

Models of stored-product pests: Their relevance to biological control in traditional storage in developing countries

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Abstract

During the past decades, models that simulate the population dynamics of stored-product pests have been developed. Some of these have been developed from an interest in ecological and evolutionary processes that shape populations. Others have been constructed with the ultimate aim of improving control of these pests. We discuss both approaches in relation to biological control of stored-product pests in developing countries.

Storage of food products in developing countries differs from that in industrialized countries. Food is often stored at a small scale, it is mostly intended for private consumption, and insect incidence is high. Biological control of these insect pests is considered an interesting alternative to traditional and chemical control methods. The situation of control of bruchids in stored cowpea is presented as a case.

Existing 'applied' models do not answer the type of questions that arise from the system of stored cowpea. They often do not include natural enemies, they are only validated for relatively low insect densities and temperatures, they assume control practices which are not appropriate to resource-poor farmers, and they often draw upon empirical relationships. We suggest that a model that predicts which measures will improve the biological control status of tropical stored-product pests should combine the 'ecological realism' of theoretical ecology with the accuracy of the 'pest management' models.

Introduction

Storage of food products in developing countries differs from that in industrialized countries in many respects (Table 1). Cereals and pulses, stored in traditional granaries, are often

seriously infested by insect pests (Compton et al., 1993, Gahukar, 1994). Traditional methods of controlling these pests, such as the use of sand or wood-ash as protectants, fall short in effectivity and efficiency for large quantities (see Compton et al., 1993). Chemical control is too expensive and imposes health risks, especially for illiterate subsistence farmers. For such systems, biological control of stored-product pests is an interesting option (Haines, 1984, Van Huis, 1991, Van Huis et al., 1991), especially because the tolerance for insect presence and cosmetic damage in stored products is high (Haines, 1984).

A simulation model can be useful in selecting a natural enemy for biological control, because it can predict the effects of characteristics of individuals at the population level. Simulation models can also be used to study the sensitivity of the system to changes in management or changes in one of its parameters. This can be helpful in determining the best control strategy for a particular system.

A large number of models deal with the biology of arthropod pests that occur in stored products (Throne, 1995, Longstaff, 1991). We examine the existing literature on these models for their relevance to biological control situations in traditional storage of small-holders in developing countries. The system of bruchids in stored cowpea in West Africa is used as an example.

We start with an introduction to bruchids in cowpea and to the research questions that have arisen from previous work on this system. Subsequently, we briefly characterize and discuss existing models and evaluate their importance to stored-product protection in the tropics. Finally, we discuss future prospects for models of the type we have in mind.

Biological Control of Bruchids in Stored Cowpea in West Africa

West Africa, cowpea, and bruchids

Many countries in West-Africa, especially in the Sahel region, have poor economies and a relatively low standard of living (measured by such criteria as Gross National Product per capita and life-expectancy at birth) (Barratt Brown, 1995: 151, Michel, 1996: A87). This region, where

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agriculture is one of the main activities (FAO, 1986, 16, Ben Yahmed, 1993), is a main area of cowpea production (FAOSTAT Internet database, Ben Yahmed, 1993, Nwokolo & Ilechukwu, 1996) Cowpea (*Vigna unguiculata* Walp) is an important source of protein for low income families (Nwokolo, 1996, Van Alebeek, 1996) Cowpea, like sorghum, millet and maize, is stored during the dry season. In rural areas, cowpea is normally stored on-farm in traditional granaries, which are made of natural materials such as wood, straw, and clay (Sagnia & Schutte, 1992, Koné, 1993) Cowpeas are often stored as whole-pods, and only when needed for consumption or for sale, they are threshed and stored as grains in smaller containers (e.g., clay jars) Typically, a subsistence farmer stores several hundred kilograms of cowpeas (Sagnia & Schutte, 1992) Cowpeas are not only stored for home consumption but also for the market, as the price of cowpea increases towards the end of the storage season (Caswell, 1974, Sagnia & Schutte, 1992)

Unfortunately, stored cowpea is often heavily attacked by bruchids, of which *Callosobruchus maculatus* Fab (Coleoptera: Bruchidae) is the most important one (Jackai & Daoust, 1986, Singh et al., 1990) The bruchid infestation starts in the field, where adult females lay single eggs on ripening pods Larvae that emerge from these eggs penetrate the seeds, in which they develop and pupate The adult emerges through an emergence hole in the bean The total development time is approximately three weeks at 32°C Adult females live for about a week, during which they may lay some 100 eggs Populations of *C. maculatus* can grow rapidly in stored cowpea After several months of storage, the stock may be totally destroyed due to the larval feeding

The nutritional value and the quality of stored beans decline as a result of bruchid infestation (Modgil & Mehta, 1994, 1996) Although it is difficult to determine exact losses (Boxall, 1991), quantitative losses are also severe The loss to bruchids in northern Nigeria in terms of weight has been estimated at 3.5–4% per year (Caswell, 1981) This corresponds to approximately 20–30% of the beans being infested Weight losses in stored beans in Ghana after five months of storage were as high as 20 or 45%, depending on whether the beans were stored unthreshed or shelled, respectively (Adams, 1977, Schulten, 1982)

Control methods

A large variety of control methods against bruchids in stored cowpea is known (Van Huis, 1991, Sagnia & Schutte, 1992, Lienard & Seck, 1994) They are aimed at either preventing bruchid infestation, eliminating or minimizing bruchid populations, or a combination of these effects. The control methods can be roughly divided into three categories: traditional methods, chemical methods and

alternative methods

Traditional methods comprise among others the use of inert materials such as sand and wood-ash, and the use of plant materials with insecticidal or insect-repellant action (Javaid & Ramatlapapela, 1995, Apuuli & Villet, 1996, Ofuya, 1986) Although these methods are often effective, they are generally laborious and not suitable for large quantities (e.g. Taylor, 1975, Compton et al., 1993) Some methods require a lot of labour when labour demand is already high because of the harvest. In addition, some 'natural insecticides' may have chronic negative effects on human health (Schulten, 1991, Compton et al., 1993)

Chemical control methods equally have several disadvantages. Some pesticides do not kill all the larvae and pupae inside the seeds, while they do kill the natural enemies of the bruchids, which are often more sensitive to insecticides (Caswell, 1973, Haines, 1984, Brower et al., 1996) In addition, pesticides are expensive for subsistence farmers, and not always available (Lienard & Seck, 1994) Moreover, farmers are generally not trained in the use of pesticides, this results in a low efficacy of their use and an increased health risk (Schulten, 1991, Dinham, 1993, Compton et al., 1993, Schwab et al., 1995, Udoh, 1998)

Alternative methods of control, such as storage of beans in hermetically closed plastic bags or oil drums, have shown promising results (Caswell, 1974, Lienard & Seck, 1994) Hermetically closed storage suffocates insects within a relatively short time. However, to most Sahelian farmers, empty oil drums or a sufficient number of strong plastic bags are as yet not available or too expensive (S. Sagnia, and A. Adandonon, personal communications, C. Stolk, personal observation, Gahukar, 1994) Another disadvantage of plastic bags is that they have to be stored in such a way that they cannot be damaged by e.g. rodents, as even a small hole in the bag will nullify the suffocating effect. This is probably hard to achieve. Even the bruchids themselves may sometimes perforate plastic bags (Lienard & Seck, 1994) It may also prove difficult to prevent re-infestation if the bags are opened frequently for the purpose of selling beans.

For many farmers no adequate method of control of bruchid pests in cowpea is therefore available. What is needed is a sustainable method of control that is (1) effective, (2) practically and economically feasible, (3) environmentally safe, and (4) flexible within a changing social and agricultural environment. Biological control of bruchids may meet all these requirements.

Biological control

The most important natural enemies of bruchids of cowpea are parasitoids. Larval parasitoids (*Dinarmus basalis* and *Eupelmus* spp.) and egg-parasitoids (*Uscana* spp.) have been proposed as candidates for biological control of bruchids in tropical storage (Monge & Hugnard, 1991) We

concentrate on *Uscana lariophaga* Steffan (Hymenoptera Trichogrammatidae). Egg parasitoids have the advantage that they kill their host already before it has done any damage (contrary to larval parasitoids).

U lariophaga is indigenous to West Africa. In the field and in storage it is responsible for a substantial amount of mortality of *C maculatus* (Lammers & Van Huis, 1989, Sagnia, 1994). Its life-history, functional response and host location have been investigated in the laboratory (Van Alebeek, 1996). We are investigating possibilities to increase the impact of *U lariophaga* on *C maculatus* populations, using a 'conservation strategy' of biological control. This strategy is aimed at conserving the populations of natural enemies that are already present in the system (rather than introducing exotic natural enemies, or producing and regularly releasing large numbers of natural enemies) (Arbogast, 1984, Van Huis, 1991, Van Huis et al., 1991, Waterhouse, 1992). Conservation biological control is especially interesting for resource-poor farmers (Waterhouse, 1992). In this particular case, promising options are (Van Alebeek, 1996): (1) manipulating the storage environment, such that conditions for *U lariophaga* are optimized, (2) offering food to the adult parasitoids to enhance their longevity and fecundity, (3) inoculating the cowpea storage with *Uscana* from locally available resources, and (4) adding plants or plant extracts to the stored beans which kill or repel the bruchids but do not harm the natural enemies. These strategies can of course be combined, for example, plant extracts (option 4) and *Uscana* (option 3) could be added at the same time. The four options, and the possible role of simulation modelling, are discussed below.

(1) Manipulation of the storage environment. Temperature is one of the main driving forces of insect development and population dynamics. Insect species differ in their temperature responses. It is therefore possible that at certain temperature regimes, a natural enemy performs relatively better, and its host worse, than at other temperatures. A simulation model, based on experimentally determined temperature-dependent development rates of both host and parasitoid, could help establish whether such a temperature regime exists. If it exists, it would be worthwhile to investigate whether such temperatures can be achieved by simple changes in the placement and construction of traditional granaries (Van Huis et al., 1994). For example, a granary can be placed in the shadow or in the sunlight (Van Huis et al., 1994), or a roof which allows for increased ventilation in the granary could be constructed (J. Mumford, personal communication, see also Haines, 1984). Meanwhile, Van Huis et al. (1994) have shown that, when *U lariophaga* is offered an excess of eggs, its r_m value at 35°C is double the value at 20°C, while the r_m of *C maculatus* remains constant and is always

below that of *U lariophaga*. However, when the availability of bruchid eggs is limited, the r_m value of *U lariophaga* may be lower.

(2) Offering food to parasitoids. Access to honey increases the fecundity of *Uscana lariophaga* by three times, and its longevity by five times, as compared to parasitoids that are starved (Van Huis et al., 1991). If such a result could be achieved in storage, it would probably exert influence on the bruchid population (see Wakers, 1998, Wakers, in prep.). Whether enhanced pest control as a result of additional food is to be expected, and how much the longevity and fecundity should be increased in order to obtain an adequate effect, can be assessed using a computer simulation model. If simulations indicate that feeding the parasitoids has a sufficient negative effect on the bruchid populations, 'field' experiments could be set up in order to test this prediction. However, practically feasible ways of administering food to the parasitoids should be found.

(3) Inoculating the cowpea storage with *Uscana*. There are many bruchid species which infest pulses of leguminous trees (e.g. Woegan, 1995). Those bruchids are not associated with cowpea, and many have only a few generations per year. The same bruchids are also hosts to *Uscana* spp., which in turn are also capable of attacking the bruchids of cowpea (A. Van Huis, C. Schutte & S. Sagnia, unpublished results). These resources of natural enemies could be used in bruchid control by adding pulses of these trees to cowpea stocks, at a time when the bruchid population is most vulnerable to an increased density of parasitoids. Farmers could even set up small temporary rearings of natural enemies, based on this leguminous plant material, and release them into their granary. Leguminous trees are relatively abundant in the dry Sahel zone, and farmers are familiar with these trees because they use the leaves for medical purposes, flavouring food, and as food protectants, and the pulses are used as animal feed (D. K. Kossou, personal communication). Rearing of parasitoids at village level is feasible, as demonstrated by farmers in Mexico who rear parasitoids for the control of the coffee berry borer (Galvez, 1992). Rearing of parasitoids on bruchids in pulses from leguminous trees is currently under investigation in Togo (I. A. Glitho & S. F. Bolevane, personal communication). Computer simulations, together with data obtained from population-dynamics experiments, could help decide at which time in the storage season inoculations with parasitoids are most likely to be effective, and how many parasitoids should be used. These predictions can then be tested in experimental granaries.

(4) Dried leaves and other parts of many plants are used in traditional control methods. Some of these plant products may not be harmful to the parasitoids of bruchids, depending on the properties of the plant species. The parasitoid population that is left behind after treatment with these

products might be able to prevent resurgence of the beetle population. This can be tested with a model, based on mortality data of both host and parasitoid. This option is especially interesting in combination with inoculation of granaries with *Uscana*.

Research questions

From the above, it appears that questions like, 'At which moment during the storage season should granaries be inoculated with extra natural enemies in order to be effective in biological control?', and 'Can additional food to natural enemies reduce the damage inflicted by bruchids?' are of practical relevance.

However, other questions have also emerged from work on this system. These questions are more fundamental in nature, but they are also important for our understanding of the level of control *U. lariphaga* may offer. For instance, in the absence of food, *U. lariphaga* has a very short adult longevity and generation time compared to *C. maculatus*. At 30°C and without access to food, *U. lariphaga* has an adult longevity of 1–2 days and a generation time of 8 days, while adults of *C. maculatus* live about a week, and their generation time is approximately 3 weeks. This implies that, if *C. maculatus* populations would occur in age cohorts which are more than two weeks apart, extinction of *Uscana* in those communities is likely to occur (Van Alebeek, 1996, Van Huis et al., submitted). Separate age cohorts may occur in insect populations as a result of activity of larval parasitoids (Godfray & Hassell, 1987, 1989), or as a result of a differential response to relatively low temperatures of different immature stages. The question is whether this occurs in *C. maculatus* populations in stored cowpea. Such temporal separation of generations would have important implications for the expected results of *Uscana* as a biological control agent. Another question is whether the metabolic heat that is developed by the beetles (larvae and adults) is of such a magnitude that it affects the developmental time of the both the beetles themselves and the parasitoids. There are indications that this might be the case (Van Huis et al., submitted). If it is, it should be taken into account in predictions of the efficacy of biological control. We will get back to this in the final section.

Models with a Theoretical and with a Practical Aim

Models of stored-product pests have been developed from two quite different backgrounds. Theoretical biologists have used stored-product insects for studies of population dynamic phenomena and the mechanisms that are responsible for those phenomena. They have developed mathematical models that describe these processes (Mertz, 1972).

Questions that are central to theoretical ecology are, 'What causes oscillations in population density?' and 'what causes populations of a host and a parasitoid to coexist?' Stored-product insects (especially *Tribolium* and *Callosobruchus* species) have often been used in ecological studies because they show interesting population dynamics, they are easy to rear, easy to handle, and because their biology is well-described (Mertz, 1972, Hassell et al., 1989, Throne, 1995). Moreover, the larvae of many bruchid species use a discrete food resource to feed upon, which is selected by their mother (as in parasitoids). This has provoked studies on optimal foraging and life-history evolution in these species (Wilson, 1988, 1994, Messina, 1991, Sibly et al. 1991, Colegrave, 1994, Horng, 1994). In this paper we will emphasize 'ecological' and population dynamical models because they are more relevant to the issue of biological control in storage. The models that are used in theoretical ecology are mainly analytical, explanatory models that contain biologically meaningful parameters which are incorporated into mechanistic relationships. These models mainly yield qualitative predictions.

Researchers that are interested in control of stored-product pests, on the other hand, have also developed models that simulate the development of insect populations in stored grain (Throne, 1995). However, these 'pest management' models have been developed to answer questions like, 'Can we expect a pest to develop in a grain storage with these specific initial conditions?' and 'When should a storage manager start cooling his grain?' (e.g. Thorpe et al., 1982, Sinclair & Alder, 1985, Maier et al., 1996, Flinn et al., 1997, Woods et al., 1997). These models are mainly phenomenological, designed in order to accurately and quantitatively predict population development, based on accurate sampling and temperature and humidity data from the grain store. They are almost always simulation models, and often draw upon empirical relationships. Temperature is often included as a driving variable, and developmental rates depend on ambient temperature. Models of this type can also be incorporated into 'expert systems' or other 'decision support' tools (see e.g. Norton & Mumford, 1993). These are software products which help the storage manager decide what he should do to prevent or control insect infestations in the stored product. Models have been developed for most insect pests that are of importance in grain storage in industrialized countries.

The models that have been developed in both disciplines (theoretical and practical) are generally very different in purpose and appearance. Historically, both types of models have been labeled 'strategic' and 'tactic', respectively (Nisbet & Gurney, 1982). In the next two sections, we will discuss the models in both categories in more detail. Subsequently, we will focus on the relevance of the existing

models to the subject of our interest. The literature on 'theoretical' models of stored-product pests has also partly been reviewed by Mertz (1972) and Throne (1995). The literature on 'practical' simulation models has been reviewed by Longstaff (1991) and Throne (1995). The use of expert systems and decision support in stored product protection has been discussed by Wilkin & Mumford (1994) and Longstaff (1997). For an explanation of some basic terms we refer to textbooks and general papers on modelling in biology (e.g. Rabbinge et al., 1989, Renshaw, 1991, Brown & Rothery, 1994).

Models from Theoretical Ecology

Theoretical ecology models are here defined as those that deal with the question, 'What regulates the dynamics of population densities?' Many different mechanisms have been proposed to explain oscillations in population densities, or the absence of them. Three major ones can be distinguished (either alone or in combination): Density-dependent processes, interactions with natural enemies, and spatial heterogeneity.

Density-dependent reproduction and survival

Density-dependent reproduction or survival has been included in many models to account for the fact that population growth is not unlimited (Hassell, 1975). At high population densities, mortality rates increase and/or reproduction rates decrease. However, density-dependent processes can also create interesting oscillations in population size. These oscillations tend to disappear after some time, unless there is a time-lag associated with the density-dependent relationship (Hastings & Constantino, 1987, Shimada & Tuda, 1996). In such so-called delayed density-dependent systems, one life stage exerts at high densities a negative effect on another life stage, rather than on its own life stage (e.g. adults eating juveniles when adult densities are high). This creates a time-delay in the effect of high densities, because it takes some time for the cohort of affected life stages (e.g., the juveniles) to develop into the cohort which can itself produce density-dependent effects (e.g., the adults). The oscillations in delayed density-dependent systems typically have a period of two to four times the maturation period (Gurney & Nisbet, 1985). However, direct density dependence may in some cases also produce strong fluctuations (Gurney & Nisbet, 1985). They can be distinguished from delayed density dependence because they have a period which approximately equals the maturation period. We will discuss in this section some examples of both direct and delayed density dependence in stored-product pests.

Mathematically, density-dependent relationships are often of the form of the logistic difference equation, or

modifications of it (Utida, 1967, Hassell, 1975, Shimada, 1989). However, the mechanism underlying such density-dependence is not always specified. These models do not give a strictly mechanistic explanation but rather a phenomenological description of processes observed at the population level (e.g. Utida, 1967, see Gordon et al., 1988). Explicitly formulated mechanistic density-dependent processes include cannibalism, competition for energy, nutrients and space, and a reduction in fecundity as a result of crowding. Note that these processes are not of the same integration level (Fig. 1), competition for energy, for instance, may result in a reduced fecundity. Cannibalism can be seen as a special form of competition.

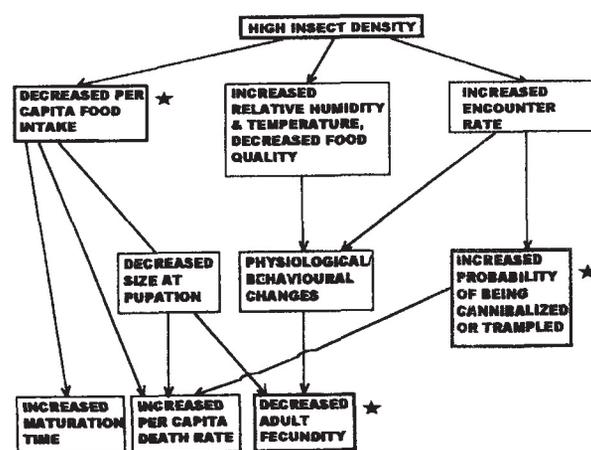


Fig. 1 Mechanisms that produce density-dependence in stored-product insect populations (partly based on Gurney & Nisbet, 1985). An asterisk (★) indicates the mechanisms which are treated in the text.

Cannibalism has mainly been studied in *Tribolium*, where mobile stages cannibalize on immobile and/or younger stages (Mertz, 1972, Desharnais & Liu, 1987, Hastings & Constantino, 1987). In *Tribolium*, cannibalism occurs randomly, such that the risk of being cannibalized increases at higher insect densities (Hastings & Constantino, 1987). There is convincing evidence that this is indeed responsible for fluctuations in densities of laboratory populations of *Tribolium*, although Fujii (1976) argued that food renewal schedules also create cyclicity, especially in the immature stages.

In the bruchid species *Callosobruchus chinensis* and *C. maculatus*, whose larvae develop inside a single bean, cannibalism does not play a role of any importance. Instead, density-dependent survival through competition between the larvae, and decreased reproduction as a result of crowding has received more attention in models of these species (Bellows, 1982a,b, Shimada, 1989, Tuda & Shimada, 1993, Tuda, 1993, Kuno et al., 1995, Shimada & Tuda,

1996) At high larval densities, the larvae compete for nutrients, energy and space (direct density dependence) At high adult densities, females lay fewer eggs, and eggs are damaged by trampling adults and because of toxic effects of the oviposition marker pheromone (delayed density dependence) (Bellows, 1982b, Oshima et al in Kuno et al , 1995) Although both processes contribute to damped oscillations or a monotonic approach towards a stable equilibrium density, only the increased egg mortality as a result of large numbers of old adults in overlapping-generation systems of *C. chinensis* prolonged the oscillations (Shimada & Tuda, 1996)

Gurney & Nisbet (1985) have shown that, if the effect of larval competition is expressed directly on the larvae themselves (direct density dependence), strong fluctuations with a period approximately equal to the maturation time can arise In other words, separate generations may occur in populations whose larvae suffer an increased death rate or maturation time at high larval densities Discrete generations in insect populations can therefore be an intrinsic property of the system, they are independent of external cues (such as food renewal schedule) or initial conditions They have been observed in experimental populations of the Indian meal moth, *Plodia interpunctella* (Gurney et al , 1983 in Gurney & Nisbet, 1985), and in models and experimental systems of *Callosobruchus* spp (Bellows, 1982a, Hassell et al , 1989)

Most of the models mentioned so far are capable of producing chaotic dynamics at certain parameter values However, Hassell et al (1976) have shown that in most single-species cases density-dependence will probably produce monotonic damping, rather than chaotic or unstable oscillations Indeed, the models discussed in this section, using realistic biological parameter values, show either a monotonic or oscillatory approach towards a stable equilibrium, or stable limit cycles Constantino et al (1995, 1997) have shown that quasiperiodic cycles and chaos, which is predicted by their model of *Tribolium* for certain parameter values, can be achieved by artificially imposing certain adult recruitment and death rates in laboratory population of *Tribolium*

Nuttall (1989) developed a very detailed model of the population dynamics of the stored product beetle *Ptinus tectus* His model illustrates the dynamic processes that have been treated in this section, including density dependence, delayed density dependence, and all types of fluctuations in population numbers

Interaction with a parasitoid or predator

Numerous studies have been devoted to the dynamics of systems with one or more herbivores and one or more natural enemies In contrast to the density-dependence literature, the question that is behind most herbivore-

natural enemy models is 'how can hosts and natural enemies coexist, or how can their populations become stable?' rather than 'how can population oscillations arise?' (Hassell & May, 1973, Reeve, 1990) Reviews of the literature on host-parasitoid models have recently been published (Godfray & Hassell, 1994, Jones et al , 1994, Mills & Getz, 1996) Although many of these models have not been developed specifically for stored-product systems, the theory is so general that it can be applied to such systems as well Here we will refer mainly to the reviews, in addition we will cite some examples from work on stored-product insects

Numerous mechanisms that promote stability have been identified (Reeve, 1990, Godfray & Hassell, 1994, Jones et al , 1994, Mills & Getz, 1996) For convenience we have combined the most important into four groups In general, stability or long-term coexistence of hosts and parasitoids is promoted by the following mechanisms

- 1 A relatively low efficiency of the parasitoid at low host densities (Godfray & Hassell, 1994) This can be related to learning behaviour of the parasitoid, or to refuges for the host Learning behaviour implies that parasitoids search more efficient at higher host densities, because they become familiar with this particular host Such parasitoids search less efficiently at low host densities Physical refuges provide shelter for a number of hosts, which also results in a reduced attack rate at low host densities However, host refuges need not be only physical Phenological and physiological refuges are also possible (Godfray & Hassell, 1994) Phenological asynchrony (the host emerges before or after the period in which parasitoids are active) results in a temporal refuge, and the term physiological refuge is used to indicate that some hosts may escape parasitism as a result of e.g. encapsulation of the parasitoid eggs These mechanisms, too, promote stability Low parasitoid efficiency at low densities of the host is graphically represented by a sigmoidal functional response curve
- 2 A relatively low efficiency of the parasitoid at high parasitoid densities (Hassell & May, 1973, Godfray & Hassell, 1994) At high parasitoid densities the encounters between parasitoids become more frequent, and this results in relatively fewer hosts being parasitized Even without physical encounters, many parasitoids notice the presence of conspecifics by chemical cues (Godfray & Hassell, 1994) It has been observed that this leads to a reduced net efficiency
- 3 Inclusion of more species (Jones et al , 1994) The introduction of an extra parasitoid or host species may contribute to stability Competition between a specialist and a generalist parasitoid, for instance, can result in a stable equilibrium where the interaction between the host and the generalist alone would not be

stable. Similarly, a system of two hosts and a parasitoid which switches to the host which is most abundant at any particular time is potentially stable

- 4 Spatial heterogeneity in host density, combined with environmental variation or variation in parasitoid attack (Reeve, 1990, Jones et al., 1994, Godfray & Hassell, 1994) Spatial heterogeneity or patchiness may contribute to stability of a system, because if the host and/or the parasitoid become extinct in one patch, the same patch can be colonized again in the next time step. Of the four mechanisms mentioned, this one is also a very powerful persistence-promoting mechanism (Jones et al., 1994). It may be the most important force behind coexistence in successful biological control situations (Beddington et al., 1978, Mills & Getz, 1996)

A general criterion for stability, based on these mechanisms, could be heterogeneity or variability in the risk of being parasitized (Godfray & Hassell, 1994). It should be noted, however, that stability also depends on the model context. Some of the mechanisms mentioned above do not create stability in discrete-time models (Nicholson-Bailey), while they do so for continuous-time models (Lotka-Volterra) (Reeve, 1990, Godfray & Hassell, 1994, Miss & Getz, 1996). This is due to the time-delay which is inherent to the discrete-time models. As was concluded in the previous section, delayed density dependence often creates instability.

Ecological theory concerning host-parasitoid relationships is illustrated by several examples with *Callosobruchus chinensis* and *C. maculatus*. Hassell et al. (1985) showed that *Anisopteromalus calandrae* and *Heterospilus prosopidis* both show inverse density dependence in an environment with patchily distributed hosts (the fraction of host larvae parasitized in a patch decreased with increasing host density in a patch). This was due to a lack of density-dependent aggregation of the parasitoid and a relatively low maximum attack rate per parasitoid within a patch. According to Hassell et al. (1985), this mechanism, like normal density dependence in a patchy environment, can contribute to persistence of the system. Hassell & May (1988) mention that *A. calandrae* and *C. chinensis* coexisted in a patchy experimental system, whereas the homogeneous system was unstable. The dynamics of both bruchid species and the larval parasitoid *Lariophagus distinguendus* were investigated in a model context by Bellows (1988). Tuda & Shimada (1995) did the same for *C. chinensis* and *H. prosopidis*. In both studies, age-structured models were used. The model of Bellows (1988) predicted erratic fluctuations which were similar to those found in laboratory systems. These fluctuations were the result of the age structure and complex interactions between parasitoid attack of host stages and competition between the

host themselves. Tuda & Shimada (1995) investigated the persistence of the host-parasitoid system at different temperatures. Persistence of host and parasitoid appeared to depend very precisely on ambient temperature.

Spatial processes in single-species systems

Compared to spatial aspects of the interaction between hosts and parasitoids, relatively little attention has as yet been paid to spatial aspects of single-species systems of storage pests. Hassell et al. (1989) investigated the stability of patchy systems with *C. maculatus* or *C. chinensis* in an experimental and model context. Stability appeared to depend on the reproduction rate and the spatial distribution of the females. A high reproduction rate, combined with little aggregation (low patchiness) results in instability of the system. A high degree of patchiness can cause the system to stabilize (and also results in a smaller population size due to unequal resource utilization combined with density-dependent effects). However, the experimental systems were all in the zone of damped oscillations, the degree of patchiness in this case had little effect on stability.

Tuzinkevich (1991) developed a model which could quantitatively predict the results of an experiment which Newman, Park & Scorr had carried out in 1956. In this experiment, the spatial distribution of *Tribolium* beetles in a cubic container, filled with flour, was studied. The highest concentrations of beetles occurred near the walls of the container, and near the surface of the flour mass. The model of Tuzinkevich (1991), of which basic features were mortality as a result of competition with nearby individuals, and random movement of beetles, described the experimental data well. He also discussed other models which had been developed to explain the observations.

There are many models that do not fit into any of the categories that have been discussed so far (e.g. Jones et al., 1990). However, the models described in this section show which aspects of storage pest ecology have received most attention.

'Pest Management' Models

Pest management models have been developed primarily by research teams in Australia, North-America and the United Kingdom (Throne, 1995). They deal mainly with storage of wheat, but also with storage of maize (Subramanyam & Hagstrum, 1991, Smith, 1994, Throne, 1994, Maier et al., 1996) or rice (Ryoo & Cho, 1988). Models that deal with other types of stored produce, such as fruit (Jang, 1996), are not considered here because the system is very different from cereal storage.

Most attention has been paid to five coleopteran pests, namely *Cryptolestes ferrugineus*, *Oryzaephilus*

sunnamensis, *Rhizopertha dominica*, *Sitophilus oryzae* and *Tribolium castaneum* (Table 2) These are the most important pests in grain storage in industrialized countries. Relatively little attention has been paid to lepidopteran storage pests.

The control techniques that have been considered in a model context include chemical, physical (e.g. aeration and cooling), cultural (e.g. harvest date, storage of resistant grain varieties), genetic, and biological control (Table 2). There is considerable attention for non-chemical control methods or environmentally and ecologically safe use of pesticides. This includes the prevention of resistance against pesticides in populations of stored-product pests (e.g. Longstaff, 1988). The use of natural enemies to control stored-product pests is considered in only two models, which are used to evaluate release strategies of *Auisopteronialus calandriae* against *Sitophilus zeamais* (Smith, 1994) and *Cephalonomia waterstoni* against *Cryptolestes ferrugineus* (Flinn & Hagstrum, 1995).

Temperature is included in most models as the main variable driving insect development. Many of these models can therefore be used for prediction of insect population growth based on actual temperatures measured in the granary. In addition, some models also predict the temperature inside the granary (e.g., at the center of the grain mass) based on ambient temperature and solar irradiation. The latter models include physical sub-models which describe the conduction of heat through a grain mass (e.g. Thorpe et al., 1982, Flinn et al., 1992, Maier et al., 1996, Woods et al., 1997). These physical models are not included in this overview, for a review see Jayas (1995).

Models which predict population size as a function of temperature normally incorporate models which predict rates of development, mortality, and oviposition as a function of temperature. These models are sometimes published separately (e.g. Hagstrum & Milliken, 1991). They are only included if it is clear that they were developed to be used in pest-management models.

Most models predict variables such as the number of insects present per kilogram of grain. In general, the 'practical' models are simulation models which are characterized by empirical relationships. Some exceptions to this rule include the parasitoid-host interactions in Smith (1994) and Flinn & Hagstrum (1995) which have features of mechanistic models, physical submodels, which are mechanistic and often also analytic, and models of Longstaff (1981, 1988) and Thorpe et al. (1982), in which an analytical approach to investigate pest-management issues was used. In addition, some models of insect development rate employ biochemically meaningful parameters which renders them mechanistic (e.g. Rvoo & Cho, 1988, Subramanyam & Hagstrum, 1991, 1993).

Many population models are incorporated into decision-support tools or expert systems (e.g. Kawamoto et al., 1992, 1992, for reviews and discussions see Longstaff, 1991, Wilkin & Mumford, 1994, Longstaff, 1997). Well-known examples include the Stored Grain Advisor (Flinn & Hagstrum, 1990b, 1991) and PestMan (Longstaff & Cornish, 1994). These are software packages that can be used on either a PC or Macintosh computer. They advise farmers which action to take based on such data as storage date, grain moisture, and insects found in grain samples. Some models are used as a teaching device for storage managers rather than an on-the-spot decision support tool (Norton, 1987, Maier et al., 1996, Mann et al., 1997).

Relevance of the Existing Models to Storage in Developing Countries, Particularly Stored Cowpea in West Africa

Aspects considered essential to tropical storage are (1) the specific pest organisms involved, (2) high temperatures and sometimes high humidity, which create an ideal environment for many pest insects (Jones et al., 1993, Haines, 1995), (3) socio-economic constraints, due to which grain cooling, the application of pesticides, and other techniques commonly used in industrialized countries are not feasible, (4) the impact of natural enemies on pest populations. All these aspects should be taken into account in a relevant model that can be used to develop a sound biological control strategy for stored-product pests in developing countries.

Pest organisms

In pest management models, most attention has been given to five coleopteran storage pests. However, the insects which cause most problems in developing countries are not necessarily the same (see Allotey, 1991, Khan & Mannan, 1991, Gahukar, 1994, Haines, 1995). For instance, after its introduction from Central America in the 1980s, *Prostephanus truncatus* (Coleoptera: Bostrichidae) has become a severe pest of stored maize in Africa (Boxall, 1991, Gahukar, 1994). Similarly, liposcelids (Psocoptera) seem to be a much bigger problem in tropical grain stores than in temperate zones (Haines, 1995). Finally, bruchids are known, no pest management model that deals with bruchids has yet been developed. However, a number of models that deal with bruchids have been developed in theoretical ecology (e.g. Bellows, 1982a,b, 1988).

High temperatures and high densities of insects

Many of the models that have been developed in

theoretical ecology take into account high densities of insects. This is not surprising, because theoretical ecologists are interested in the factors which regulate the dynamic size of a population. However, in these studies the densities of insects are generally so high that they are not relevant for (tropical) grain stores (see e.g. Hassell et al., 1989, Jones et al. 1990). Moreover, in the studies on *Tribolium* and *Callosobruchus*, the food source is typically renewed at regular intervals (e.g. Fujii, 1976, Hassell et al., 1989). This does not resemble a normal storage situation: the storage manager, on the other hand, wants to control pest populations below levels which are of interest of theoretical ecologists. As a consequence, the typical pest management model deals primarily with insects at very low densities where population dynamic processes are qualitatively different from those at higher densities.

Temperatures in cowpea granaries in West Africa can exceed 40°C (Van Huis et al., submitted, C. Stolk et al., unpublished results). These temperatures need not be lethal for the adult bruchids (see e.g. Heinrich, 1993) but mortality of the larvae may increase. Tuda & Shimada (1993) have shown experimentally and theoretically that a rather small increase in ambient temperature (from 30°C to 32°C) results in a significant decline in the equilibrium population size of *Callosobruchus chinensis*. This may be due to a decreased larval survival at 32°C compared to 30°C (Tuda, 1993). Tuda & Shimada (1995) have shown (both experimentally and in a model context) that the persistence of a larval parasitoid of this bruchid, *Heterospilus prosopidis*, is greater at 30°C than at 32°C. Additionally, their model predicted that the parasitoid would go extinct earlier at 28°C than at 32°C. These results suggest that relatively small differences in temperature may have a significant effect on biological control, as we referred to in the second section of this paper. Most practical pest-management models, however, are not validated for high temperatures.

Socio-economic constraints

Compton et al. (1992) and Jones et al. (1993) have developed an expert system for pest control in bagged maize in the tropics. This computer-based model is intended for large-scale stores (Jones et al., 1993) and is not appropriate for Sahelian subsistence farmers who store their cereals and beans privately. The lack of financial means and the poor state of infrastructure (electricity, roads) imposes constraints on the methods that can be used to control storage pests in these systems. The control methods that are considered in most pest management models are not appropriate in this case.

Rather than a decision support tool for farmers, we want to develop a model that enables researchers and possibly extension workers to e.g. select a natural enemy or a yearly 'release date' for the natural enemy which will prove most

effective in suppressing the pest populations.

Natural enemies

While a large part of theoretical ecology deals with natural enemies, the type of questions that is treated there are often not appropriate to storage conditions. For instance, the paradigm of an ecological equilibrium has dominated for the past decades (Mills & Getz, 1996). However, it is questionable whether the 'search for stability' can be justified from the viewpoint of pest control in stored product. It may be beneficial if the natural enemy and its host coexist at a very low equilibrium density in storage, but a high equilibrium density is obviously destructive to the stored product. Nonetheless, concepts and techniques which have been developed in theoretical ecology may be used in determining which aspects of a storage system need to be included in a simulation model. For instance, Godfray & Hassell (1987, 1989) show how natural enemies may create separate generations in tropical insect species. As mentioned in the second section of this paper, such distinct generations may limit the ability of *U. lamophaga* to suppress bruchid populations.

Natural enemies have only been considered in a pest-management model in two cases (Table 2). However, there is now increased attention for biological control in stored products in industrialized countries (Arbogast, 1984, Brower et al., 1996). This may accelerate the development of pest management which incorporate natural enemies.

Conclusions and Perspectives for the Future

There is a distinction between models from theoretical ecology and pest management models in terms of the type of questions and the methods they employ (Fig 2). Both approaches have proven to be very useful and fruitful areas of research, and in order to be able to develop guidelines for biological control in traditional storage in industrialized countries, we need to combine the 'ecological realism' of theoretical ecology with the accurate, quantitative predictions of pest management models. Existing pest-management models have mainly been constructed for use in industrialized countries. They do mostly not entail natural enemies, while these are important for stored-product protection in developing countries. Natural enemies of stored-product pests are firmly embedded in ecological theory, however, the type of research questions and predictions that are yielded by these models do not meet the needs of people who are interested in practical biological control in developing countries. The same is true for other aspects that are specific to traditional storage in developing countries.

MODEL FEATURES ↓	MODEL AIM →	THEORETICAL ECOLOGY QUALITATIVE PREDICTIONS	PEST MANAGEMENT QUANTITATIVE PREDICTIONS
<ul style="list-style-type: none"> •NATURAL ENEMIES •HIGH INSECT DENSITIES •MECHANISTIC RELATIONSHIPS 			RELEVANT FOR TROPICAL STORAGE
<ul style="list-style-type: none"> •NO NATURAL ENEMIES •LOW INSECT DENSITIES •EMPIRICAL RELATIONSHIPS 		(e.g. exponential growth)	

Fig. 2 A model that quantitatively predicts the result of different management practices, aimed at conserving the natural enemies in a tropical storage system is not available. Requirements are: Incorporation of natural enemies, validation for high temperatures, and probably incorporation of mechanistic relationships.

We favour a model approach that combines the best of both worlds. However, that does not mean that we propose a 'model of everything' in which all possible interactions are mechanistically modelled. Rather, we have in mind a situation in which for instance a more qualitative analysis is used to help decide which processes are important to the system and should be incorporated into the 'quantitative' model. In this quantitative model, use can be made of concepts that have been developed in theoretical ecology, e.g. the importance of spatial heterogeneity and of variation between individuals. However, a pragmatic procedure to model processes, including the use of empirical relationships, may sometimes be followed. An example of a model which successfully integrates concepts from theoretical ecology with quantitative predictions, is the individual-based, stochastic model of biological control of the greenhouse whitefly *Trialeurodes vaporariorum* in tomato greenhouses with the parasitoid *Eucarsia formosa* (Van Roermund et al., 1997).

Apart from advocating the incorporation of concepts and techniques from theoretical ecology into pest management models, we also argue that theoretical ecology itself may benefit from more cross-fertilization with pest-management practitioners. Several aspects of the biology of stored-product pests are interesting from both points of view, but have as yet received little attention from theoretical ecologists. Two examples are metabolic heat production of stored-product insects, and evolution of stored-product insects.

Stored-product pests, like all organisms, produce metabolic heat. Since this heat can be retained by the grain

mass, metabolic heat production sometimes results in so-called 'hot spots' in grain (Howe, 1943, 1962, Sinha & Wallace 1966). In such hot spots, insects and fungi develop more rapidly, causing severe deterioration of the grain quality. The amount of metabolic heat production under different circumstances has been measured in several stored-product pests (e.g. Cofie-Agblor et al., 1995, 1996). Longstaff (1991, 1997) and Throne (1995) have both pointed out the need to incorporate the influence of metabolic heat production on grain temperature models of stored-product protection. Nevertheless, a robust model that predicts insect population growth and heat production based on ambient temperature and initial grain conditions is not yet available. Such a model would both be useful for the development of pest-management models, and interesting from a theoretical point of view. It would be useful because it could help decide whether the heat generation for a given insect species and climatic range is such that it should be incorporated into a pest management model, and if it should be incorporated it will give an idea of how it can be incorporated. It would be interesting because metabolic heat production is normally regarded as loss of energy, while in the case of stored-product insects it may actually accelerate population growth. The situation becomes even more complex if we consider the fact that superoptimal or lethal temperatures are sometimes reached, causing emigration of the adults or increased mortality of the immobile stages present in the hot spot (Howe, 1943, see also Tuda, 1993).

The other example is the question as to what extent stored-product pests and their natural enemies have been able to adapt themselves in an evolutionary sense to the storage environment. While some attention has been paid to evolution of storage pests (Imura, 1990, Credland, 1991, Smith, 1991, Via, 1991), almost nothing is known about the possible adaptation of natural enemies of these insects to the storage environment. Storage of food products as practiced today is probably a relatively young phenomenon (Levinson & Levinson, 1994, 1996). However, evolution of life-histories may occur rapidly (e.g. Reznick et al., 1997). Whether such adaptation occurs or has occurred depends among others on whether a 'field' population (on wild and cultivated plants) of the species involved still exists, and if it does, to which degree field-populations of the insect contribute to the gene pool of the species. However, little is known about field populations of storage pests (Throne, 1995). It is possible that individuals of typical storage pests (and their natural enemies) that are found in the field, are merely emigrants of storage populations, and that they contribute little to the gene pool in the next generation. The opposite is also possible: 'Storage' populations are always founded by 'field' individuals. Intermediates between these two extremes are

also possible 'Filed' individuals regularly enter storages and interbreed there with 'storage' individuals. Knowledge about the evolution of storage pests and their natural enemies could give important information concerning (biological) control of storage pests.

Several insects develop easily on stored cereals and pulses. For that reason, they are both a nuisance to the storage manager, and an opportunity to the scientist who seeks to understand population ecology. Storage managers and theoretical ecologists need collaborate for safe and effective control of those insects in storage. As Haines (1995) has pointed out, a thorough analysis of the ecology of tropical stored-product pests is needed if we want to control those pests. Natural enemies will have to be included in such an analysis for the development of biological control of stored-product pests in developing countries.

Acknowledgements

We thank Frank van den Bosch, Joop van Lenteren and PhD students of the Laboratory for Entomology for valuable comments on previous versions of this paper. Many of the ideas presented in this paper have emerged from the work of Frans van Alebeek. We thank Felix Wackers for interesting discussions. Gerard Pesch assisted with the literature references. Use was made of a literature database which was previously maintained by Frans van Alebeek.

References

- Adams, J. M. 1977. A review of the literature concerning losses in stored cereals and pulses, published since 1964. *Tropical Science* 19: 1–28.
- Allotey, J. 1991. Storage insect pests of cereal in small scale farming community and their control. *Insect Science and Its Application* 12: 697–693.
- Apuuli, J. K. K. and Villet, M. H. 1996. The use of wood ash for the protection of stored cowpea seed (*Vigna unguiculata* (L.) Walp.) against Bruchidae (Coleoptera). *African Entomology* 4: 97–99.
- Arbogast, R. T. 1984. Biological control of stored-product insects: status and prospects. In F. J. Baur (ed.), *Insect management for food storage and processing*. The American Association of cereal chemists, St. Paul, Minnesota, U.S.A. pp. 226–238.
- Barratt Brown, M. 1995. Africa's choices. After thirty years of the World Bank. Penguin Books, London, U.K. (etc.) 443p.
- Beddington, J. R., Free, C. A. and Lawton, J. H. 1978. Characteristics of successful natural enemies in models of biological control of insect pests. *Nature* 273: 513–519.
- Bellows Jr., T. S. 1982a. Analytical models for laboratory populations of *Callosobruchus chinensis* and *C. maculatus* (Coleoptera, Bruchidae). *Journal of Animal Ecology* 51: 263–287.
- Bellows Jr., T. S. 1982b. Simulation models for laboratory populations of *Callosobruchus chinensis* and *C. maculatus*. *Journal of Animal Ecology* 51: 597–623.
- Bellows Jr., T. S. and Hassell, M. P. 1988. The dynamics of age-structured host-parasitoid interactions. *Journal of Animal Ecology* 57: 259–268.
- Ben Yahmed, B. (ed.) 1993. L'atlas du continent africain. Jeune Afrique and Les Editions du Jaguar, Paris, France. 175p.
- Boxall, R. A. 1991. Post-harvest losses to insects: a world overview. In H. W. Rossmore (ed.), *Biodeterioration and biodegradation* 8: 160–175.
- Brower, J. H. and Tilton, E. W. 1975. Potential for control of *Cadra cautella* (Walker) by release of fully or partially sterile males. *International Journal of Applied Radiation and Isotopes* 26: 720–725.
- Brower, J. H., Smith, L., Vail, P. V. and Flinn, P. W. 1996. Biological control. In B. Subramanyam and D. W. Hagstrum (eds.), *Integrated management of insects in stored products*. Marcel Dekker, Inc., New York (etc.) pp. 223–286.
- Brown, D. and Rotherv, P. 1994. *Models in biology: Mathematics, statistics and computing*. John Wiley and Sons, Chichester, England. 688p.
- Campbell, A. and Sinha, R. N. 1990. Analysis and simulation modelling of population dynamics and bioenergetics of *Cryptolestes ferrugineus* (Coleoptera: cucujidae) in stored wheat. *Researches on Population Ecology* 32: 235–254.
- Caswell, G. H. 1973. The storage of cowpea. *Samaru Agricultural Newsletter* 15(2): 73–75.
- Caswell, G. H. 1974. The development and extension of nonchemical control techniques for stored cowpeas in Nigeria. *Proceedings of the First International Working conference on Stored Product Entomology*, Savannah, Georgia, U.S.A., October 7–11, 1974. pp. 63–67.
- Caswell, G. H. 1981. Damage to stored cowpea in the northern part of Nigeria. *Samaru Journal of Agricultural Research* 1: 11–19.
- Colegrave, N. 1994. Game theory models of competition in closed systems: Asymmetries in fighting and competitive ability. *Oikos* 71: 499–505.
- Compton, J. A. F., Tyler, P. S., Hindmarsh, P. S., Golob, P., Boxall, R. A., and Haines, C. P. 1993. Reducing losses in small farm grain storage in the tropics. *Tropical Science* 33: 283–318.
- Compton, J. A. F., Tyler, P. S., Mumford, J. D., Norton, G. A., Jones, T. H. and Hindmarsh, P. S. 1992. Potential for an expert system on pest control in tropical grain stores. *Tropical Science* 32: 295–303.
- Constantino, R. F., Cushing, J. M., Dennis, B. and

- Desharnais, R A 1995 Experimentally induced transitions in the dynamic behaviour of insect populations *Nature* 375 227–230
- Constantino, R F, Desharnais, R A, Cushing, J M and Dennis, B 1997 chaotic dynamics in an insect population *Science* 275 389–391
- Credland, P F 1990 Biotype variation and host change in bruchids: Causes and effects in the evolution of bruchid pests. In K Fuji, A M R Gatehouse, C D Johnson, R Mitchell and T Yoshida (eds), *Bruchids and legumes: economics, ecology and Coevolution*. Proceedings of the Second International Symposium on Bruchids and Legumes, Okayama, Japan, September 6–9, 1989 pp 271–287
- Cuff, W R and Hardman, J M 1980 A development of the Leslie matrix formulation for restructuring and extending an ecosystem model: the infestation of stored wheat by *Sitophilus oryzae* *Ecological Modelling* 9 281–305
- Desmarschelier, J M 1988 The relationship between wet-bulb temperature and the intrinsic rate of increase of eight species of stored-product coleoptera *Journal of Stored Products Research* 24 107–113
- Dinham, B 1993 *The pesticide hazard: A global health and environmental audit*. Zed Books, London and New Jersey 228p
- FAO 1986 *Atlas of African agriculture*. Food and Agriculture Organization of the United Nations, Rome 72p
- Flinn, P W and Hagstrum, D W 1990a Simulations comparing the effectiveness of various stored-grain management practices used to control *Rhyzopertha dominica* (Coleoptera: Bostrichidae) *Environmental Entomology* 19 725–729
- Flinn, P W and Hagstrum, D W 1990b Stored Grain Advisor: a knowledge-based system for management of insect pests of stored grain *AI Applications* 4 44–52
- Flinn, P W and Hagstrum, D W 1991 An expert system for managing insect pests of stored grain. In F Fleurat-Lessard & P Ducom (eds), *Proceedings of the Fifth International Working conference on Stored-product Protection*, Bordeaux, France, September 9–14, 1990 Vol 3 pp 2011–2017
- Flinn, P W and Hagstrum, D W 1995 Simulation model of *Cephalonomia waterstoni* (Hymenoptera: Bethyliidae) parasitizing the rusty grain beetle (Coleoptera: Cucujidae) *Environmental Entomology* 24 1608–1615
- Flinn, P W, Hagstrum, D W, Muir, W E and Sudavappa, K 1992 Spatial model for simulating changes in temperature and insect population dynamics in stored grain *Environmental Entomology* 21 1351–1356
- Flinn, P W, Hagstrum, D W and Muir, W E 1997 Effects of time of aeration, bin size, and latitude on insect populations in stored wheat: a simulation study *Journal of Economic Entomology* 90 646–651
- Fujii, K 1976 Simulation models for population dynamics of stored-product insects: A case study with *Tribolium* species. In *Proceedings of the Joint U.S./Japan Seminar on Stored-Product Insects*, Manhattan, Kansas pp 20–34
- Gahukar, R T 1994 Storage of food grains and insect control in developing countries *Insect Science and its Application* 15 383–400
- Galvez, G C 1992 El control biologico de la broca como una alternativa viable para centroamerica *Boletin de Promecafe* 57 6–11
- Godfray, H C J and Hassell, M P 1987 Natural enemies may be a cause of discrete generations in tropical insects *Nature* 327 144–147
- Godfray, H C J and Hassell, M P 1989 Discrete and continuous insect populations in tropical environments *Journal of Animal Ecology* 58 153–174
- Godfray, H C J and Hassell, M P 1994 How can parasitoids regulate the population densities of their hosts? *Norwegian Journal of Agricultural Sciences Supplement* 16 41–57
- Gordon, D M, Gurney, W S C, Nisbet, R M and Stewart, R K 1988 A model of *Cadra cautella* larval growth and development *Journal of Animal Ecology* 57 645–658
- Gurney, W S C and Nisbet, R M 1985 Fluctuation periodicity, generation separation, and the expression of larval competition *Theoretical Population Biology* 28 150–180
- Hagstrum, D W 1996 Monitoring and predicting population growth of *Rhyzopertha dominica* (Coleoptera: Bostrichidae) over a range of environmental conditions *Environmental Entomology* 25 1354–1359
- Hagstrum, D W and Flinn, P W 1990 Simulations: Comparing insect species differences in response to wheat storage conditions and management practices *Journal of Economic Entomology* 83 2469–2475
- Hagstrum, D W and Flinn, P W 1994 Survival of *Rhyzopertha dominica* (Coleoptera: Bostrichidae) in stored wheat under fall and winter temperature conditions *Environmental Entomology* 23 390–395
- Hagstrum, D W and Milliken, G A 1988 Quantitative analysis of temperature, moisture, and diet factors affecting insect development *Annals Entomological Society of America* 81 539–546
- Hagstrum, D W and Milliken, G A 1991 Modeling differences in insect developmental times between constant and fluctuating temperatures *Annals Entomological Society of America* 84 369–379
- Hagstrum, D W and Throne, J E 1989 Predictability of stored-wheat insect population trends from life-history

- traits *Environmental Entomology* 18 660–664
- Haines, C P 1984 Biological methods for integrated control of insects and mites in tropical stored products III The use of predators and parasites *Tropical Stored Products Information* 48 17–25
- Haines, C P 1995 Grain storage in the tropics In D S Jayas, N D G White and W E Muir (eds), *Stored-grain ecosystems* Marcel Dekker Inc., New York pp 55–99
- Hardman, J M 1978 A logistic model simulating environmental changes associated with the growth of populations of rice weevils, *Sitophilus oryzae*, reared in small cells of wheat *Journal of Applied Ecology* 15 65–87
- Hassell, M P 1975 Density-dependence in single-species populations *Journal of Animal Ecology* 44 283–295
- Hassell, M P and May, R M 1973 Stability in insect host-parasite models *Journal of Animal Ecology* 42 693–726
- Hassell, M P and May, R M 1988 Spatial heterogeneity and the dynamics of parasitoid-host systems *Annales Zoologici Fennici* 25 55–61
- Hassell, M P, Lawton, J H and May, R M 1976 Patterns of dynamical behaviour in single-species populations *Journal of Animal Ecology* 45 471–486
- Hassell, M P, Lessells, C M and McGavin, G C 1985 Inverse density dependent parasitism in a patchy environment a laboratory system *Ecological Entomology* 10 393–402
- Hassell, M P, Taylor, V A and Reader, P M 1989 The dynamics of laboratory populations of *Callosobruchus chinensis* and *C. maculatus* (Coleoptera: Bruchidae) in patchy environments *Researches on Population Ecology* 31 35–51
- Hastings, A and Constantino, R F 1987 Cannibalistic egg-larva interactions in *Tribolium* an explanation for the oscillations in population numbers *American Naturalist* 130 36–52
- Heinrich, B 1993 *The hot-blooded insects: Strategies and mechanisms of thermoregulation* Springer-Verlag Berlin (etc) 601 p
- Horng, S -B 1994 What is the oviposition decision rule by the bean weevil, *Callosobruchus maculatus* *Zoological Studies* 33 278–286
- Imura, O 1990 Life histories of stored-product insects In K Fuji, A M R Gatehouse, C D Johnson, R Mitchell and T Yoshida (eds), *Bruchids and legumes: economics, ecology and evolution* Proceedings of the Second International Symposium on Bruchids and Legumes, Okayama, Japan, September 6–9, 1989 pp 257–269
- Jackai, L E N and Daoust, R A 1986 Insect pests of Cowpeas *Annual Review of Entomology* 31 95–119
- Jang, E B 1996 Systems approach to quarantine security Postharvest application of sequential mortality in the Hawaiian grown ‘Sharwil’ avocado system *Journal of Economic Entomology* 89 950–955
- Javadi, I and Ramatlapakela, K 1995 The management of Cowpea weevils [*Callosobruchus maculatus* (Fabricius)] in Cowpea seeds by using ash and sand *Journal of Sustainable Agriculture* 7 147–154
- Jayas, D S 1995 Mathematical modeling of heat, moisture, and gas transfer in stored-grain ecosystems In D S Jayas, N D G White and W E Muir (eds), *Stored grain ecosystems* Marcel Dekker Inc., New York pp 527–567
- Jones, A E, Gurney, W S C, Nisbet, R M and Gordon, D M 1990 Food degradation as a mechanism of intraspecific competition among the larvae of secondary stored-product pests *Functional Ecology* 4 629–638
- Jones, T H, Hassell, M P and May, R M 1994 Population dynamics of host-parasitoid interactions In B A Hawkins and W Sheehan (eds), *Parasitoid community ecology* Oxford University Press, Oxford pp 371–394
- Jones, T H, Mumford, J D, Compton, J A F, Norton, G A and Tyler, P S 1993 Development of an expert system for pest control in tropical grain stores *Postharvest Biology and Technology* 3 335–347
- Kawamoto, H, Sinha, R N and Muir, W E 1992 computer simulation modelling for stored-grain pest management *Journal of Stored Products Research* 28 139–145
- Kawamoto, H, Sinha, R N and Muir, W E 1992 Ecosystem modelling to provide early warning of pest infestation of stored grain In F Fleurat-Lessard & P Ducom (eds), *Proceedings of the Fifth International Working conference on Stored-product Protection*, Bordeaux, France, September 9–14, 1990 pp 2019–2026
- Kawamoto, H, Sinha, R N, Muir, W E and Woods, S M 1991 Simulation model of *Acarus siro* (Acari: Acaridae) in stored wheat *Environmental Entomology* 20 1381–1386
- Kawamoto, H, Woods, S M, Sinha, R N and Muir, W E 1989 A simulation model of population dynamics of the rusty grain beetle, *cryptolestes ferrugineus* in stored wheat *Ecological Modelling* 48 137–157
- Khan, A R and Mannan, A 1991 Stored-products entomology in the tropics *Agricultural Zoology Reviews* 4 67–95
- Kone, S 1993 Traditional storage of farm products *ILEA Newsletter* 9(3) 12–13
- Kuno, E, Kozai, Y and Kubotsu, K 1995 Modelling and analyzing density-dependent population processes comparison between wild and laboratory strains of the bean

- weevil, *Callosobruchus chinensis* (L.) Researches on Population Ecology 37 165–176
- Lammers, P M and Van Huis, A 1989 *Uscana lariophaga* Steffan (Hym Trichogrammatidae), egg parasitoid of the stored insect pests *Callosobruchus maculatus* and *Bruchidius atrolineatus* Pic (Col Bruchidae) population studies in the field and in storage in Niger Proceedings Integrated Pest Management in Tropical and Subtropical Cropping Systems, Bad Dürkheim, Germany, February 8–15, 1989 Vol 3 pp 1013–1021
- Lienard, V and Seck, D 1994 Revue des méthodes de lutte contre *Callosobruchus maculatus* (F.) (Coleoptera Bruchidae), ravageur des graines de niébe (*Vigna unguiculata* (L.) Walp) en Afrique tropicale Insect Science and its Application 15 301–311
- Longstaff, B C 1981 The manipulation of the population growth of a pest species: an analytical approach Journal of Applied Ecology 18 727–736
- Longstaff, B C 1988 Temperature manipulation and the management of insecticide resistance in stored grain pests: a simulation study for the rice weevil, *Sitophilus oryzae* Ecological Modelling 43 303–313
- Longstaff, B C 1991 The role of modelling in the management of stored-product pests In F Fleurat-Lessard and P Ducom (eds), Proceedings of the Fifth International Working conference on Stored Product Protection, Vol 3, Bordeaux, France, 9–14 September 1990 pp 1995–2007
- Longstaff, B C 1997 Decision tools for grain storage pest management Journal of Stored Products Research 33 99–114
- Longstaff, B C and Cornish, P 1994 PestMan: A decision support system for pest management in the Australian central grain-handling system AI Applications 8 13–23
- Longstaff, B C and Cuff, W R 1984 An ecosystem model of the infestation of stored wheat by *Sitophilus oryzae*: a reappraisal Ecological Modelling 25 97–119
- Maier, D E, Adams, W H, Throne, J E and Mason, L J 1996 Temperature management of the maize weevil, *Sitophilus zeamais* Motsch (Coleoptera Curculionidae), in three locations in the United States Journal of Stored Products Research 32 255–273
- Mann, D D, Jayas, D S, White, N D G, Muir, W E and Evans, M S 1997 A grain storage information system for Canadian farmers and grain storage managers Canadian Agricultural Engineering 39 49–56
- Mertz, D B 1972 The Tribolium model and the mathematics of population growth Annual Review of Ecology and Systematics 3 51–78
- Messina, F J 1991 Life-history variation in a seed beetle: adult egg-laying vs Larval competitive ability Oecologia 85 447–455
- Michel, J H (ed) 1996 Development co-operation efforts and policies of the members of the Development Assistance committee 1995 report Organisation for Economic co-operation and Development 234 p
- Mills, N J and Getz, W M 1996 Modelling the biological control of insect pests: a review of host-parasitoid models Ecological Modelling 92 121–143
- Modgil, R and Mehta, U 1994 Effects of different levels of *Callosobruchus chinensis* (L.) infestation on proximate principles, true protein, methionine and uric acid contents of green gram and red gram Journal of Food Science and Technology 31 135–139
- Modgil, R and Mehta, U 1996 Effect of *Callosobruchus chinensis* (L.) (Coleoptera Bruchidae) on carbohydrate content of chickpea, green gram and pigeon pea Nahrung 40 41–43
- Monge, J P and Huignard, J 1991 Population fluctuations of two bruchid species *Callosobruchus maculatus* (F.) and *Bruchidius atrolineatus* (Pic) (Coleoptera Bruchidae) and their parasitoids *Dinarmus basalis* (Rondani) and *Eupelmus veulleti* (Crawford) (Hymenoptera, Pteromalidae, Eupelmidae) in a storage situation in Niger Journal of African Zoology 105 187–196
- Nisbet, R M and Gurney, W S C 1982 Modelling fluctuating populations John Wiley and Sons, Chichester, U K (etc) 379p
- Norton, G 1987 Developments in expert systems for pest management at Imperial college, U K Review of Marketing and Agricultural Economics 55 167–171
- Notron, G A and Mumford, J D (eds) 1993 Decision tools for pest management CAB International, Wallingford, U K 279p
- Nuttall, R G 1989, Simulated population dynamics of a stored-products' pest (*Ptinus tectus*, Coleoptera) Ecological Modelling 48 291–313
- Nwokolo, E 1996 The need to increase consumption of pulses in the developing world In E Nwokolo and J Smartt (eds), Food and feed from legumes and oilseeds Chapman & Hall, London pp 3–11
- Nwokolo, E and Ilechukwu, S N 1996 Cowpea (*Vigna unguiculata* (L.) Walp) In, E Nwokolo and J Smartt (eds), Food and feed from legumes and oilseeds Chapman & Hall, London pp 229–242
- Ofuya, T I 1986 Use of wood ash, dry chilli pepper fruits and onion scale leaves for reducing *Callosobruchus maculatus* (Fabricius) damage in cow-pea seeds during storage Journal of Agricultural Science (Cambridge) 107 467–468
- Rabbinge, R, Ward, S A and Van Laar, H H (eds) 1989 Simulation and systems management in crop protection Simulation Monographs, Pudoc, Wageningen, The Netherlands 420p

- Reeve, J D 1990 Stability, variability and persistence in host-parasitoid systems *Ecology* 71 422–426
- Renshaw, E 1991 Modelling biological populations in space and time Cambridge University Press 403p
- Reznick, D N, Shaw, F H, Rodd F H and Shaw, R G 1997 Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*) *Science* 275 1934–1937
- Ryoo, M I and Cho, K-J 1988 A model for the temperature-dependent developmental rate of *Sitophilus oryzae* L (Coleoptera Curculionidae) on rice *Journal of Stored Products Research* 24 79–82
- Sagnia, S B and Schutte, C 1992 Le système de stockage du niébe en milieu villageois dans l'état de Kano, Nigeria *Sahel PV Info* 46 6–15
- Sagnia, S B 1994 Mortality factors affecting *Callosobruchus maculatus* (F) (Coleoptera Bruchidae) under field conditions in Niger *Journal of Stored Products Research* 30 71–74
- Schulten, G G M 1982 Post-harvest losses in tropical Africa and their prevention *Food and Nutrition Bulletin* 4 (2) 2–9
- Schulten, G G M 1991 Stored-products protection in warm climates In F Fleurat-Lessard and P Ducom (eds), *Proceedings of the Fifth International Working Conference on Stored-product Protection*, Bordeaux, France, Sept 9–14, 1990 pp 1557–1570
- Schwab, A, Jager, I, Stoll, G, Gorgen, R, Prexler-Schwab, S and Altenburger, R 1995 Pesticides in tropical agriculture Hazards and alternatives Margraf Verlag, Weikersheim, Germany 281 p
- Shimada, M 1989 Systems analysis of density-dependent population processes in the azuki bean weevil, *Callosobruchus chinensis* *Ecological Research* 4 145–156
- Shimada, M and Tuda, M 1996 Delayed density dependence and oscillatory population dynamics in overlapping-generation systems of a seed beetle *Callosobruchus chinensis* *Matrix population model Oecologia* 105 116–125
- Sibly, R M, Smith, R H 1991 Evolutionary demography of a bruchid beetle IV Genetic trade-off, stability selection and a model of optimal body size *Functional Ecology* 5 594–601
- Sinclair, E R and Alder, J 1985 Development of a computer simulation model of stored product insect populations on grain farms *Agricultural Systems* 18 95–113
- Singh, S R, Jackai, L E N, Dos Santos, J H R 1990 Insect pests of cowpeas In Singh, S R (ed), *Insect pests of tropical food legumes* John Wiley and Sons, Chichester, UK (etc) pp 43–89
- Smith, L 1994 Computer simulation model for biological control of maize weevil by the parasitoid *Anisopteromalus calandrae* In E Highley, E J, Wright, H J Banks and B R Champs (eds), *Stored Product Protection, Proc 6th Int Working conf Stored-prod Prot, Vol II CAB Int*, Willingford, U K pp 1147–1151
- Smith, R H 1990 Adaptation of *Callosobruchus* species to competition In K Fuji, A M R Gatehouse, C D Johnson, R Mitchell and T Youshida (eds), *Bruchids and legumes economics, ecology and coevolution Proceedings of the Second International Symposium on Bruchids and Legumes*, Okayama, Japan, September 6–9, 1989 pp 351–360
- Subramanyam, B and Hagstrum, D W 1991 Quantitative analysis of temperature, relative humidity, and diet influencing development of the larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera Bostrichidae) *Tropical Pest Management* 37 195–202
- Subramanyam, B and Hagstrum, D W 1993 Predicting development times of six-stored-product moth species (Lepidoptera Pyralidae) in relation to temperature, relative humidity, and diet *European Journal of Entomology* 90 51–64
- Taylor, T A 1975 Effects of orange and grapefruit peels on *Callosobruchus maculatus* infestation of cowpea *Ghana Journal of Agricultural Science* 8 169–172
- Thorpe, G R, Cuff, W R and Longstaff, B C 1982 Control of *Sitophilus oryzae* infestation of stored wheat an ecosystem model of the use of aeration *Ecological Modelling* 15 331–351
- Throne, J E 1989 Effects of noncatastrophic control technologies that alter life history parameters on insect population growth a simulation study *Environmental Entomology* 18 1050–1055
- Throne, J E 1994 Life history of immature maize weevils (Coleoptera Curculionidae) on corn stored at constant temperatures and relative humidities in the laboratory *Environmental Entomology* 23 1459–1471
- Throne, J E 1995 computer modeling of the population dynamics of stored-product pests In D S Jayas, N D G White and W E Mur (eds), *Stored-grain ecosystems* Marcel Dekker Inc, New York pp 169–195
- Tuda, M 1993 Density dependence depends on scale, at larval resource patch and at whole population *Researches on Population Ecology* 35 261–271
- Tuda, M and Shimada, M 1995 Developmental schedules and persistence of experimental host-parasitoid systems at two different temperatures *Oecologia* 103 283–291
- Tuda, M and Shimada, M 1993 Population-level analysis on reduction in equilibrium population size of the azuki bean beetle *Researches on Population Ecology* 35 231–239
- Tuzinkevich, A V 1991 Modelling of spatial-temporal dynamics of the bisexual population of *Tribolium*

- confusum *Ecological Modelling* 58 185–198
- Udoh, A J 1998 Safety research study Nigerian farm household hazards *Pesticide News* 40 8–9
- Utida, S 1967 Damped oscillation of population density at equilibrium *Researches on Population Ecology* 9 1–9
- Van Alebeek, 1996 Foraging behaviour of the egg parasitoid *Uscana lariophaga* Towards biological control of bruchid pests in stored cowpea in West Africa PhD thesis, Wageningen Agricultural University, Wageningen, The Netherlands 176 pp
- Van Huis, A 1991 Biological methods of bruchid control in the tropics a review *Insect Science and its Application* 12 87–102
- Van Huis, A, Arendse, P W, Schilthuisen, M, Wieggers, P P, Heering, H, Hulshof, M and Kaashoek, N K 1994 *Uscana lariophaga*, egg parasitoid of bruchid beetle storage pests of cowpea in West Africa the effect of temperature and humidity *Entomologia Experimentalis et Applicata* 70 41–53
- Van Huis, A, Kaashoek, N K and Maes, H M 1991 Biological control of bruchids (Col Bruchidae) in stored pulses by using egg parasitoids of the genus *Uscana* (Hym Trichogrammatidae) a review In F Fleurat-Lessard & P Ducom (eds), *Proceedings of the Fifth International Working conference on Stored-product Protection*, Bordeaux, France, September 9–14, 1990 pp 99–108
- Van Huis, A, Schutte, and Sagna, S Submitted The impact of the egg parasitoid *Uscana lariophaga* (Hymenoptera Trichogrammatidae) on *Callosobruchus maculatus* (Coleoptera Bruchidae) and the damage to cowpea in a traditional storage system
- Van Roermund, H J W, van Lenteren, J C, and Rabbinge, R 1997 Biological control of greenhouse whitefly with the parasitoid *Encarsia formosa* on tomato an individual-based simulation approach *Biological control* 9 22–36
- Via, S 1991 Variation between strains of the flour beetle *Tribolium castaneum* in relative performance of five flours *Entomologia Experimentalis et Applicata* 60 173–182
- Wackers, F L 1998 Food supplements to enhance biological control in storage systems Effects of hosts and honey on the longevity of the bruchid parasitoids *Anisopeteromalus calandreae* and *Heterospilus prosopidis* In M J Sommeijer and P J Francke (eds), *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society (N E V)*, Amsterdam, The Netherlands, December, 1997 pp 47–52
- Wackers, F L In preparation The effect of food supplements on parasitoid-host dynamics in the tritrophic system of cowpea, *Callosobruchus chinensis* and *Anisopeteromalus calandreae*
- Waterhouse, D F 1992 Biological control a viable strategy for the tropics In P A C Ooi, G S Lim and P S Teng (eds), *Biological control issues in the tropics Proceedings of the biological control session, 3rd international conference on plant protection in the tropics held in Genting Highlands, Malaysia, 20–23 March, 1990* pp 1–13
- White, G G 1987 Effects of temperature and humidity on the rust-red flour beetle, *Tribolium castaneum* (Herbst) (Coleoptera Tenebrionidae) in Wheat Grain *Australian Journal of Zoology* 35 43–59
- Wilkin, D R and Mumford, J D 1994 Decision support systems for integrated management of stored commodities In E Highlight, E J Wright, H J Banks and B R Champ (eds), *Stored Product Protection Proceedings of the 6th International Working conference on Stored-product Protection*, CAB International, Wallingford, U K Vol 2 pp 879–883
- Wilson, K 1988 Egg laying decisions by the bean weevil *Callosobruchus maculatus* *Ecological Entomology* 13 107–118
- Wilson, K 1994 Evolution of clutch size in insects II A test of static optimality models using the beetle *Callosobruchus maculatus* (Coleoptera Bruchidae) *Journal of Evolutionary Biology* 7 365–386
- Woegan, A Y 1995 contribution au recensement de quelques le gummeuses spontanees, hotes de bruchidae en zone guineenne au Togo These DEA de Biologie de Developpement, University of Benin, Togo 53p
- Woods, S M, White, N D G and Sinha, R N 1997 Simulation of generation times of the rusty grain beetle, *Cryptolestes ferrugineus*, in farm-stored grain in the Canadian prairies, 1952–1990 *Researches on Population Ecology* 39 47–56