11. The center line of the capsid was determined by minimizing the function

$$Q = A\Sigma(F - F_{real})^2/\Sigma(F + F_{real})^2$$

where F is the computer-calculated, equatorial Fourier transform; F_{real} is the real part of F; and A is a normalization factor such that a value of $Q = 1.0$ corresponds to random agreement between F and F_{real}.

12. The position of the glide line was determined by minimizing the function $Q = A\Sigma[F_{left} - F_{right} \cdot \exp(i\pi kb)]^2/\Sigma[F_{left} + F_{right} \cdot \exp(i\pi kb)]^2$, where F_{left} and F_{right} are the Fourier coefficients symmetrically related to the left and right sides of the meridian; b is the repeat distance in the direction of the glide, and A is the normalization factor. The position of the mirror line was determined by minimizing $Q = A\Sigma(F_{left} - F_{right})^2/\Sigma\ (F_{left} + F_{right})^2$ where all symbols are defined as above.

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Social Facilitation and Development in Ephestia kühniella Z.

Abstract. *Total time required for larval and pupal development in* Ephestia kühniella *Z. was significantly modified when habitable space of the food mass was increased by dilution with a nontoxic sawdust. Doubling the living space resulted in an increased developmental rate, presumably due to a reduction in the number of larval interactions. Tripling the living space, however, produced a somewhat unexpected delay in development, accompanied by a marked increase in variance about the means for both males and females.*

Studies of the development of *Ephestia kühniella* Z. (Mediterranean flour moth) from egg deposition to adult eclosion have shown that, within limits, an inverse proportionality exists between available food and the average time required for complete development. Other effects that have been related directly to an increase in population density in a food mass are an increase in mortality and decreases in weight, length of body, and wing length (*1*). Moreover, crowding is accompanied by a reduction in egg (or progeny) production (*2*). Still, these phenomena are only a partial function of the size of the food mass; some cornmeal remains in excess after all larval feeding has been completed in all cultures, regardless of the degree of crowding.

It has been suggested (*3*) that byproducts of development (such as excreta) that accumulate in the food mass are contacted increasingly through ingestion or chemoreception in crowded cultures, and thus indirectly influence the growth of individual larvae. A similar phenomenon has been observed in *Kalotermes flavicollis*; the maintenance of the polymorphism of this social termite is dependent on direct contact, and pheromone transfer, between individuals (*4*). Direct observations of crowded meal moth cultures have shown that physical encounters between larvae increase as a result of crowding (*5*). Resulting from each contact is a burst of activity that may include biting, butting, or rapid movement through the food tunnel. These behavioral responses interfere with quiet feeding and food storage.

Hence, the thesis was developed that increasing habitable space while holding the amount of food (cornmeal) per animal constant would decrease the likelihood of chance encounters, and thus decrease both first-order effects (direct physical contact) and second-order effects (chemical perception of metabolites) between the individual larvae. A reduction in the avoidance or aggressive responses to other feeding larvae could then result in a reduction of the time required for the larval phase of development, and thus for total developmental time from egg deposition to eclosion of the adult moth.

A nontoxic substance, basswood sawdust, was used to dilute the cornmeal, either one or two volumes of sawdust per volume of cornmeal, and thus double or triple the living space. The test animals were F_1 hybrids of the *aa0* (red eye) and *wawa0* (white eye) stocks. Newly hatched larvae (less than 4 hours after emergence) were isolated, and 360 were transferred in groups of ten to three series of plastic bowls, 9.0 cm in diameter. The sawdust for the 1 : 1 or 1 : 2 dilutions was mixed thoroughly with the standardized volume of food before being poured into the bowl containing the larvae. The food was commercially available enriched and degerminated cornmeal; each volume contained 9.7 g, or approximately 1.0 g per larva. Vented soft plastic snap lids were fitted to each bowl before shelving. An experimental set consisted of three bowls that were filled in sequence with food only (control), food-sawdust 1 : 1, and food-sawdust 1 : 2. Twelve replicate sets were established on the same day and were maintained on the same shelf in a darkened room at 20 ± 1°C. After the onset of pupation, the cultures were surveyed daily at 0900, and all adults were collected, sexed, and scored. The data of the daily collections, which were separated by sex and pooled, are presented in Fig. 1.

For the determination of the eclosion distributions, day 1 was taken as the first day when adults appeared in any of the 36 culture bowls; the first adults in some cultures were not recorded until day 2 or 3. In the control (food only) cultures, the mean time required for eclosion of all adults was shorter for females (group A) than for males (group D) (Fig. 1), but the difference was not significant (*t*-test, $.10 < P < .50$).

The sawdust used to dilute the food mass apparently had minimal toxicity. Of 240 larvae introduced into bowls containing cornmeal diluted with sawdust, 239 were obtained as adult moths (< 1 percent mortality), whereas only 112 adults of the initial 120 first-instar larvae completed eclosion in the control cultures with undiluted cornmeal

Table 1. Values of *t* and *P* for *t*-test comparisons of the mean times of eclosion for males and females in the control (groups A and D) and experimental sets of cultures of *Ephestia kühniella.* The cornmeal-sawdust ratio was 1 : 1 for groups B and E and 1 : 2 for groups C and F.

Group and sex	Group and sex									
	A♀		B♀		C♀		D♂		E♂	
	t	*P*	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*
B♀	1.33	.10–.50								
C♀	3.78	< .01	5.33	< .01						
D♂	1.12	.10–.50								
E♂			0.22	.50			3.32	< .01		
F♂					1.36	.10–.50	1.48	.10–.50	3.68	< .01

(6.6 percent mortality). However, the eclosion values of the experimental groups indicate that two different effects resulted from the two food dilutions.

Doubling of habitable space by addition of an equal volume of sawdust produced adults with shorter mean eclosion times than those for the control animals. The decrease was significant for experimental males (group E) compared to male controls (group D) ($P<.01$), but not for the experimental females (group B) compared to control females (group A) ($.10<P<.50$). However, comparison of mean eclosion values for groups B and E yielded the smallest value of t in the three sets of male-female comparison (Table 1). For these groups, distributions of the pooled eclosions show a tighter clustering about the mean values (Fig. 1).

Data for animals reared in cornmeal diluted 1 : 1 with sawdust thus seem to support the hypothesis that reduction in direct physical contact between larvae or reduction in the concentration of developmental metabolites in the surrounding culture medium results in less time required for total development. Thus, it was expected that *Ephestia* with living space tripled would either maintain the gain in development speed observed for larvae in the 1 : 1 dilution, or would develop even faster.

However, in the group with food mass diluted 1:2 with sawdust, the major effects were (i) delayed eclosion and (ii) an increase in the variance of the mean values for female and male eclosion (Fig. 1). The mean eclosion value for females (group C) is significantly larger ($P<.01$) than those for control females (group A) and females in the 1 : 1 dilution (group B). For males in the 1 : 2 experimental cultures (group F), the mean eclosion value is again the largest for the three groups of males, and is significantly different ($P<.01$) from that for males in the 1 : 1 dilution (group E), although not from that of control males (group D).

This major delay of development which is evident from the increased eclosion values may be related to the following factors acting alone or in combination: an increase in food-seeking time, especially in early larval instars; increased consumption of the nonnutritive wood fragments; or greatly reduced perception of siblings and the stage of their development through physical and second-order contacts. The end result is a reduction in the temporal coherence of initiation of cocoon formation and of eclosion of adults.

The shift of the distribution of eclosion values to the right in the 1:2 dilution group is probably less important for the potential survival of this cryptic moth species than the greatly reduced clustering of eclosions about the mean (Fig. 1). The consequence of a flattened distribution of eclosions is the decreased probability of an adult emerging from the food mass in the presence of a potential mate. This reduced likelihood of reproductive success is especially important to the short-lived adults of a cryptic species in contrast to the longer-lived moths of aposematic species (*6*).

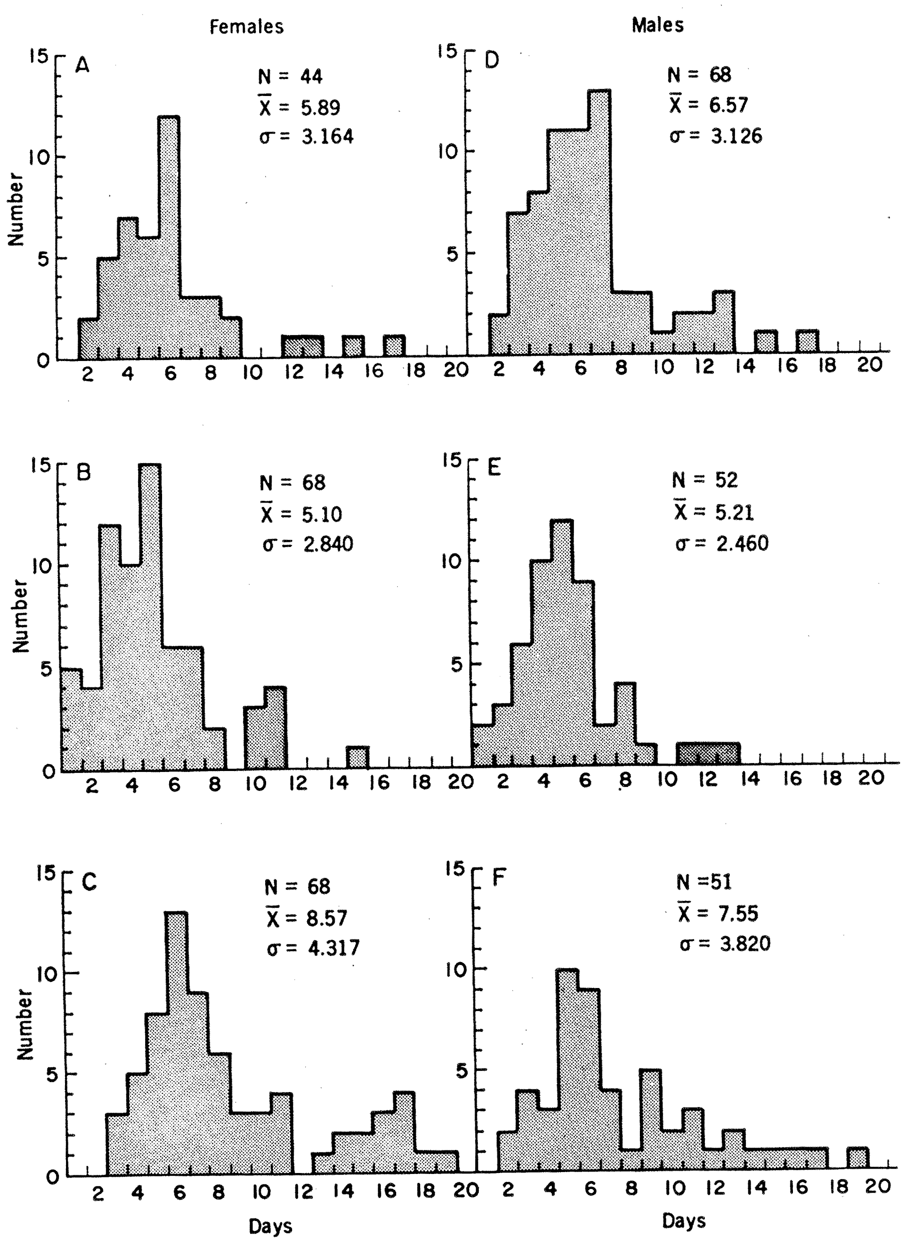

Fig. 1. Histograms of pooled eclosion values with means ($\overline{X}$) and variances (σ) for female and male *Ephestia kühniella* in the cornmeal dilution experiments. Groups were as follows: A and D, controls (cornmeal only); B and E, cornmeal diluted 1 : 1 with sawdust; and C and F, cornmeal diluted 1 : 2 with sawdust.

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7. I thank B. Curtin for preparing the statistical analysis of the data.

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