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Biocontrol of Arthropods Affecting Livestock and Poultry

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19. Computer Simulation Modeling of Fly Management

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Management of arthropod pests of livestock and poultry is a complex process requiring a mixture of control strategies according to the species of pests and the different types of animal production systems (Axtell 1981, 1986a). Computer simulation models are needed to effectively deal with these complexities. Integrated pest management (IPM) is a part of the total livestock management system; the design and implementation of management techniques requires analysis of the pest population dynamics, among other factors. Critical to practical IPM is pest population monitoring and the use of pest population predictive models together with management predictive models to elucidate the appropriate management actions (Figure 1).

Biocontrol is a major management option which is becoming more important as the application of IPM principles increases. Greater use of biocontrol is also encouraged by the trend to low-input sustainable agriculture (LISA) along with desires to minimize the use of chemicals in animal production systems. Population dynamics models of biocontrol agents are as important as models of the pests themselves in the development of livestock and poultry IPM programs.

Computer simulation models of pest management in livestock and poultry production are needed to organize and visualize the complexities and interactions which are too numerous and subtle to be comprehended without assistance. Further, models allow predictions of the consequences of environmental and management changes. The validity of a simulation model, however, depends on the accurate conceptualization of the system, the reliability of the input data, and the proper mathematical expressions for components of the model and for manipulation of data. It is inevitable that lack of data and knowledge on relationships requires

Figure 1. Diagram of the major components in the development and operation of an IPM program for livestock (including poultry) production systems. Adapted from Axtell (1981, 1986a).

the use of assumptions in the modeling effort. Such assumptions must be reasonable and explicit.

Filth fly management, among the pest problems of livestock and poultry production, is amenable to computer simulation modeling (Weidhaas 1986). The need is substantial due to the complex mixture of biological, cultural, and chemical methods required for fly management. Further, fly management is a problem common to all confined-animal production systems throughout the world. These systems present manure-management problems and an ideal habitat for fly production. Because confined-animal production systems are artificial ecosystems, designed and managed by humans, they are especially adaptable to the application of the IPM concept and to the use of pest management modeling. The increase in confined systems for dairy, swine, and poultry has intensified the filth fly problem, with the house fly, *Musca domestica*, being the most abundant pest species. Therefore, we have chosen to conceptualize and model house fly management. Our approach is based on the situation in caged poultry production, but with modifications is applicable to fly management in other types of confined-animal production systems as well as to other fly species.

MODELING CONCEPT

In our overall concept of house fly management, as shown in Figure 2, the population of adult flies in a confined-animal facility is variable due to the following major factors: 1) immigration/emigration, 2) habitat conditions (temperature and moisture) in the house and in the accumulated manure, 3) the fly management practices used, including cultural (mainly timing and methods of manure handling and disposal), biological (enhancement of the population of natural enemies), and chemical (type and application methods), and 4) the populations of natural enemies in the habitat. The natural enemies or "biocontrol agents" include predators, parasites, pathogens, and competitors. In poultry houses, predators (*Macrocheles* mites and *Carcinops* beetles) and pteromalid parasites (*Muscidifurax* and *Spalangia*) are especially important. There are likely to be considerable interactions among the species of natural enemies and among the other components in the fly management conceptualization. Likewise, the impacts of management strategies are interrelated. Further, the habitat conditions in the housing results from modifications of the ambient temperature and moisture

Figure 2. Major components in a model of house fly management for confined-animal production systems.

by the interacting impacts of animal type and management, type of housing, and system of manure handling and disposal. Figure 2 conveys the major relationships, without inclusion of all possible interactions and interrelationships, in order to provide a practical framework for fly management modeling.

Biological Components. Understanding the biology and behavior of the house fly and its natural enemies is basic to developing a realistic fly management model. Identification and quantification of the sources of fly mortality (in all life stages) are critical to the elucidation of the fly population dynamics. Further details and references on the ecology and management of the house fly and its natural enemies are provided by Axtell 1986b,c; Axtell and Arends 1990; Patterson and Rutz 1986; Rueda and Axtell 1985. Briefly, some of the major considerations are as follows.

The house fly life cycle (Figure 3) in poultry manure requires six to ten days in a warm house. The eggs are deposited in batches in manure that has the most attractive odor and moisture level. Eggs hatch within a day to first-instar larvae (L1), which undergo development and molting through two additional instars (L2, L3). Larval stages move through the manure, though usually not very deeply owing to the anaerobic conditions. When there is no alternative, the larvae can tolerate rather liquid conditions. The third-instar larva develops into the pupal stage within its thickened integument (puparium). Pupation occurs in the drier portions of the manure near the surface and edges. An adult fly emerges from the puparium and disperses after hardening of the cuticle. It often remains in the vicinity if the habitat is conducive to feeding, mating, and oviposition. Adult flies spend considerable time on the surface of the manure in the daytime, but at night rest on surfaces, mostly in the upper parts of the poultry house.

Other species of flies (as well as certain beetles) may compete with development of the house fly in the manure (Axtell and Arends 1990). The soldier fly, *Hermetia illucens*, has robust larvae which churn the manure and physically render the habitat less suitable for the house fly. Larvae of *Ophyra* spp. flies occupy the same manure microhabitats as the house fly and also may prey on the house fly larvae. Under certain conditions, *Ophyra* flies may become the dominant species in poultry houses. It is unclear how much this may be due to competition versus predation on the house fly. Several species of *Fannia* larvae develop in the manure, occasionally become quite abundant, and conceivably may be competitors. In most circumstances, however, there appears to be

Figure 3. Diagram of house fly, *Musca domestica*, life cycle and factors affecting population size.

little evidence of house fly development being seriously impeded by competitors in the poultry manure.

Predators and parasites of the house fly are major suppressors of fly populations (Axtell and Rutz 1986). The most abundant predators on eggs and first-instar larvae of the house fly (and other muscids) are the mite, *Macrocheles muscaedomesticae*, and the histereid beetle, *Carcinops pumilio* (Geden and Axtell 1988, Geden et al. 1988). Mite and beetle predators are most abundant and effective in manure that is not too wet and accumulates in a distinct pile. These predators are most abundant at or near the crest and slightly beneath the surface of the pile, in the areas most likely to have house fly eggs and first-instar larvae. Mites develop rapidly (Figure 4), with only two to three days required under warm favorable conditions to complete the life-cycle from egg to adult (with intermediate larva, protonymph, and deutonymph stages). Most predation by mites is by the adult feeding on house fly eggs and first-instar larvae, with a preference for the eggs. Alternate foods for the adult and earlier life stages are nematodes, acarid mites, and other dipterous eggs and small larvae. Adult mites exhibit phoresy, with the house fly the most common carrier. This phoresy is regulated by olfactory responses to the flies and the aging manure, resulting in dispersal to the most favorable fly breeding areas.

The predator *C. pumilio* has a longer life cycle (Figure 5), requiring about forty days for development from egg to adult (with two intermediate larval stages and a pupal stage) in the warm conditions of a poultry house. Adults have a mean longevity of almost 100 days at 27°C. Adults (and to a much lesser extent, larvae) feed on eggs and first-instar larvae of the house fly. Alternate foods are eggs and small larvae of other Diptera in the manure. Beetles require an undisturbed site in the manure for normal pupation.

Hymenopterous parasites (Pteromalidae) are a major factor in destroying house fly pupae in poultry facilities (as well as in other livestock operations). Several species in the genera *Muscidifurax* and *Spalangia* are common (Rueda and Axtell 1985). Intergeneric differences in searching abilities and competitiveness exist. All species have the same basic life cycle (Figure 6) with development from egg to adult on the fly pupae (within the puparium) requiring about three weeks under poultry house conditions. One adult parasite emerges from each puparium and destroys the fly pupa during development. Adult parasites destroy additional flies by host feeding. Development on the fly pupae is through three larval

Figure 4. Diagram of macrochelid mite predator, *Macrocheles muscaedomesticae*, life cycle and factors affecting population size.

Figure 5. Diagram of histerid beetle predator, *Carcinops pumilio*, life cycle and factors affecting population size.

Figure 6. Diagram of pteromalid parasite (*Muscidifurax* and *Spalangia*) life cycle and factors affecting population size.

instars and a pupal stage. There are species of fly parasites in other genera that differ in their biology, particularly *Nasonia*, which develops several parasites on one fly pupa and *Tachinaephagus* (Encyrtidae), which parasitizes fly larvae. These genera of parasites are generally considered of less importance in suppressing house fly populations.

Fly pathogens have received less attention as suppressors of house fly populations in poultry houses. The fungus *Entomophthora muscae* is a common pathogen of adult flies (Mullens et al. 1987). With more research, it may become obvious that the population dynamics of it, and perhaps other pathogens, should be modeled. Since pathogens undoubtedly have some effect on fly mortality, they need to be included in the conceptualization of a fly management model.

Physical Components. Populations of the house fly and its natural enemies are temperature-dependent (Ables and Shepard 1976, Ables et al. 1976, Lysyk and Axtell 1987, Weidhaas et al. 1977). Although the temperature range in a poultry house is restricted to maintain suitable poultry management conditions, there is still considerable variation, which affects the arthropod population dynamics. Air temperature obviously directly affects the adult fly and parasite activities. Manure temperature is more directly related to immature stages of the house fly and parasites, and to all stages of the predaceous mites and beetles. Because it is more practical to routinely monitor air temperature, it is important to relate manure temperatures to air temperatures.

Moisture is also a major factor affecting populations of the house fly and its natural enemies (Fatchurochim et al. 1989). The manure moisture level influences the degree of oviposition by house flies and the survival of immature stages of the fly. It affects the survival of all stages of the predaceous mites and beetles. Manure that is very wet is unsuitable for survival of mites and beetles, while very dry manure does not support immature stages of the house fly. Air moisture (relative humidity) affects the rate of manure drying, and the activity and survival of adult flies and parasites. Relating moisture, both manure and air, to arthropod population dynamics is extremely difficult and only approximations and crude estimates are possible at this time.

Management Components. Management approaches to house fly (and other filth fly) control in poultry production are empirically understood. A judicious meshing of cultural, biological, and chemical techniques, along with appropriate monitoring of the fly populations are required (Axtell 1986a, Lysyk and Axtell

1986a,b). Although details vary with the type of housing, manure handling system, and climatic situation, the principles of fly management are universal. Cultural methods are primary and basically involve keeping the manure dry in order to discourage fly development and to encourage a heterogeneous population of predators and parasites that occur naturally and provide biological control of the fly population. Chemical control measures are supplements to cultural and biological methods. Since most insecticides that are effective against the house fly are also quite toxic to the predators and parasites, routine use of larvicides in the poultry manure is not compatible with maintenance of the biological control agents. Routine adulticides may be detrimental to the populations of adult parasites. Some selectivity is obtained by limited spot treatment of manure, residual surface treatments of areas where adult flies rest in the upper parts of the structure, and fly toxicant-baits. Timing of these control measures is facilitated by monitoring adult fly populations with standardized techniques, such as spot cards and baited jug-traps.

Submodels. The overall conceptualization of house fly management requires relating the above considerations and others, in a scheme with several interacting submodels. Thus we include submodels for: the house fly (FLYMOD), mite predators (MACMOD), beetle predators (CARMOD), and pteromalid parasites (PARMOD), based on the conceptualizations presented in Figures 3, 4, 5, and 6, respectively.

These population dynamics models are temperature-dependent and the relevant temperature will be that of the manure and/or air as described previously. Several alternatives for relating manure to air temperature are being developed by Wilhoit (personal comm.). Linkage of these submodels provides a base for input of the estimated impacts of various management strategies such as the timing and methods of manure removal, pesticide applications, and parasite and/or predator augmentation. Techniques for modeling this fly management scheme are available based on modeling efforts with other pest management problems, but selection of the most appropriate techniques and adapting them to this particular situation are critical.

MODELING METHODS

In modeling the population dynamics of the house fly, its predators and parasites, we have used a modification of the approach described by Wilkerson et al. (1986). This same paradigm is used for each of the species involved, so that many of the same subroutines are called by the different species' population generator ("bookkeeper"). This generator is a cohort "bookkeeper," using two arrays for each stage. The elements of the first array contain the densities per unit area, D , of individuals which entered that stage 0, 1, 2, 3, . . . N time units ago (Figure. 7). N is the maximum number of time units an individual can remain in a given stage. Summing the elements gives the total density of individuals presently in the given stage. Within a stage, at the beginning of a new time step, individuals in a given element are multiplied by survival during that time and moved to the next ("older") element.

$$D(j,t+1) = D(j,t) * S(j, \Delta t) \quad \text{Eq. (1)}$$

where: $D(j,t)$ = density of individuals in stage j , which entered that stage t time units ago.

$S(j, \Delta t)$ = survival of individuals in stage j during time Δt .

The second array contains elements, A , representing the median physiological age of the corresponding D element. Within a stage, at the beginning of a new time step, the median development rate, R , occurring during the time step is calculated, added to the previous physiological age, and the sum moved to the next element.

$$A(j,t+1) = A(j,t) + (R * \Delta t) \quad \text{Eq. (2)}$$

where: $A(j,t)$ = median physiological age of individuals in stage j who are t time units old chronologically.

Δt = time step.

The developmental increment, Q , which equals $R * \Delta t$, (and, thus, physiological age) is temperature dependent. We use median (50%) development rate rather than the mean rate because of the way in which developmental variability is modeled (see below). For virtually all poikilotherms, development rate is a nonlinear function

Figure 7. Density (D) and physiological age (A) compartmental flow used in population model. Q is developmental increment and S is survival. See text for explanation.

of temperature (Sharpe and DeMichele 1977, Wagner et al. 1984), although many other models have assumed the relationship to be linear (i.e., day-degree models). As an example, Figure 8 shows the median development rate, R , versus temperature, T , for *Spalangia endius* (Mann et al. 1990b), fit with the Sharpe-DeMichele (1977) model.

$$R = \frac{b_1 * \frac{T}{298.15} * \exp \left[\frac{-b_2}{1.987} \left(\frac{1}{298.15} - \frac{1}{T} \right) \right]}{1 + \exp \left[\frac{b_3}{1.987} \left(\frac{1}{b_4} - \frac{1}{T} \right) \right]} \quad \text{Eq. (3)}$$

where: R = median rate of development.

T = temperature (degrees Kelvin).

b_1, b_2, b_3, b_4 = estimated parameters.

Since this submodel is computationally expensive, in our population models we simply have an array of the rates (previously calculated) for temperatures from 1 to 45°C.

Median physiological age at time t , A_t , is simply the sum of the ratio over time. For a cohort beginning development at time = 0.

$$A_t = \sum_{i=0}^t R * \Delta t \quad \text{Eq. (4)}$$

where: A_t = median physiological age at time t .

R = rate of development for temperature at time i ,
from Eq. (3)

Δt = time step

Eq. (4) is the equivalent of Eq. (2), taken over multiple time steps. It is important to recognize that for each median rate, there is an entire distribution of development times (Figure 9) for any temperature. If these distributions are plotted against median physiological age from Eq. 4, then all of these distributions collapse to a single distribution (Figure 10), dependent on median

Figure 8. Median development rate as a function of temperature for *Spalangia endius*.

Figure 9. Cumulative proportion of individuals developed to adult for *Spalangia endius* for different temperatures.

Figure 10. Cumulative proportion of individuals developed to adult for *Spalangia endius* as a function of physiological age, estimated from Eqs. 3 and 4.

physiological time. This "same-shape" assumption has been tested and is valid for all of the species involved in our efforts. Note that at a median physiological age of 1.0, 50% of the individuals have developed to the next stage. Given this, it is possible to calculate the proportion of individuals completing development, G , as a function of physiological age during time Δt , using the algorithm of Stinner et al. (1975):

$$G(j, \Delta t) = (P(j, t+\Delta t) - P(j, t)) \quad \text{Eq. (5)}$$

where: $P(j, t)$ = cumulative proportion of stage j individuals completing development by time t .

$$P(t) = \frac{kz^2}{(1 - z)}$$

$$z = (\max(j) - A(j, t)) / (\max(j) - \min(j))$$

$\max(j)$ = median physiological age at which the slowest individual in stage j develops to the next stage, generally 1.25-1.35.

$\min(j)$ = median physiological age at which the fastest individual in stage j develops to the next stage, generally 0.7-0.8.

k = empirical constant, calculated from $\max(j)$ and $\min(j)$ (see Stinner et al. 1975).

For immature *S. endius* development in our example, $\max(1)$, $\min(1)$, and k are 1.3, 0.8, and 2.1013, respectively.

In the models, transfer (development) to the next stage is based on the above, with all individuals entering the O element of the next stage density array, with their physiological age reset to zero. To account for individuals already molted, G must be divided by the proportion of individuals left $(1 - P(j, t))$:

$$D(j+1,0) = \sum_{t=1}^N D(j,t) * [G(j, \Delta t)/(1 - P(j,t))] \text{ Eq. (6)}$$

For example, with *S. endius* (Figure 8), the median rate of development, R_d , at constant 30°C is 0.06135. At 30°C, individuals (in different proportions) from 14 to 22 days old will molt to adults (Figure 9). Note that once 100% ($G = 1.0$) is reached, all the individuals have molted (and in the model transferred to the next stage). For chronological ages greater than 22 days, G is equal to one, but the corresponding densities of immatures older than 22 days are all zero (they have already molted). For 25°C, the median development rate is 0.03175 (Figure 8) and individuals from twenty-six- to thirty-eight-days-old molt, in different proportions, into adults (Figure 9). Since the development rate itself is lower, it takes longer to develop and 100% molting does not occur until day 38.

Obviously, for the adult to egg transfer:

$$D(1,0) = \sum_{t=1}^N D(\text{adult}, t) * S * F * G(\text{adult}, \Delta t) \text{ Eq. (7)}$$

where: S = proportion females.

F = lifetime fecundity.

$G(\text{adult}, \Delta t)$ = proportion of total eggs laid during Δt .

For any population dynamics model, development, immature survival, adult longevity, reproduction, and immigration/emigration must be considered. For predators and parasites, additional information on attack and parasitism processes are needed. Of these processes, only development, as discussed above, can be modeled as a general process for most species. How we have approached modeling these other processes for each species or species group is discussed below. Since both experiments and modeling efforts are still in progress, the exact functional forms of many of the relationships are subject to change. Many of the specific relationships are complex, based on data from multiple sources, and require detailed justifications and analyses beyond the scope of this chapter.

FLYMOD. In addition to temperature-dependent development, the house fly dynamics model includes: immature survival, adult longevity, and fecundity. To calculate survival rates, eggs and first instars are subject to predation by *Macrocheles muscaedomesticae* and *Carcinops pumilio* (Geden and Axtell 1988, Geden et al. 1988), and pupae are parasitized by pteromalid parasites of the genera *Spalangia* and *Muscidifurax* (Mann et al. 1990a,b). Additionally, all stages are assumed to be killed by temperatures below 0°C. Immature survival is limited to between 35 to 75% moisture in the manure and outside this range, survival is assumed to be zero (Fatchurochim et al. 1989).

Adult flies can live a considerable time beyond their reproductive life. Thus, it is necessary to model both longevity and oviposition (Fletcher et al., submitted). Longevity is modeled as described for development. Median longevity rate, L , is defined as:

$$L = \exp(bl(T-b2)-1) \quad \text{Eq. (8)}$$

where: T = temperature (°C)

$bl, b2$ = estimated parameters

Adult physiological age is calculated from Eq. (4), and adults die of "old age," using Eq. (5), with minimum age, maximum age, and k equal to 0.118, 2.496, and 1.8382, respectively. Reproduction (eggs/female/4 hours) is modeled as a function of current temperatures and physiological age. Since we are concerned with the population, and not individual females, it was assumed that inclusion of the oogenesis cycles of individuals is not necessary. Total fecundity (based on current 4-hour mean temperature) is calculated first. This relationship is described by Eq. (3), with total fecundity, F , replacing R . This value, multiplied by the proportion of that total fecundity which should be laid during the time interval, (Eq. (5)), based on the physiological age of each female adult cohort, simulates eggs laid/female during Δt . This result is then multiplied by the female adult density in each cohort and summarized over cohorts to provide total eggs laid during the 4-hour interval.

Ages and densities of eggs and larvae are recalculated every four hours, including production of new eggs and large larval transfer to the pupal stage. Because pupae and adults have considerably longer transit times (times in those stages), their physiological ages and survivals are updated only daily.

MACMOD. The mite *Macrocheles muscaedomesticae*, as a predator of eggs and first instars of house fly, has been the subject of considerable research which has facilitated modeling (see data and references in Geden and Axtell 1988, Geden et al. 1988, and Geden et al. 1990). A detailed description of the model, its assumptions, and data sources is presented in Geden et al. (1990), although a number of the functions used have already been revised (Wilhoit, pers. comm.). Immature survival is considered a function of crowding, habitat size, and habitat quality. Since it has not been feasible to determine when mortality occurs in the immature stages, survival proportion is simply accounted for as the immatures transfer to adults.

As with the house fly, this mite lives beyond its reproductive period. Adult aging and longevity are considered temperature-dependent only. The adult physiological longevity rate is calculated as proportional to a mean longevity of 21.2 days at 27°C. Mortality due to age is calculated from Eq. (5), with minimum and maximum ages set at 0.8 and 1.3, respectively.

Reproduction is calculated similar to the house fly, except that the resultant eggs/4-hour interval is reduced as a function of the quantity and quality of prey to allow for the effect of alternate prey. Additionally, mite crowding was found to decrease fecundity significantly, and a negative exponential, scaled 0-1, modifies the potential to actual reproduction. Potential lifelong fecundity, F , is defined as:

$$F = b1 * Z^{b2} * (1-Z)^{b3} \quad \text{Eq. (9)}$$

where: $Z = (40-t)/(40-15)$

$t =$ temperature within the range of 40°C maximum and 15°C minimum

The proportion of eggs laid during a given time interval, P , is calculated using Eq. (5) ($P = G$ of Eq. (5)), with minimum and maximum physiological ages set at 0.089 and 0.833, respectively. The maximum fecundity during a time interval, FEC , is thus:

$$FEC = F * P$$

This maximum fecundity is reduced by the effect of prey density and potential lower nutritional value of alternate prey, if available.

Details and justification for the above are presented in Geden et al. (1990).

Predation on house fly eggs and first instars is based on a maximum rate related to prey density at 27°C, with proportional changes determined by temperature (relative to 27°C), mite crowding, and deflection to alternate prey (if present).

As with the house fly, adult mites live considerably longer than the immatures. Therefore, immature development, reproduction and attack rates use a 4-hour time step, while adult aging and longevity have a 1-day time step.

CARMOD. Modeling of the histerid beetle, *Carcinops pumilio*, is in progress using an approach similar to that used for MACMOD (Wilhoit, pers. comm.). The major difference is in dealing with longevity, since the median adult longevity of the beetle is almost 100 days at 27°C. Because our prediction horizon is 30 days or less, adult aging is not considered in this model. Thus, fecundity, after the prereproductive phase, is considered constant, except for effects of temperature and beetle density.

Immature development, as related to temperature, is being described by Fletcher et al. (pers. comm.), using Eq. (3). Attack rates were determined by Geden and Axtell (1988) and Geden et al. (1988), with additional functional forms being explored by Wilhoit (pers. comm.).

PARMOD. The four pteromalid pupal parasites, *Spalangia endius*, *S. cameroni*, *Muscidifurax raptor*, and *M. zaraptor* have been the subject of considerable research (Rueda and Axtell 1985). Mann et al. (1990a,b) provide most of the data on temperature and density effects on development, parasitism, and pupal attack rates used in the parasite models. Surprisingly, all four species exhibited similar responses. Development is modeled in the same manner described for the other submodels. Immature parasite survival is assumed equal to fly pupal survival. Because the adult parasites host feed, in addition to ovipositing in fly puparia, separate values for pupal kill and parasite reproduction have to be calculated. A daily time step is used for both adults and immatures, but attacks occur with a 4-hour time step. A full description of the parasite model is being prepared.

For all four species, both pupal kill and parasitism are assumed to be functions of temperature and host/parasite ratios. In a series of experiments with both host and parasite densities varying (Mann et al. 1990a), no effect could be found of either host or parasite density alone that was not accounted for by using an asymptotic function of host/parasite ratio. That is, there were no

apparent crowding effects. For all four species, both number killed/parasite, P_k , and number parasitized/parasite, P_p , are described by:

$$P_k \text{ or } P_p = w_1 \{1 - \exp[-w_2(H/P)]\} \quad \text{Eq. (10)}$$

where: w_1 = temperature-dependent maximum asymptote
calculated from Eq. (3);
 w_1 = R of Eq. (3)

w_2 = estimated parameter

H/P = host pupa/adult parasite ratio

For all species, w_1 for the P_k equation is greater than w_1 for the P_p equation.

At this time, longevity is considered a function of temperature only, but it will be necessary to incorporate the findings of Ables and Sheppard (1976) that the longevity is affected by the pattern of reproduction during the adult life time. Since both immatures and adults are long-lived, compared to the immatures of other species in this overall model, a one-day time step is used for both.

An additional problem which arises with these parasites is that host pupae are susceptible to parasitism only when young (approximately the first 25% of their time as pupae). Mann's (1990a,b) experiments on density effects were conducted with young susceptible pupae only. Should older, nonsusceptible pupae be considered in density relationships (e.g., do parasites "waste" time probing these pupae)? Will parasites host-feed on the older pupae? Because the parasite responses are quite sensitive to density, these questions must be resolved.

Species interactions. Among the most difficult modeling problems to resolve is how to handle species interactions. For competing predators or parasites, during a time step, which species is allowed to attack first, or can rules be developed to partition fly hosts or prey appropriately within a time step? Is the present 4-hour time step sufficiently small that the order of attack makes no difference? Given the difficulty in executing multispecies validation studies, the answers to these questions are not easily obtained. Wilhoit (pers. comm.) is exploring model sensitivities to alternative hypotheses regarding host/prey partitioning.

FUTURE PROSPECTS

To use the house fly system model in actual management situations requires that we include potential management strategies (e.g., pesticide scheduling, manure management alternatives, augmentation of natural enemies, alterations in the temperature and moisture conditions) in terms of their impact on survival and/or emigration for each of the species and their respective stages. The completion of this management model will also necessitate inclusion of economic information, and will be implemented within an expert system frame. The latter is necessary if we are to include subjective information necessary for decisions, but not appropriate for simulation modeling, *per se*. The prospects are promising for the construction of a practical fly management model for use in an expert system. Eventually such a model should be incorporated into a multi-pest management expert system for poultry production as well as be modified for application to other types of confined-animal production systems.

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