11 Ecological Modeling for Pesticide Risk Assessment for Honey Bees and Other Pollinators

V. Grimm, M.A. Becher, P. Kennedy, P. Thorbek, and J. Osborne

CONTENTS

11.1 Introduction 149
11.2 Example Model: Common Shrew 150
11.3 Rationale and Approaches of Mechanistic Effect Modeling 152
11.4 Modeling Practice for Risk Assessment 154
11.5 Existing Models of Pollinators 155
11.6 Discussion 159
References 160

11.1 INTRODUCTION

Current pesticide risk assessment for honey bees is based on laboratory tests and on semi-field and field studies. Risk assessment schemes focus on quotients of the hazard imposed by a compound and the predicted exposure to this compound in the field. Depending on this quotient, in a tiered approach, individual larvae and adults or entire experimental colonies are tested under confined or open field conditions. This scheme provides a wealth of important information for risk assessment. Test methods, experimental designs, standardization, and new and comprehensive endpoints are under continuous development and will help improve the efficiency and reliability of current risk assessment schemes. There are, however, a number of questions relevant for ecological risk assessment that cannot be fully answered with laboratory and field studies. Ecological risk assessment tries to determine unacceptable risk on populations but it remains unclear how to establish whether an effect is unacceptable or not (Hommen et al., 2010). Tests focusing on the individual organisms deliver information on mortality or sublethal effects under laboratory conditions, but leave uncertain what these effects mean at the population level, for example, whether or not they impair the ability of the entire colony to persist, to cope with other stressors, and to reliably provide services such as honey production and pollination.

To assess effects on natural populations in general, ecological factors such as adaptive behavior, population structure, density dependence, exposure patterns, landscape structure, and species interactions need to be taken into account (Forbes et al., 2009). In addition, for social insects such as honey bees, it needs to be considered that the reproductive unit is not the individual worker bee but the entire colony and its queen. The colony and its functioning can be considered as a complex net of buffer mechanisms that has evolved to increase the fitness of the queen. The loss of individual worker honey bees might thus be less significant than in solitary species; beekeepers may see it differently if honey harvest is impaired. On the other hand, buffer mechanisms

Pesticide Risk Assessment for Pollinators, First Edition. Edited by David Fischer and Thomas Moriarty.
© 2014 John Wiley & Sons, Inc. Published 2014 by John Wiley & Sons, Inc.

UNCORRECTED PROOF

ED_013166_00000030-00001

have only certain capacities. We cannot easily know these capacities and how they are affected by other stressors such as varroa mites (*Varroa destructor*), viruses, changes in landscape, or beekeeping practices.

Semi-field and field studies allow inclusion and manipulation of some ecological factors, but certainly not all of them in all possible combinations within experimentally controlled conditions. They are expensive, time-consuming, require interpretation by experts, and may still be inconclusive as sufficiently controlled conditions are rarely achievable under field conditions. In addition, behavioral responses of colonies and foraging bees show large variations that can make it difficult to obtain any identifiable effects of a certain factor on honey bee populations.

Ecological models provide a tool to overcome limitations of empirical studies. They are widely used in theoretical and applied ecology because ecological systems are usually too complex, develop too slowly, and cover areas that are too large to be studied solely via controlled laboratory or field experiments. In the context of regulatory risk assessment, ecological models are often grouped with organism-level models addressing toxicokinetics and toxicodynamics (TK–TD) or dynamic energy budgets (DEB) to "mechanistic effect models" (Grimm et al., 2009). This terminology was introduced to distinguish these models, which simulate processes related to effects of pesticides on organisms and populations, from fate models which focus on the fate of pesticides in water and soil, and from statistical or empirical models, which establish correlative, but not causal relationships between factors. Ecological models can address all levels of organization beyond the individual, but ecological risk assessment usually focuses on populations (Galic et al., 2010; Schmolke et al., 2010a). In this chapter, we give a brief introduction into the rationale and approaches of ecological modeling of population dynamics. We present an example model to demonstrate the potential insights that can be gained from such ecological models, summarize current modeling practice, and describe recent attempts to establish good modeling practice (GMop), which is needed to make mechanistic effect models applicable for regulatory risk assessment. We then provide an overview of existing models of honey bee colonies and give recommendations for the potential use of these models for pesticide risk assessment. Although this chapter focuses on honey bees, we will also briefly discuss how ecological modeling could support risk assessment of non-*Apis* pollinators. We will not discuss models addressing ecosystem services, which are important but belong to a different category of models and address different questions (Kevan et al., 1997; Williams et al., 2010).

11.2 EXAMPLE MODEL: COMMON SHREW

The following example model demonstrates how well-tested population models can be used to extrapolate the effects of toxicants observed at the individual level to the population level while considering different exposure patterns and landscape structures. Since such a demonstration does not yet exist for honey bees or other pollinators, we use a model of the common shrew (*Sorex araneus* L.). Wang and Grimm (2007) developed an individual-based population model of this species, which is a common insectivore. The purpose of the model was to explore the population-level consequences of acute mortality induced by pesticides.

The key behavior of the common shrew, which determines its response to heterogeneity in habitat quality and to the local density of conspecifics, is territoriality, that is, the aggressive defense of a certain area to secure resources and habitat. Therefore, the model is spatially explicit and represents each individual of the population, its life cycle, and its territorial behavior. The habitat consists of hexagonal units of 5 m diameter which are characterized by habitat type (e.g., grassland or hedge) and level of food resources on a given calendar day. Individuals are characterized by the variables age, gender, developmental stage (lactating offspring, subadult, adult), fertility (fertile, infertile; applies to females only), pregnancy, and home range. Home ranges are a set of habitat units occupied by a certain individual.

The processes of the model comprise development, mortality, reproduction, home range dynamics, dispersal, and mating. The model proceeds in daily time steps and covers an area of 25 ha. A full description of the model is given in Wang and Grimm (2007) using the standard format for describing individual-based

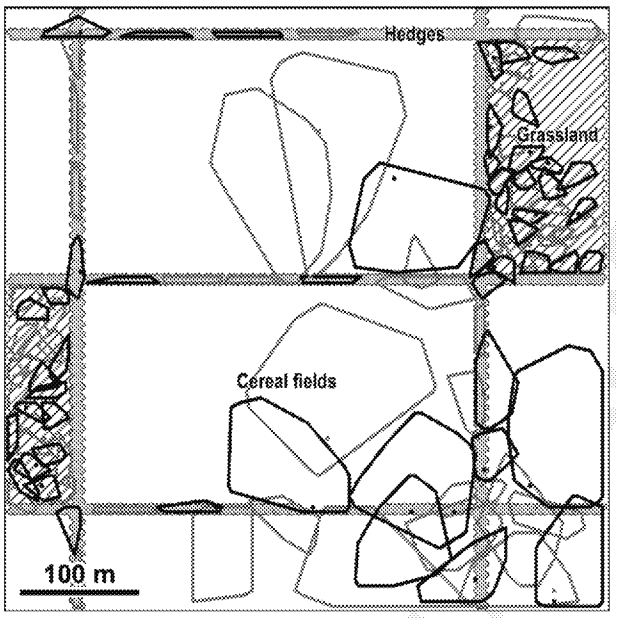

FIGURE 11.1 Output of an individual-based model of the common shrew (Wang and Grimm, 2007) on a certain day of the simulation. Black lines delineate home ranges of males, gray lines of females. Home ranges in cereal fields need to be larger than in grassland or hedges because of lower resource levels. Home ranges are drawn as minimum convex polygons by connecting the outmost cells occupied by their owners (from Wang and Grimm, 2007).

models (IBMs), ODD (Overview, Design concepts, Details; Grimm et al., 2006; 2010). The model allows the fate of each individual and its territory to be followed, day by day, in heterogeneous landscapes consisting of different habitat types (Figure 11.1).

Parameters affecting home range sizes were calibrated to match observations of a certain field study. Likewise, daily mortality was calibrated to obtain populations able to persist in good habitats. All other model parameters were taken from field studies. To make sure that the model captures important features of the internal organization of real populations of the common shrew, it was compared to multiple patterns observed in reality (Grimm et al., 2005; Grimm and Railsback, 2005, 2012). Home range size and location varied with season, habitat type, and shrew density qualitatively similar to what is known from the field. Further patterns successfully tested were: proportion of pregnant and lactating females and the age distribution of juveniles and subadults. Thus, although the model certainly is not realistic in the sense that it takes into account all aspects of real populations, it is realistic enough to qualitatively predict the response of populations to additional mortality.

Accordingly, Wang and Grimm (2010) explored various hypothetical scenarios by applying pesticide-induced mortality on either April 1 or July 15; on that day, all individuals had an additional probability of 10% or 20% of dying. They contrasted orchards with and without 10% or 20% hedges, and compared different endpoints such as population size, daily population growth rate, recovery time, and extinction risk. They found that population size is more sensitive for detecting short-term effects than population growth rates; and that the landscape structure and timing of application had strong impacts on population recovery. For example, with 20% additional mortality on April 1, the population stabilized in orchards including 20% hedges, but continually declined in landscapes without hedges (Figure 11.2).

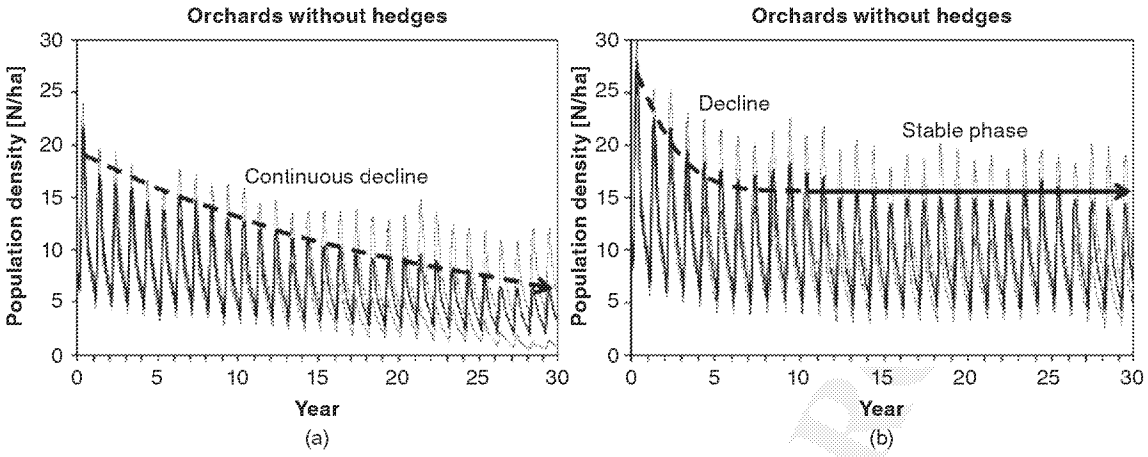

FIGURE 11.2 Population dynamics in orchards with and without 20% hedges with a yearly application of 20% additional mortality on April 1 (from Wang and Grimm, 2010).

The model of Wang and Grimm (2007, 2010) can in principle be used for regulatory higher-tier risk assessments of small mammals. Its main limitation is that only few empirical studies exist that can be used for parameterizing, testing, and validating the model. But it clearly demonstrates the potential of well-tested ecological models for risk assessment of pesticides. A further exemplary demonstration of this potential can be found in Topping et al. (2009), who analyze, using much more detailed models, scenarios including skylarks, beetles, spiders, and field voles. Galic et al. (2010) give an overview of the types of insights for ecological risk assessment that can be gained from population models. Population models are all based on a model's ability to assess population status after integrating lethal and sublethal effects including behavioral changes, at the individual level.

11.3 RATIONALE AND APPROACHES OF MECHANISTIC EFFECT MODELING

Ecological models have to be based on conceptual models that reflect our current understanding of the system represented in the model. Conceptual models are usually formulated verbally or graphically, which by itself provide no means for testing whether they are consistent and complete. Modelers, therefore, use formal notations, based on mathematics and computer logics, to translate conceptual models into a framework that allows rigorous calculation of their consequences. Ecological models are thus, broadly speaking, tools for studying if–then scenarios: *if* we agree on a certain set of simplifying assumptions, *then* we have to accept the consequences predicted by the model.

At the beginning of modeling projects, we are usually unhappy with their consequences because they do not match observations, so we revise our assumptions. Model development is, therefore, an iterative process (Figure 11.3).

The "Modeling Cycle" depicted in Figure 11.3 is relevant for any type of model, but many different types of model design and formulation exist (Schmolke et al., 2010a). Simple models, which are formulated via one or a few coupled differential equations, keep track of the processes causing changes in population size, such as mortality, reproduction, or disturbances. They are easy to communicate and understand but usually too poor in structure and mechanisms to be predictive and testable. Matrix models go beyond population size and consider the age, size, or stage structure of populations. They are frequently used to predict population growth

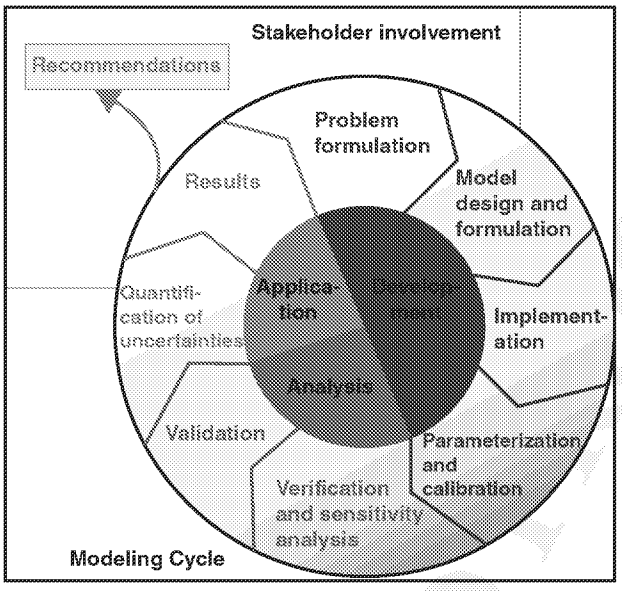

FIGURE 11.3 Tasks of the "Modeling Cycle," that is, of the iterative process of formulating, implementing, testing, and analyzing ecological models (after Schmolke et al., 2010b). Full cycles usually include a large number of subcycles, for example, verification leading to further effort for parameterization or reformulation of the model. The elements of this cycle are used to structure a new standard format for documenting model development, testing, analysis, and application for environmental decision making, TRACE (Schmolke et al., 2010b). (For a color version, see the color plate section.)

rate and the sensitivity of growth rate to changes in mortality or reproduction of certain classes of individuals. Again, matrix models are easy to communicate but, once they are designed to include stochasticity, spatial effects, or density dependence, they have to be run on computers and are, therefore, no longer very different from IBMs. Simple matrix models have a standard format and are relatively easy to parameterize and analyze. They project current average conditions into the future and can, therefore, be used for initial screening, corresponding to lower tier tests in risk assessment, with small or negative population growth rate indicating risk.

IBMs are computer simulation models in which each individual and its life cycle is represented explicitly (see the common shrew model presented above). Population dynamics and growth rates emerge from what individuals do and how they interact with each other and their environment. IBMs are harder to communicate, parameterize, test, and understand than simpler mathematical models, but nevertheless used when one or more of the following factors are assumed to be essential for explaining population dynamics: local interactions, differences among individuals, and adaptive behavior (Grimm and Railsback, 2005). IBMs are no longer new but routinely used not only in ecology but also in many other disciplines ranging from behavioral ecology to social sciences, where they are usually referred to as "agent-based" models (Railsback and Grimm, 2012). Strategies exist to optimize model complexity (Grimm et al., 2005) and to formulate and communicate IBMs according to a standard format, the ODD ("Overview, Design concepts, Details") protocol (Grimm et al., 2006, 2010).

To use models for pesticide risk assessment, two conflicting criteria for assessing the suitability of models are critical: on the one hand, models need to be complex enough to deliver testable predictions which enable decisions about whether or not the model is a sufficiently good representation of the real world. On the other

hand, models need to be simple enough to be thoroughly analyzed and fully understood. Modeling thus requires finding the optimal level of model complexity (Grimm et al., 2005, Grimm and Railsback, 2012).

Understanding the main process within a model is decisive, otherwise we would be asking for blind faith in output from the equivalent of a black box. For some questions, simpler models can be sufficient, correctly predicting trends and general mechanisms without making quantitative predictions. For other questions, more accurate predictions are required, which is possible if the models are driven by first principles, such as physiology, stoichiometry, or adaptive behavior, and if enough data are available to directly or indirectly estimate model parameters with sufficient certainty. Highly ecological predictive models have been developed (e.g., Railsback and Harvey, 2002; Topping et al., 2009; Stillman and Goss-Custard, 2010), but all required more than 5 person years before first versions could be used to support decision making. However, once a predictive model exists, it pays off extremely well because it can then be used as a virtual laboratory to answer a wide range of questions regarding population dynamics under different and possibly new environmental conditions.

11.4 MODELING PRACTICE FOR RISK ASSESSMENT

Claims about the high potential of ecological modeling for pesticide risk assessment are not new and have been made for at least 20 years (Barnthouse, 1992). In fact, approximately 100 academic publications exist that use population or other ecological models to explore the effects of pesticides at the population level (Schmolke et al., 2010a). Galic et al. (2010) summarize the scientific insights of these studies, which are certainly important and contribute to our understanding of the significance of individual-level effects at the population level. Nevertheless, the use of models is still limited to a few recent exceptions. Why is this so? Schmolke et al. (2010a) found that most models in this field are not fit for being used for pesticide registrations. The main reason is that criteria for being accepted as a scientific publication, such as novelty, focusing on one main aspect, simplicity, or generality, are less relevant for making a model suitable for basing environmental decisions on their output. In most cases, choice of model structure and complexity was not justified, endpoints directly relevant for regulatory risk assessments were not considered, sources of parameter values were unclear, uncertainty of model output was not communicated, and most importantly, little effort was made to demonstrate that the model was a sufficiently good representation of the real population such that insights gained in the model world could be transferred to the real world with sufficient confidence.

This situation is, however, changing in Europe. Two main challenges to make models fit to be used for regulatory risk assessment are (1) the establishment of GMoP, so that both industry and regulators have clear criteria for how to create and assess models, and (2) the lack of researchers who are well-trained both in ecological modeling and risk assessment (Thorbek et al., 2010). Therefore, CREAM (Chemical Risk Effects Assessment Models), a large research and training network funded by the European Commission, was launched in 2009 (Grimm et al., 2009; http://cream-itn.eu), includes 13 academic institutions and 10 partners from industry, consulting firms, and regulatory authorities, will run until 2013, and will deliver both guidelines for GMoP and more than 20 young researchers trained in modeling and risk assessment. Moreover, models will be developed which, for indicator species and risk assessment questions, are good demonstrations for how models can be used for regulatory risk assessments.

Elements of GMoP have long been identified but are still widely ignored. The real challenge is to get these elements accepted and used in practice. Schmolke et al. (2010b) found that for this, regulators or, more generally, decision makers need to be involved, direct benefits for modelers who follow GMoP (which usually requires extra effort) need to be identified, and a consistent terminology needs to be established. Therefore, the basic approach of CREAM in establishing GMoP is to define and use a standardized documentation framework, Transparent and Comprehensive Ecological Modeling (TRACE). Schmolke et al. (2010b) suggest the use of the structure of the iterative modeling cycle (Figure 11.3) as the basis for a general and standardized

document structure. As a result, all models that are to be used to support pesticide registration and come with a TRACE documentation as a supplementary document, can be assessed in exactly the same way. Regulators will know that, for example, sensitivity analysis will be described in Section 2.2, the conceptual model underlying the model's design can be found in Section 1.2. Modelers, on the other hand, will know that regulators will expect to see, for example, a documentation of sensitivity analysis, at some point, so they can use the TRACE format as a checklist. The direct benefit for the modeler is that the TRACE format helps keeping notes in the "modeling notebook," which corresponds to "lab journals" in laboratories, in a format that later can directly be transferred to TRACE documents.

Once a critical number of example TRACE documents exist, by the end of the CREAM project, more specific assessment guidelines can be developed that help standardize the use of ecological models for regulatory risk assessment. This includes the agreement on standard scenarios, species, landscapes, ecoregions, and population-level endpoints. Honey bees and pollinators will play an important role in this context, due to their unique significance for biodiversity and ecosystem services.

11.5 EXISTING MODELS OF POLLINATORS

Quite a few models exist that address various aspects of honey bee behavior and ecology (for an overview, see Section 5.4. in Schmickl and Crailsheim, 2007). However, there are surprisingly few sufficiently described models addressing dynamics of non-swarming, managed colonies which include the full life cycle of worker bees from a single hive over several years such that the colony-level effects can be assessed (Table 11.1).

Two of these models are interesting from an academic point of view, but too simple to be tested against observed data (Omholt, 1986; Khoury et al., 2011). Nevertheless, theoretical insights can guide the design and

TABLE 11.1

Colony Models That Include the Full Life Cycle of Worker Bees and Run Long Enough, that is, Two or More Years, to Assess Status and Survival of a Model Colony. The Third Column Lists Additional Factors Included in the Model That Can Affect Colony Status and Survival

Reference	Purpose of Model/Question Addressed	Additional Factors
Omholt (1986)	Explain brood-rearing peaks in non-swarming colonies	
DeGrandi-Hoffman et al. (1989)	Simulate honey bee population dynamics to support management	
Martin (2001)	Explain the link between varroa mite infestation and honey bee colony failure, including the effects of virus diseases	Varroa and virus infections
Al Ghamdi and Hoopingarner (2004)	Develop a tool for research and management; interaction between varroa and honey bees	Varroa
Thompson et al. (2005), (2007)	Explore effect of an insecticide on colony dynamics	Pesticides
Schmickl and Crailsheim (2007)	Explore significance of important feedback loops, pollen supply, and brood cannibalism	Swarming
Becher et al. (2010)	Does temperature during development affect colony survival?	
Khoury et al. (2011)	Impact of increased forager mortality on colony growth and development	

UNCORRECTED PROOFS

analysis of more complex models. For example, Khoury et al. (2011) implement two feedback mechanisms: between colony size and brood production and between the number of foragers and recruitment to foraging, which have been referred to as "social inhibition" (Leoncini et al., 2004). They found that if forager mortality exceeds a certain threshold, the colony can no longer maintain itself and will decline to extinction. These feedback mechanisms have been observed empirically and the results of Khoury et al. (2011) suggest that their significance should be further tested in more detailed models, containing a colony's age structure, nectar and pollen stores, further feedback mechanisms, and variable environmental drivers.

Au: Please provide complete details for the reference citation "Thompson et al., 2007" to be included in the reference list

The model by Thompson et al. (2005, 2007) is also simple and considers the abundance of brood, in-hive and forager bees. This model was originally used in combination with a more detailed population model of varroa mites (Wilkinson and Smith, 2002), but Thompson et al. left out the varroa part and added assumptions about the effects of a certain type of pesticide (insect growth regulators), based on observations from their own experiments. Such reuse of models for new questions can be problematic, since the model's design may not be appropriate for the new questions. In this case, model resolution is likely to be too coarse to make robust predictions, still, the model serves as a demonstration of how, in principle, individual-level effects of pesticides can be included in colony models of honey bees.

The models presented by Martin (2001) and Al Ghamdi and Hoopingarner (2004) are modifications of BEEPOP (DeGrandi-Hoffman et al., 1989), a simulation model proceeding in time steps of one day and representing cohorts (or age classes) of eggs, brood, and adults of both worker bees and drones (Figure 11.4). BEEPOP distinguishes between in-hive and foraging bees, whereas the other two models do not. Colony dynamics are driven by the queen's egg-laying rate, which is mainly driven by weather, in particular

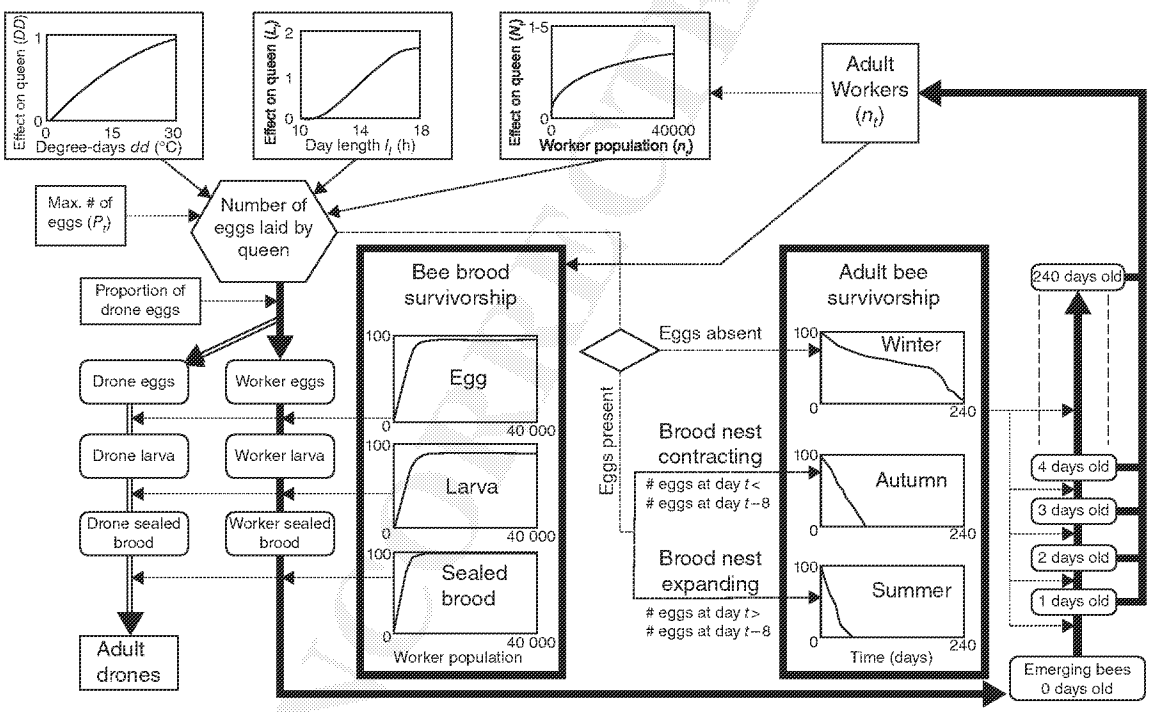

FIGURE 11.4 Conceptual diagram of the colony model of Martin (2001). Solid lines represent the flow of individuals between developmental stages and dotted lines represent influences (from Martin, 2001).

temperature and photoperiod. Additionally, these models include feedbacks between egg laying and colony size. Drones are mainly included because mites are more attracted by drone cells and mite reproduction is higher in drone cells, so that the proportion of drone cells has an important impact on the dynamics and effects of varroa infestation.

BEEPOP has been augmented by detailed modules for including effects of pesticides (Bromenshenk et al., 1991). The module BEETOX included a toxicity database for more than 400 chemicals and calculated lethal and sublethal effects for specific exposures; the module BEEKILL allowed the linkage these effects to exposure scenarios and feed the resulting changes in mortality, development, and longevity into the colony model. Unfortunately, details of these modules were not published and the software implementing them, PC BEEPOP, is unlikely to run on modern computers. It also seems that it has never been used for regulatory risk assessment of pesticides, probably because it was very much ahead of its time. Nevertheless, the design of PC BEEPOP is interesting since it allows one to test effects of pesticides on honey bee colonies in a standardized way.

Becher et al. (2010) include the effect of colony size and structure on heating and the resulting temperature in the brood chamber. It had been observed that brood developed under higher temperatures proceeds faster from in-hive tasks to foraging. It turns out, however, that this has little effect on the dynamics and status of the colony. This is a good example of the role of models for relating individual-level effects to colony-level phenomena. Without the model, it would have been impossible to predict this relationship for the temperature effect, simply because colony structure, environmental drivers, and feedback mechanisms are too complex to be even qualitatively assessed just by reasoning. Negative results, as in this case, that is, the working hypothesis is shown to be false, are no less important than positive results.

The most complex colony model is HoPoMo (Schmickl and Crailsheim, 2007). In contrast to all other colony models, HoPoMo is not entirely driven by demographic rates, such as egg-laying rate of the queen and age- and task-dependent mortalities. Rather, the current number, stage, age, and task of bees are used to calculate the estimated requirements of the colony for nectar and pollen. Depending on current stocks of these two resources, the proportion of worker bees devoted to different tasks is dynamically reallocated every day. The three different tasks distinguished are nursing, food processing, and foraging. HoPoMo includes a large number of further feedbacks between the current state of the colony, or parts of it, and process rates.

HoPoMo consists of 60 difference equations, which are all well documented and biologically justified. The model has been thoroughly tested, including sensitivity analyses and exploration of certain mechanisms. It reproduces several empirical patterns and correctly predicts at least one feature of real colonies that was not used to calibrate or design the model, but emerged during analysis of the full model: in smaller model colonies, with no more than 20,000 brood cells, the number of unsealed brood cells shows oscillations similar to what has been observed in real experimental hives. The model has, however, not yet been used to answer any specific question about how colonies respond to environmental stress, such as exposure to a pesticide.

Two of the colony models in Table 11.1 also consider infestation with varroa mites. Phoretic mites, that is, mites attached to worker bees, enter brood cells about one day before they are sealed and reproduce within these brood cells. Emerging mites try to infest another brood cell or become phoretic, and thereby spread varroa infestation. During the interaction with brood and worker bees, mites transfer viruses, for example, deformed wing virus (DWV), or acute paralysis virus (APV). The model of Martin (2001) integrates honey bee and mite population dynamics and the effects of viruses. It shows, for example, that the less virulent DWV will become more widely spread than APV, and that mite control measures need to be taken before the longer-lived overwintering bees emerge. Further varroa models, which focus on various aspects of varroa population dynamics, but are coupled to much simpler colony models than BEEPOP, include Omholt and Crailsheim (1991), Fries et al. (1994), Martin (1998), Calis et al. (1999), Wilkinson and Smith (2002), and DeGrandi-Hoffman and Curry (2005). For the purpose of pesticide registration, it seems necessary to use models that allow inclusion of varroa infestation because at least in Europe and North America, varroa is a

ubiquitous stressor. It remains as an open question, the way in which varroa infestation could or should be taken into account for pesticide registration. Should decisions be made to ensure safety under a worst-case assumption of high infestation where colonies have high risk of collapsing even without exposure, under an assumption of effective varroa management by beekeepers, or should average infestation levels based on national or international surveys be used? These questions cannot be answered scientifically, but robust, well-tested, and predictive colony models which allow inclusion of varroa and possibly other stressors would support decisions by quantitative arguments.

Currently, only the model by Martin (2001) is suitable to consider different, but simultaneous stressors. On the other hand, HoPoMo is a more realistic model and includes feedback mechanisms which seem to be important for the functioning of a colony; in particular, HoPoMo is driven by pollen and nectar stores, demand, and availability in the landscape. If HoPoMo could include a module representing varroa infestation and virus effects, it would currently be the most suitable model for pesticide risk assessment. However, changes in landscape structure, crop plants and their rotation, and agricultural practice also affect honey bee colony performance so that, for registration purposes, a model should also allow such factors to be represented with sufficient detail regarding spatial structure, crop dynamics and rotation, and foraging behavior. Adding such a module to HoPoMo would make an already very complex model even more complex and, therefore, harder to test and understand. Therefore, a colony model that includes varroa, viruses, and foraging in heterogeneous landscapes should preferably be similar in design to the model of Martin (2001) but include the most important feedbacks included in HoPoMo.

A well-tested prototype of such a model, dubbed "BEEHAVE," was developed by M. Becher and coworkers at Rothamsted Research, UK, in 2009–2013. Its purpose is not pesticide registration *per se*, but to explore the possible reasons for honey bee decline and collapse as well as devising strategies for improving honey bee health. For this purpose, the model includes varroa, viruses, and explicit foraging in heterogeneous landscapes. The option to include pesticide effects, or other additional stressors subsequently shown to be important, was considered from the beginning of this modeling project and a design developed to enable this to be relatively straightforward. The model and its computer code and user manual will be made available in the summer of 2013, so that other researchers can test the model independently and use it or the model for various purposes.

As for non-*Apis* pollinators, fewer models exist than for honey bees. The population model of the solitary red mason bee, *Osmia rufa* (L.) (Ulbrich and Seidelmann, 2000) shows, however, that if sufficient empirical knowledge of a species ecology and behavior exists, developing a population model is straightforward and can lead to important insights. The purpose of the *Osmia* model was predicting the risk of extinction of this solitary species in different types of habitat, which are characterized by the amount and quality of food they provide. The model is individual-based and focuses on cell construction and maternal investment in brood cells. The life stages distinguished are eggs, larvae, imagines in cocoons, males, pre-nesting females, and nesting females. A key decision of nesting females is the sex determination of their brood. The first brood cells are always daughter cells, but at some point, the mother bee switches to construction of son cells. In the model, it is assumed that this switching depends on the mother's weight, that is, heavier bees produce more daughter cells. Likewise, size of progeny is related to their mother's weight. As a measure of habitat quality, time for cell construction was used as a proxy (Gathmann, 1998). In this way, the model can be linked to habitat quality without explicitly representing habitat and foraging. As stressor, parasites were taken into account, with parasitism rates being higher for longer cell construction times. Mean population size and extinction risk were taken as population-level endpoints.

Mitesser et al. (2006) developed a colony model for the halictid bee *Lasioglossum malachurum* to explore the emergence of activity cycles, which are typical for some annual eusocial "sweat bees" (Halictidae). The model is very simple and includes only two state variables, the numbers of workers and of sexuals; the time horizon considered is so short that mortality of sexuals could be ignored. Still, there is no principle reason

why it should not be possible to develop an age-structured model, similar to BEEPOP or BEEHAVE that includes the full life cycle.

A very interesting IBM of bumble bees was developed by Hogeweg and Hesper (1983). It includes the full life cycle of individuals and different types of behaviors, and is, like HoPoMo, to a large degree driven by food collection and consumption and time budgets for certain activities. Focus, though, is less on colony dynamics *per se* but on explaining division of labor within the colony and the so-called "dominance interactions," by which this division emerges. This model was about 20 years ahead of its time as IBMs, which go beyond demographic rates and include behavior, have only become more widely used within the last 10 years. It would certainly be worthwhile to reimplement this model and try to adapt it to new questions. Whether or not it would be sufficient to just assume division of labor, or have mechanisms included that allow this division to emerge, remains an open question.

In general, eusocial non-*Apis* pollinators have simpler and smaller colonies. This implies that, although they benefit from cooperative activities, they do not maintain buffer mechanisms and reserves which would be as powerful as in honey bee colonies. They also show greater foraging activity, to compensate for the lack of maintained reserves, potentially increasing the risk of pesticide exposure.

A bottleneck for developing models for non-*Apis* pollinators might be the lack of data about their foraging behavior in real landscapes since exposure to pesticides to a large extent depends on foraging. Detailed foraging models need to be developed and parameterized and tested using corresponding field studies and experiments (Everaars, 2012; Everaars and Dormann, 2013).

11.6 DISCUSSION

Sophisticated tests and schemes exist to assess the risk that pesticides impose to honey bees. Current regulations and thresholds seem to be conservative but still leave many questions open. The difficulty is that to confirm whether or not the sublethal or lethal effects of pesticides, observed in laboratories or field experiments, translate into a significant risk to the functioning and/or survival of a colony, controlled, long-term experiments are required to take into account the individual and combined effects of pesticides and other stressors on colonies at the landscape scale. For example, if on a normal day an average of 100 dead bees is found around the hive, and during acute pesticide exposure 300 dead bees are found, is this of any significance to the colony? Likewise, if larvae develop more slowly, or worker bees have a shortened lifespan due to pesticides, how does this affect colony functioning in terms of honey production and pollination? Answering such questions with real experiments might be possible to some degree, but would require enormous resources.

Ecological models could, in principle, compensate for this limitation of empirical approaches. And there are, indeed, fields where models are used to support environmental decision making. For example, recent regulations of wildlife diseases, such as rabies or classical swine fever, are based on predictions of models which are quite similar to the common shrew model presented earlier (Thulke and Grimm, 2010). In some federal states of Germany, forest management plans on the timescale of 10–20 years are based on predictions of the individual-based forest model SILVA (Pretzsch et al., 2002). Common features of these and other ecological models used for decision making is that their development took at least 5 years, and their acceptance by the responsible decision makers about 10 years.

Establishing the use of ecological models to assess risk of pollinators, in particular honey bees, can nevertheless be achieved faster. Well-tested and documented models already exist, which can at least be used, preferably in joint workshops, to discuss and learn the use of such models for higher-tier risk assessments. BEEHAVE, the model currently developed in the UK, holds further promise, in particular because it includes the main potential stressors of colonies and foraging in heterogeneous landscapes. Ideally, to make BEEHAVE fit for use with pesticide registrations, it would need to be used in one or more workshops where researchers from all three sectors involved in pesticide risk assessment, industry, regulators, and academia, agree on

standard model scenarios, endpoints, and risk assessment schemes. BEEHAVE is described in a standard format (Grimm et al., 2006, 2010), its development and analysis will be available as a TRACE document, and it is implemented in a software platform, NetLogo (Wilensky, 1999), that is freely available and easy to learn. BEEHAVE is thus designed to be tested, used, and developed not only by its developers but by the scientific and user community involved in honey bee research and management.

The good news is that honey bee models are less limited by data for parameterization than models of most other species. Experimentally managed colonies are relatively easy to observe in the laboratory and field. Bee behavior has been investigated a lot, and beekeepers accumulated sound empirical knowledge on how colonies respond to environmental events and beekeeping practices. Foraging still is a bottleneck in empirical knowledge, but remote sensing techniques can be used now to follow the flight path of individual foragers (Riley et al., 1996; Osborne et al., 1999). Moreover, in response to the decline or collapse of honey bees in Europe and North America, large international networks such as COLOSS (Neumann and Carreck 2010) compile and analyze huge amounts of data, which can be used to test model predictions.

Ecological models are no silver bullet to solve all problems of pollinator risk assessment, but they are a valuable and needed tool for extrapolating individual-level effects to the colony-level, to overcome important limitations of field studies, and to explore endpoints that quantify adverse effects not only on pollinators *per se* but also on biodiversity and ecosystem services.

REFERENCES

Al Ghamdi A, Hoopingarner R. 2004. Modeling of honey bee and varroa mite population dynamics. *Saudi. J. Biol. Sci.* 11:21–36.

Barnthouse LW. 1992. The role of models in ecological risk assessment: a 1990s perspective. *Environ. Toxicol. Chem.* 11:1751–1760.

Becher MA, Hildenbrandt H, Hemelrijk CK, Moritz RFA. 2010. Brood temperature, task division and colony survival in honeybees: a model. *Ecol. Model.* 221:769–776.

Bromenshenk IJ, Doskocil J, Olbu GJ, DeGrandi-Hoffman G, Roth SA. 1991. PC BEEPOP, an ecotoxicological simulation-model for honey-bee populations. *Environ. Toxicol. Chem.* 10:547–558.

Calis NM, Fries I., Ryrie SC. 1999. Population modelling of *Varroa jacobsoni* Oud. *Apidologie* 30:111–124.

DeGrandi-Hoffman G, Roth SA, Loper GL, Erickson EH. 1989. Beepop—A honeybee population-dynamics simulation-model. *Ecol. Model.* 45:133–150.

DeGrandi-Hoffman G, Curry R. 2005. Simulated population dynamics of Varroa mites in honey bee colonies: Part II—What the VARROAPOP model reveals. *Am. Bee. J.* 145:629–632.

Everaars J. 2012. The response of solitary bees to landscape configuration with focus on body size and nest-site preference. PhD dissertation, Martin-Luther-University.

Everaars J, Dormann CF. 2013. A simulation model for non-*Apis* bees: solitary bees foraging and competing for pollen. In: Devillers, J. (ed.) In *Silico Bees*. CRC Press. In press.

Au: Please update the reference "Everaars & Dormann, 2013"

Forbes VE, Hommen U, Thorbek P, Heimbach F, van den Brink P, Wogram J, Thulke H-H, Grimm, V. 2009. Ecological models in support of regulatory risk assessments of pesticides: developing a strategy for the future. *Integr. Environ. Assess. Manag.* 5:167–172.

Fries I, Camazine S, Sneyd J. 1994. Population dynamics of *Varroa jacobsoni*—a model and a review. *Bee World* 75:5–28.

Galic NG, Hommen U, Baveco JM, Van den Brink PJ. 2010. Potential application of population models in the European ecological risk assessment of chemicals: II review of models and whether they can address the protection aims. *Integr. Environ. Assess. Manag.* 6:338–360.

Gathmann A. 1998. Bienen, Wespen und ihre Gegenspieler in der Agrarlandschaft: Artenreichtum und Interaktionen in Nisthilfen, Aktionsradien und Habitatbewertung. Göttingen: Cuvillier Verlag.

Grimm V, Railsback SF. 2005. *Individual-Based Modeling and Ecology*. Princeton University Press, Princeton, NJ.

Grimm V, Railsback SF. 2012. Pattern-oriented modelling: a "multiscope" for predictive systems ecology. *Philos. T. Roy. Soc. B.* 367:298–310.

UNCORRECTED PROOF

Grimm V, Revilla E, Berger U, Jeltsch F, Mooij WM, Railsback SF, Thulke H-H, Weiner J, Wiegand T, DeAngelis DL. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* 310:987–991.

Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T, Heinz SK, Huse G, Huth A, Jepsen JU, Jørgensen C, Mooij WM, Müller B, Pe'er G, Piou C, Railsback SF, Robbins AM, Robbins MM, Rossmanith E, Rüger N, Strand E, Souissi S, Stillman RA, Vabø R, Visser U, DeAngelis DL. 2006. A standard protocol for describing individual-based and agent-based models. *Ecol. Model.* 198:115–126.

Grimm V, Ashauer R, Forbes V, Hommen U, Preuss TG, Schmidt A, van den Brink PJ, Wogram J, Thorbek P. 2009. CREAM: a European project on mechanistic effect models for ecological risk assessment of chemicals. *Environ. Sci. Pollut. Res.* 16:614–617.

Grimm V, Berger U, DeAngelis DL, Polhill G, Giske J, Railsback SF. 2010. The ODD protocol: a review and first update. *Ecol. Model.* 221:2760–2768.

Hogeweg P, Hesper B. 1983. The ontogeny of the interaction structure in bumble bee colonies: a MIRROR model. *Behav. Ecol. Sociobiol.* 12:271–283.

Hommen U, Baveco JM, Galic NG, Van den Brink PJ. 2010. Potential application of ecological models in the European environmental risk assessment of chemicals I: review of protection goals in EU directives and regulations. *Integr. Environ. Assess. Manag.* 6:325–337.

Kevan PG, Greco CF, Belaousoff S. 1997. Log-normality of biodiversity and abundance in diagnosis and measuring of ecosystem health: pesticide stress on pollinators in blueberry heaths. *J. Appl. Ecol.* 34(5):1122–1136.

Khoury DS, Myerscough MR, Barron AB. (2011). A quantitative model of honey bee colony population dynamics. *PLoS ONE.* 6(4):e18491. doi:10.1371/journal.pone.0018491

Leoncini I, Le Conte Y, Costagliola G, Plettner E, Toth AL. 2004. Regulation of behavioral maturation by a primer pheromone produced by adult worker honey bees. *Proc. Nat. Acad. Sci. USA.* 101:17559–17564.

Martin S. 1998. A population model for the ectoparasitic mite *Varroa jacobsoni* in honey bee (*Apis mellifera*) colonies. *Ecol Model.* 109:267–281.

Martin SJ. 2001. The role of Varroa and viral pathogens in the collapse of honeybee colonies: a modelling approach. *J. Appl. Ecol.* 38:1082–1093.

Mitesser O, Weissel N, Strohm E, Poethke H-J. (2006). The evolution of activity breaks in the nest cycle of annual eusocial bees: a model of delayed exponential growth. *BMC. Evol. Biol.* 6:45. doi:10.1186/1471-2148-6-45

Neumann P, Carreck C. (2010). Honey bee colony losses: a global perspective. *J. Apic. Res.* 49:1–6.

Omholt SW. 1986. A model for intracolonial population dynamics of the honeybee in temperate zones. *J. Agric. Res.* 25:9–21.

Omholt SW, Crailsheim K. 1991. The possible prediction of the degree of infestation of honeybee colonies (*Apis mellifera*) by *Varroa jacobsoni* OUD by means of its natural death-rate: a dynamic model approach. *Norw. J. Agric. Sci.* 5:393–400.

Osborne JL, Clark SJ, Morris RJ, Williams IH, Riley JR, Smith AD, Reynolds DR, Edwards AS. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *J. Appl. Ecol.* 36:519–533.

Pretzsch H, Biber P, Dursky J. 2002. The single tree-based stand simulator SILVA: construction, application and evaluation. *Forest. Ecol. Manag.* 162:3–21.

Railsback SF, Harvey BC. 2002. Analysis of habitat selection rules using an individual-based model. *Ecology.* 83:1817–1830.

Railsback SF, Grimm V. 2012. *Agent-Based and Individual-Based Modeling: A Practical Introduction.* Princeton University Press, Princeton, NJ.

Riley JR, Smith AD, Reynolds DR, Edwards AS, Osborne JL. 1996. Tracking bees with harmonic radar. *Nature.* 379:29–30.

Schmickl T, Crailsheim K. 2007. HoPoMo: a model of honeybee intracolonial population dynamics and resource management. *Ecol. Model.* 204:219–245.

Schmolke V, Thorbek P, Chapman P, Grimm V. 2010a. Ecological modelling and pesticide risk assessment: a review of current modelling practice. *Environ. Toxicol. Chem.* 29:1006–1012.

Schmolke A, Thorbek P, DeAngelis DL, Grimm V. 2010b. Ecological modelling supporting environmental decision making: a strategy for the future. *Trends. Ecol. Evol.* 25:479–486.

Stillman RA, Goss-Custard JD. 2010. Individual-based ecology of coastal birds. *Biol. Rev.* 85:413–434.

ED_013166_00000030-00013

Thompson HM, Wilkins S, Battersby AH, Waite RJ, Wilkinson D. 2005. The effects of four insect growth-regulating (IGR) insecticides on honeybee (*Apis mellifera* L.) colony development, queen rearing and drone sperm production. *Ecotoxicology*. 14:757–769.

Thorbek P, Forbes V, Heimbach F, Hommen U, Thulke HH, van den Brink PJ, Wogram J, Grimm V (eds.) 2010. *Ecological Models for Regulatory Risk Assessments of Pesticides: Developing a Strategy for the Future*. CRC Press, Boca Raton, FL (in collaboration with the Society of Environmental Toxicology and Chemistry (SETAC), Pensacola, FL).

Thulke H-H, Grimm V. 2010. Ecological models supporting management of wildlife diseases. In: Thorbek P, Forbes V, Heimbach F, Hommen U, Thulke HH, van den Brink PJ, Wogram J, Grimm V (eds), *Ecological Models for Regulatory Risk Assessments of Pesticides: Developing a Strategy for the Future*. CRC Press, Boca Raton, FL (in collaboration with the Society of Environmental Toxicology and Chemistry (SETAC), Pensacola, FL), pp. 67–76.

Topping CJ, Dalkvist T, Forbes VE, Grimm V, Sibly RM. 2009. The potential for the use of agent-based models in ecotoxicology. In: Devillers J. (ed.) *Ecotoxicology Modeling*, Springer, pp. 205–237.

Ulbrich K, Seidelmann K. 2000. Modeling population dynamics of solitary bees in relation to habitat quality. *Web. Ecol.* 2:57–64.

Wang M, Grimm V. 2007. Home range dynamics and population regulation: an individual-based model of the common shrew. *Ecol. Model.* 205:397–409.

Wang M, Grimm V. 2010. Population models in pesticide risk assessment: lessons for assessing population-level effects, recovery, and alternative exposure scenarios from modelling a small mammal. *Environ. Toxicol. Chem.* 29: 1292–1300.

Wilensky U. (1999). *Center for Connected Learning and Computer-Based Modeling*, Northwestern University, Evanston, IL. http://ccl.northwestern.edu/netlogo/

Au: PLease provide the last accessed date for the reference "Wilensky, 1999"

Wilkinson D, Smith GC. 2002. A model of the mite parasite, *Varroa destructor*, on honeybees (*Apis mellifera*) to investigate parameters important to mite population growth. *Ecol. Model* 148:263–275.

Williams NM, Crone EE, Roulston TH, Minckley RL, Packer L, Potts SG. 2010. Ecological and life history traits predict bee species responses to environmental disturbances. *Biol. Cons.* 143:2280–2291.

UNCORRECTED PROOFS