the nearest 0.1 mg. Honeydew concentration (c) was computed as $c = (x - z)/[(y - x) + (x - z)]$.

In both experiments, attribute variances often differed significantly between imbibing treatments (variance-ratio test). Treatment differences in such cases were analyzed nonparametrically by the Wilcoxon two-sample test. Otherwise, treatment differences were analyzed parametrically by F- and Student t-tests. Because honeydew-water was expected to have positive effects, most testing was one-tailed.

"Infertile" here refers to females not producing viable eggs whether mated or not. Standard deviation is abbreviated SD.

RESULTS

Preliminary experiment. Of 28 pupal and adult containers set up for the honeydew-water imbibing treatment, and 29 set up for the plain-water imbibing treatment, 9 and 19, respectively, produced viable eggs and complete reproductive attribute records. Shortfalls were caused

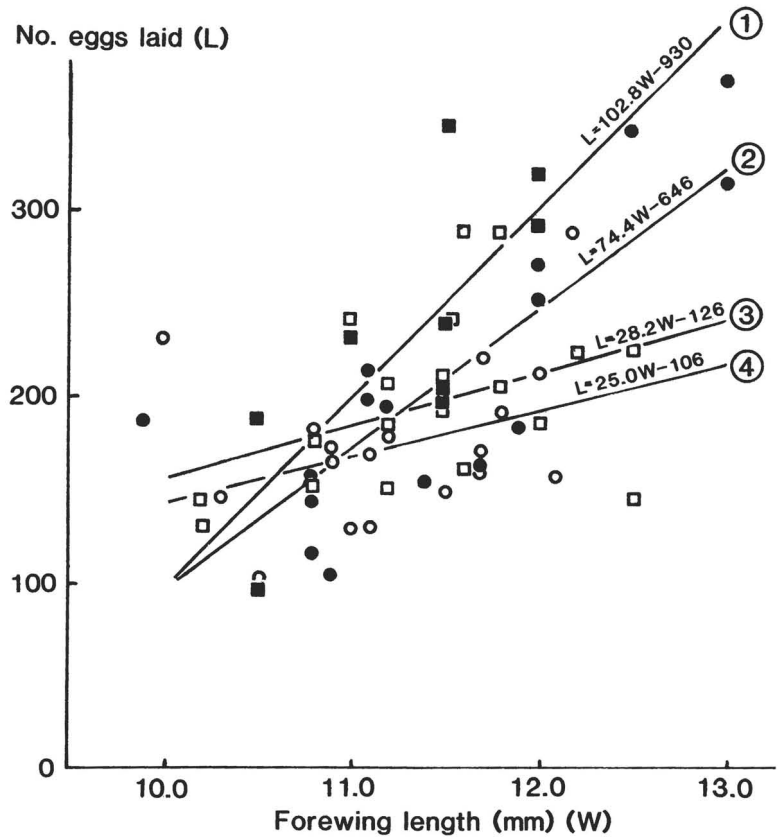

FIG. 1. Role of spruce budworm female body size in determining number of eggs laid in response to honeydew- and plain-water imbibing treatments. Each symbol represents one female. Line ① (closed squares) and line ② (closed circles) depict honeydew-water imbibers in the preliminary and main experiments, respectively; line ③ (open squares) and line ④ (open circles), plain-water imbibers.

by sexing errors, asynchronous eclosions, moth escapes, and unexplained infertility.

Females given honeydew-water outperformed those given plain water in four of seven reproductive attributes tabulated (Table 1). On average, honeydew-water imbibers had a 1.5-day (17%) longer oviposition span, matured 45 (22%) more oocytes, and contained 33 (26%) fewer immature oocytes at death. Some tests were not robust enough to detect biologically relevant attribute differences. The prime example concerns number of eggs laid (Table 1, Fig. 1). In this and all attributes except total oocyte number and egg viability, the effect of honeydew interacted with body size. Thus an 11.0-mm female on honeydew-water laid 201

eggs (11.0 × 102.8 − 930 = 200.8) while one on plain water laid 184 (11.0 × 28.2 − 126 = 184.2) (9% difference); but a 12.5-mm female on honeydew-water laid 355 eggs (12.5 × 102.8 − 930 = 355.0) while one on plain water laid 226 (12.5 × 28.2 − 126 = 226.5) (57% difference). Forewing length of females in the honeydew- and plain-water treatments averaged 11.3 mm (SD = 0.6, range 10.5–12.0) and 11.2 mm (SD = 0.7, range 10.2–12.5), respectively. For attributes with variances shown in Table 1 (in SD, or square-root form), variances for the honeydew-water treatment are usually greater numerically, two of them greater statistically ($P < 0.05$, variance-ratio test), than for the plain-water treatment.

In 2-h-old freeze-killed females, egg maturity averaged 7% (n = 8). On average, these females contained 266 oocytes (SD = 40, range 228–333), 60–73 fewer than the 326 and 339 totals shown in Table 1 for imbibing females. The differences arose not because of inherently different oocyte numbers, but because freeze-killed females were smaller. Their forewing lengths, averaging 10.5 mm (SD = 0.7, range 9.5–11.6 mm), were 0.7–0.8 mm less than for imbibing females. Regressions of oocyte counts on forewing lengths among freeze-killed and imbibing females did not differ significantly ($P > 0.75$, F-test of slope-coefficient differences).

Dry-weight constituents of hemispherical scale honeydew (including other water-soluble substances that also may have been on yucca leaf surfaces) were fructose, 23.7%; glucose, 19.8%; sucrose, 12.8%; total nitrogen, 0.6%; nonsugar and non-nitrogenous matter, 43.1%. These amounts are similar to those previously reported for scale and aphid honeydews (Auclair 1963).

Main experiment. Of 26 pupal and adult containers set up for the honeydew-water imbibing treatment, and an equal number for the plain-water imbibing treatment, 16 and 18, respectively, produced viable eggs and complete reproductive attribute records. Shortfalls were caused by the same factors as in the preliminary experiment.

Pairs given honeydew-water outperformed those given plain water in 4 of 11 reproductive attributes tabulated (Table 2). On average, honeydew-water imbibers had a 0.7-day (6%) longer female lifespan, a 1.8-day (23%) longer oviposition period, and contained 41 (68%) fewer immature oocytes at death. As in the preliminary experiment, some tests were not robust enough to detect attribute differences, and number of eggs laid is again the prime example (Table 2, Fig. 1). In this and all attributes except total oocyte numbers and egg viability, the effect of honeydew interacted with body size. Thus an 11.0-mm female on honeydew-water laid 172 eggs (11.0 × 74.4 − 646 = 172.4) while one on plain water laid 169 (11.0 × 25.0 − 106 = 169.0) (2% difference);

TABLE 2. Performance of spruce budworm pairs imbibing plain water and honeydew-water in the main experiment. SD preceded by ±, range in parentheses.

Attribute	Mean or other value		Departure from plain-water group (%)
	Plain water [18 pairs]	Honeydew-water [16 pairs]	
Preoviposition period, days	2.2 ± 0.7 (1–3)	2.3 ± 0.8 (1–4)	
Lifespan, days			
Female	10.7 ± 2.0 (7–14)	11.4 ± 3.4 (6–17)	6[a]
Male	9.4 ± 2.8 (5–14)	8.7 ± 3.8 (4–17)	−7
Oviposition period, days	7.7 ± 2.2 (4–11)	9.5 ± 3.6 (4–15)	23[b]
No. eggs and oocytes			
Total	238 ± 60 (104–332)	233 ± 80 (126–404)	−2
Matured	177 ± 43 (104–288)	214 ± 78 (111–372)	21
Laid	175 ± 43 (102–288)	210 ± 79 (104–370)	20
Change in no. laid (L) as function of fore-wing length (W)	25.0	74.4	198[c]
Viable	156 ± 36 (98–245)	181 ± 78 (59–325)	16
Unlaid immature	60 ± 41 (0–134)	19 ± 29 (0–104)	−68[d]

[a] $P < 0.01$, 1-tailed Wilcoxon 2-sample test.
[b] $P < 0.05$, 1-tailed Student t-test.
[c] $P < 0.01$, F-test. Values are slope coefficients from the regressions $L = 25.0W - 106$ ($r = 0.36$) and $L = 74.4W - 646$ ($r = 0.81$).
[d] $P < 0.01$, 1-tailed Student t-test.

but a 12.5-mm female on honeydew-water laid 284 eggs (12.5 × 74.4 − 646 = 284.0) while one on plain water laid 206 (12.5 × 25.0 − 106 = 206.5) (38% difference). For 9 of the 10 attributes with variances shown in Table 2 (in SD, or square-root form), variances for the honeydew-water treatment are greater numerically, four greater statistically ($P < 0.05$, variance-ratio test), than those for the plain-water treatment.

In 2-h-old freeze-killed females, egg maturity averaged 10% (n = 13). On average, these females contained 259 oocytes (SD = 83, range 132–424), a number not inherently different from the 238 and 233 totals shown in Table 2 for imbibing females ($P > 0.75$, F-test of differences in slope coefficients of oocyte number–forewing length regressions). Forewing length of freeze-killed females averaged 10.7 mm (SD = 1.2, range 10.1–12.7).

Daily oviposition records in both imbibing treatments were similar until the latter half of the oviposition period (Fig. 2). Beyond day 8 of adulthood, live female-days/female averaged 3.5 in the honeydew-water group and 1.7 in the plain-water group, and respective numbers of eggs laid/female were 35 and 10.

Individual females were monitored for imbibing more than 150 times

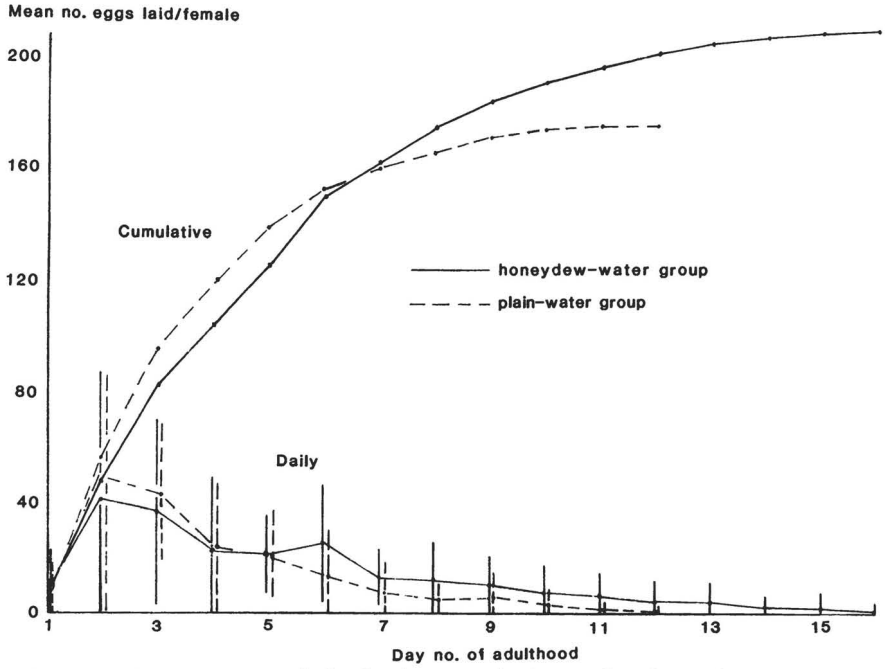

FIG. 2. Oviposition records for fertile spruce budworm females in the main experiment. Sixteen females in the honeydew-water group, 18 in the plain-water group. Vertical bars represent SD.

during the daily period of liquid availability. Imbibing started within 20 min after liquids were offered, usually much sooner, and individual imbibing episodes lasted as long as 5 min. No monitored female imbibed more than once daily, and none was seen excreting liquids anally. After drying, honeydew presumably was not consumed until the next misting.

Females did not imbibe on the first or second days of adulthood (n = 11 and 12, respectively). During days 3–12 of adulthood, fertile females imbibed more often than infertile ones, the former using 78% of their opportunities (62/79), the latter 50% (23/46). The difference is significant ($P < 0.01$, 2×2 contingency table, G-test).

Among fertile females, imbibing frequency was unrelated to presence or absence of honeydew. During days 3–12 of adulthood, sample females in the plain-water treatment imbibed essentially as often as those in the honeydew-water treatment, the former using 77% of their opportunities (33/43), the latter 80% (29/36). Imbibing frequency was affected by female age, however. Thus imbibing frequency rose from 60% on days 3–4 of adulthood to 97% on days 7–8, then fell to 54% on days 11–12 (Table 3). Pooling by two-day intervals in Table 3 increased the base and reliability of percentages.

TABLE 3. Imbibing frequencies by age of fertile spruce budworm females offered honeydew-water or plain water in the main experiment.

Day no. of adulthood	No. females observed	Percent of females imbibing[1]
3–4	5	60
5–6	15	80
7–8	30	97
9–10	16	69
11–12	13	54

[1] Underlying frequencies significantly dependent on female age ($P < 0.01$, 2 × 5 contingency table, G-test with Williams correction).

For 10 fertile females monitored for imbibing on two successive days, 30% imbibed both days (3/10), and 70% imbibed one day only (7/10). These females were in the 5th to 11th day of adulthood at the first observation, averaging day 8.

Regressing weights of fertile females determined just before daily imbibing episodes (M, range 13.8–86.0 mg) on forewing length (F, range 9.8–13.0 mm) and day number of adulthood (D, range 1–12) produced the equation $M = 11.7F - 4.6D - 70.8$ ($R = 0.91$, $n = 37$). Based on this equation, live weights of honeydew-water imbibing females of average forewing length on days 1, 4, 7, and 10 of adulthood were, respectively, 59.2, 45.4, 31.6, and 17.8 mg. Such weight decline during adulthood reflects egg laying and depletion of stored reserves. Forewing length of females in the honeydew- and plain-water treatments averaged, respectively, 11.5 mm (SD = 0.9, range 9.3–13.0) and 11.25 mm (SD = 0.6, range 10.0–12.2).

Intake per imbibing episode did not differ significantly between plain- and honeydew-water or fertile and infertile classifications in any partition of data in Table 4 ($P > 0.13$, one-tailed Student t-tests); it likewise varied independently of female size and age (r-range 0.03–0.57, none approaching $P = 0.05$). Intake per episode averaged 4.5 mg

TABLE 4. Intake per investigated imbibing episode by individual spruce budworm females offered liquids daily in the main experiment. SD preceded by ±, range in parentheses.

Fertility status	No. observed	Mean age (days)	Mean forewing length (mm)	Amount imbibed (mg)
		Plain-water imbibers		
Fertile	9	8.1 ± 2.4 (5–12)	11.1 ± 0.3 (10.5–11.7)	3.9 ± 2.3 (0.9–8.1)
Infertile	5	4.6 ± 1.8 (3–7)	10.7 ± 0.6 (9.8–11.2)	4.3 ± 1.5 (2.7–6.5)
		Honeydew-water imbibers		
Fertile	7	8.0 ± 1.0 (7–10)	11.7 ± 0.8 (10.8–13.0)	5.2 ± 2.5 (1.7–10.0)
Infertile	7	5.1 ± 1.3 (4–7)	10.8 ± 0.5 (9.8–11.2)	3.0 ± 1.8 (1.0–6.5)
		All imbibers		
Mixed	28	6.7 ± 2.3 (3–12)	11.1 ± 0.7 (9.8–13.0)	4.5 ± 2.4 (0.9–10.0)

of liquid (Table 4), or 8, 10, 14, or 25% of the live female weights computed above on days 1, 4, 7, and 10 of adulthood.

Honeydew concentration in honeydew-water on yucca leaf segments averaged 6.5% by weight (SD = 2.1, range 3.5–9.4, n = 5).

During and immediately after adult eclosions observed under a binocular microscope (4 females, 2 males), the paired galeae were separate for most of their length as reported for lepidopterans generally (Hepburn 1971). Within 15–30 min after pupal skin splitting, however, galeae had engaged along their full lengths to form proboscises. During much of the engagement process, which seemed assisted by the narrow corridor formed by palpi, galeae twitched and intertwined. In two cases, a droplet of clear fluid appeared near the base of galeae during the engagement period.

DISCUSSION

Honeydew in imbibed water clearly had positive reproductive effects. In both experiments, these effects were prolonged female lifespan, oocyte maturation, and oviposition, the latter two causing redistributions within apparently fixed total oocyte complements (Tables 1 & 2). Effects were strongest in the largest females (Fig. 1).

With only 7–10% of oocytes mature at female eclosion, a range consistent with observations by Outram (1971), much oocyte maturation necessarily takes place after eclosion. Thus an opportunity exists for adult imbibing to influence oocyte maturation. However, females were slow to begin imbibing under a regime that provided a once daily opportunity. There was no evidence that they imbibed on the first or second days of adulthood; even after four days, 40% of fertile females still had not imbibed (Table 3). This explains why preoviposition period was unaffected in this study, and perhaps also why positive reproductive effects appeared late in adulthood. Preoviposition period was affected in earlier work when the period lasted longer, and a stronger nutrient solution (15% bee honey) was available constantly (Miller 1987). Abstinence from imbibing in early adulthood did not appear to be morphological in origin; proboscises were formed and presumably functional within 0.5 h after eclosion.

In imbibing frequency and intake per imbibing episode, females showed no clear preference for honeydew-water over plain water. This result suggests that the moths merely respond to liquid.

Products (I) of age-specific imbibing frequencies (Table 3) and average intake per imbibing episode (4.5 mg, Table 4) plotted on female age (A) resulted in a nearly straight line. This line is closely described by the equation $I = 3.45A - 7.7$, and computed I-values differ by no more than 7% from actual ones. Based on this equation, lifetime expected honeydew-water intake for fertile females of average lifespan

(11.4 days, Table 2) is 31.6 mg. Since honeydew concentration in honeydew-water on yucca leaf segments averaged 6.5% by dry weight, corresponding honeydew intake is 2.05 mg (31.6 × 0.065 = 2.05). Attribute departures among honeydew-water imbibing females may therefore be ascribed to average consumption of ca. 2 mg of dry honeydew per individual, or ca. 3.5% of initial live weight of females of average forewing length in the main experiment (2.05/59.2 = 0.035).

The greater attribute variability (variances) noted among honeydew-water imbibers in both experiments probably results from the interaction between honeydew effect and female body size. However, in an experiment in which bee-honey concentration was a constant 15%, and honey-water was constantly available, no tendency to heterogeneous variability appeared (Miller 1987).

How much the positive reproductive effects of imbibed honeydew might influence the dynamics of natural populations would seem to hinge on how long females survive in nature, as well as on how readily available honeydew is to them.

ACKNOWLEDGMENTS

Ingman Laboratories Inc., Minneapolis, Minn., performed the chromatography, and University of Minnesota Soil Science Analytical Services the Kjeldahl analysis. I thank Jana Campbell for help in collecting pupae, J. M. Muggli for the honeydew source, A. B. Hamon for expert identification of hemispherical scale, R. L. Jones for laboratory space, D. A. Andow for statistical advice, G. T. Harvey, R. W. Hansen, D. W. Ragsdale and three anonymous readers for useful manuscript reviews, and R. C. Lederhouse for serving as special *Journal* editor for this manuscript.

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Received for publication 14 November 1987; accepted 8 May 1989.