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MACMOD: A Simulation Model for *Macrocheles muscaedomesticae* (Acari: Macrochelidae) Population Dynamics and Rates of Predation on Immature House Flies (Diptera: Muscidae)

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ABSTRACT The development, population dynamics, and predation rates on the eggs and first instars of the house fly, *Musca domestica* L., of the manure-inhabiting mite, *Macrocheles muscaedomesticae* (Scopoli), were simulated in a FORTRAN77 model. Effects of mite crowding on fecundity were determined experimentally, and long-term population dynamics experiments were conducted under simulated field conditions for model development; other data used in development of the model were obtained from the literature. Features of the model include: nonlinear development, longevity, and attack rate routines for variable temperatures; mite fecundity as a function of temperature, mite crowding levels, physiological age, and prey quantity and type; attack rates as a function of mite crowding and prey quantity and type; mite survival as a function of crowding and habitat size and quality; and a house fly submodel that tracks deposition, aging, and destruction of fly immatures. Mite populations are updated by the model every 4 h. Comparison of predicted mite populations with actual populations from validation experiments were in close agreement, and improvements in agreement were achieved by empirical adjustments of mite survival as a function of changes in habitat quality over time.

KEY WORDS Insecta, arachnida, *Musca domestica*, biological control

HOUSE FLIES, *Musca domestica* L., constitute one of the primary arthropod pest problems associated with poultry production because of public nuisance concerns and the potential role of flies in the maintenance and spread of human and avian pathogens. Efforts during the past 15 yr to use biological control agents in fly integrated pest management programs (IPM) have emphasized pteromalid parasitoids of fly pupae (Olton & Legner 1975; Morgan & Patterson 1977; Rutz & Axtell 1979, 1980a,b; Rueda & Axtell 1985; Mullens et al. 1986). In recent years, there has been renewed interest in predators of fly eggs and young larvae in poultry manure (Pfeiffer & Axtell 1980; Morgan et al. 1983; Axtell & Rutz 1986; Geden et al. 1987, 1988; Geden & Axtell 1988).

The mite *Macrocheles muscaedomesticae* (Scopoli) is one of the most abundant predators of fly immatures in poultry production systems (Peck & Anderson 1969; Axtell 1970; Geden & Stoffolano 1987, 1988). The mite's short development time (about 3 d at 27°C [Filipponi & Petrelli 1967]), high attack rate (reviewed by Axtell 1969), ability to reproduce on alternative prey (Filipponi & Delupis 1963, Ito 1973), proclivity for dispersal into new fly breeding areas via phoresy (Farish & Axtell 1971), and the fact that large numbers of mites can be reared in the laboratory make *M. muscaedomesticae* a particularly attractive biocontrol agent.

Exploitation of this mite and other biocontrol agents in fly IPM programs requires a thorough understanding of the interactions of predators, parasitoids, the house fly, and other prey species with each other and with the manure habitat. Simulation models can assist in describing these interactions and ultimately can be developed into expert systems to aid in fly management decision making. Our objectives in this study were to develop a simulation model that predicts population dynamics and attack rates of the mites under constant and variable temperature regimes; takes manure quality, habitat size, and the presence of alternate prey into account; and is linked to a rudimentary fly development model that will allow the subsequent integration of other members of the manure arthropod community into a more comprehensive model.

Materials and Methods

Model Description. MACMOD was developed as an interactive computer simulation model that predicts populations of *M. muscaedomesticae* in accumulating poultry manure when provided with the following user-supplied initialization parameters: initial mite densities, immature survival, immigration and emigration of adult female mites,

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oviposition by house flies, availability and quality of alternative prey, and beginning and ending Julian days. In addition, the model provides for optional external file inputs for the age structure of the initial mite population for variable hourly house fly oviposition. All biological processes in the model are driven by temperature, which can be a single constant temperature or an external file of hourly temperatures. The default habitat size for simulations is a patch (1 m by 1 m by 5 cm) of accumulating poultry manure (50,000 cm³), on the assumption that the mites and fly eggs and first instars are restricted to the surface region of the manure. The user is allowed to specify other habitat dimensions and to allow for variable depth of usable habitat.

The model updates densities and age structure of the mites and available house fly prey at 4-h intervals and outputs mite densities and fly immatures destroyed per day to an external file named by the user. A house fly submodel tracks physiological age of house fly immatures and removes them from available prey after they develop beyond the stage of vulnerability to predation by mites (eggs and first instars). Because male mites have no substantial effect on developing house fly immatures (unpublished data), they are accounted for in the model by reducing fecundity by the user-defined sex ratio and are not tracked beyond oviposition.

Equations used in modeling individual biological relationships within the model were generally selected on the basis of providing an appropriate curve form for the data under consideration. Unless stated otherwise, no claim is made for biological significance of equation parameters.

MACMOD is written in FORTRAN77 and compiled under UNIX System V on an NCR Tower 32 supermicrocomputer. Source code listings and documentation can be obtained as hard copies or on diskette by corresponding with C. J. G. or R. E. S.

***Macrocheles muscaedomesticae* Submodel.** *Development and Longevity.* Temperature-dependent development of immature mites was determined by applying a four-parameter biophysical model of poikilotherm development with high-temperature inhibition (Schoolfield et al. 1981) to development rate data in Table 4 of Filipponi & Petrelli (1967) (shown here in Fig. 1). A computer program (Wagner et al. 1984) designed for the Statistical Analysis System (SAS Institute 1982) was used to derive parameter estimates for the model:

$$r(T) = \frac{RHO25 \cdot \frac{T}{298.15} \cdot \exp\left[\frac{HA}{1.987}\left(\frac{1}{298.15} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{HH}{1.987}\left(\frac{1}{TH} - \frac{1}{T}\right)\right]} \quad (1)$$

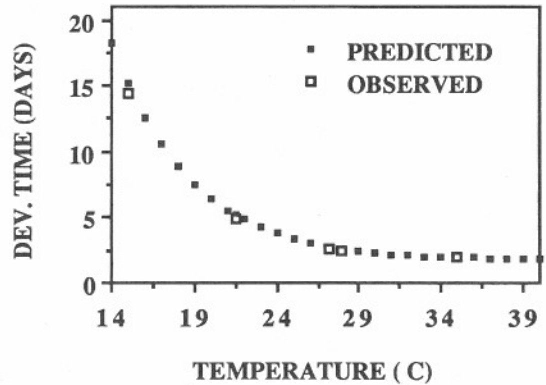

Fig. 1. Simulated (closed boxes) and actual (open boxes) development times (egg to adult) of *M. muscaedomesticae* in relation to temperature. Actual data from Filipponi & Petrelli (1967); predicted points from Equation 1.

where $r(T)$ is the development rate (days^{-1}) of immature female mites at temperature T (in °K), $RH025$ is the development rate at 25°C, HA is the enthalpy of activation of a hypothetical reaction catalyzed by a single, rate-controlling enzyme, TH is the temperature (°K) at which the rate-controlling enzyme is half-inactivated by high temperature inhibition, and HH is the change in enthalpy associated with the inactivation.

The derived parameter estimates (Table 1) were used to calculate development rates at temperatures from 1 to 45°C, then these rates (1/[days from egg to adult]) were adjusted to development per 4-h time step and placed in a single-dimension 45-address array (RATE). At the beginning of each 4-h time step in the model, hourly temperatures during the time step are used in a table lookup to determine development rate. This development is then partitioned into two immature stages, eggs and mobile immatures (larvae, protonymphs, and deutonymphs), by dividing total immature development rate by 0.1223 and 0.8777, respectively (Wade & Rodriguez 1961). This is equivalent to multiplying development times by the proportion of time spent in each of the two stages. These incremental increases in development are then added to the physiological age of the mites at the beginning of the time step. As the physiological age of the eggs and immatures enter the range of 0.8–1.3, a cumulative probability function (PHEN [Stinner et al. 1975]) calculates the proportion of individuals that will molt to the first age class (physiological age 0.0) of the next life stage (mobile immatures or adults). Densities of mites molting to the adult stage are multiplied by immature survival (maximum, 0.805 [from Table 5 of Filipponi & Petrelli 1967]).

The relationship between adult longevity and temperature was described from data in Table 2 of Filipponi & Petrelli (1967) (shown here in Fig. 2). Because mite longevity in their experiment was extraordinarily long, longevity at all temperatures

Table 1. Parameter estimates for relationships used in development of the model

Equation no.	Parameter	Parameter estimate (SE)
1	*RHO25*	0.5 (0.02)
	HA	32,641.0 (324.9)
	TH	300.0 (0.3)
	HH	36,378.0 (249.1)
3	*B1*	293.4 (166.9)
	B2	0.567 (0.327)
	B3	1.025 (0.416)
5	*B1*	1.351 (0.103)
6	*B1*	2.967 (0.446)
	B2	0.363 (0.056)
7	*B1*	7.916 (1.320)
	B2	0.365 (0.025)
8	*B1*	1.163 (0.105)
	B2	0.041 (0.003)
10	*B1*	4.058 (0.692)
	B2	0.884 (0.256)

was reduced by 0.767. This proportional reduction was determined by comparing interpolated longevity at 27°C in the above-cited experiment (27.6 d) with the mean of three other longevity figures in the same paper at 27°C (16.6, 19.6, and 18.0 d in three other experiments), and a fourth longevity figure at this temperature (24.1 d) observed by Wade & Rodriguez (1961). The mean longevity from these five experiments (21.2 d) was used as a reference standard longevity at 27°C. Longevity at temperatures 1–45°C were read off the curve, converted to amount of aging per 4-h time step (where death is physiological age 0.8–1.3), and placed in a 45-address array (ARATE). Functions QUIP and PHEN use this array to simulate mean aging during the time step and the proportion of aging individual mites that die during the time step, respectively.

Oviposition. At the beginning of each time step, the model calculates oviposition by each mite in the habitat according to the following sequence: (1) determination of maximal lifelong fecundity as a function of temperature, (2) determination of the proportion of this reproductive output that is expended during the time step as a function of physiological age at the beginning and end of the time step, (3) reduction of fecundity as a function of the quantity and quality of prey in the habitat, and (4) elimination of males from the model by the sex ratio.

The relationship between temperature and total lifelong fecundity was described from data in Table 3 of Filipponi & Petrelli (1967). No oviposition was observed in this study at temperatures <15°C

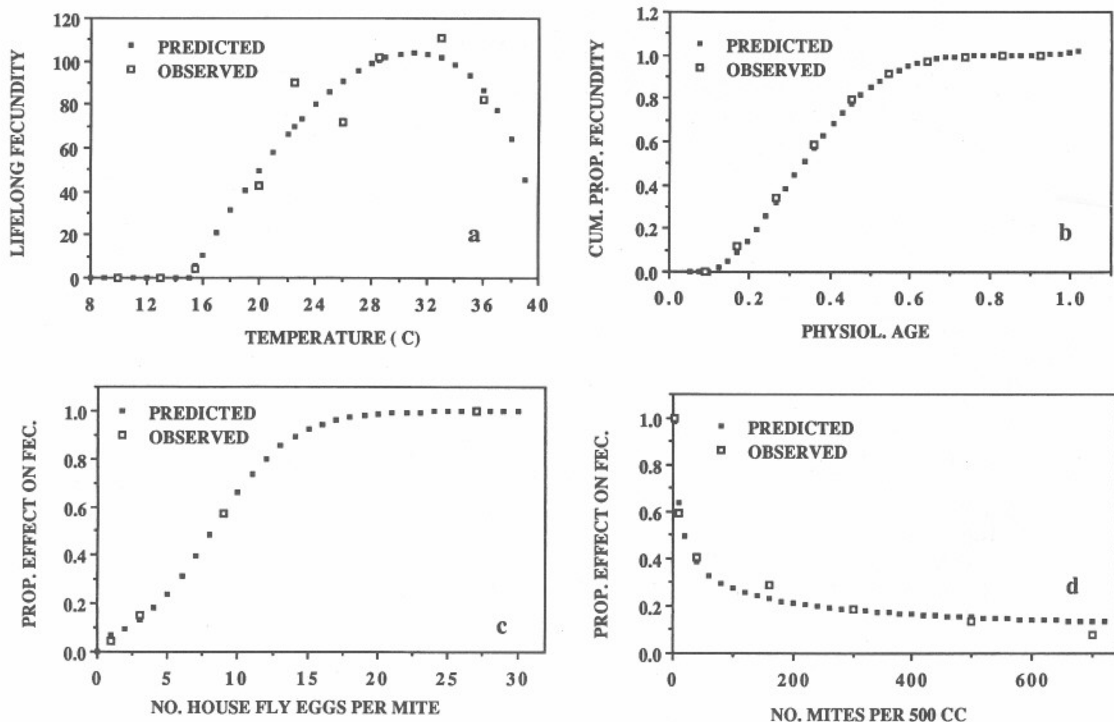

Fig. 2. Simulated (closed boxes) and actual (open boxes) fecundity of *M. muscaedomesticae*. (a) Total lifelong fecundity as a function of temperature (actual data from Filipponi & Petrelli [1967]; predicted points from Equation 3). (b) Cumulative fecundity (as a proportion) as a function of physiological age (actual data from Filipponi & Petrelli [1967]; predicted points from Equation 5). (c) Fecundity (as a proportion of maximum fecundity) as a function of house fly prey availability (actual data from Filipponi & Petrelli [1967]; predicted points from Equation 6). (d) Fecundity (as a proportion of maximum fecundity) as a function of mite crowding (actual data from Table 2; predicted points from Equation 7).

and >40°C (Fig. 2a). Temperatures were converted to a standardized variable, Z1, which takes on values from 0 to 1 as temperatures decrease from 40 to 15°C:

$$Z1 = (40 - X)/(40 - 15), \quad (2)$$

where X is the temperature in degrees Celsius. Nonlinear regression was used (Proc Nlin of the SAS [SAS Institute 1982]) to estimate parameters $B1$, $B2$, and $B3$ for:

$$Y = B1 \cdot (Z1 ** B2) \cdot ((1 - Z1) ** B3) \quad (3)$$

where Y is the total lifelong fecundity at standardized temperature Z1 of Equation 2. Lifelong fecundity was then determined at temperatures 15–40°C using the derived parameter estimates for Equation 3 (Table 1), and these values were placed in a 25-address array (FEC). At the beginning of each time step, MACMOD selects the second of the four hourly temperatures during the time step and uses the temperature as an array address in a table lookup of FEC.

Fecundity schedules throughout adult life as a function of physiological age were derived from data in Table 7 (strain 1) of Filipponi & Petrelli (1967) (shown here in Fig. 2b), with two additional assumptions: the prereproductive stage (not reported with precision in the experiment) is set at adult physiological age 0.089 (from Wade & Rodriguez 1961), and this proportion is assumed to be constant over the temperature range for mite reproduction; mean longevity in the experiment was adjusted to the reference standard of 21.2 d at 27°C, as discussed in the section on development. After making these adjustments, fecundity data were expressed as cumulative proportional egg output (0.0–1.0) as a function of physiological age during the fecund phase of adult life (0.089–0.833). Physiological age during the fecund phase was then converted to a standardized variable, Z2, which takes on values from 0 to 1:

$$Z2 = (0.833 - X)/(0.833 - 0.089) \quad (4)$$

where X is physiological age. Nonlinear regression (Proc Nlin of SAS [SAS Institute 1982]) was then used to obtain an estimate of $B1$ for:

$$Y = (1 - Z2) \cdot (B1 \cdot (Z2 ** 2)) \quad (5)$$

where Y is cumulative proportional egg output at standardized physiological age Z2 of Equation 4 (Fig. 2b). Function PHEN is used again to determine the proportion of lifelong reproduction that is expended during the time step as a function of physiological age at the beginning of the time step and the amount of aging that occurs during the time step (calculated in the temperature-dependent longevity routine described previously). This proportion is then multiplied by the total number of eggs that could be produced in a lifetime (from array FEC) to give maximal possible fecundity during the time step if the mites were provided with unlimited prey.

The relationship between house fly prey availability and fecundity was described from data in Table 1 of Filipponi & Petrelli (1967) (shown here in Fig. 2c). Because Filipponi & Petrelli (1967) used live house fly eggs, the apparent decline in fecundity at 1,000 fly eggs/mite is probably an artifact of fly larval disturbance of the substrate, and we disregarded the test results at that prey density. We also assumed that fecundity would level off at a maximum of 10 mite progeny/female per day, and converted fecundity data to represent the proportion of this maximal fecundity that was observed at the different prey levels (0–10 mite progeny per female per day, 0.0–1.0). Using Proc Nlin of SAS (SAS Institute 1982), estimates of $B1$ and $B2$ were obtained for

$$Y = 1/(1 + \exp(B1 - B2X)) \quad (6)$$

where Y is the proportion of maximum fecundity at X house fly immatures available per mite (Table 1). In the model, this proportion is multiplied by the maximum fecundity figure determined in the previous section. Determination of house fly prey availability is discussed in the section on the house fly immatures submodel.

The model also allows for the presence of alternative prey for the mites in the form of acarid mites, sphaerocerid fly larvae, or saprophytic nematodes (Ito 1977). If alternative prey are present in the habitat, the contribution to fecundity attributable to house fly immatures is first reduced by a factor that accounts for deflection of predation away from house fly immatures in the presence of the alternative prey. The predation deflection value is 1.0 (no deflection) for acarid mites, 0.43 for immatures of sphaerocerid flies, and 0.39 for saprophytic nematodes (data from Geden & Axtell 1988). Then, the contribution to fecundity attributable to alternative prey is determined by multiplying the difference between maximum possible fecundity and prey-limited fecundity by the proportional nutritional value of the alternative prey (VALNUT, supplied by the user). For the nematodes used as alternative prey in our experiments, VALNUT was estimated as 0.36, close to the value of 0.32 found in Filipponi & Petrelli (1967). No data are available at present on values of VALNUT for acarid or sphaerocerid prey. The fecundity contributions from house fly and alternative prey are then summed, and the sum is checked to ensure that it does not exceed maximum possible fecundity levels for the mites. Because data are not available on the effect of the relative abundance of alternative prey on mite fecundity or deflection of predation from house fly immatures, these factors are assumed to be constants.

After fecundity during the time step has been determined as a function of mite age, temperature, and prey type and availability, males are eliminated from the model by multiplying the final fecundity figure by the sex ratio (proportion female, 0.3657 from our crowding experiment; see below).

Table 2. Effect of mite crowding on production of new adult *M. muscaedomesticae* ($\bar{x}$ ± SE)

Initial no. ♀♀	No. new adults per ♀ after 4.5 d			Proportional decrease in reproduction	Sex ratio, proportion ♀
	♀♀	♂♂	Total		
3	4.00 ± 1.03	7.83 ± 1.21	11.83 ± 1.54	1.00	0.305 ± 0.067
10	2.14 ± 0.32	4.90 ± 0.52	7.04 ± 0.70	0.595	0.302 ± 0.033
40	1.67 ± 0.36	3.13 ± 0.26	4.80 ± 0.60	0.406	0.308 ± 0.036
160	1.78 ± 0.54	1.67 ± 0.42	3.44 ± 0.95	0.291	0.478 ± 0.050
300	1.01 ± 0.32	1.28 ± 0.26	2.28 ± 0.50	0.193	0.399 ± 0.072
500	0.75 ± 0.23	0.87 ± 0.10	1.62 ± 0.27	0.137	0.418 ± 0.066
700	0.34 ± 0.07	0.60 ± 0.06	0.95 ± 0.12	0.080	0.350 ± 0.033

Effect of Mite Crowding on Fecundity. An experiment was conducted to evaluate the effect of crowding levels on net recruitment of new adult female mites into the population. Mites for the tests were collected from manure in a North Carolina poultry house and cultured as described by Geden et al. (1988). Three days before introducing the mites, 500 cm³ of a 1:1 mixture of poultry manure and prepared (dry medium, brewers yeast and water) fly larval rearing medium (CSMA medium, Ralston Purina Company, St. Louis, Mo.) was added to each of 14 screen-topped plastic containers (12 cm high, 16 cm diameter, about 2 liters volume). The medium ranged in depth from 1 to 5.7 cm. The medium in each container was inoculated with 250,000 to 500,000 *Diplogasteroides* sp. nematodes (from a culture that was originally isolated from poultry manure) as a supplementary food for the mites (Geden & Axtell 1988). Three days later, adult female mites of undetermined age were added at 3, 10, 40, 160, 300, 500, and 700 mites per container (two containers per mite density). Frozen house fly eggs (17,000 per container) were added to the containers daily for 5 d (at 27°C), then the mites were extracted through Tullgren funnels into 80% ethanol and counted. The experiment was replicated on three separate occasions for a total of six observations per mite density treatment.

Assuming no mortality among the founding populations, the data were expressed as new adult individuals produced per initial female mite (Table 2). Crowding effects were then expressed as a proportional reduction in the maximum production of new adults, and parameter estimates (Proc Nlin of SAS [SAS Institute 1982]) were obtained (Fig. 2d) for

$$Y = B1 \cdot (X ** (- B2)) \qquad (7)$$

where Y is the proportional reduction of production of new adult mites and X is the initial number of mites present, expressed as the number of females present in the model's default habitat size (1 m² by 5 cm deep). In the model, this crowding effect is calculated during each 4-h time step (after adjusting for user-defined changes in the habitat size) and applied to mite fecundity.

Destruction of House Fly Immatures. Destruction of house fly immatures by the mites is calculated during each 4-h time step according to the following sequences: (1) determination of maximum daily predation rates (number of fly immatures destroyed per mite per day) as a function of the availability of house fly immatures at 27°C; (2) adjustment to account for temperature effects; (3) reduction in predation because of mite crowding; (4) reduction in predation because of the presence of alternative prey, if such prey are present; and (5) conversion of the final predation rate into mite-induced mortality of the house fly prey during the time step.

The relationship between availability of house fly immatures and predation rates under conditions where mite crowding was inconsequential was described from data in Table 1 of Geden & Axtell (1988), using only the results of experiments involving five mites per assay cup (Fig. 3a). Nonlinear regression (Proc Nlin of SAS [SAS Institute 1982]) was used to obtain estimates of $B1$ and $B2$ for Holling's (1959) disc equation:

$$Y = (B1 \cdot X)/(1 + [B1 \cdot B2 \cdot X]) \qquad (8)$$

where Y is the number of house fly immatures destroyed per mite per day at 27°C when presented with X house fly immatures per mite (Table 1).

Temperature effects on predation were accounted for by using the temperature-dependent predation rate model of Geden & Axtell (1988) to estimate predation rates at temperatures from 1 to 45°C. These rates were then divided by the estimate for 27°C (18.8 fly immatures destroyed per mite per day) and the resulting proportions placed in a 45-address array (PRTEMP). In the model, function QUIP is used as a table look-up function to PRTEMP to access the proportional temperature effects at each of the 4 h during the time step using the hourly temperatures as array addresses. The resulting mean proportion is multiplied by the predation rate determined in the previous section.

Crowding effects on predation were described from pooled data from all mite experiments that were conducted at 27°C in Geden et al. (1988) and Geden & Axtell (1988). From these data, we made the following assumptions: that mite crowding does not have a significant effect until densities reach 10 mites per assay cup (about 3,000 mites per default habitat size in the model), with no additional effect at densities above 40 mites (about 12,000 per model habitat); and using the observed maximum

and minimum predation rates (21.3 and 10.0 fly immatures destroyed per mite, respectively), that the proportional effect of mite interference could range only from 0.4695 (maximum interference) to 1.0 (no interference) (Fig. 3b). Mite densities were converted to a new variable, Z3, which takes on values from 0 to 1:

$$Z3 = (12{,}000 - X)/(12{,}000 - 3{,}000) \quad (9)$$

where X is the number of mites per standardized habitat of 1 m by 1 m by 5 cm. Nonlinear regression (Proc Nlin of SAS [SAS Institute 1982]) was used to obtain estimates for $B1$ and $B2$ for:

$$Y = 0.4695 + 0.5305 \cdot (Z3 ** (B1 \cdot (1 - Z3) ** B2)) \quad (10)$$

where Y is the proportional reduction of the predation rate attributable to mite crowding at standardized density Z3 of Equation 9 (Table 1). In the model, this proportion is multiplied by the predation rate determined in the previous section.

The effect of the presence of alternative prey (defined by the model user) on predation rates is accounted for in the model by multiplying the predation rate by the deflection constants described in the fecundity section.

The resulting daily rate of house fly destruction per individual mite is multiplied by the number of mites in the habitat (total destruction of fly immatures per day) and divided by the number of fly immatures present (fly mortality per day). This mortality is then converted to survival of house fly immatures during the 4-h time step:

$$Y = (1 - X) ** 0.1667 \quad (11)$$

where Y is survival of fly immatures during the time step and X is mite-induced mortality during 1 d. Survival of fly immatures during the time step is passed to the house fly immature submodel, described below.

Musca domestica **Immatures Submodel.** The house fly submodel tracks the age structure and densities of house fly immatures as a function of oviposition rates (supplied by the user), temperature, and mortality from predation (passed from the mite submodel). Fly immatures are removed from the model when they have developed beyond the stage of vulnerability to predation. No attempt is made to model adult flies. During each 4-h time step, the model updates the population of fly immatures in the simulated habitats according to the following sequences: (1) application of mite-induced mortality, (2) development of surviving fly immatures as a function of temperature, and (3) deposition of newly laid fly eggs into the habitat.

Mortality from mites is passed from the mite submodel as fly survival (as a proportion) during the time step. This proportional survival is then multiplied by the densities of fly immatures in all vulnerable age classes (defined below).

The relationship between temperature and development of fly immatures was described by using the model of Lysyk & Axtell (1987) to estimate total fly development (egg to adult) at temperatures from 2 to 45°C. On the assumption that house fly immatures are vulnerable to predation by the mites for about 1 d at 27°C (i.e., eggs and first instars), and that this vulnerability period represents a constant proportion of total development at the temperatures normally experienced by the flies (0.0772 [Geden & Axtell 1988]), development times from oviposition to the end of vulnerability period were determined by multiplying total development time by 0.0772 for temperatures from 1 to 45°C. These times were converted to development per 4-h time step and placed in a 45-address array (FLYDEV). Function QUIP is called by the model during each time step as a table look-up function to FLYDEV to determine mean development using hourly temperatures as array addresses. This developmental increment is added to the physiological age of the fly immatures in the habitat, and immatures are removed when they reach physiological age 1.0 (the end of the vulnerability period).

New fly inputs into the habitat are calculated during each time step by summing hourly oviposition as specified by the user and assigning physiological age 0.0 to these newly deposited eggs. At the end of the time step, total numbers of fly immatures in each physiological age class are totalled,

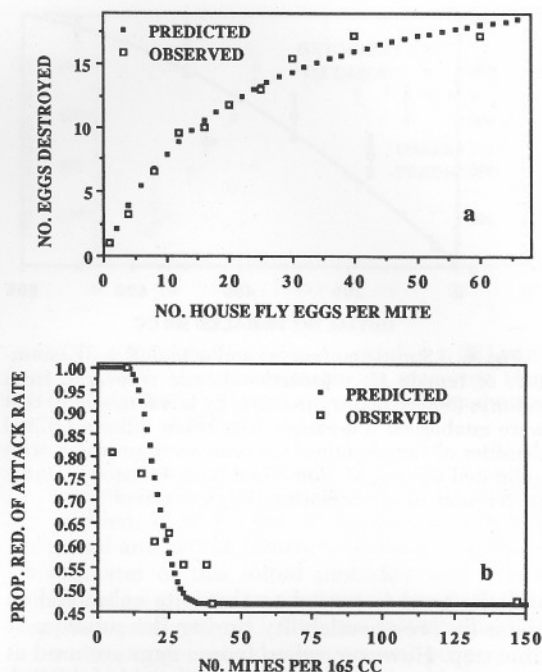

Fig. 3. Simulated (closed boxes) and actual (open boxes) attack rates of female *M. muscaedomesticae* on house fly immatures. (a) Attack rate as a function of fly egg availability (actual data from Geden & Axtell [1988]; predicted points from Equation 8). (b) Attack rate as a function of mite crowding (actual data from Geden et al. [1988]; predicted points from Equation 10).

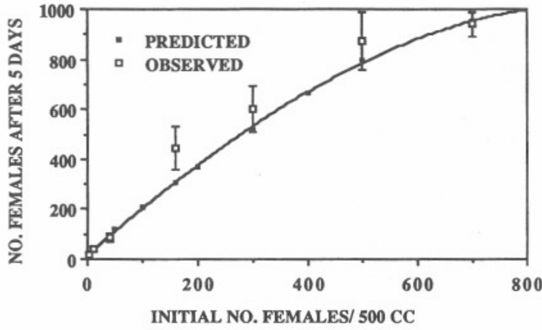

Fig. 4. Simulated (curve) and actual ($\bar{x} \pm$ SE) numbers of female *M. muscaedomesticae* recovered from cultures (500 cc poultry manure–fly larval medium) that were established 5 d earlier with seven different initial densities of female mites. Cultures were provided with unlimited fly egg (*M. domestica*) and nematode (*Diplogasteroides* sp.) prey during the experiment.

and the total is passed to the mite submodel as house fly prey availability during the subsequent time step. However, when frozen eggs are used as prey, it is assumed that they are available for 2.2 d.

Validation Experiments. Three population dynamics experiments were conducted using identical protocols except for the temperature regimes, which were constant, moderately variable, and highly variable. Tests at constant temperatures were conducted in a rearing room maintained at a constant temperature of 27 ± 0.5°C. A moderately variable temperature regime was achieved by holding cultures in a room with a modest degree of temperature regulation. Tests at highly variable temperatures were conducted by holding mite cultures in an open-sided poultry house in Wake County, N. Car., under spring–summer conditions (18 May to 16 July 1987). Temperatures in the first two temperature treatments were monitored by continuously recording thermographs that were placed in the rooms where the cultures were held. Independent measurements of air and media temperatures indicated that media temperatures averaged 1–2°C higher than the monitored air temperatures. Therefore, 1°C was added to these air temperatures in subsequent simulations. Hourly temperatures in the cultures held in the poultry house were monitored by thermocouple probes that lead from the center of the medium in two sample cultures to a Speedomax G (Leeds & Northrup Company, Philadelphia, Pa.) recorder.

In each experiment, 500 cm³ of a 1:1 (wt/wt) mixture of prepared fly larval rearing medium: poultry manure was placed in each of 32 screen-topped plastic containers (12 cm high, 16 cm diameter; about 2 liters) and inoculated with *Diplogasteroides* sp. nematodes as described in the mite crowding experiment. One day later, 25 female mites and 1,000 frozen house fly eggs were added to each container. Cultures were subsequently given frozen fly eggs (1,000 per feeding during the first 2 wk, 2,000 per feeding thereafter), 25 cm³ of fresh manure–fly larval medium, and about 10 cm³ of a nematode-rich medium 3 d/wk for the next 8 wk. Fly eggs were generally frozen within 6 h of deposition; nematode-rich media were prepared as described in Geden & Axtell (1988).

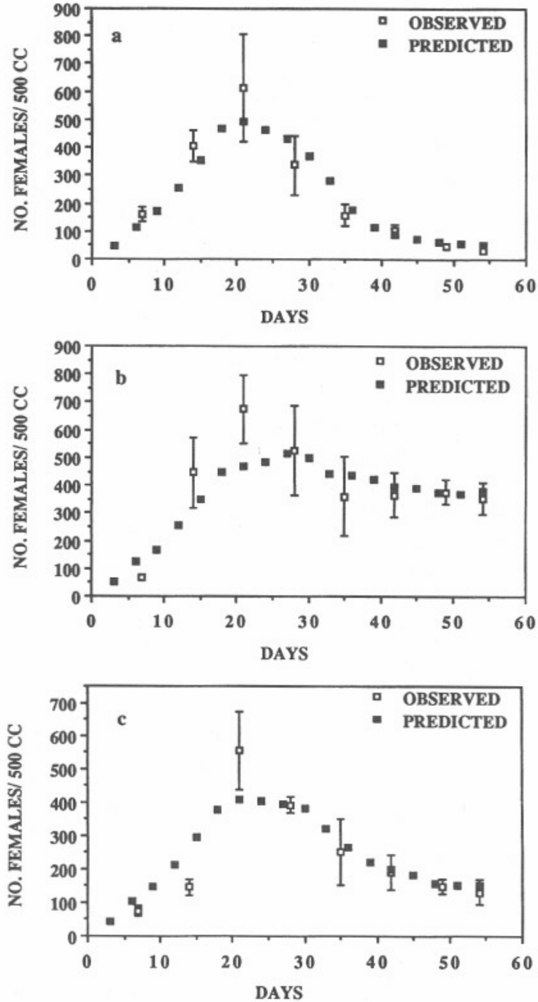

Fig. 5. Simulated (curve) and actual ($\bar{x} \pm$ SE) numbers of female *M. muscaedomesticae* recovered from cultures (500 cc of poultry manure–fly larval medium) during an 8-wk population dynamics experiment under constant (a), moderately variable (b), and highly variable (c) temperature regimes. Cultures were started with 20 female mites each and provided with fly egg and nematode prey using prey dose rates and schedules as described in the text.

Mite predation on house fly eggs was not monitored directly, but the close relationship between prey consumption and fecundity within the model allowed us to monitor the precision of the attack rate routines indirectly by measuring changes in mite population sizes. Four cultures per week during the 8 wk after establishment of the cultures

were selected at random and extracted through Tullgren funnels into 80% ethanol. Counts were made of all adult mites in each culture.

Initial simulations of the constant temperature "validation" revealed that additional assumptions relating to longer term dynamics were necessary. Therefore the following relationships were added to the model.

First, because cannibalism in *Macrocheles* has been documented (Axtell 1969), it was assumed that immature mortality from adult predation (Y) is directly proportional to adult density per 50,000 cc (X_1), fly predation rate (X_2), and the ratio of immature mites to total prey (fly prey + immature mites, X_3), taking the form:

$$Y = B \cdot X_1 \cdot X_2 \cdot X_3 \quad (11)$$

where B was estimated as 0.000015 by grid search over the parameter space, using the constant-temperature "validation" data.

Second, it was assumed that proportional adult longevity (Y) decreases with increasing adult density/cc (X):

$$Y = 1.0/(1.0 + B \cdot \exp(X ** 2)) \quad (12)$$

where B was estimated as 0.025, as described above.

Finally, it was obvious during the validation experiments that habitat "quality" decreased significantly after approximately 3 wk. It was assumed that this affected immature survival. The simplest approach, a ramp function, was incorporated to allow user control. Initial survival is set at optimum, 0.805 (Filipponi & Petrelli 1967), for a selected number of days (for our experiments, 19 d). After this time, survival is decreased by a daily amount until some lower level is reached; both values are supplied by the user because they are habitat dependent.

Results and Discussion

Because additional density effects were added, it is appropriate to compare complete model simulations with data from the crowding study to demonstrate that results from the model in whole are consistent with this earlier experiment (Fig. 4). For the same reason, the constant temperature "validation" test does not constitute validation, but it is presented here to demonstrate the "goodness-of-fit" of the model (Fig. 5a).

For both experiments, the simulations and data are in agreement. For the constant temperature "validation," habitat-related immature survival after 19 d was allowed to decrease by 0.40 to a minimum of 0.14.

Simulations for moderately and highly varying temperatures (Fig. 5b and c) required a change in the final habitat-related immature survival only (0.50 and 0.28, respectively). For both simulations, simulated mite densities during the first 1–2 wk were higher than actual densities. However, the model assumes no initial adult mortality during

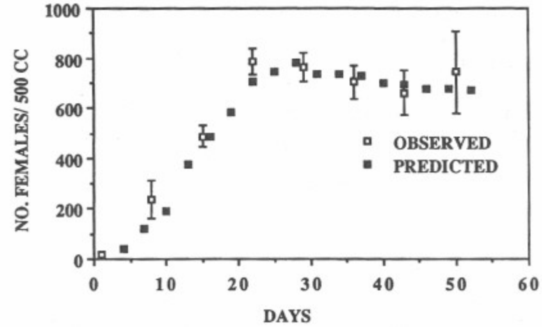

Fig. 6. Simulated (curve) and actual ($\bar{x} \pm$ SE) numbers of female *M. muscaedomesticae* recovered from cultures (825–840 cc) during a 7-wk population dynamics experiment at 27°C.

transfer of mites. When various initial mortalities are applied, it is possible to force agreement of simulated and actual densities. Given that we have no estimates of this initial mortality and that it would not be a factor in continuing populations in a poultry production facility, we felt that adding this to the model would serve no real purpose.

Additional validation was made possible by comparison of simulations with unpublished data obtained in 1967 (unpublished data). These experiments were conducted in a manner similar to our constant temperature "validation" experiment, except that mites were provided with 20,000 frozen fly eggs, three times per week, with media volume equal to 825–840 cc. Again, simulated and actual results are in close agreement (Fig. 6). However, for these simulations, it was necessary to change the initial time of habitat degradation to day 13, with a final immature survival of 0.27.

It is obvious that more information is needed on what constitutes "habitat suitability." Our model does not consider factors such as moisture or other natural enemies, except through user-defined immature survival. In spite of this, simulated and actual mite densities are in agreement, and the *Macrocheles* model is sufficiently complete to be coupled with a fly population dynamics model currently under development.

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