

Effect of Diet and Temperature on Development Rates, Survival, and Reproduction of the Indianmeal Moth (Lepidoptera: Pyralidae)

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ABSTRACT Developmental rates, egg hatch, survival, adult weight, and reproductive potential were determined for Indianmeal moth, *Plodia interpunctella* (Hübner), reared on wheat bran diet, almonds, pistachios, and walnuts at four temperatures. Developmental rate and adult weight were highest on bran diet. Developmental rates on almonds and pistachios were similar, although development on almonds was faster at higher temperatures. Developmental rate and survival were lowest on walnuts. At 35°C, no Indianmeal moth completed development on walnuts and developmental rates on all other diets decreased, indicating that the thermal threshold had been surpassed. Diet had no significant effect on reproductive potential of adults reared at temperatures of 25 and 28.3°C. At 31.7°C, adults reared on bran diet produced the most progeny; adults reared on walnuts produced the fewest progeny. No progeny resulted from adults reared on any diet at 35°C. Suitability of diet for Indianmeal moth development was correlated with diet moisture content; however, the poor performance of walnuts may have been due to the development of rancidity. The results of this study illustrate the difficulty in developing a model for the diverse conditions that exist in California's Central Valley.

KEY WORDS Insecta, *Plodia interpunctella*, developmental rates, temperature

THE INDIANMEAL MOTH, *Plodia interpunctella* (Hübner), will develop on a variety of grains, nuts, beans, meals, dried fruits, and processed foods (Simmons & Nelson 1975). As a result, this insect is a major problem in California during processing and storage of dried fruit and nut commodities. Current control practices often rely on scheduled fumigation with methyl bromide or hydrogen phosphide. Concern over the possible loss of these fumigants through regulatory action or the development of resistance has generated interest in reducing the number of fumigation treatments. One approach is to fumigate only when needed. Unfortunately, because of inadequate information on insect developmental rates and useful sampling methods for these commodities, it is difficult to determine when treatment is necessary.

Commercially available lures for Indianmeal moth allow monitoring of the first spring flights. By combining this technique with a phenological model, it would be possible to time fumigations for maximum efficacy. Developmental rate, survival, and reproduction of Indianmeal moth is

known to be affected by larval diet (Savov 1973a, LeCato 1976, Hoppe 1981, Cline & Highland 1985). Therefore, any model developed to predict phenology must take diet into account. Here, we report the results of a study to determine the effect of larval diet and temperature on developmental rate, survival, and reproductive potential of Indianmeal moth. Comparisons of Indianmeal moth development on shelled almonds, walnuts, and pistachios, as well as on a standard wheat bran diet, were made.

Materials and Methods

The Indianmeal moth isolate used in the study was obtained from a walnut packinghouse in Modesto, Calif., in November 1967. Test insects were maintained continuously on a wheat bran diet modified from Finney & Brinkman (1967) (Tebbetts et al. 1978). Normal rearing conditions were 28°C, 60% RH, and a photoperiod of 14:10 (L:D). The temperatures ($\pm 0.5^\circ\text{C}$) used to determine developmental rates were 25, 28.3, 31.7, and 35°C. Temperatures were maintained in environmental chambers kept at $50 \pm 5\%$ RH and 14:10 (L:D).

In addition to normal wheat bran-based rearing medium, 'Nonpareil' almonds, 'Hartley' walnuts, and 'Kerman' pistachios were used to determine the effect of food source on develop-

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mental rate. The nuts were ground in a food processor and passed through screens to obtain particles between 1.4 and 0.6mm. The nuts were kept in cold storage after grinding so that the same source could be used throughout the study.

Test units consisted of 0.48-liter glass canning jars. The lid of each jar was replaced with filter paper (9.0 cm) overlying copper screen (40 mesh). Each jar contained either 125 g of bran diet or 150 g of ground nuts. Five jars were used for each diet and temperature. The moisture content of all food sources was equilibrated by holding the jars in the environmental chambers for 3–4 wk before the experiment was begun. Moisture content of the food sources was determined periodically throughout this period to determine that equilibrium was reached. Toluene distillation was used to determine moisture content of the bran diet; moisture content of the nuts was determined in a vacuum oven (Horowitz 1980).

Indianmeal moth eggs were collected from adults 1–2 d after emergence. Oviposition jars containing 100–150 adults of both sexes were set up at 1600 hours (PST) and placed under normal rearing conditions. Eggs were collected \approx 40 h later. Eggs were cleaned of scales by gently shaking the collection container under a fume hood. An analytical balance was used to weigh out 2.1 mg of eggs (\approx 100 eggs) into plastic weighing dishes (4.3 by 4.3 cm). After a count of the eggs was made, one dish was placed on the surface of the food source in each jar, and the jars were placed in the environmental chambers. One week later, unhatched eggs in the dishes were counted to determine egg hatch.

Jars were monitored periodically for adult emergence. Once emergence began, adults were removed daily. All adults not needed for subsequent studies were immediately frozen. These adults were later counted and weighed and their sex was determined. Once a 5-d period passed during which no adults emerged, the contents of the jars were frozen and examined for adult moths.

To determine the effect of diet and temperature on mating and reproductive potential, progeny numbers per female were determined. Fifteen mating pairs were selected from adults (0–24 h old) emerging from each diet and placed in 0.48-liter jars containing 125 g of bran diet. The jars were returned to the adult rearing conditions and examined daily for adult survival and subsequent progeny emergence. Adult progeny were collected daily and frozen for later counting and sex determination. Once a 5-d period passed without any emergence, the contents of the jars were frozen and examined for any remaining adults.

The average time in days from oviposition to adult emergence was calculated as mean developmental duration. Developmental rate was expressed as the reciprocal of duration. Survival

was taken as the percentage of adults emerging from each egg sample. Treatments considered for statistical analysis were temperature and diet for all variables except weight, which was measured separately for males and females. Because variances (among replicates) were found not to be consistent among treatment combinations based on Bartlett's test for homogeneity of variance, weighted statistical analyses were performed using the reciprocal of the variance as the weighting factor. SAS procedure GLM (SAS Institute 1987) was used to compute a two-way analysis of variance (ANOVA) to test for the effects of temperature, diet, and their interaction for mean developmental duration, egg hatch, survival, and progeny number. In the case of weight, sex and all interactions with it were added, yielding a three-way analysis. Multiple comparisons among diets were computed within temperatures using the least significant difference (LSD) method with $P \leq 0.05$. The SAS GLM procedure was also used to compute weighted regression for median developmental rate on temperature for all diets.

Results

The equilibrium moisture content for each diet is shown in Table 1. Bran diet had the highest moisture content at all temperatures. Moisture levels for almonds and pistachios were similar at all but the lowest temperature and were 53–66% less than moisture levels for bran diet. Moisture levels for walnuts were 72–78% less than those for bran diet and 26–48% less than for the other nuts. Developmental rate was significantly correlated with moisture content at the three lowest temperatures, with R values of 0.98, 0.98, and 0.97 for 25, 28.3, and 31.7°C, respectively. Rate and moisture content were not significantly correlated at 35°C, with an R of 0.92. The effect of moisture content on other variables is further discussed later.

Two-way ANOVAs showed significant interactions between temperature and diet for all variables. Consequently, further discussion of the effect of diet on each variable will look at each temperature separately. At all temperatures, Indianmeal moth development on bran diet was significantly faster than on the nuts (Table 1). Development on almonds and pistachio was not significantly different at the two lower temperatures. At the two highest temperatures, development on almonds was significantly faster than on pistachios. Development on walnuts was significantly slower than the other diets at all temperatures. For bran diet, almonds, and pistachios, development was slower at 35 than at 31.7°C. No adults emerged from walnuts kept at 35°C.

Developmental rates for each diet are regressed against temperature, as shown in Fig. 1. Values for 35°C were not included in the regres-

Table 1. Initial diet moisture content and mean developmental times ($n = 5$) for Indianmeal moth reared on different diets

Temp, °C	Diet	% Moisture content	Mean no. surviving adults	Development time, $\bar{x} \pm \text{SEM}$
25.0	Bran	13.1	94.4	28.0 \pm 0.05a
	Almonds	4.5	99.0	38.6 \pm 0.29b
	Pistachios	6.1	106.0	38.2 \pm 0.22b
	Walnuts	3.2	33.8	47.2 \pm 0.37c
28.3	Bran	14.0	105.8	22.6 \pm 0.28a
	Almonds	4.8	96.4	31.4 \pm 0.26b
	Pistachios	4.8	99.0	31.3 \pm 0.09b
	Walnuts	3.1	43.2	38.2 \pm 0.29c
31.7	Bran	12.1	109.0	20.2 \pm 0.07a
	Almonds	4.3	104.8	28.4 \pm 0.10b
	Pistachios	4.3	100.8	29.0 \pm 0.10c
	Walnuts	3.2	59.8	35.4 \pm 0.26d
35.0	Bran	10.3	103.6	25.1 \pm 0.41a
	Almonds	4.3	81.6	34.1 \pm 0.71b
	Pistachios	4.7	33.0	42.4 \pm 3.55c
	Walnuts	2.9	0	—

For each temperature, means within columns followed by the same letter are not significantly different ($P < 0.05$ level; LSD test [SAS Institute 1987]).

sion analysis. From the lack of overlapping 95% CL for bran diet, development on this diet was shown to be significantly faster. Overlapping 95% CL for almonds and pistachios indicated that these lines were not significantly different. Developmental rates for walnuts were significantly lower than the other diets. Regression analysis indicated that the lines for all diets had a similar curvature. From the fitted quadratic equations, lower developmental thresholds were estimated as 16.6, 17.5, 17.1, and 18.0°C for bran, almonds, pistachios, and walnuts, respectively.

Egg hatch was erratic and difficult to interpret (Table 2). Eggs did not come in direct contact with the diet and should not have been affected; however, significant differences in hatch were detected between diets. Neonate larvae were

seen dragging unhatched eggs off the plastic dishes, which may account for the erratic results. Many dead neonate larvae were observed in the plastic dishes on walnuts at 35°C. Although the dishes did not appear oily, oil from the walnuts may have come in contact with the eggs, causing their suffocation.

The effect of diet on overall survival was more consistent (Table 2). Survival on walnuts was always significantly less than on the other diets. No adults survived on walnuts at 35°C. Survival on bran diet was similar to, or significantly higher than, on almonds and pistachios at all temperatures. At the two lower temperatures, survival on almonds and pistachios was not statistically different; survival was higher on almonds at 31.7 and 35°C.

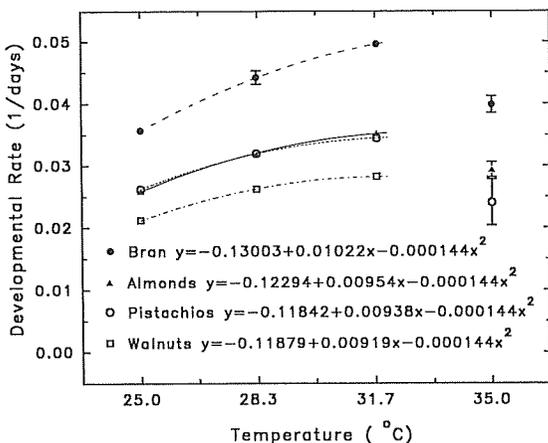


Fig. 1. Developmental rates for Indianmeal moth reared at constant temperatures on different diets. Lines represent the regression of data from 25 to 31.7°C. Missing error bars are smaller than the point symbols.

Table 2. Effect of temperature and diet on egg hatch and survival of Indianmeal moth ($\bar{x} \pm \text{SEM}$; $n = 5$)

Temp, °C	Diet	% Hatch	% Survival
25.0	Bran	91.8 \pm 0.86b	85.8 \pm 0.97a
	Almonds	96.4 \pm 0.51a	87.4 \pm 1.50a
	Pistachios	84.8 \pm 2.35c	84.0 \pm 1.84a
	Walnuts	92.0 \pm 0.71b	30.2 \pm 2.18b
28.3	Bran	96.2 \pm 0.20a	93.8 \pm 0.80a
	Almonds	95.4 \pm 0.51ab	86.4 \pm 0.75b
	Pistachios	94.8 \pm 0.86ab	90.4 \pm 2.06ab
	Walnuts	92.8 \pm 1.59b	39.2 \pm 2.85c
31.7	Bran	97.6 \pm 0.24a	92.4 \pm 1.44a
	Almonds	98.2 \pm 0.37a	90.4 \pm 0.93a
	Pistachios	97.6 \pm 0.40a	86.4 \pm 1.21b
	Walnuts	92.6 \pm 0.75b	51.0 \pm 2.12c
35.0	Bran	97.6 \pm 0.68a	87.6 \pm 1.97a
	Almonds	98.6 \pm 0.35a	70.5 \pm 2.55b
	Pistachios	96.0 \pm 1.49a	34.5 \pm 8.87c
	Walnuts	62.5 \pm 12.70b	0

For each temperature, means within columns followed by the same letter are not significantly different ($P < 0.05$ level; LSD test [SAS Institute 1987]).

Table 3. Effect of rearing temperatures and diet on reproduction of Indianmeal moth ($\bar{x} \pm \text{SEM}$; $n = 15$)

Temp, °C	Diet	No. adult progeny
25.0	Bran	280.8 \pm 11.54a
	Almonds	274.1 \pm 21.26a
	Pistachios	—
28.3	Walnuts	258.5 \pm 23.85a
	Bran	328.0 \pm 7.43a
	Almonds	308.5 \pm 6.49a
31.7	Pistachios	317.2 \pm 7.56a
	Walnuts	291.3 \pm 22.08a
	Bran	339.1 \pm 12.27a
35.0	Almonds	311.3 \pm 4.63b
	Pistachios	301.1 \pm 3.78b
	Walnuts	262.9 \pm 15.95c
	Bran	0
	Almonds	0
	Pistachios	0
	Walnuts	0

For each temperature, means within columns followed by the same letter are not significantly different ($P < 0.05$ level; LSD test [SAS Institute 1987]).

Because of an unavoidable delay in obtaining pistachios, the developmental study for this product at 25°C was done later than the other diets. The quality of the bran diet used for progeny determination differed slightly from earlier tests, causing progeny numbers to be skewed. For this reason, progeny numbers for adults reared on pistachios at 25°C were excluded from the analysis (Table 3). At 31.7°C, progeny production was significantly higher for bran and significantly lower for walnuts than for the other diets; progeny numbers from almonds and pistachios were not statistically different. Although the means follow the same order at the two lowest temperatures, differences were not significant.

At 35°C, no progeny were produced from adults reared on any of the diets. Of the 15 mating pairs used from each diet, 8 (53.3%) of those from bran diet, 6 (40%) of those from almonds, and none of those from pistachios remained in copulo until death. The remaining females were dissected to confirm successful mating by determining the presence of spermatophores. Five (33.3%) of the females reared on bran diet and on pistachios, and seven (46.7%) of those reared on almonds had mated. No spermatophores were found in two females reared on bran diet and on almonds, and 10 (66.7%) of those on pistachios.

Adult weight of females reared on bran diet was significantly higher than those on any other diet (Table 4). Weights of females reared on almonds and pistachios were not statistically different at 28.3 and 35.0°C. Weights of females reared on pistachios at 25.0 and 31.7°C were significantly higher than for females reared on almonds. For all temperatures, weights of females reared on walnuts were not significantly different from, or significantly lower than, for females reared on almonds and pistachios.

Table 4. Effect of rearing temperature and diet on weight of adult Indianmeal moths ($\bar{x} \pm \text{SEM}$; $n = 5$)

Temp, °C	Diet	Wt, mg	
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25.0	Bran	15.4 \pm 0.18a	9.9 \pm 0.14a
	Almonds	13.5 \pm 0.19c	8.2 \pm 0.07b
	Pistachios	14.0 \pm 0.13b	7.9 \pm 0.10c
28.3	Walnuts	13.3 \pm .019	8.3 \pm 0.24bc
	Bran	13.8 \pm 0.26a	8.4 \pm 0.40a
	Almonds	11.7 \pm 0.33b	6.9 \pm 0.19b
31.7	Pistachios	11.4 \pm 0.13b	6.7 \pm 0.10b
	Walnuts	11.6 \pm 0.17b	6.9 \pm 0.09b
	Bran	12.1 \pm 0.14a	7.0 \pm 0.09a
35.0	Almonds	10.6 \pm 0.23c	6.2 \pm 0.12c
	Pistachios	11.4 \pm 0.15b	6.8 \pm 0.15ab
	Walnuts	10.9 \pm 0.26bc	6.6 \pm 0.13b
	Bran	12.5 \pm 0.51a	7.8 \pm 0.44a
	Almonds	6.8 \pm 0.40b	4.2 \pm 0.13b
	Pistachios	5.7 \pm 0.69b	3.9 \pm 0.36b
	Walnuts	—	—

For each temperature, means within columns followed by the same letter are not significantly different ($P < 0.05$ level; LSD test [SAS Institute 1987]).

Weight of adult males reared on bran diet was significantly higher than males reared on other diets at all temperatures except 31.7°C, where weights of adults reared on pistachios were not significantly different. Weights of males reared on pistachios and walnuts were similar at all temperatures. At all temperatures, weights of males reared on pistachios and walnuts were not significantly different. At 25.0°C, weights of males reared on almonds were significantly higher than those on pistachios but not significantly different from those on walnuts. Weights of males from almonds were not significantly different from those from pistachios and walnuts at 28.3 and 35.0°C and were significantly lower at 31.7°C. Weight for both females and males reared on any diet generally decreased as rearing temperature increased. This tendency was most pronounced in adults reared on almonds and pistachios at 35°C, where adult weight was 32–50% lower than weight of adults reared on almonds and pistachios at 31.7°C.

In the present study, a linear correction for moisture content was applied to the data, and ANOVAs were recomputed for all variables. This correction made almost no change in the means for egg hatch. Means for mean development and progeny numbers were brought closer together, but significant differences remained unchanged. However, for survival and weight, the apparent superiority of bran diet was reduced. At 35°C, bran diet still showed significantly better survival and weight (both females and males). However, at the two lowest temperatures, corrected weights for bran diet were not significantly different from either almond or walnut values. For 31.7°C, weights of females from bran were significantly lower than those from pistachios, and weights of males reared on bran were signifi-

cantly lower than those from all other diets. When corrected for moisture, survival was significantly lower on bran than on almonds or pistachios at the two lowest temperatures, and lower than pistachios at 31.7°C. Survival on bran remained significantly better than on walnuts for all temperatures. Because mean development after correction for moisture content still was significantly better on bran for all temperatures in the study, it would appear that moisture was not the only factor contributing to developmental differences. Because the desirability of correcting for moisture content is questionable, it was considered preferable to report results on the uncorrected data and discuss the corrected results.

Discussion

Our results show that, for the culture used in the study, development and survival was best on bran diet. Although this might be interpreted as adaptation of the culture to its rearing medium, we have found that newly isolated Indianmeal moth strains have developmental rates similar to those in our laboratory culture, also developing faster on bran diet than on nuts (J.A.J., unpublished data). Overall, response of Indianmeal moth reared on almonds and pistachios was similar, although development and survival at higher temperatures was better on almonds than on pistachios. Development and survival was poorest on walnuts, especially at higher temperatures.

Suitability of diet was correlated with moisture levels; developmental rates and survival were lowest on the driest diet. Humidity and moisture content of diets have been found to affect both survival and development of Indianmeal moth and related pyralids. Abdel-Rahman et al. (1968) showed that higher moisture contents of corn varieties were often more suitable for development of Indianmeal moth. Similar results were found by Warren (1956) for Angoumois grain moth, *Sitotroga cerealella* (Olivier). Mbata & Osuji (1983) showed that relative humidities of 70–80% were best for Indianmeal moth development on peanuts, but that 60% RH slowed development and decreased adult weight.

Dietary moisture content may not be the only reason for the differences in development seen in our study. Development of both Indianmeal moth and Angoumois grain moth varied considerably between different corn varieties of identical moisture contents (Warren 1956, Abdel-Rahman et al. 1968). Savov (1973a) found that Indianmeal moth reared on walnuts and almonds had shorter developmental times than those reared on dried fruits, which are normally of higher moisture content than nuts. In preliminary experiments (J.A.J., unpublished data), developmental rates and survival of Indianmeal

moth on raisins were much lower than on nuts, although raisin moisture content was between 10 and 12%. Swatonek (1973) found a negative correlation between larval developmental rates and mortality of Indianmeal moth reared on different paprika varieties with capsaicin content. When the data from this study were corrected for dietary moisture content, only survival and weight showed major adjustments in mean separation. For these two variables, bran diet lost its superiority. For mean development, egg hatch, and progeny numbers, only minor changes were noted. Therefore, it is reasonable to assume that dietary factors other than moisture content may have contributed to the observed differences in Indianmeal moth development.

Oxidative rancidity occurs in walnuts at a faster rate than in almonds or pistachios because walnuts are much higher in polyunsaturated fatty acids (Peterson & Johnson 1978). Possible end products of rancidification include volatile aldehydes and ketones that may be toxic to insects. Rancidity in walnuts can be induced by storage at high temperatures and by grinding (Musco & Cruess 1954). Thus, the observed relative unsuitability of walnuts for Indianmeal moth egg hatch and development, especially at 35°C, may be from the production of toxic compounds during rancidification.

The decrease in developmental rates observed at 35°C on all diets shows that the upper temperature threshold has been surpassed. Mbata & Osuji (1983) found developmental periods under different humidity regimes were longer at 35 than at 30°C. Savov (1973a) found that mortality was high and development was inhibited when Indianmeal moth was reared at 34°C on various dried fruits and nuts. The inability of Indianmeal moths reared at 35°C to reproduce also shows that an upper threshold has been reached. Bell (1975) found that *Ephestia elutella* (Hübner) and *E. kuehniella* (Zeller) were unable to reproduce when reared at 30°C. Lum (1977) found that eupyrene sperm development was inhibited in Indianmeal moth pupae and prepupae exposed to 35°C for ≥ 3 d, resulting in a reduction in egg production. Our results indicate that many moths reared at 35°C were unable to mate, separate, or transfer spermatophores.

In California, most commercial nut storage includes silos kept at ambient temperatures, which may peak above 35°C during summer months. Any model to predict population trends in these silos must take into account an upper temperature threshold, both for development and reproduction.

Savov (1973b) determined the lower developmental temperature threshold for Indianmeal moth to be 13.5°C. The developmental thresholds obtained from our data ranged from 16.6 to 18°C. These temperatures may be too high to be accurate. More temperatures should be included

in the regression analysis to obtain a valid estimate. However, larvae reared at temperatures below 20°C enter diapause (Tzanakakis 1959, Bell 1976). In preliminary experiments, attempts to measure developmental rates at 21.1°C resulted in about half of the test larvae entering diapause. We were thus limited to temperatures above 22°C for developmental rate determinations. A more practical method of obtaining a lower developmental threshold for use in a predictive model would be to determine developmental rates for Indianmeal moth eggs and pupae. Difficulties imposed by diapause induction would be avoided and effects of diet would be minimized.

The results of our study illustrate the difficulty in developing predictive models for insects with wide host ranges. A different model will likely be required for each product attacked. In California's Central Valley, a variety of nuts and dried fruits, all susceptible to infestation by Indianmeal moth, are produced and processed in the same area, sometimes in the same packing plant. Also, not all product within a single packing plant are stored under the same temperature and humidity conditions. All of these factors add to the complexity of any proposed model. Despite these difficulties, information on Indianmeal moth developmental rates, along with data on diapause induction and termination and pheromone trapping studies, should eventually lead to more efficient fumigation schedules.

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