A SIMULATION MODEL OF HOUSE FLY (DIPTERA: MUSCIDAE) DEVELOPMENT IN POULTRY MANURE

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Abstract

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Developmental times were determined at constant temperatures for egg–larval (prepupal) and egg–larval–adult (preadult) house flies in poultry manure. Developmental time decreased as temperature increased but declined at temperatures above 35°C. The average time from oviposition to pupation ranged from 26.8 days at 16°C to 5.2 days at 35°C, and the average time to adult emergence ranged from 43.1 to 8.8 days. Pupae were formed at 41°C, but no adults emerged above 38°C. The relationship between developmental rate and temperature was determined and used in a rate summation model to simulate prepupal and preadult developmental times in poultry manure, with manure bed temperature as input. The model was tested on the basis of developmental times determined in a poultry house during the fly-breeding season. The observed mean time to pupation under field temperatures ranged from 6.7 to 15.6 days, and adult emergence required from 12.5 to 27.1 days. Simulations were closest to the observed times when actual manure bed temperatures were used as input; however, soil temperatures obtained from a nearby weather station also provided satisfactory simulation results after an empirical correction was used.

Résumé

Les temps de développement de la mouche domestique jusqu'aux stades pupal et adulte dans le fumier de volaille ont été mesurés à des températures constantes. Ces temps diminuaient plus la température était élevée, jusqu'à 35°C. Le temps moyen de l'oviposition à la pupation a varié de 26,8 jours à 16°C, à 5,2 jours à 35°C, tandis que l'intervalle des temps moyens jusqu'à la sortie des adultes a été de 43,1 à 8,8 jours. À 41°C, il y a eu formation de pupes, mais aucun adulte n'a émergé à plus de 38°C. La relation entre la vitesse du développement et la température a été déterminée, et la fonction obtenue a été utilisée dans un modèle de sommation pour la simulation des températures de développement jusqu'aux stades pupal et adulte dans le fumier de volaille où la température du lit de fumier était la donnée de départ. Le modèle a été contrôlé avec des données sur les temps de développement mesurés dans un poulailler durant la saison de reproduction de la mouche. Les temps moyens observés jusqu'à la pupation aux températures locales ont varié de 6,7 à 15,6 jours, et il a fallu de 12,5 à 27,1 jours jusqu'à l'émergence des adultes. Les données de simulation se rapprochent le plus des temps observés lorsque les températures du lit de fumier sont employées comme données de départ; toutefois, les données sur la température du sol obtenues d'une station météorologique de la région ont également permis une simulation satisfaisante après une correction empirique.

Introduction

Temperature has been used to model development for several species of Diptera of medical-veterinary importance (Greenham 1972; Berry *et al.* 1977; Palmer *et al.* 1981; Moon 1983). Such models provide a useful basis for predicting life-history events in the field, and aid in the understanding of a species' population dynamics.

The house fly, *Musca domestica* (L.), is an important pest in poultry rearing systems. Adults oviposit in accumulated poultry manure. The larvae feed in the manure and pass through three instars before pupation. The relationship between temperature and minimum developmental time for the house fly egg, larval, and pupal stages in a mixture of pig and horse dung was reported by Larsen and Thomsen (1940). However, mean developmental

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rates and the cumulative distribution of developmental times at several constant temperatures are required to formulate stochastic models of temperature-dependent development (Curry *et al.* 1978). As information is lacking for house flies developing in poultry manure, this study was conducted to (1) determine the relationship between constant temperature and mean developmental rates for immature house flies in poultry manure, (2) develop a model that uses temperature data to simulate developmental times under field conditions, and (3) compare simulations with house fly developmental times observed under field conditions.

Materials and Methods

House fly eggs were obtained from a colony initiated with wild flies collected from a poultry house in Wake County, North Carolina, 6 weeks before the study. Adult flies were kept in screen cages and fed a diet of milk and sugar. Larvae were reared in a mixture of fly rearing medium (Ralston-Purina, St. Louis, MO), yeast, and water (CSMA media).

Manure was collected 6 days before use by suspending 45 by 150 cm plastic-covered wooden boards 60 cm beneath cages of white Leghorn laying hens. Manure was collected from the boards after 24 h, frozen for 3 days to kill any invading arthropods, and thawed 1 day before use. Water was added to the thawed manure to bring it to the consistency of fresh manure.

Observations on the developmental times of house fly immatures were made using standard manure cups inoculated with house fly eggs. To collect eggs, plastic dishes containing tissue paper soaked with milk and several drops of 6% ammonium hydroxide as an oviposition stimulant were placed for 4 h in cages containing ca. 3000 adult house flies, 4–5 days old. After collection, the eggs were washed with tap water and groups of 50 were placed on pieces of moistened blotting paper (2.5 by 2.5 cm). The thawed manure was placed in 350-mL plastic cups (ca. 250 g of manure per cup), and a piece of blotting paper containing house fly eggs was placed egg side down on the surface of the manure in each cup. The cups were tightly covered with organdy cloth to allow ventilation and prevent ingress of indigenous predators and flies.

Constant-temperature experiments. Temperature cabinets were set at 16, 19, 22, 26, 31, 35, 38, and 41°C. Fifty cups of manure, each containing 50 eggs, were placed in each cabinet. One cup was removed daily from each cabinet, and the contents were mixed with 25% sodium chloride to separate fly immatures from the manure for inspection. When pupae were first observed at a particular temperature, three cups per sampling interval were removed and examined. Sampling was conducted at 24-h intervals for flies held at 16, 19, 22, and 41°C, at 12-h intervals for 26°C, and at 8-h intervals for 31, 35, and 38°C. House fly larvae and pupae were separated from the manure by flotation. The proportion that had pupated was used to determine the cumulative probability of pupation through time at each temperature.

When pupation was complete at a given temperature, all pupae were extracted from the remaining manure cups, placed in individual vials, returned to the same temperature at which they were reared, and held until emergence. The vials were examined daily until adult emergence started, after which they were examined with the same frequency as during pupation. The cumulative probability of adult emergence through time was determined. The mean time required to develop from egg to pupa (prepupal development) and egg to adult (preadult development), as well as the mean rates of prepupal and preadult development, were calculated for each constant temperature, the midpoint of the inspection interval being used as the measure of time.

Field experiments. The time required for prepupal and preadult development of house flies under field conditions was determined throughout the fly-breeding season in North Carolina. Experiments were conducted in a narrow caged-layer poultry house 4.9 m long

by 3.1 m wide located in Wake County, NC. The sides of the house were 2 m high, and the roof rose to a central peak 3 m above a middle walkway. On each side of the walkway were two tiers of 10 standard commercial cages containing a total of 80 white Leghorn laying hens. Manure accumulated on the ground for 4 weeks before the beginning of the experiments, and continued to do so throughout the experiments.

Cups containing manure and fresh house fly eggs were prepared as described previously, and were placed in the manure bed in the poultry house directly beneath the cages of laying hens. Five separate cohorts of eggs were placed in the manure bed from May to October 1984, the season that corresponds to the time of greatest activity for the house fly in North Carolina (Lysyk and Axtell 1986). Starting dates for each cohort were 22 May, 16 June, 18 July, 15 August, and 22 September. Each cohort consisted of 50 manure cups containing 50 house fly eggs each, placed in the manure beds on each side of the poultry house. As the cups were placed directly beneath the cages of laying hens, a method to prevent fouling of the surface of the cups with chicken droppings had to be devised. A 15-cm piece of white PVC pipe (ca. 10 cm diameter) was placed around each manure cup, and a plywood board (10 by 10 by 0.6 cm) was attached with wire clips to two pieces of smaller PVC pipe (7.5 cm long by 1.8 cm diameter) glued lengthwise to the tops of the larger cylinders. The boards were elevated to allow airflow and light to enter, and prevented manure from accumulating on the cups.

Sampling to determine the times for prepupal and preadult development was conducted daily for the May–August cohorts, and every second day for the September cohort. Before pupation, samples consisted of two cups of manure selected at random from the manure bed. The contents were floated in 25% sodium chloride for inspection. When the first pupae in a cohort were detected, six cups per day were examined to determine the distribution of pupation through time. When pupation was complete, the remaining cups were left in the manure bed and examined daily for adult emergence. The mean time for prepupal and preadult house fly development was calculated.

The temperature of the manure beds was recorded at 3-h intervals at one location on each side of the house, and the average daily manure temperature was calculated. Air and soil temperatures were obtained from a synoptic weather station located within 1 km of the study site.

Data analysis and model development. Mean rates of development for prepupal and preadult house flies at constant temperatures were fitted to a four-parameter thermodynamic model of poikilotherm development with high temperature inhibition (Sharpe and DeMichele 1977) which has the form:

$$r(K) = \frac{\text{rho25}\ \frac{K}{298.15}\ \exp\left(\frac{\text{HA}}{R}\left(\frac{1}{298.15} - \frac{1}{K}\right)\right)}{1 + \exp\left(\frac{\text{HH}}{R}\left(\frac{1}{\text{TH}} - \frac{1}{K}\right)\right)} \quad [1]$$

where $r(K)$ = mean rate of development (days $^{-1}$) at temperature K, K = temperature in Kelvin (= °C + 273.15), and R = 1.987 cal degree $^{-1}$ mol^{-1}. Rho25, HA, TH, and HH are constants associated with a single rate-controlling enzyme and are described by Schoolfield *et al.* (1981). Estimates of these constants were determined separately for prepupal and preadult house flies on the basis of data from the constant temperature experiments and the non-linear regression routine outlined by Wagner *et al.* (1984*a*).

The distributions of development at each constant temperature were normalized using the mean developmental time at each temperature as the normalizing constant (normalized time = developmental time/mean time). The normalized distributions from constant temperatures of 19–35°C were pooled for both prepupal and preadult developmental times, and Weibull functions were fitted to the data according to methods similar to those outlined

by Wagner *et al.* (1984*b*). This assumes that the distribution of development on the normalized scales is the same at each constant temperature. The cumulative Weibull distribution has the form:

$$F(x) = 1 - \exp(- ((x - \gamma)/ \beta)^{**}\eta) \quad [2]$$

where $F(x)$ is the cumulative proportion of individuals that have completed development at the normalized time x. The mean developmental times on the normalized time scales are represented by 1, and no development is represented by 0. The parameters η, β, and γ are determined by non-linear regression, and γ represents the time (in normalized units) at which the first individuals complete development.

A FORTRAN algorithm was written incorporating Eqs. [1] and [2] so that measurements of poultry manure temperature taken in the field could be used to simulate the proportion of house flies from a single cohort that had completed prepupal and preadult development under variable temperature regimes. The fractional age (age measured in normalized units) of a cohort of house fly immatures after exposure to a temperature regime for a given period was calculated from:

$$\text{fractional age} = \Sigma r(K)dt \quad [3]$$

where $r(K)$ is obtained by solution of Eq. [1] with the average temperature (in K) to which the cohort is exposed and dt is the length of the exposure interval measured as a portion of 1 day (Stinner *et al.* 1974). Two physiological time scales were used, one for prepupal and the other for preadult development. Fractional age was calculated separately along the two scales, with mean prepupal developmental time corresponding to fractional age = 1 on the first scale and mean preadult developmental time corresponding to fractional age = 1 on the second. This was accomplished by solving Eq. [1] using the appropriate parameter values from Table 2 for prepupal and preadult development. The cumulative proportion of individuals of a cohort that completed development at a fractional age was then estimated by solving Eq. [2] with the appropriate estimates of the distribution parameters from Table 2.

To test the model, temperatures recorded during the field experiments were used as input to simulate patterns of house fly development after exposure to variable temperatures. The simulated results were compared graphically to the patterns of development observed during the field experiments. Linear regression was used to determine the relationship between simulated and observed means.

Results and Discussion

Constant-temperature experiments. The mean rates and times for house fly preadult and prepupal development at constant temperatures are shown in Table 1. Developmental times are similar to those reported by Larsen and Thomsen (1940). Although pupae were formed at 41°C, no adult emergence occurred at this temperature; this suggests that the lethal limit for pupae is between 38 and 41°C, and is lower than for the larvae.

The relationship between the rate of development and temperature for prepupal and preadult house flies is shown in Figure 1 and has a shape similar to that observed for other Diptera (Moon 1983; Palmer *et al.* 1981; Berry *et al.* 1977). Development was fastest near 36°C, in agreement with Larsen and Thomsen (1940).

Parameter estimates for the four-parameter poikilotherm development model for prepupal and preadult house flies are shown in Table 2. The Sharpe and DeMichele (1977) model fitted the observed data well, as evidenced by the high R^2 for prepupal ($R^2 = 0.996$) and preadult ($R^2 = 0.997$) developmental rates. The parameter estimates for the distribution functions are also listed in Table 2. The Weibull function fitted the pooled normalized distributions of prepupal and preadult development well, having R^2 values of 0.95 and 0.96, respectively (Fig. 2*a*, *b*).

Table 1. Developmental times (days) and rates (days^{-1}) for prepupal and preadult house flies reared at different constant temperatures

	Prepupal development					Preadult development				
Temp (°C)	*n*	Mean time	(SD)	Mean rate	(SD)	*n*	Mean time	(SD)	Mean rate	(SD)
16	556	26.8	(4.12)	0.0386	(0.0057)	107	43.1	(2.89)	0.0233	(0.0015)
19	183	17.9	(2.10)	0.0570	(0.0058)	16	30.6	(1.41)	0.0327	(0.0014)
22	462	12.7	(1.56)	0.0796	(0.0091)	138	22.9	(1.09)	0.0438	(0.0018)
26	1000	8.1	(0.69)	0.1262	(0.0114)	226	14.6	(0.71)	0.0690	(0.0035)
31	602	5.2	(0.37)	0.1989	(0.0209)	301	9.4	(0.47)	0.1069	(0.0056)
35	547	4.9	(0.33)	0.2352	(0.0196)	370	8.8	(0.41)	0.1145	(0.0060)
38	82	5.2	(0.50)	0.1953	(0.0205)	38	9.0	(0.62)	0.1124	(0.0083)
41	35	6.6	(0.85)	0.1550	(0.0448)	No development				

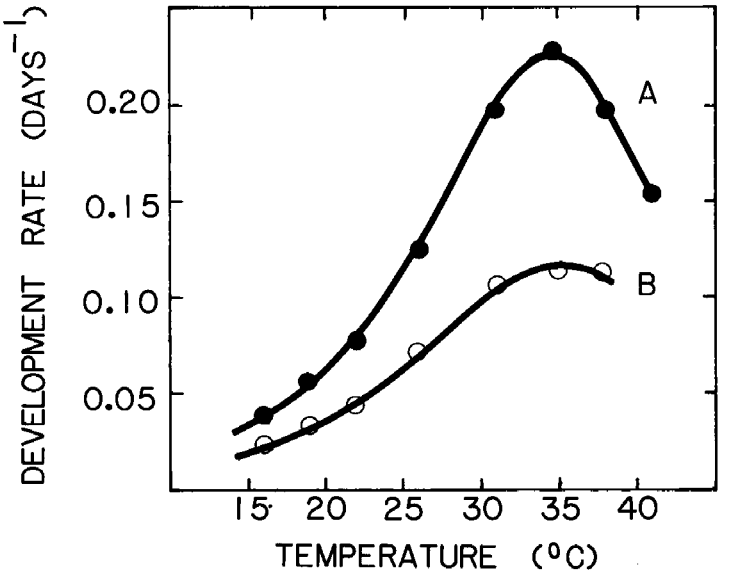

FIG. 1. Relationship between temperature and developmental rate for prepupal (solid circles) and preadult (open circles) house flies. The solid lines are the rate equations from Table 1 for (A) prepupal and (B) preadult development.

Field experiments. The mean times to pupation and standard deviations (shown in parentheses) were 8.0 (0.36), 7.1 (0.37), 6.7 (0.34), 7.7 (0.34), and 15.6 (2.19) days for cohorts started in May, June, July, August, and September. The average times to emergence were 14.7 (0.42), 13.1 (0.44), 12.5 (0.66), 14.4 (0.42), and 27.1 (0.92) days for each cohort. The longest developmental period was more than twice the shortest for both prepupal and preadult flies. The length of the developmental period for each cohort was reflected in the temperature of the manure beds during the time the cohort was in the field. The ranges in mean daily manure temperature were 18.4–28.3, 25.6–29.2, 25.3–29.1, 23.9–29.4, and 17.2–25.0°C for the cohorts started in May, June, July, August, and September, respectively. Although seasonal variations in manure temperature were large, temperatures in the manure bed were quite stable during each 24-h period. The largest observed range in manure bed temperature was 9°C during a 24-h period, and generally the daily range was 2–6°C.

Table 2. Parameter estimates (SE) for model of temperature-dependent immature house fly developmental rates (Eq. [3]) and parameter estimates for the distribution of development (Eq. [4])

	Parameter estimates			
	Prepupal development		Preadult development	
(A) Rate				
rho25	0.1178	(0.0037)	0.0666	(0.0047)
HA	20782.2990	(1104.2294)	19929.2714	(1900.0856)
TH	309.5055	(0.6947)	309.8486	(1.5784)
HH	56291.4258	(3562.8401)	46394.1083	(8121.5837)
(B) Distribution				
γ	0.8558	(0.0229)	0.9038	(0.0436)
η	0.1724	(0.0267)	0.1232	(0.0461)
β	1.4929	(0.2600)	2.0674	(0.9207)

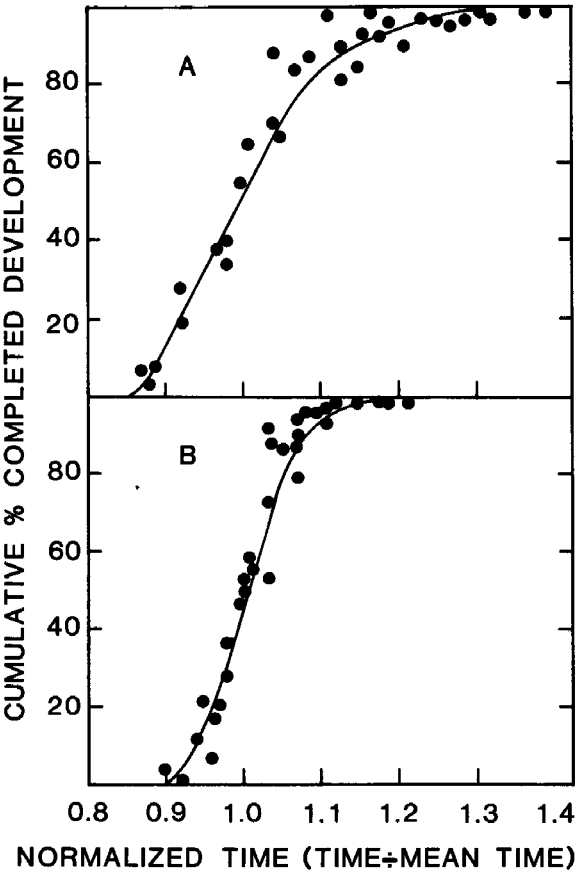

FIG. 2. Cumulative distribution of developmental times for (A) prepupal and (B) preadult house flies on the normalized time scales.

Total immature survival was calculated on the basis of the number of adults emerging in the manure cups that remained at the end of each cohort trial. The proportions surviving and standard deviation (shown in parantheses) for the duration of each cohort were 0.734 (0.017), 0.701 (0.016), 0.761 (0.015), 0.545 (0.019), and 0.546 (0.019). Daily survival rates were calculated as $s = S^{1/x}$ where s = daily survival rate, S = total cohort survival rate, and x = mean time to emergence in days. The daily survival rates of the immature house flies were 0.979 (0.002), 0.973 (0.002), 0.978 (0.002), 0.959 (0.002), and 0.978 (0.001) for each cohort. These survival rates are estimates of physiological mortality as natural enemies were excluded.

Simulation results. The results of the simulations of prepupal and preadult developmental times for each cohort are shown in Figures 2 and 3. As manure bed temperatures showed little within-day variation, the average daily manure bed temperature was used to drive the simulation model. Increments of 0.1 day (dt) were used to estimate the times of mean pupation and emergence. The date on which eggs were collected was used to initiate the simulation for each cohort. Simulated mean times to pupation for each cohort differed little from observed mean pupation times. The differences between the observed and simulated mean pupation times (observed − simulated) were 0.7, 0.1, 0.5, 0.7, and 1.9 days for cohorts started in May, June, July, August, and September, respectively. The simulated

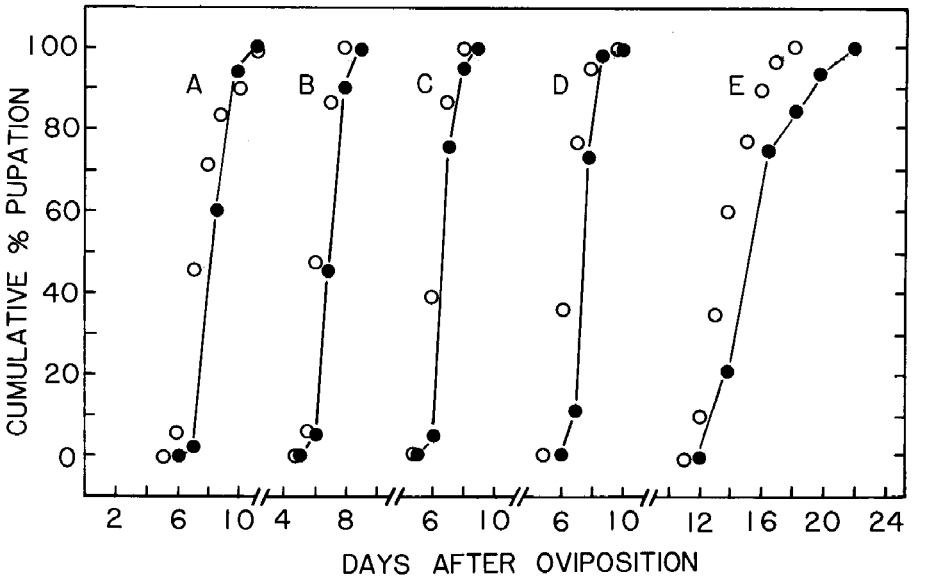

FIG. 3. Simulated (open circles) and observed (solid circles) pupation in the field. A = May cohort, B = June cohort, C = July cohort, D = August cohort, E = September cohort.

variability profiles reflected well the observed variation in pupation (Fig. 3). Simulations of adult emergence times also reflected the observed variability (Fig. 4), and the differences between the observed and simulated mean emergence times were -0.7, 0.8, 0.2, 0.9, and 2.4 days for the May, June, July, August, and September cohorts. The relationship between simulated and observed mean pupation and emergence times as determined by linear regression was as follows: observed = 0.29 + 1.05 simulated ($p < 0.01$, $r^2 = 0.98$, $\text{se}(b_1) = 0.05$). The intercept and slope were not significantly different from 0 and 1, respectively ($t = 0.45$, $p < 0.66$; $t = 1.47$, $p < 0.32$), an indication that the model functioned well in estimating mean developmental times.

As records of poultry manure bed temperatures are scanty, the possibility of using weather station data to drive the model was investigated to expand its simulation capabilities. The relationships between average daily manure temperature and daily averages of soil (5 cm depth) and air temperatures were determined by multiple linear regression. These relationships were as follows:

$$y = -18.86 + 2.89\,x - 0.04\,x^2 \quad (p < 0.01, R^2 = 0.87) \qquad [4]$$

$$y = 18.05 - 0.31\,z + 0.03\,z^2 \quad (p < 0.01, R^2 = 0.71) \qquad [5]$$

where y = mean daily manure temperature (°C), x = mean daily soil temperature (°C), and z = mean daily air temperature (°C). Temperatures in the manure bed were consistently higher than soil or air temperatures (Figs. 5 and 6); therefore, the use of Eqs. [4] and [5] to correct the weather station records to manure temperatures was necessary. The relationship between the observed and simulated means, with converted soil temperatures (Eq. [5]) used to drive the model was as follows: observed = −0.42 + 1.06 simulated ($p < 0.01$, $r^2 = 0.98$). Deviations of the simulated from the observed means ranged from −1.1 to 2.0 days. When converted air temperature records (Eq. [5]) were used to drive the model, the relationship between the observed and simulated mean developmental times became: observed = −2.05 + 1.18 simulated ($p < 0.01$, $r^2 = 0.90$). The deviations of the simulated from the observed means ranged from −2.9 to 4.4 days. Therefore, air temperature records are less satisfactory for driving models of house fly development in

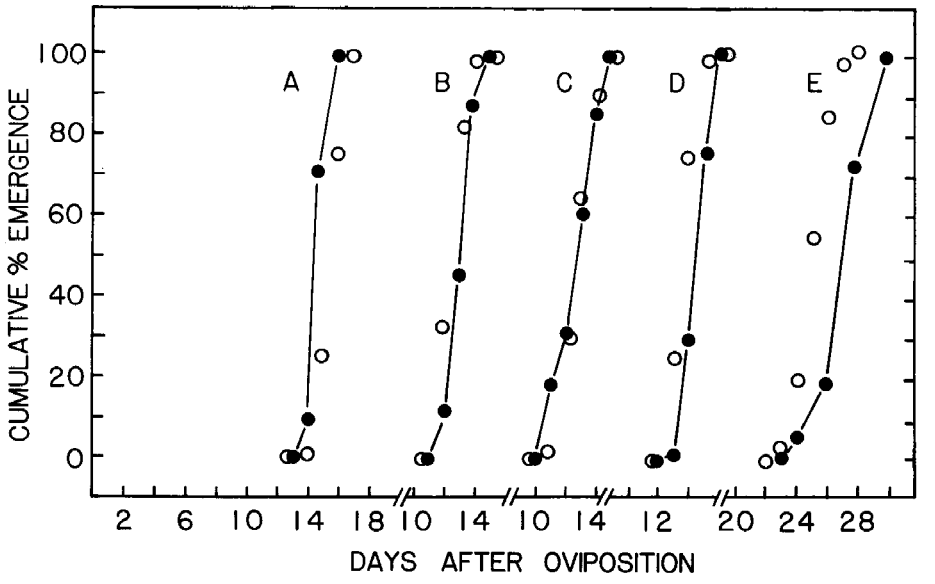

FIG. 4. Simulated (open circles) and observed (solid circles) emergence in the field. A = May cohort, B = June cohort, C = July cohort, D = August cohort, E = September cohort.

poultry manure than are actual manure temperatures or empirically corrected soil temperature records. Soil temperatures more closely resemble the temperatures in the manure bed, and although the relationship used for correction was empirical, it can serve as a useful base for temperature inputs to simulate house fly development in poultry manure.

Regardless of the source of data for temperature input, the simulated mean times were consistently higher than observed mean times, and this suggests the presence of a systematic error. One likely source of error may have arisen as a result of placement of the PVC

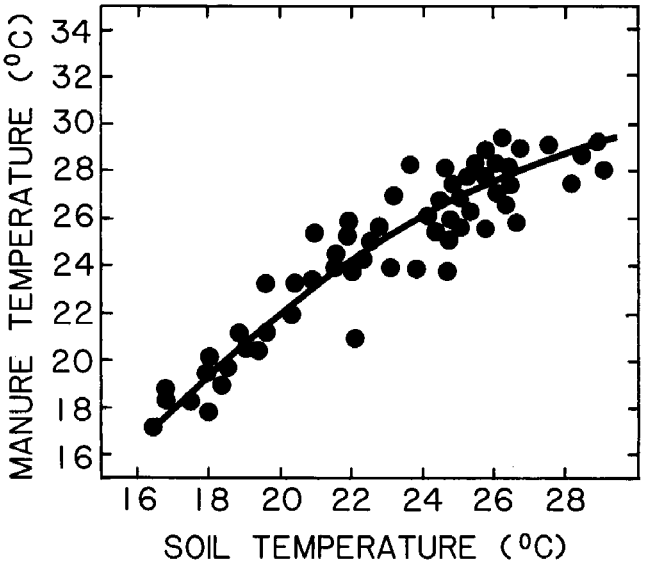

FIG. 5. Relationship between average daily soil and manure bed temperature.

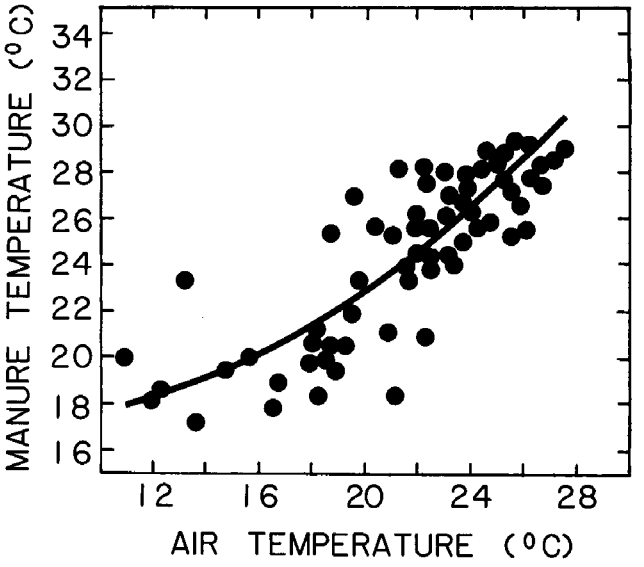

FIG. 6. Relationship between average daily air and manure bed temperature.

cylinders around the manure cups. The white PVC may have acted to reflect solar radiation and thus lowered temperatures inside the manure cups in relation to the manure bed where the temperature recordings were made. This would have resulted in prolonged developmental times for the house fly immatures within the manure cups. Temperatures were not recorded within the PVC cylinders; however, additional simulations were conducted to determine by what amount the actual temperatures in the manure cups had to differ consistently from the recorded temperatures to minimize the squared deviations of the simulated from the observed means $((\text{obs}-\text{sim})^2/\text{obs})$. This value was -0.62°C, and when it was used to correct the recorded manure temperatures, the relationship between the observed and simulated means became: observed $= -0.11 + 1.01$ simulated ($p < 0.01$, $r^2 = 0.99$). The intercept and slope of the regression are closer to 0 and 1, respectively, than for simulations that use uncorrected manure temperatures. The deviations of the simulated from the observed means when corrected temperatures were used ranged from -1.5 to 1.0 days, indicating an improvement in accuracy. This correction should not be necessary for simulating developmental times in other situations as the presence of the PVC cylinders was artificial, but it is necessary to protect the manure cups from being fouled by droppings from the caged hens above.

Other factors may cause errors in simulation, but were not incorporated into the model at this time. Temperatures to which the larvae are exposed may vary throughout the manure bed and can be affected by factors such as topographic relief, evaporative cooling, or solar radiation. Also, developmental rates may vary depending on food quantity, quality, or genetic differences between strains (Boyne *et al.* 1985).

This model will be useful for simulating development of cohorts of immature house flies in larger models of house fly population dynamics.

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