Great tits (*Parus major*) foraging for caterpillars contribute to biological control in apple orchards

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Chapter 1

General introduction

GENERAL INTRODUCTION

The damage caused by herbivores such as caterpillars is not only an important aspect of reproduction of plants, but also a major economic factor in the commercial growth of fruit. The extent to which the density of caterpillars can be effectively reduced by birds and the extent to which this can lead to a reduction of damage to commercial crops is poorly understood. It depends critically on the foraging behaviour of the insectivorous birds in the period during which damage is inflicted. These considerations led to the study reported on in this thesis, in which the foraging behaviour of the great tit (*Parus major*) was studied with particular emphasis on its potential role in reduction of damage in apple orchards.

To set the stage, I will first review the current situation of pest control in agricultural systems with emphasis on commercial apple growing and the role of birds in agricultural systems. Next I will review what is known and what needs to be known about foraging behaviour of birds to assess their role as biological control agents.

History of pest control and present status in apple orchards

Before the end of the nineteenth century farmers had no means to protect their crops against pests and diseases. It was only around World War II that DDT was discovered and used against a broad spectrum of insects. However, an increasing number of insects became resistant to DDT and the negative effect of DDT and related pesticides on predators higher up in the food web, such as birds and fish, became apparent in the nineteen-sixties. The first legislation on chemical control measures was merely aimed at ensuring that the chemical products would indeed terminate the insects they claimed to work against (Anonymous, 2002). It was only after the publishing of the book "Silent Spring" by the environmentalist Rachel Carson (1962) that discussion about the negative effects of pesticides on the environment and human health started. In the nineteen-seventies the legislation was adjusted and also aimed to reduce the negative effects of pesticides on the environment and human health as much as possible (Anonymous, 2002). As a consequence pesticide use was reduced.

In apple orchards a change in management away from regular application of broad-spectrum pesticides into so-called Integrated Pest Management (IPM) occurred around 1975. Pesticides were no longer applied at regular intervals but only if a certain control threshold was exceeded. This resulted in a decrease of insecticide application (Blommers, 1994). Furthermore, the implementation of biological control of phytophagous mites by predatory mites restricted the use of pesticides to those safe for predatory mites and, if possible, to other natural enemies. IPM has now become standard practice in most Dutch apple orchards (van den Ende *et al.*, 1996).

From the nineteen-seventies onwards, more and more attention has been paid to the use of natural enemies and biological control measures, such as plant substances, natural enemies (including bacteria and viruses) and disruption of mating by pheromones. In Organic Farming (OF) only these biological measures are used and no

synthetic pesticides, herbicides or chemical fertilisers are applied. Increased consumer awareness of food safety issues and environmental concerns has contributed to the growth in organic farming over the last few years. Given the adverse public attitudes to pesticides, the resistance of harmful insects to pesticides and the fact that legislation increasingly restricts the use of pesticides gives rise to renewed interests in natural enemies such as birds to help control pests in agricultural systems.

Birds as biological control agents in agricultural systems
In both farming systems, IPM as well as OF, natural enemies are used to control or suppress pest species in combination with other control measures. At present, the search for agents that can contribute to biological control is mainly focussed on parasitoids (Cross *et al.*, 1999) and predatory insects such as predatory mites, earwigs, lacewings, mirids and anthocorids (Solomon *et al.*, 2000). The usefulness of birds was investigated in several agricultural systems in the first half of the twentieth century (Kirk *et al.*, 1996). However, the study of contributions made by birds to population control was often anecdotal and was totally discarded after the appearance of broad-spectrum pesticides such as DDT until there was a renewed interest around the nineteen-seventies. Most studies show a reduction in insect population size due to foraging by birds. Quiring and Timmins (1988) studied the American crows, *Corvus brachyrhynchos* (Brehm), which reduced *c.* 50% of the overwintering European corn borer, *Ostrinia nubilalis* (Hübner), in southwestern Ontario without causing damage to crops themselves. Bendell *et al.* (1981) found redwinged blackbirds (*Agelaius phoeniceus* L.) preying on these larvae as well, but these birds caused more damage then that they prevented. Flocks of the Oregon junco, *Junco hyemalis*, predating on pear psyllas (*Cacopsylla spp.*) caused a sizeable reduction although the relative significance was questioned due to the relative small segment of the psylla population overwintering in orchard leaf litter (Fye, 1982). Several authors (Glen & Milsom, 1978; MacLellan, 1958, 1959; Solomon & Glen, 1979; Solomon *et al.*, 1976; Subinprasert, 1987; Wearing & McCarthy, 1992; Zajac, 1979) report that birds reduce survival of mature larvae of codling moth, *Cydia pomonella* L. in autumn and winter. Some studies show a reduction in plant damage caused by leaf-chewing insects (Atlegrim, 1989; Greenberg *et al.*, 2000; Marquis & Whelan, 1994; Spiller & Schoener, 1990). But an increase in biomass production of plants, which were less damaged by herbivores in the following year, was not found (Strong *et al.*, 2000). In forestry studies, the main conclusion is that birds generally are not able to break down insect pests, but they can be important in preventing insect outbreaks (Bruns, 1960; Otvos, 1979; Tinbergen, 1960).

   Although most of these studies show the potential of birds to act as control agents by reducing the population sizes of harmful insect species, they do not link the reduction in population numbers to actually achieved reduction in crop damage. Here lies one of the challenges in this field of research to directly link damage reduction to the reduction of insect populations by birds in agricultural systems.

Great tits as a biological control agent in apple orchards

A good model system to directly investigate the effect of birds on damage reduction in an agricultural system is the reduction of caterpillar damage in apple orchards by great tits. One of the key pests in apple orchards are caterpillars of winter moths *Operophtera brumata* L. and tortricid moths (Cross *et al.*, 1999; Solomon *et al.*, 2000). These caterpillars cause a distinct type of damage to apples in spring, which is characterised by corked scar tissue on the apple harvested in autumn. Reduction of this type of damage can therefore easily be assessed.

The great tit has a number of features that make it suitable to act as a control agent for caterpillars in orchards. They are largely insectivorous birds with a preference for caterpillars, especially when feeding their nestlings (Betts, 1955; Gibb & Betts, 1963; Gruys, 1982; Naef-Daenzer *et al.*, 2000; Royama, 1966; van Balen, 1973). The nestling rearing period, when the number of prey items caught is high, coincides with the time that caterpillars occur in orchards. The great tit is also a common species that breeds readily in nest boxes, and hence the local density of great tits can be increased easily by putting up nest boxes in orchards. The modern growing type of apple trees, i.e. spindle bush trees, does not hinder great tits to breed in these surroundings.

The orchard system does not only supply an environment where the direct effect of great tits on damage reduction can be tested, but also provides an opportunity to study the foraging behaviour of great tits in more detail. The orchard system with its uniform positioned apple trees is simpler than forests and has a limited number of available prey of which the density can be assessed with reliable methods. Furthermore, the resulting caterpillar damage to the apples can be used to test the predicted foraging behaviour of great tits**.**

Foraging behaviour: where, what and how many

To explain and predict the effect of great tits on the reduction of caterpillar damage in apple orchards, insight is needed in the foraging behaviour of great tits. Three aspects of foraging behaviour are important in the context of this study. To be effective in reducing caterpillar damage in orchards great tits should preferably forage within the orchard, provide their nestlings mainly with caterpillars (i.e. the pest species) and remove a high quantity of caterpillars.

One of the tools to predict where animals should forage are optimal foraging models. For cases in which a forager has to bring food back to a fixed location, such as a nest, Orians and Pearson (1979) introduced the term "central place foraging". In central place models the basic patch models are extended to make specific predictions about how patches should be used and at what distances from the central place items should be attacked (Stephens & Krebs, 1986). These models capture the situation of great tits provisioning their nestlings in orchards. The decision where to forage by a central place forager, when energy costs are included in the foraging strategy (Houston, 1987; Kacelnik & Houston, 1984), depends on the difference in energetic and time costs of travel and search. Predictions can be made with this model where

the great tit will forage within the orchard given different spatial distribution and densities of prey items, but it does not give information on how many prey items will be removed, which is the main interest of this study.

To estimate the total number of prey gathered by a central place forager within a day, the absolute search time within patches is needed. This requires the relationship between density and search time to be estimated. With this relationship the model can predict the effect of individual behaviour of great tits on the population reduction of caterpillars in orchards. Furthermore, we need to know if there is an effect of depletion. If depletion causes an increase in search time, the estimated number of prey removed by great tits would be overestimated when ignoring it. The relation between prey density and search time, and the possible effect of depletion, has to be estimated to be able to link the individual behaviour of great tits in orchards to the number of caterpillars removed and thereby to the amount of damage reduction.

The final piece of information needed on the foraging behaviour, is the diet composition of great tits in orchards. To predict the effect of great tits on the different caterpillar species in the orchard, it would be ideal to know for which caterpillar species great tits have a preference and how this preference changes with population densities of these specific caterpillars. Although foraging behaviour and thereby diet composition is normally difficult to assess, the nestling rearing period gives the opportunity to study diet composition of nestlings with video recordings. However, determining caterpillars to species level was not possible from video recordings. This study therefore considers the whole group of caterpillars in the diet compared to all other prey items and links proportion of caterpillars in the diet to caterpillar densities in the orchard. Moreover we know that all caterpillars found in the orchards can cause damage to the apples.

Outline of the thesis
Most orchards in the Netherlands are run under a regime of integrated pest management (IPM) and only few have a biological control system. Control measures both in Organic as in IPM orchards are only taken if numbers of harmful insects exceed thresholds of economic damage and thus the objective is to assess whether great tits can reduce damage and thereby allow higher threshold numbers for control measures in the presence of great tits.

Whether great tits contribute to biological control of caterpillars and thereby reduce damage by caterpillars in apple orchards and under which circumstances damage reduction can be expected is investigated with three complementary approaches i) experimental work in the experimental orchard "de Schuilenburg", ii) monitoring in regular Integrated Pest Management and Organically Farmed orchards and iii) theoretical modelling. The work in the experimental orchard in plots with high caterpillar densities aimed to prove whether great tits in principle could reduce damage. However, if great tits are to serve as natural control agents they also have to be effective under regular farming regimes of IPM or OF orchards. Given a reduction

in caterpillar damage by great tits under ideal conditions, I show in the next step whether a similar effect can be found under commercial regimes. In several IPM and OF orchards caterpillar densities and damage were assessed in areas with and without breeding pairs of great tits to answer this part of the question. However, these observations cannot explain the variation in reduction of caterpillars damage by great tits between orchards and years. Therefore the last step is to use a theoretical model that predicts the foraging behaviour of great tits for different patterns of spatial variation and densities of caterpillars and thereby the reduction of caterpillars and damage in the orchard. Furthermore this model allows exploring whether the current control threshold used in IPM and OF for caterpillars can be shifted in the presence of great tits. The combination of the three approaches i.e. experimental work, monitoring and theoretical modelling will provide more insight in the process of reduction of caterpillar damage by great tits and in the foraging behaviour of great tit.

To be effective as a biological control agent in reducing fruit damage inflicted by caterpillars in spring, great tits must remove caterpillars before damage has occurred. It is unclear when great tits start removing caterpillars in sufficient numbers to reduce fruit damage. **Chapter 2** examines when great tits start removing caterpillars and whether this time of removal is before the damage to the apples has occurred. An experiment was designed in the experimental orchard "de Schuilenburg" to determine from which larval stage onwards damage is inflicted to apples by caterpillars and in which period great tits can reduce this damage. The experiment shows that great tits can reduce damage at the higher caterpillar densities of the experimental orchard.

This raises the question under which range of conditions great tits can reduce damage. To answer this question we cannot do measurements in the field. An alternative is to study how the spatial distribution and densities of caterpillars affect foraging decisions of great tits and consequently how the foraging behaviour affects caterpillar densities. Ecological theories on foraging behaviour give us tools to make a model to predict the foraging behaviour of great tits in orchards. The trade-off between travel- and search time is the most important factor to determine the place where birds search for food. However, little is known about the relationship between caterpillar density and search time in apple trees and the effect of depletion on search time in general. **Chapter 3** reports on an experiment to assess search time in relation to density in two situations. In the first situation birds were offered initial densities. In the second situation birds were offered densities that were created by the previous bird(s). With this set-up not only the relation between search time and density and the influence of depletion on search time could be assessed but also some basic assumptions of foraging models were tested.

The results of chapter 3 were implemented in a central place foraging model (Kacelnik & Houston, 1984) (**chapter 4**). The model was designed to predict the number of caterpillars removed in an orchard of 1 ha given different spatial distributions and densities of caterpillars. With the information on the time of removal and the number of removed caterpillars, the level of damage reduction by great tits can be calculated and compared to field data. The model simulations fill the gap in

knowledge about the expected damage reduction by great tits for caterpillar densities other than the high densities in the experimental orchard "de Schuilenburg" and the low densities in commercial orchards. The influence of number of breeding pairs and their nest box positions, breeding parameters of great tits and physical parameters in the model on the estimated damage are evaluated. It is discussed whether the caterpillar threshold densities at which pesticides are currently applied in IPM as well as OF orchards can be adjusted in the presence of great tits.

In **chapter 5** the factors that influenced the level of damage reduction in the model of chapter 4 are placed in the light of the underlying processes, which determine the damage reduction. The number of caterpillars removed by great tits and the time of removal are the main component that determines the level of damage reduction. The influence of hatching date, date and number of nestlings on the total number of feeding trips as well as on the number of caterpillars brought to nestlings is estimated. The number of feeding trips are calculated with different methods and compared. Given the ecological constraints that great tits face in reducing considerable numbers of caterpillars in the orchard, the expected maximum consumption of caterpillars is calculated.

In the final **chapter 6**, the conclusion is drawn that great tits reduce fruit damage inflicted by caterpillars in spring in apple orchards. Thus, for the same initial caterpillar densities the level of fruit damage will be lower in the presence of great tits. Therefore the current control thresholds can be adjusted when great tits breed in the orchard.

Chapter 2

Great tits can reduce caterpillar damage in apple orchards

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SUMMARY

1. The potential contribution of vertebrate predators to biological control in orchards has been largely overlooked to date. A few studies have shown that birds reduce numbers of pests, but data are scarce on the effects on pattern or timing of damage. Consequently, the practical value of birds as biocontrol agents remains unclear.

2. This study considered whether great tits *Parus major* can reduce caterpillar numbers and fruit damage by caterpillars and increase biological yield in an experimental orchard of apple trees with high caterpillar numbers. The outcome would depend on the coincidence of the period during which great tits forage and the period during which caterpillars cause damage. In the first experiment nets were put over trees at different times of the growing season, thus creating different periods during which great tits had access to the trees. In the second experiment caterpillars were removed from trees at different times in the growing season. In both experiments, the resultant caterpillar damage to apples was assessed in autumn.

3. The longer the period of foraging by great tit, from the start of egg incubation until fledging of young, the less the overall damage to fruit. Damage caused by caterpillars was greater the later they were removed, from the young apple stage onwards.

4. The effect of great tits on caterpillar damage to apples was small (percentage damage was reduced from 13.8% to 11.2%) but significant ($P<0.05$) and the yield of fruit increased significantly (from 4.7 to 7.8 kg apples per tree, $P<0.05$). The only cost to the producer was that of erecting nest boxes (*c.* 2 ha^{-1}) to encourage great tits to breed in the orchard. Depending on the great tits' numeric response to insect densities, their relative impact may be greater at lower densities more typical of commercial orchards and, if so, the presence of breeding great tits may allow control thresholds to be set at higher initial densities of caterpillars. Furthermore, the contribution of natural predators to biological control of insect pests may be useful in organic orchards and in the future when a further reduction of pesticide use may be enforced.

INTRODUCTION

There is increasing interest in biological control of pests in apple *Malus domestica* Borkh. orchard systems because adverse public attitudes to pesticides have intensified (Solomon *et al.*, 2000), resistance of harmful insects to pesticides is an ongoing problem and legislation increasingly restricts the use of pesticides (Anonymous, 2001). The main focus in the search for pest control agents that can contribute to biological control has been on parasitoids (Cross *et al.*, 1999) and predatory insects such as predatory mites, earwigs, lacewings, mirids and anthocorids (Solomon *et al.*, 2000). The potential contribution of vertebrate predators such as birds is mostly overlooked. The main reason given for ignoring vertebrate predators is their presumed lack of a sufficient numerical response to outbreaks of pests. However, most of the studies on birds as biological pest control agents do show a reduction in the

population size of the harmful insect species (Table 1 and 2; see also Kirk *et al.*, 1996) thereby demonstrating their potential. However because these studies have not investigated whether the insect reduction leads to actual damage reduction to the crop, it remains unclear whether they have practical value.

In this study we investigated whether great tits *Parus major* L. can reduce fruit damage inflicted by caterpillars in spring in apple orchards. Great tits are partly insectivorous birds with a preference for caterpillars especially when they are feeding their nestlings (Betts, 1955; Gibb & Betts, 1963; Gruys, 1982; Naef-Daenzer *et al.*, 2000; Royama, 1966; van Balen, 1973). The nestling rearing period, when the number of prey items caught is high, coincides with the time that caterpillars of winter moths *Operophtera brumata* L. and tortricid moths occur in orchards. These caterpillars are key pests in apple orchards (Cross *et al.*, 1999; Solomon *et al.*, 2000). Great tit is also a common species that breeds readily in nest boxes, and hence the local density of great tits can be increased easily by putting up nest boxes in the orchards. Together, features suggest that great tits have the potential to contribute to the control of caterpillar pests.

To be effective as biological control agents against caterpillar damage, great tits must remove caterpillars before damage is inflicted on the fruit. Surprisingly, the time at which caterpillars actually inflict damage is not clearly known. It is also unclear when great tits start removing caterpillars in sufficient numbers to reduce fruit damage. It is presumed that their activity during the chick-rearing period is the most effective but predation during their egg-laying and incubation period might also be important because caterpillars are then removed at an early larval stage. It is also unknown if removal of late larval stages causes a reduction in fruit damage. In this study, we examined whether great tits can reduce caterpillar damage, by assessing the period that i) caterpillars cause, and ii) foraging great tits reduce, fruit damage. The impact great tits have as biological pest control agents depends on the overlap between these periods. This impact was quantified by determining the magnitude of damage reduction.

MATERIALS AND METHODS

Study site

Two experiments were carried out in 2000 in the experimental orchard 'De Schuilenburg' at Kesteren (51°70'N 5°31'E) in the Netherlands. The apple orchard consisted of 12 blocks of "small spindle bush" trees that were planted in 1984 and 1988. The area contained 36 nest boxes within these blocks (three per block) and 15 boxes in an older part of the orchard on the border of the 1988 blocks. Nest boxes were inspected at least once a week to determine laying date, clutch size, hatching date and the number of young fledged of great tits.

Table 1 Review of studies that investigated the effect of bird predation on insect populations in agricultural systems.

Harmful insect	Bird species	Measured effect	Authors
Codling moth *Cydia pomonella* in apple orchards	Two species of woodpeckers *Dendrocopos* spp.	-Removal of more than 50% of overwintering codling moth larvae	MacLellan (1958)
Codling moth *Cydia pomonella* in apple orchards	Great tits *Parus major*, blue tits *Parus caeruleus*, tree-creepers *Certhia familiaris*, woodpeckers *Dendrocopos* spp. and nut-hatches *Sitta europea*	-Removal of 94.9% of overwintering codling moth larvae -The more larvae the greater the proportional reduction	Solomon *et al.* (1976)
Codling moth *Cydia pomonella* in apple orchards	Great tits *Parus major* and blue tits *Parus caeruleus*	-Removal of 47% of the initial number of overwintering codling moth larvae -Birds annually reduce the population to very low levels	Glen & Milsom (1978)
Codling moth *Cydia pomonella* in apple orchards	Mainly blue tits *Parus caeruleus* and some great tits *Parus major*	-Removal of 95% of the initial density of overwintering codling moth larvae -The more larvae the greater the proportional reduction, but at a declining rate	Solomon & Glen (1979)
Codling moth *Cydia pomonella* in apple orchards	Silvereyes *Zosterops lateralis*	-The more larvae, the higher the consumption rates	Wearing & McCarthy (1992)
Codling moth *Cydia pomonella* in apple orchards	Mainly great tits *Parus major*	-Removal of 46-99% of overwintering codling moth larvae -The more larvae the greater the proportional reduction	Zajac (1979)
Pear psyllas *Cacopsylla spp.* in pear orchards	Oregon juncos *Junco hyemalis*	-Sizeable reduction but may be relatively insignificant due to the small segment of psylla population overwintering in orchard duff	Fye (1982)
European corn borer, *Ostrinia nubilalis* in fields of maize	American crows *Corvus brachyrhynchos*	-Survival of overwintering larvae was *ca*. 50% less on uncaged than on caged plants	Quiring & Timmins (1988)
Banded fruit weevil *Phlyctinus callosus* in apple orchards	Helmeted guineafowls *Numida meleagris*	-No reduction of weevil numbers by guineafowl	Witt *et al.* (1995)
Arthropods in general in coffee plantations	Forest birds in general	-Removal of 64-80% of large arthropods, no reduction in small arthropods -Small increase in leaf damage when birds are excluded	Greenberg *et al.* (2000)
Cutworm *Agrotis spp.*, weevils *Sphenophorus spp.*, aphids *Rhopalosiphum maidis*, European corn borer, *Ostrinia nubilalis* and the Northern corn rootworm *Diabrotica longicornis* in grain- and cornfields	20 Bird species including the american robins *Turdus migratorius*, red-winged blackbirds *Agelaius phoeniceus* and the song *Melospiza melodia* and chipping sparrows *Spizella passerina*	-Higher densities of cutworms and weevils when birds are excluded -Trend of higher densities of aphids and corn borer but no difference in density of corn rootworm	Tremblay *et al.* (2001)

Table 2 Review of studies that investigated the effect of bird predation on (a) insect populations and (b) leaf damage in forests**.**

	Harmful insect	Bird species	Measured effect	Author(s)
a) insect populations	*Ernarmonia conicolana* in plantations of Scots pine *Pinus sylvestris*	Mainly blue tits *Parus caeruleus* and coal tits *Parus ater*	-Removal of 45% of the overwintering larvae -The more larvae per cone the greater the proportional reduction	Gibb (1958)
	Sawfly *Pristiphora erichsonii* on tamarack *Larix laricina* in bog forests	Forest birds in general	-Birds influence sawfly population trends at low insect densities	Buckner & Turnock (1965)
	Herbivorous insects on striped maple *Acer pensylvanicum*	Forest birds in general	-Removal of 37% of the caterpillars per week -Birds cannot prevent insect outbreaks but extend the time between outbreaks	Holmes *et al.* (1979b)
	Forest insects	Forest birds in general	-Birds cannot prevent insect outbreaks but extend the time between outbreaks	Otvos (1979) and references therein
	Roaches *Blattidae*, spiders *Arachnida*, crickets *Gryllidae* and katydids *Tettigoniidae* in a moist tropical forest understory	Checker-throated antwrens *Myrmontherula filiventis*	-Removal of 50% of the preferred prey -Exclusion of birds significantly improved insect survival	Gradwohl & Greenberg (1982)
	Spruce budworm *Choristoneura fumiferana* in spruce- fir stands *Picea abies*	Forest birds in general among which the black-capped chickadees *Parus articapillus* and some warbler species *Dendroica spp.* were the most important ones	-The more larvae the more larvae eaten but the proportion eaten decreases	Crawford & Jennings (1989)
	Leaf-mining moth *Cameraria hamadryadella* in woodland	Carolina chickadees *Poecile carolinensis*	-The more larvae per leaf the lower the proportional reduction	Conner *et al.* (1999)
	Pine processionary caterpillar *Thaumetopoea pityocampa*	Hoopoes *Upupa epops*	-Removal of *ca.* 70% of the pupae	Battisti *et al.* (2000)
	Geometrid moth *Epirrita autumnata* in mixed coniferous forest	Forest birds including great tits *Parus major*, pied flycatchers *Ficedula hypoleuca* and willow wablers *Phylloscopus trochilus*	-Exclusion of birds significantly improved larval survival	Tanhuanpaä *et al.* (2001)
b) leaf damage	Mainly larvae of geometrids, tortricids and sawflies on bilberry in 5 forest stands mostly dominated by *Pinus abies*	Hazel hen chicks *Tetrastes bonasia* great tits *Parus major*, pied flycatchers *Ficedula hypoleuca*	-Exclusion of birds significantly increased shoot damage -Removal of 63% of the larvae	Atlegrim (1989)
	Leaf chewing insects in general in a forest dominated by white oak *Quercus alba*	Forest birds in general	-Exclusion of birds increased leaf damage	Marquis & Whelan (1994)

Because the majority of insectivorous birds in the orchard were great tits, it was assumed that great tits were the main predators of caterpillars. Other birds occasionally observed in the orchards included blue tit, *Parus caeruleus* L., chaffinches *Fringilla coelebs* L., goldfinches *Carduelis carduelis* L., chiffchaffs *Phylloscopus collybita* Vieillot, willow warblers *Phylloscopus trochilus* L., magpies *Pica pica* L., jays *Garrulus glandarius* L., blackbirds *Turdus merula* L. and tree sparrows *Passer montanus* L. Of these birds blackbirds, magpies and goldfinches only occasionally prey upon caterpillars (Glutz von Blotzheim & Bauer, 1988, 1993a, b, 1997). Chaffinches, jays, chiffchaffs and willow warblers include caterpillars in their diet but numbers stay below 20% of the total diet (Glutz von Blotzheim & Bauer, 1991, 1993a, b, 1997). Only tree sparrows and blue tits are known to prey on caterpillars on leaves (Glutz von Blotzheim & Bauer, 1993a, 1997), but less than great tits and they foraged mainly at the edges of the orchard near their nesting sites.

Four blocks were selected in the experiment: two blocks planted in 1984 and two blocks planted in 1988. No control measures against caterpillars had been taken in these blocks for at least 4 years. Trees of the common apple variety Elstar were used for the experiment. A double row of this variety occurred twice in each block while the other varieties (Cox's orange pippin, Belle de Boskoop, Jonagold, Alkmene, and Summerred) had at least one double row per block. The blocks of approximately 0.4 ha., were 21 or 22 rows wide and about 50 trees long. The distance between trees within a row and between rows was 1.25 m and 3 m respectively.

Experimental designs

In experiment 1 we prevented great tits from foraging on apple trees by covering the trees with polyethylene nets (mesh 25 by 25 mm) at different phases of the growing season and leaving them covered until the end of July. The earliest experimental treatments were made in the early pink bud stage (e2, classification on scales according to Fleckinger 1948) of the apple trees, and the latest treatments were made 2 weeks after the end of the great tit breeding season (26 April until 26 June 2000). The early pink bud stage of the apple trees is the first stage in which caterpillars become visible.

At the start of the experiment 44 trees were covered with nets (Julian date 116, i.e. 1 February is Julian date 32 and the fact that 2000 was a leap-year was discarded). In the following 8-week period (Julian date 118-174) every Monday, Wednesday and Friday four additional trees were covered, i.e. one per block. A control group of 56 trees were never covered with nets. Great tits had access to the control trees during the whole period (i.e. the control group has Julian date 177 in the analyses). At the end of July (Julian date 205-208) all nets were removed from the experimental trees to prevent reduced growth of, or damage to, the apples.

A similar experimental design was used in experiment 2 but instead of placing nets over trees, trees were searched and caterpillars were removed by hand. These data on caterpillar numbers were used to determine how caterpillar densities changed over

time. After searching, trees were sprayed with insecticide (Condor[®]; 240 g L^{-1} active ingredient parathion-methyl; Agrevo Nederland BV, Haren, the Netherlands) at 0.1% to ensure the total removal of all caterpillars. The insecticide can also have an effect on aphids and mirids. The insecticide was sprayed with a hand lance until drip off (i.e. the trees were saturated), using approximately 1 L tree^{-1}. Caterpillars were never removed on a control group of 56 trees (i.e. control group had Julian date 177 in analyses). Thus both experiments had their own control group treated identically.

In order to distinguish treatment effects from block effects, all treatments were distributed across all blocks. Further, in order to avoid confounding of treatment effects with the effects of rows, all treatments were similarly distributed across all rows. The treatments were further randomised within rows to balance for carry-over effects so that treatments were not systematically positioned relative to each other in space within blocks and rows.

All abscissed young fruits in June (June-drop) and all full-grown apples (in October) were collected from all trees included in the experiments. June-drop apples were collected to investigate whether damaged apples are more likely to be shed, thereby reducing the treatment effects among harvested apples. All apples collected (June-drop and full-grown) were inspected for caterpillar damage, i.e. early spring damage, as described by de Reede *et al.* (1985). The other classes of caterpillar damage (July damage and late summer damage) can be distinguished easily from early spring damage, which is characterised by corked scar tissue not present in other classes of caterpillar damage. Other classes of caterpillar damage were not included in the analyses because they were caused after the time at which all experimental treatments had ended.

To prevent bias in damage evaluation, the observer was not aware of the treatment of the inspected apples. The same observer checked all apples. Besides damage levels, the number of apples per tree and biological yield (in kg) were determined. For yield all apples (damaged and undamaged) that were hanging on the experimental trees at the harvest day in October were taken into account. Any effect of treatment on yield can be due to either the number of apples per tree and/or the weight of each apple. As the number of abscissed young fruits might explain effects in the number of harvested apples June-drop apples were not only checked for damage but were also counted.

STATISTICAL ANALYSIS

To test our data on, respectively, caterpillar damage, loss of caterpillar-damaged apples in June-drop, yield, number of apples, weight per apple and number of apples lost in June-drop, we carried out 6 groups of statistical analyses.

Caterpillar damage

For variation in caterpillar damage (individual apples either did or did not have caterpillar damage; binary data) we used generalised linear models (GLIM4) with

binomial errors. We used the number of damaged apples per tree as the response variable, with the number of apples per tree as the binomial denominator (effectively weighting data points by the number of apples scored). Five trees had no apples and were therefore omitted from this analysis.

We tested date of treatment, expressed in Julian dates (i.e. 1 February is Julian date 32), as a continuous variable, and also date^2 to test for non-linear effects. Block was included as a factor, both as a main effect and in interaction with date and date^2 to control for possible differences in damage related to block. Non-significant terms were dropped from the model starting with the highest order interaction (stepwise backward procedure). Because the residual deviance was substantially larger than the residual degrees of freedom, Williams' adjustment for overdispersion was applied (Crawley, 1993), and hence the significance of terms in the model was assessed using an F-test (Crawley, 1993).

## *Loss of caterpillar damaged apples in June-drop*

The effect of treatment on the harvest might be reduced by June-drop if trees shed relatively more apples with caterpillar damage than undamaged apples. If this were the case the slope of the regression of the percentage of damage in June-drop on the percentage of damage in harvest would be significantly different from 1. Analyses were carried out on the combined data of June-drop of experiment 1 and 2. Individual trees were treated as data points in a generalised linear model, with percentage of damage in June-drop as the response variable and binomial errors and percentage of damage in the harvest as a continuous variable and block as a factor, to control for possible differences in damage related to block. The full model with its interaction was fitted and we tested whether the slope of the regression line differed from 1 (using the offset option in GLIM4).

Yield, number of apples and weight per apple

To investigate the effect of treatment on the biological yield (damaged and undamaged apples) at harvest we tested yield (in kg), number of apples and weight per apple as response variables. For these variables we used the same model structure as above but with different error distributions and link functions. The logarithm of yield and the weight per apple were treated as normally distributed variables and the number of apples per tree as a gamma distributed variable with a reciprocal link function. We included an additional covariate, the percentage of rosy aphid *Dysaphis plantaginea* Pass.-infested apples per tree, because apples on aphid infested trees were smaller.

Number of apples lost in June-drop

To investigate whether the number of June-drop apples increased with higher levels of caterpillar damage, we tested the number of apples shed in June against the total
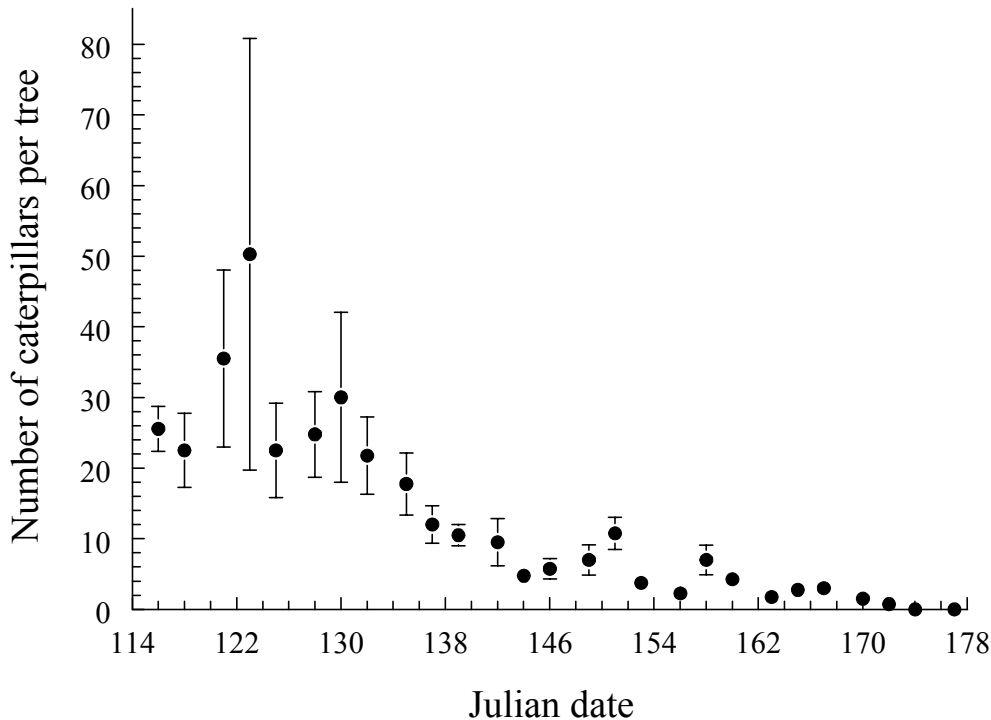
Figure 1 Changes over time in the number of caterpillars on previously untreated trees of experiment 2 where caterpillars were removed from trees at different times during the growing season (i.e. the 1st of February is Julian date 32) in the experimental orchard "de Schuilenburg". Each dot is the average count from 4 trees, except for the first dot, which is based on 44 trees.

percentage of apples with caterpillar damage. A generalised linear model with binomial errors was used with the number of apples per tree in June-drop as the response variable and total number of apples (i.e. harvest plus June-drop) as the binomial denominator. Data on number of June-drop apples in both experiments were combined. We tested total caterpillar damage (i.e. damage in June-drop and harvest) as a continuous variable with number of June-drop apples as a response variable. Block was included as a factor to control for possible differences between blocks. The full model with percentage of damage and block was fitted together with their interactions.

RESULTS

Breeding pairs and caterpillar densities

During the experiment, nine pairs of great tits bred in the vicinity of the experimental blocks. Place of breeding could not be manipulated and was a result of the birds' preferences for breeding places. The first block had one nest within and one nest in a non-experimental neighbouring block. The second block had two nests within and two

Table 3. Logistic regression of the proportion of apples per tree with caterpillar damage. In experiment 1, great tits were excluded from foraging on trees, and in experiment 2 caterpillars were removed from trees, at different times during the growing season. Date in experiment 1 is the Julian date (i.e. the 1st of February is Julian date 32) on which great tits were excluded from trees. A later Julian date for great tits exclusion implies a longer period of great tit predation and hence a lower exposure to caterpillars. Date in experiment 2 is the Julian date on which caterpillars were removed from the tree. A later Julian date means higher exposure to caterpillars.

		increase in deviance	df	F	P	estimate	
experiment 1:	great tits excluded[a]						
	block	44.2	3	14.7	< 0.001	1[b]	-1.1
						2[b]	-1.4
						3[b]	-1.3
						4[b]	-1.8
	date	4.9	1	4.9	< 0.05		$-3.7 \, 10^{-3}$
experiment 2:	caterpillars destroyed[a]						
	block	32.1	3	10.8	< 0.001	1[b]	-16.6
						2[b]	-17.1
						3[b]	-16.7
						4[b]	-17.3
	date	15.7	1	15.8	< 0.001		0.2
	date^2	12.5	1	12.8	< 0.001		$-5.2 \, 10^{-4}$

[a] All interactions and variables that were not significant are not listed
[b] Block number

nests in a non-experimental neighbouring block. The third and fourth blocks had no nests within but, respectively, two and one nest in a non-experimental neighbouring block. Additionally, three pairs of great tits and two pairs of tree sparrows bred on the edge of the orchard. The birds deserted one of the broods in the first experimental block and the chicks died at 7 days old. Two other broods lost one of the parents during the nestling phase but both remaining parents managed to fledge 3 chicks. Average clutch size of great tits was 8.5 eggs (SD ± 1.3, $n = 12$), out of which on average 7.6 (SD ± 1.4, $n = 12$) chicks hatched and 5.0 (SD ± 2.9, $n = 12$) chicks fledged. The hatching dates ranged from 4 to 18 May.

Caterpillar numbers were high at the start of the experiment (on average 28 caterpillars per tree; SD ± 25.3, $n = 56$) and decreased rapidly due to pupation and predation from 10 May onwards (Fig. 1). Almost no caterpillars were present after 20 June. Winter moth comprised 38.7% of the sampled caterpillars, followed by the tortricid species *Spilonota ocellana* Denis & Schiffermüller, 25.3%, *Pandemis heparana* Denis & Schiffermüller, 14.6%, and *Recuvaria leucatella* Clerck, 11.4%. All these caterpillars prefer feeding on leaves. Injury to apples is caused by accident when leaves are close to or connected with young fruits and flowers. Injuries appear as cork scars on the surface of the apple. There is no distinction between scars of different caterpillar species.

Caterpillar damage

In experiment 1, we found decreasing caterpillar damage levels with an increasing period of foraging by great tits (experiment 1; Fig. 2a and Table 3). The reduction was linear in relation to the date of exclusion ($F_{1,193} = 4.9$, $P<0.05$), with observed damage decreasing from 13.8% (SE ± 1.0%, $n = 44$), when great tits were excluded on Julian date 116 to 11.2% (SE ± 0.9%, $n = 56$), when great tits were never excluded (treatment date 177). The total percentage of caterpillar damage differed between blocks ($F_{3,193} = 14.7$, $P<0.001$) but the effect of the experimental treatment did not differ between blocks (block*date interaction was not significant; Table 3).

In experiment 2, caterpillar damage increased when caterpillars were left for a longer period on the trees. This increase in relation to the date of caterpillar destruction was approximately linear at first and flattened out after Julian date 153 (date, $F_{1,191} = 15.8$, $P<0.001$); date^2, $F_{1,191} = 12.8$, $P<0.001$); Fig. 2b and Table 3). The percentage of caterpillar damage differed between the blocks ($F_{3,191} = 10.8$, $P<0.001$), but the effect of treatment did not differ between blocks (block*date interaction was not significant; Table 3). The observed damage in the harvest increased from 2.6% (SE ± 0.5%, $n = 42$), when caterpillars were destroyed on date 116, to 11.4% (SE ± 1.2%, $n = 56$), when caterpillars were never destroyed (treatment date 177). The percentage damage for the control group of both experiments was almost equal (11.2% and 11.4%).

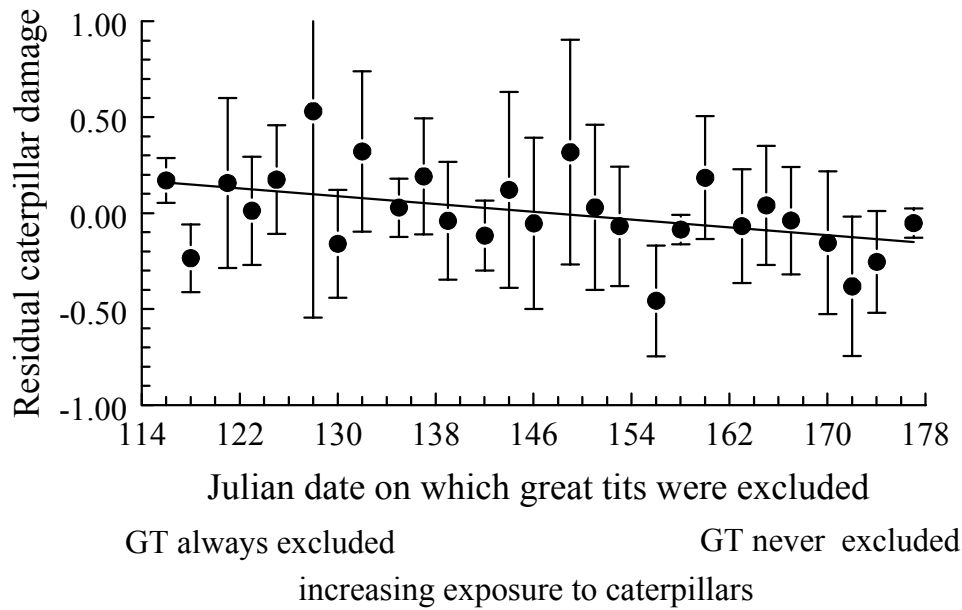*Loss of caterpillar damaged apples in June-drop*

There was no difference in the percentage of damaged apples in the June-drop and the percentage in the harvested apples ($F_{1,372} = 0.73$, $P > 0.39$). Thus the percentage of damaged apples among those harvested was not influenced by trees preferentially dropping damaged apples in June.
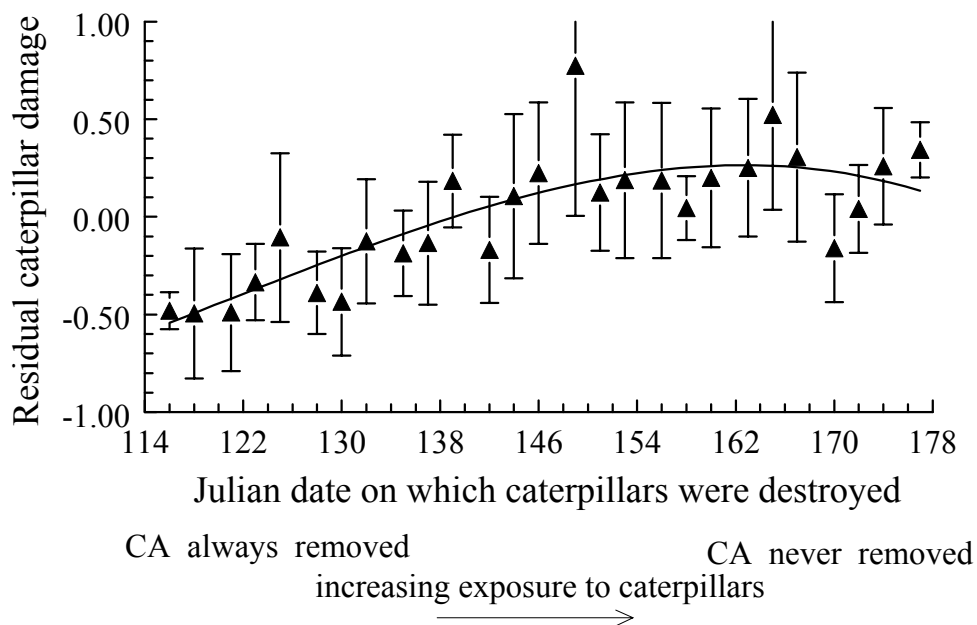
Yield

In experiment 1, yield increased non-linearly in relation to the date of exclusion of great tits (Fig. 3a and Table 4). This increase was less marked at high levels of aphid infestation (interaction date^2*aphid; Table 4). Levels of aphid infestations were not affected by the period of great tit exclusion ($F_{1,192} = 2.75$, $P = 0.10$). The observed yield per tree increased from 4.7 kg (SE ± 0.6, $n = 44$), when great tits were excluded on Julian date 116, to 7.8 kg (SE ± 0.7, $n = 56$), when great tits were never excluded (treatment date 177).

In experiment 2, no difference in the yield per tree was found when caterpillars were left longer on the trees. None of the interactions or date^2 and date had an effect on the yield per tree (Fig. 3b and Table 4). The average yield per tree was 8.1 kg (SE ± 0.42, $n = 197$). Only the percentage of aphid infestation had a significant effect on yield, with yield decreasing as the percentage of aphid infestation increased. Because the active ingredient parathion-methyl, of Condor also affects aphids, the level of aphid infestations was higher in the treatments where caterpillars were removed from the tree later in the season ($F_{(1,193)}=5.42$, $P=0.02$).

a) Experiment 1: exclusion of great tits (GT)

Julian date on which great tits were excluded

GT always excluded   GT never excluded

increasing exposure to caterpillars

b) Experiment 2: removal of caterpillars (CA)

Julian date on which caterpillars were destroyed

CA always removed   CA never removed

increasing exposure to caterpillars

Figure 2. (a) Experiment 1: Caterpillar damage (± SE) as the residual from a model including block effect only as result of a logistic regression of the proportion of apples per tree with caterpillar damage when great tits are excluded from trees, at different times during the growing season. A later Julian date for great tits exclusion implies a longer period of great tit predation and hence a lower exposure to caterpillars (indicated by arrow). (b) Experiment 2: Caterpillar damage (± SE) as the residual from a model including block effect only as result of a logistic regression of the proportion of apples per tree with caterpillar damage when caterpillars were removed from trees, at different times during the growing season. A later Julian date for caterpillar destruction implies a higher exposure to caterpillars (indicated by arrow). Julian date is the date according to the Julian calendar (i.e. the 1st of February is Julian date 32)

a) Experiment 1: exclusion of great tits (GT)

Julian date on which great tits were excluded

GT always excluded   GT never excluded

increasing exposure to caterpillars

b) Experiment 2: removal of caterpillars (CA)

Julian date on which caterpillars were destroyed

CA always removed

increasing exposure to caterpillars

Figure 3. (a) Experiment 1: Biological (damaged and undamaged apples) yield (± SE) as the residual from a model including block effect and percentage of aphid infestation only as result of a regression of the logarithm of yield per tree when great tits are excluded from trees, at different times during the growing season. The residuals values are on a log scale because yield was log transformed. A later Julian date for great tits exclusion implies a longer period of great tit predation and hence a lower exposure to caterpillars (indicated by arrow). (b) Experiment 2: Biological (damaged and undamaged apples) yield (± SE) as the residual from a model including block effect and percentage of aphid infestation only as result of a regression of the logarithm of yield per tree when caterpillars were removed from trees, at different times during the growing season. The residual values are on a log scale because yield was log transformed. A later Julian date for caterpillar destruction implies a higher exposure to caterpillars (indicated by arrow). Julian date is the date according to the Julian calendar (i.e. the 1st of February is Julian date 32).

Table 4 Regression of biological yield, weight per apple and number of apples per tree. In experiment 1 great tits were excluded from foraging on trees and in experiment 2 caterpillars were removed from trees at different times during the growing season. Date in experiment 1 is the Julian date (i.e. the 1st of February is Julian date 32) on which great tits were excluded from trees. A later Julian date means a shorter period of great tits exclusion thus implying a longer period of great tit predation and hence a lower exposure to caterpillars. Date in experiment 2 is the Julian date on which caterpillars were removed from the tree. A later Julian date means higher exposure to caterpillars.

response variable	Experiment 1 great tits excluded from foraging on trees						Experiment 2 caterpillars destroyed					
	variables in the model	increase in deviance	df	F	P	estimates	variables in the model	increase in deviance	df	F	P	estimates
Yield[a]	date	0.75	1	5.80	<0.05	0.024	aphid	1.06	1	6.31	<0.05	-0.43
	$date^2$	0.49	1	3.95	<0.05	$6.9\ 10^{-5}$	intercept					0.83
	$date^2$*aphid	0.89	1	7.36	<0.01	$1.0\ 10^{-5}$						
	intercept					-1.35						
Weight per apple[a]	aphid	0.031	1	49.78	<0.001	-0.06	aphid	0.003	1	4.66	<0.05	0.88
	date*block	0.005	3	2.73	<0.05	1[b] $9.1\ 10^{-5}$	date*aphid	0.004	1	6.69	<0.05	-0.012
						2[b] $13.1\ 10^{-5}$	$date^2$*aphid	0.005	1	7.86	<0.01	$3.6\ 10^{-5}$
						3[b] $6.9\ 10^{-5}$	intercept					0.12
						4[b] $11.3\ 10^{-5}$						
	intercept					0.11						
Number of apples[a]	block	8.14	3	5.47	<0.01	1[b] 0.039	block	8.32	3	4.50	<0.05	1[b] 0.018
						2[b] 0.041						2[b] 0.012
						3[b] 0.042						3[b] 0.019
						4[b] 0.033						4[b] 0.012
	date	6.29	1	12.68	<0.001	$-1.3\ 10^{-4}$						
	aphid	2.25	1	4.53	<0.05	$-8.4\ 10^{-3}$						

[a] All interactions and variables that were not significant are not listed

[b] Block number

Average weight per apple and number of apples
We investigated whether the increase in yield was caused by an increase in the average weight of each apple or by an increase in the number of apples. The average weight of apples increased as the period during which great tits could forage on the trees increased, but this rate of increase varied between blocks (Table 4). Furthermore, the average weight per apple decreased with increasing levels of aphid infestation. The average apple weight ranged from 104.3 g (SE ± 8.4, $n = 11$) to 124.6 g (SE ± 7.4, $n = 11$) in the different blocks in the first treatment and from 108.5 g (SE ± 6.1, $n = 14$) to 124.8 g (SE ± 4.8, $n = 14$) in the control group. In experiment 2, with varying periods of caterpillar exposure, the average weight per apple decreased when caterpillars were left longer on the trees. There was a significant interaction between experimental treatment and aphid infestation (both the interactions date*aphid and date^2*aphid were significant; Table 4): average apple weight decreased at higher levels of aphid infestation. Individual apples were larger in the first treatment (Julian date 116) than in the control (Julian date 177), on average the weight of each apple decreased from 119.1 g (SE ± 3.1, $n = 42$) to 117.7 g (SE ± 3.1, $n = 56$).

The number of apples harvested per tree increased when great tits could forage over a longer period on trees (Table 4). This increase differed between blocks. More apples were harvested when the percentage of aphid-infested apples was higher. The average number of apples ranged from 29 (SE ± 6.2, $n = 11$) to 57 (SE ± 17.2, $n = 11$) in the different blocks for the first treatment, and from 45 (SE ± 9.6, $n = 14$) to 101 (SE ± 21.6, $n = 14$) for the control group. In experiment 2, there was a marginally non-significant decrease in the number of apples with an increasing period of caterpillar exposure, depending on the degree of aphid infestation (date*aphid, $F_{1,183} = 3.40$, $P < 0.07$). The number of apples per tree varied significantly between blocks, ranging from 52 (SE ± 5.1, $n = 50$) to 83 (SE ± 8.3, $n = 50$).

Number of apples lost in June-drop
In order to explain some of the variation in the number of apples per tree, we investigated whether the number of June-drop apples increased with increasing harvest damage levels. Trees with a high percentage of caterpillar damage at the time of harvest had also dropped a larger percentage of their apples in June (percentage of caterpillar damage, $F_{1,372} = 6.81$, $P < 0.01$). The effect of damage on June-drop was the same for all blocks (interaction, $F_{3,369} = 0.64$, $P > 0.59$) but the average level of June-drop differed between blocks (block, $F_{3,372} = 9.34$, $P < 0.001$). The effect of damage levels on June-drop was small. An increase of 30% in caterpillar damage led to an increase of about 8% in June-drop.

DISCUSSION

We show clearly that great tits can reduce caterpillar damage in apple orchards. Other studies have already shown that birds can reduce insect numbers and that this reduction is dependent on prey densities (Tables 1 and 2, Kirk *et al.*, 1996). Some of these other studies also concluded that birds became ineffective when densities were either low or above a threshold insect density and that the relative impact of predation thus reaches the maximum at moderate caterpillar densities. It is unclear how the birds perceived the densities of caterpillars in the experimental orchard. Insect densities at the site have been building up over the last 10 years, during which time hardly any action was taken against caterpillars. Densities were six times higher than in commercial organic orchards in the same year, where mineral oil and the microbial insecticide, *Bacillus thuringiensis,* had been used for caterpillar control (C.M.M. Mols, unpublished data). Depending on the perception of caterpillar density by the birds, the damage reduction will either increase or decrease with increasing densities. On the other hand, if insect densities in the orchard become very low, great tits may forage more outside the orchard so that damage reduction by great tits would be lower.

The second experiment, together with the data on caterpillar abundance (Figures 1 and 2) show that caterpillars became harmful to the apples at the end of bloom (Julian date 120) and kept inflicting damage until they pupated (Julian date 156). Besides the fact that caterpillars start inflicting damage to apples at a very early stage of the growing season (before great tits exert any predation effect), the great tits' impact as a biological pest control agent is further reduced by their preference for larger prey (Betts, 1955; Gibb & Betts, 1963; Tinbergen, 1960). Naef-Daenzer *et al.* (2000) found that great tits have a preference for caterpillars larger than 10-12 mg (9-10 mm). The caterpillar species occurring in the orchard differed in full-grown size as well as in their time of appearance. At a given sample date a range of different caterpillar size classes was available to great tits, of which they preferred the relative larger caterpillars. A minimum amount of damage will therefore always occur as small caterpillars inflict damage prior to reaching 9-10 mm or larger, the preferred size of predatory great tits. However, as the relationship between time of removal by great tits and caterpillar damage is linear, few large caterpillars during a long period of time can inflict the same damage as many small ones during a short period of time.

In our experiment great tits reduced damage by 2.6 % from 13.8% to 11.2%. This damage reduction was not influenced by differential loss of damaged apples in June-drop. The remaining damage of 11.2% is far above the economic thresholds of fruit growers (either with organic or integrated pest management). Solomon *et al.* (2000) concluded for several polyphagous arthropod predators that they alone are unlikely to prevent pest damage. Our results show that this is also the case for great tits. However, their benefits should be seen when used in concert with other control measures, where it is possible, under some circumstances, that economic thresholds could be reduced in the presence of great tits.

Besides reducing damage, great tits also improved the biological yield per tree. Yield increased due to an increase in the number of apples rather than the weight per apple. In experiment 2, where caterpillars were removed, the same trend was found: lower damage was associated with more apples per tree. However, care should be taken in interpreting these results because we experimentally excluded great tits by covering trees with nets. Although mesh size was large enough to allow access by bees, the nets might have reduced pollination. However, since an effect on the number of apples was also found when caterpillars were destroyed, we are confident that the effect is due to the exclusion of great tits and not to side-effects of the nets. Moreover, June-drop appears to increase with damage, explaining part of the variation in the numbers of apples.

Although great tits on their own cannot reduce caterpillar damage within the present economic thresholds, they certainly contribute to biological control. Furthermore, the only cost to the fruit growers is that of putting-up nest boxes (*c.* 2 ha^{-1}) to allow great tits to breed in the orchards. With the tightening of regulations on the use of pesticides, resistance of harmful insects to pesticides and the adverse public attitudes to pesticides, great tits should be encouraged as a pest control agent for caterpillars in orchards.

Chapter 3

Central assumptions of predator-prey models fail in a semi-natural experimental system

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Catherine M. Lessells, Piet J. Drent & Marcel E. Visser

ABSTRACT

The relationship between the encounter rate of predators with prey and the density of this prey is fundamental to models of predator-prey interactions. The relationship determines, among other variables, the rate at which prey patches are depleted, and hence the impact of predator populations on their prey, and the optimal spatial distribution of foraging effort. Two central assumptions made in many models are that encounter rate is directly proportional to prey density and that it is independent of the proportion of prey already removed, other than via the decreased density. We show here, using captive great tits searching for winter moth caterpillars in their natural hiding positions that neither of these assumptions hold. Encounter rate increased less than directly in proportion to prey density, and it depended not only on the current density of prey, but also on the proportion of prey already removed by previous foragers. Both of these effects will have major consequences for the outcome of predator-prey interactions.

INTRODUCTION

Predator-prey interactions are common components of all ecological communities. The rate at which predators encounter prey is central to such interactions and has consequences on an ecological time scale through its influence on population dynamics as well as on an evolutionary time scale through its influence on optimal foraging strategies. Two assumptions are commonly made concerning the relationship between encounter rate and prey density. The first is that overall encounter rate is the sum of the encounter rates for individual prey items, and hence that encounter rate increases directly in proportion to prey density. This assumption is embodied in many classical mathematical models including the Lotka-Volterra predator-prey model (Lotka, 1925) and the Nicholson-Bailey parasitoid-host model (Nicholson, 1933) among population dynamic models, and the optimal diet model (Pyke *et al.*, 1977; Stephens & Krebs, 1986) among optimal foraging models. A second commonly made assumption is that encounter rate depends only on the current density of prey, and is unaffected by the proportion of prey already removed by previous predators. This implicitly assumes that there is no heterogeneity in the likelihood of being found for individual prey items. We carried out an experiment on captive great tits foraging on different densities of winter moth caterpillars in their natural hiding positions on small apple trees to test whether these assumptions hold. We tested the first assumption by allowing individual great tits to forage on previously unexploited patches with an experimentally created range of prey densities. We tested the second assumption by allowing individual great tits to forage on patches that had previously been exploited by other great tits.

METHODS

We used 17 male and 14 female great tits (*Parus major*), housed individually in 0.9 x 0.4 x 0.5 m cages connected via sliding doors to one of two observation rooms (4.2 x 2.5 x 2.3 m). The birds were let in and out the observation room without handling (Verbeek *et al.*, 1994). Birds had access to various types of food and water in their cages (Marchetti & Drent, 2000; Verbeek *et al.*, 1994) but no live insects were fed during the experimental period.

Winter moth (*Operophtera brumata* L.) caterpillars (larval stage L5, weight 63.2 mg (± 11.0 s.d.)) were placed in a Poisson distribution over groups of 5 two-year-old potted apple trees one day before these were used in the experiment. This allowed the larvae to build their natural shelters. Directly after the experiment, the trees were searched three times by different experimenters to check that the intended number of prey had been present during the experiment. If not all caterpillars that should have still been on the trees were recovered, it was assumed that they had been missing from the beginning of the test and densities were corrected in the analysis. Unexploited sets of 5 trees had densities of 2, 4, 8, 16, and 32 caterpillars. Depleted patches were created by allowing other individuals to forage successively on the same set of trees, each being allowed to remove up to 4 caterpillars. When a bird failed to find 4 caterpillars, they were removed either by a non-experimental bird with a high searching efficiency (8.2% of removed caterpillars) or by the observers (16.6%). This design resulted in 5 current densities for unexploited patches and 11 combinations of current density and level of depletion for partially exploited patches.

Before the start of the experiment great tits were trained to the test situation by being allowed to forage on four occasions on initial densities of 26, 30, 34 or 38 caterpillars offered in a random sequence. In the experiment we used a randomised Latin Square to determine the sequence in which the 16 tested combinations of current prey density and level of depletion (including previously unexploited patches) were offered to the different individuals. Each of the 31 great tits searched 15 of the 16 different combinations, because the last series of combinations could not be tested due to a lack of winter moths. In total 465 observations were made. The observation period started when the bird entered the room and ended when 4 caterpillars had been found (or 1 caterpillar at densities of 2 or 4), a total period of 30 minutes had elapsed, or the bird had stopped searching for 30 seconds. 'Search time' was the time until finding the first caterpillar minus the time spent on other activities. Date of testing, time of day, experience of the bird, observation room and observer (CMMM, KvO and LMAW) did not affect the recorded search time (P>0.15 in both analyses).

Search times were analysed using proportional hazard models (Kalbfleisch & Prentice, 1980), which can incorporate censored data such as ours. We fitted the model $h(t) = h_0(t)\exp(\beta\ln(d))$, where $\ln(d)$ is the natural log of the prey density, β its coefficient, $h(t)$ the hazard at time t, and $h_0(t)$ is the baseline function. The baseline function is time dependent and therefore accounts for, for example, birds not foraging for the first seconds at the start of a trial. We tested whether encounter rate (hazard) is

Table 1 Proportional hazard model of the time to find the first prey (search time) in great tits foraging for caterpillars. A) Test whether encounter rate (hazard) is directly proportional to prey density (unexploited patches only). The observed coefficient of log density, β (0.7807, s.e. 0.1056) is significantly smaller than the predicted β of 1 (T-test (138 d.f.) = 2.08, P<0.04). Encounter rate did not differ significantly between individuals ($\chi^2(30)$=42.58, P=0.06) or sexes ($\chi^2(1)$=1.80, P=0.18), nor was there a significant interaction between log prey density and sex ($\chi^2(1)$=3.07, P=0.08); B) Test whether search time is affected by the level of depletion [1 − (current density/initial density)] (unexploited and partially depleted patches). Search time did not differ between individuals ($\chi^2(30)$=37.29, P=0.17), nor were there significant interactions between log prey density and sex ($\chi^2(1)$=2.40, P=0.12) or depletion and sex ($\chi^2(1)$=0.004, P=0.96).

Variable	χ^2	df	P	β (s.e.)
A. Unexploited patches (n=140; 9 censored = 6.43 %)				
Ln (prey density)	64.6	1	<0.0001	0.781 (0.106)
B. Unexploited and partially depleted patches (n=453; 80 censored = 17.6%)				
Ln (prey density)	104.3	1	<0.001	0.891 (0.092)
Depletion	5.1	1	0.024	-1.246 (0.545)
Ln (prey density)* depletion	4.1	1	0.042	-0.490 (0.272)
Sex	9.8	1	0.002	-0.337 (0.106)

proportional to density by testing whether β departs from 1 for the trials involving only unexploited patches. To test for the effect of the level of depletion on encounter rate we used observations from all trials and included the level of depletion [1 − (actual density/initial density)] (which varies from 0 in unexploited patches to 0.875 in the most depleted patches used in the experiment) in the analysis.

RESULTS

When great tits searched on unexploited patches we found that encounter rate increased ($\chi^2(1)$ = 64.6, P<0.0001; Table 1a; and hence search time for the first prey decreased; Figure 1) with increasing prey density, but that this decrease was significantly less than directly proportional to density (T-test (138 d.f.) = 2.08, P<0.04). When prey density is doubled, encounter rate increases only by 72% (not 100%). This causes the search time to be 58% (not 50%) of the search time at the original prey density. This is a reduction of 42% instead of the expected 50%.

When great tits foraged on both unexploited trees and trees where other great tits had previously removed prey (see Methods), we again find an effect of prey density ($\chi^2(1)$ = 104.3, P<0.0001), but also a very clear effect of the level of depletion (both as a main effect, $\chi^2(1)$ = 5.10, P=0.024, and in interaction with prey density, $\chi^2(1)$ = 4.13, P=0.042; Table 1b). Encounter rate decreased, and hence search time increased,

dramatically with increasing depletion levels (Figure 2). Thus, when density decreases due to exploitation by other predators, encounter rate decreases much more than expected from the decrease in density alone. For example, the expected search time to find the first out of four caterpillars is almost five times higher when these are the survivors from an initial density of 32 than when they constitute the entire initial group of four prey. This effect of depletion is stronger at higher current prey densities (a significant interaction between depletion and prey density, Table 1b).

DISCUSSION

We show clearly that encounter rate increases less than directly in proportion to prey density and decreases dramatically with increasing levels of depletion. This latter effect has often been ignored and decreases in capture rate (assuming random search) within a patch have been attributed to decreases in prey abundance only (Cowie & Krebs, 1979). We do not know why encounter rate does not increase as quickly as expected with prey density in our experiment. If there is competition between winter moth larvae for resting places where they are well hidden, we would expect the opposite effect. An increase in searching rate by the great tits at high prey densities
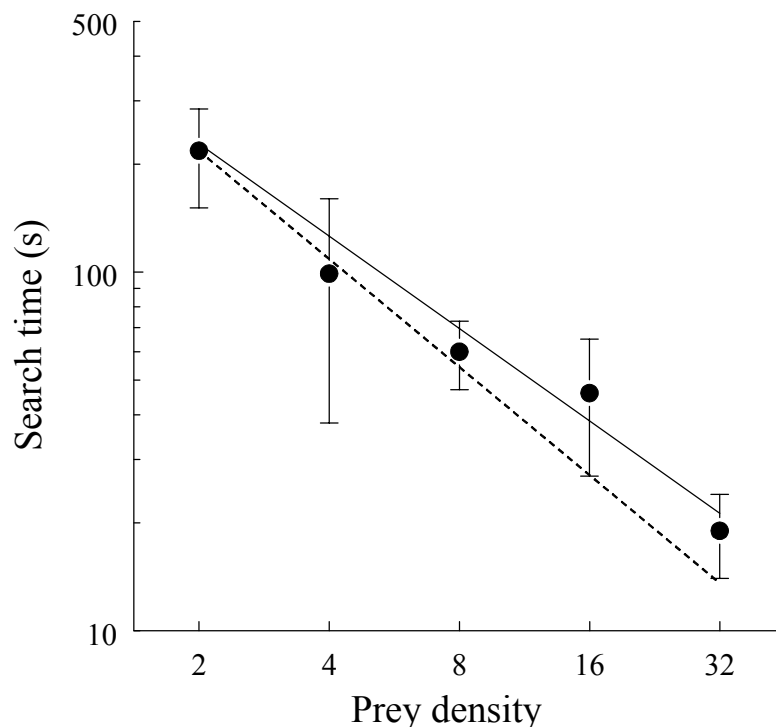
Figure 1 Median time to find the first prey ('search time'; Kaplan-Meier estimate with SE) in relation to prey density for great tits foraging for caterpillars on previously unexploited patches. Solid line is calculated from the proportional hazard model with β = 0.7807 (see Table 1a); broken line is the predicted line when search time is directly inversely proportional to prey density.
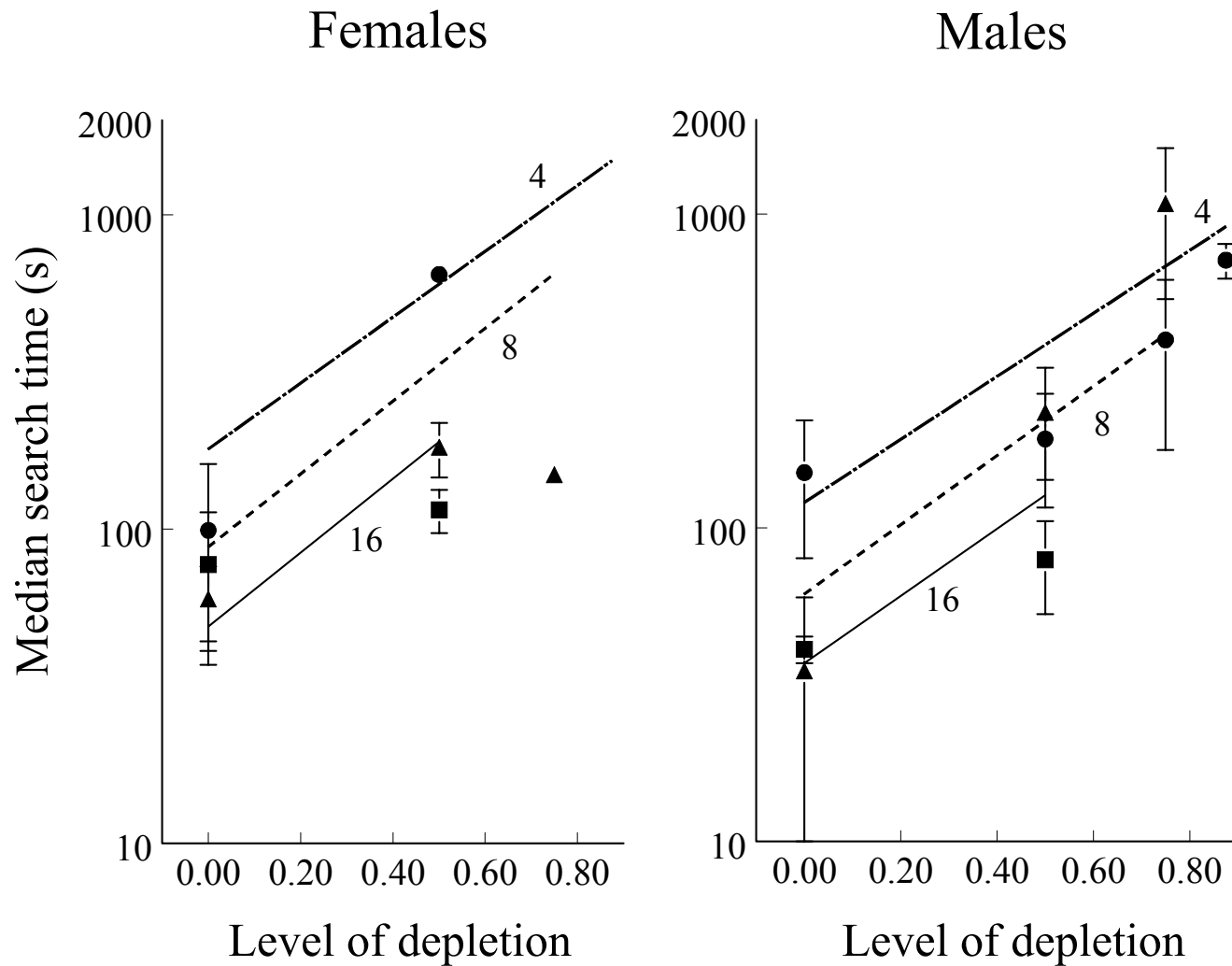
Figure 2 Median time to find the first prey ('search time'; Kaplan-Meier estimate with s.e.) in relation to the level of depletion for 3 current prey densities (dots = 4, triangles = 8, squares=16 prey) for male and female great tits foraging for caterpillars the two sexes. Lines are calculated from the proportional hazard model (see Table 1b for co-variates and their estimated coefficients).

would also produce the opposite effect, but in any case is not expected in our experimental results because we analysed only the search times for the first prey, when foraging great tits had no information about the current prey density. The effect of depletion on prey availability has been addressed by Charnov *et al.* (1976) who gave three explanations. Prey may change their behaviour and become more difficult to capture (behavioural depression), they may change their position such that they become harder to encounter or capture (microhabitat depression), or the prey that is easiest to find are taken first because of heterogeneity in either the prey or environment. The prey items in our experiment were confined to their self-built shelters (see Methods), so behavioural and microhabitat depression is unlikely. We therefore attribute the effect of previous exploitation in our experiment to heterogeneity in encounter rates, with the easiest prey to find being removed first, leading to a decrease in the average encounter rate of the individual remaining prey.

Clearly, the effects that we found will have a profound effect on predator-prey interactions in natural environments, particularly because prey often have a clumped distribution, and exploitation is often initially concentrated in the high-density patches (as for example assumed by ideal free distribution models (Sutherland, 1996). The effects found in our experiment can lead to a paradoxical situation in partly depleted environments, where patches with a relatively low current density, but little previous exploitation, may offer the best foraging opportunities. The reduced encounter rate in partially exploited patches will also effectively create refugia from predation, and hence may profoundly influence population dynamics. Some recent models of predator-prey interactions do take into account heterogeneity in encounter rates between prey (Anderson & May, 1991; Sibly *et al.*, 2002). However, this is often limited to easily recognisable classes of prey such as age, size or sex. The fact that we have found effects of previous exploitation when both the prey size distribution and environment are more homogeneous than in most natural situations, and that we have found an unexplained departure from direct proportionality between encounter rate and the density of previously unexploited prey, warns us for uncritical acceptance of the plausible assumptions of classical predator-prey models, even in seemingly uniform environments.

ACKNOWLEDGEMENTS

Chapter 4

Reduction of caterpillar damage in apple orchards by great tits (*Parus major*)

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& Marcel E. Visser

ABSTRACT

Alternative ways to control caterpillar pests and reduce the use of pesticides in apple orchards are in the interest of the environment, farmers and the public. Great tits are known predators of caterpillars and reduce damage under high caterpillar density when they are breeding in nest boxes in an experimental apple orchard. We tested whether this reduction also occurs under practical conditions of Integrated Pest Management as well as Organic Farming, by setting up an area with nest boxes while leaving a comparable area as control within 12 commercial orchards. We showed that in areas with breeding great tits apples had less caterpillar damage than in control areas. This demonstrates that great tits also can reduce damage under commercial management. In addition to the field study, a model was developed to predict damage reduction in the range between the low caterpillar densities in commercial and the high densities in an experimental orchard. Furthermore the model was used to evaluate the influence of the biological and physical parameters on the level of damage reduction. In the model the amount of damage reduction by great tits depended mainly on the hatching date of the chicks relative to the appearance of caterpillars and the number of breeding pairs in the orchard. The field data and the model show that damage is reduced in the presence of great tits. Therefore the caterpillar densities at which pesticides are applied can be shifted to higher densities in the presence of great tits, thereby reducing the amount of pesticides applied.

INTRODUCTION

Interest in biological control of pests is increasing for several reasons. Resistance of harmful insects to pesticides is a problem that persists, adverse public attitudes to pesticides have intensified (Solomon *et al.*, 2000), and legislation increasingly restricts the use of pesticides (Anonymous, 2001). The main focus in the search for biological pest control agents has been on parasitoids (Cross *et al.*, 1999) and predatory insects such as predatory mites, earwigs, lacewings, mirids and anthocorids (Solomon *et al.*, 2000). The potential contribution of vertebrate predators such as birds has mostly been overlooked. The main reason given for ignoring vertebrate predators is their presumed lack of a sufficient numerical response to outbreaks of pests. However, most of the studies on birds as biological pest control agents do show a reduction in the population size of harmful insect species (review see Kirk *et al.*, 1996; Mols & Visser, 2002 this thesis, chapter 2). These studies therefore show that birds have the potential as biological pest control agents in particularly in crops such as apples.

The great tit *Parus major* is a common species in the Netherlands and breeds readily in nest boxes. Putting up nest boxes can easily enhance the local density of great tits (Gosler, 1993 and personal data). When gathering food, great tits mainly forage for caterpillars, which is the preferred food for their nestlings (Betts, 1955;

Naef-Daenzer *et al.*, 2000; Royama, 1966; van Balen, 1973). Caterpillars in orchards, such as winter moths *Operophtera brumata* L. and tortricid moths, are key pests (Cross *et al.*, 1999; Solomon *et al.*, 2000). These features together suggest that great tits can serve as a biological control agent for caterpillars in orchards. Mols and Visser (2002 this thesis, chapter 2) showed that foraging by great tits reduced caterpillar damage on apples in an experimental orchard with high caterpillar densities. The question remains however whether great tits can also be effective in reducing damage under commercial management with lower caterpillar densities.

In this study we investigated whether great tits can reduce caterpillar damage in apple orchards with either Integrated Pest Management (IPM) or Organic Farming (OF) in areas with and without breeding great tits by measuring caterpillar densities and damage levels. In orchards with IPM, pesticides are only used if the control threshold is exceeded (Blommers, 1994). Furthermore, implementation of the biological control of phytophagous mites by predatory mites restricted the use of pesticides to those safe for predatory mites and, if possible, to other natural enemies. In orchards with OF biological control measures, such as, plant substances, natural enemies (including bacteria and viruses) and disruption of mating by pheromones are used and no synthetic pesticides, herbicides or chemical fertilisers are applied.

Compared to the experimental orchard, caterpillar densities were low in these IPM and OF orchards. Information at high densities in the experimental orchard and low densities in commercial orchards leave a gap of information at intermediate densities that were not present in the field during the research period. It is of importance to fill this gap as in the near future caterpillar densities in orchards are expected to increase due to new legislation which increasingly restricts the use of pesticides (Anonymous, 2001). We therefore modelled the expected damage reduction for low to high caterpillar densities and compared these model predictions with field data of the experimental (Mols & Visser, 2002 this thesis, chapter 2) and IPM and OF orchards. We evaluate the influence of number of breeding pairs and their nest box positions, breeding parameters of great tits and physical parameters in the model on the estimated damage and show that the caterpillar densities at which pesticides are currently applied in Integrated Pest Management as well as orchards with Organic Farming can be adjusted in the presence of great tits.

METHODS

Field measurements

The research was carried out in 12 apple orchards (6 IPM and 6 OF) over a period of 4 years (1997-2000). Of these 12 orchards 6 were sampled in one, 5 in two and 1 in three of the years of the research period. All orchards had two equivalent areas of 2 ha and it was randomly determined in which of the two areas nest boxes were put up. Nest boxes (15 to 25) were systematically placed in the inner 1.5 ha of the nest box

area to attract great tits. The main apple varieties in the orchards were Elstar and Jonagold.

In the orchards the breeding parameters of great tits, such as laying date, clutch size and number of fledgelings, were determined by checking nest boxes on a weekly basis from half April until all nests had fledged. Caterpillar densities were determined in the control and nest box area at the end of apple bloom. We determined caterpillar densities on 40 trees in both areas. On each tree a standardised branch was sampled i.e. the third branch from below. The orchards had at least one pair of breeding great tits.

In autumn we checked 25 apples of 40 trees (in total 1000 apples) for caterpillar spring damage, as described by De Reede *et al.* (1985), in both the nest box and the control area. Caterpillar spring damage is easily distinguished from other caterpillar damage because it is characterised by corked scar tissue not present in other classes. Caterpillar damage was classified as small (< 0.25 cm^2), medium (0.25- 1.0 cm^2) and large (>1.0 cm^2) but these classes were grouped for analysis because we were interested in the total caterpillar damage. The percentage of damage was calculated per tree and averaged per area (nest box and control) per orchard. We tested whether the average percentage of caterpillar damage in the nest box area was lower than on the control area using a paired T-test. Furthermore, we tested whether management type, the difference between caterpillar numbers in the nest box and control area and the number of breeding pairs in the nest box area had an effect on the degree of damage reduction using an ANOVA.

Simulation model

An individual-based model was developed in the framework of OSIRIS (Mooij & Boersma, 1996). This model was used to calculate the amount of damage caused by caterpillars in an orchard with and without great tits assuming different initial caterpillar densities. Great tits were foraging in a virtual apple orchard of 1 ha. This orchard consisted of 32 by 83 grid cells of 3 by 1.2 meter each. Each grid cell represents one apple tree. The cell size was chosen to represent the normal distances between rows (3 m) and trees (1.2 m) within a row in commercial orchards. The great tits in the model have complete knowledge of their environment and are restricted to forage within the 1 ha orchard. Prey types are grouped as a single prey type with one weight dependent energetic value. The weight of the prey increases with its age (see Appendix). Per feeding trip only one prey item can be taken because generally great tits are single prey loaders (Houston & McNamara, 1985; Royama, 1966). The great tits in the model do not feed themselves but only forage for their offspring. Per nest box two parents are feeding the nestlings, each supplying half of the energy requirement of the young.

In the model, a pair of great tits starts removing caterpillars from the orchard from the moment their nestlings hatch. Hatching date of chicks can be varied. Each foraging trip starts from the assigned nest box position and leads to the grid cell with

the highest difference between the energy gain rate for the chicks and the foraging costs for the individual model tit. A slightly modified model of Kacelnik & Houston (1984) is used to calculate the net energy gain rate per prey for each cell (see Appendix). With each visit to an individual grid cell one prey is subtracted from the (current) density in that cell. The model keeps track of the current as well as the initial density of cells for the calculation of the search time to find a prey within cells (see Appendix).

With every feeding trip the time spent flying, searching and provisioning is added to the total time spent foraging, the energy spent is added to the energy expenditure of that day and the energy content of the prey is added to the energy intake of the chicks. Before the next feeding trip starts, the model checks whether i) the total time spent foraging is less than the available daily foraging time i.e. average daylight in May (KNMI), ii) the energy expenditure of the parents is lower than their maximum daily energy expenditure (DEE_{max}) (Tinbergen & Dietz, 1994) and iii) the energy intake of the nestlings is lower then their daily energy requirement (after Royama, 1966). To account for the fact that both parents feed the young, the maximum daily energy requirement is split equally over both parents. In case one of these three criteria is reached, the model shifts to the next day and the age of the nestlings and prey are updated, all counters are reset to zero and the whole procedure starts again. Otherwise the next foraging trip is made. The simulations are finished when the age of the chicks becomes 18 days (i.e. assumed fledging age of great tits) or when there are no more caterpillars found in the virtual orchard.

Several pairs of great tits can forage simultaneously in the orchard and can be assigned to different nest box positions (see Appendix). The calculation which grid cell had the highest net energy gain is done after the density in the grid cell where the previous bird has foraged is reduced. All counters are kept per individual as described above.

In the field, caterpillars are Poisson distributed (Mols, unpublished data) and therefore the assigned densities to individual cells in the model follow Poisson distributions as well. Caterpillar dynamics were modelled assuming that all caterpillars appear on the 1 May and decrease linearly over a period of 50 days in presence and absence of great tits (see Appendix). The linear decline in the number of caterpillars was implemented by dividing the total number of caterpillars in all grid cells by the number of remaining days (i.e. 50 days minus number of day the caterpillars have already been growing). The number of caterpillars eaten, if any, was first subtracted from the remaining density before this calculation was done (see Appendix).

The cumulative number of caterpillar days was calculated by adding up all remaining caterpillars at the end of one day over the period of 50 days. The cumulative number of caterpillar days was used to estimate the percentage of damage caused (see Appendix). The model was parameterised using field, laboratory and literature data (see Appendix) to reflect the natural situation as best as possible.

The simulations were done with a default setting for 5 different caterpillar densities, namely 2, 4, 8, 16 and 32, and with 5 replicates per simulation. Furthermore we determined the sensitivity of the model for the main physical and biological parameters (Table 1). For background information on parameters and values see Appendix.

RESULTS

Field data

We found a significantly lower percentage of damaged apples in the nest box area compared to the control area (one tailed paired T_{test}= -2.71, *P*<0.01, n=19). The average percentage of damaged apples was 4.5% (SE ± 0.7) in areas with and 6.0% (SE ± 0.9) in areas without great tits (Fig. 1).

In the analysis, data of all IPM and OF orchards were pooled because no difference in damage levels between nest box and control areas for the different management regimes could be detected ($F_{(1,14)}$=2.63, *P*=0.13). The difference in average damage between the area with and without great tits was, respectively, 2.8% (SD ± 3.4) and 0.8% (SD ± 1.5) in IPM and OF orchards. Due to the large variation we could not show a significant difference between IPM and OF orchards (power analysis β=0.52).
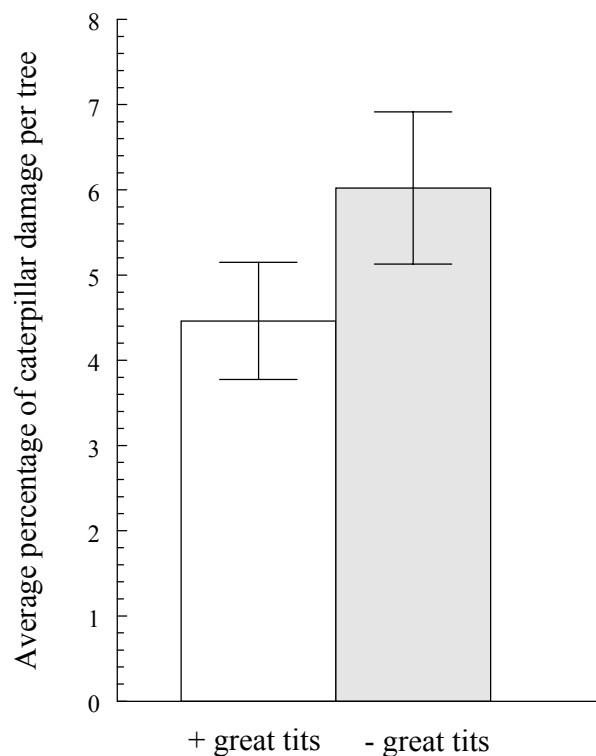
Figure 1 Average percentage of caterpillar damage (± SE) of 40 trees, of which 25 apples each were sampled, in pairs of 2 ha areas with and without breeding great tits in 6 IPM and 6 OF orchards.

Besides management regime also the number of breeding pairs and the difference in caterpillar density between the two areas were tested. Number of breeding pairs varied between 1 and 6 resulting in a low number of replicates and thus power was not sufficient to detect a difference in this set up ($F_{(1,14)}$=1.71, P=0.21). The difference in initial caterpillar density at bloom per area was small and had no significant effect on the amount of damage reduction ($F_{(1,14)}$=0.26, P=0.62). The average difference between the two areas was 0.2 caterpillars (SD ± 1.2) when numbers of caterpillars in the control area were subtracted from the nest box area with a minimum difference of – 0.8 and a maximum of 4.2 caterpillars per tree.

Caterpillar densities in OF orchards were slightly higher than in IPM orchards. The extrapolated numbers of caterpillars per tree were 7.1 (SD ± 1.0) for OF and 6.1 (SD ± 0.3) for IPM around the end of bloom. This was much lower then the 39.3 (SD ± 13.2), 11.4 (SD ± 5.2), 36.2 (SD ± 30.0) and 15.7 (SD ± 11.9) per tree found in block 1 to 4 in an experimental orchard (for details see Mols & Visser, 2002 this thesis, chapter 2). The species composition in OF orchards was 4.3% winter moths and 80.8% tortricid moths (remaining items unidentifiable), while in IPM orchards 58.1% winter moths and only 15.2% tortricid moths occurred. The lower number of tortricid moths in IPM orchards is caused by chemical control measures against these species, which is not accepted in OF orchards. In the experimental orchard the species composition varied between blocks with the percentage of winter moth varying between 9.7 in block 2 up to 49.8 in block 3 and tortricid moths between 49.4 in block 3 and 86.8 in block 2.

Model predictions

Simulations under default setting as given in Table 1 were made for the caterpillar densities 2, 4, 8, 16 and 32. The model predicts the percentage of caterpillar damage in the presence and absence of great tit and predicts higher percentages of damage in a model orchard without great tits (Fig. 2). The difference in predicted damage with and without great tits increases with increasing caterpillar densities.

The sensitivity of the model for variation in biological and physical parameters was tested. The predicted damage by the model is sensitive for alterations in two of the six biological parameters namely, the number of breeding pairs in the orchard and the hatching date of the chicks relative to the appearance of caterpillars (Table 1). When the number of breeding great tits increases the predicted damage reduction increases as well (i.e. the difference between the lines with and without great tits) (Fig. 2), but not proportional to the increase in the number of breeding pairs. At low caterpillar densities (2 and 4) the model only predicts a small 0.1 to 0.3% damage reduction i.e. the predicted value with great tits minus the value without great tits. At higher densities this difference is more pronounced and can run up to 1 to 1.4% damage reduction with respectively 2 or 4 breeding pairs at an initial density of 16 caterpillars per tree. Variation in hatching date also has an effect on damage reduction but less than the number of breeding pairs. When chicks hatch later than average in the season

Table 1 Parameter values (see Appendix for calculation of values) used in the model and altered values to test the sensitivity of the model and their effect on damage all relative to the run with the default parameter values: ++ relative large increase, + relative small increase, = no difference -- relative large decrease and - relative small decrease.

Parameter	Default	Alternative value	Change in predicted damage reduction
Biological parameter			
Number of pairs	1	2	-
		4	--
Number of chicks	9	7	=
		11	=
Nest box position	middle	2/3 between corner and centre	=
		1/3 between corner and centre	=
		corner	=
Hatching date	12	5	-
		19	+
Energy need of chicks	Table A3	default – 50%	=
		default + 50%	=
Time to forage (daylight)	16	12	=
		14	=
Physical parameter			
Costs of searching	3.25	default – 50%	=
		default + 50%	=
Costs of flying	14	default – 50%	=
		default + 50%	=
Energy content prey	21.35	default – 50%	=
		default + 50%	=

the damage reduction is less and when hatching is earlier the average damage reduction is slightly larger for low density and increases with higher densities (Fig. 3). At the caterpillar densities of 2 and 4 caterpillars per tree, the model only predicts very small changes in damage in comparison to the default value of minus 0.06 and 0.1% and plus 0.4 and 0.9% when hatching dates were respectively a week earlier or later than the default average hatching date. Again differences are more pronounced at higher densities. The predicted damage reduction increases from 0.6 to 0.8% when chicks of one breeding pair hatch one week earlier and decreases to 0.4% damage reduction when chicks hatch one week later. The predicted damage in Figure 2 and 3 does not pass through the origin because of the shape of the relationship between the cumulative number of caterpillar days and damage (see Appendix). This relationship was derived from field data of the experimental orchard were caterpillar densities per tree were measured at different times in the growing season (Mols & Visser, 2002 this thesis, chapter 2). Due to mortality, early pupating or mobility of caterpillars some trees were found to have no caterpillars but did have caterpillar damage in harvest.
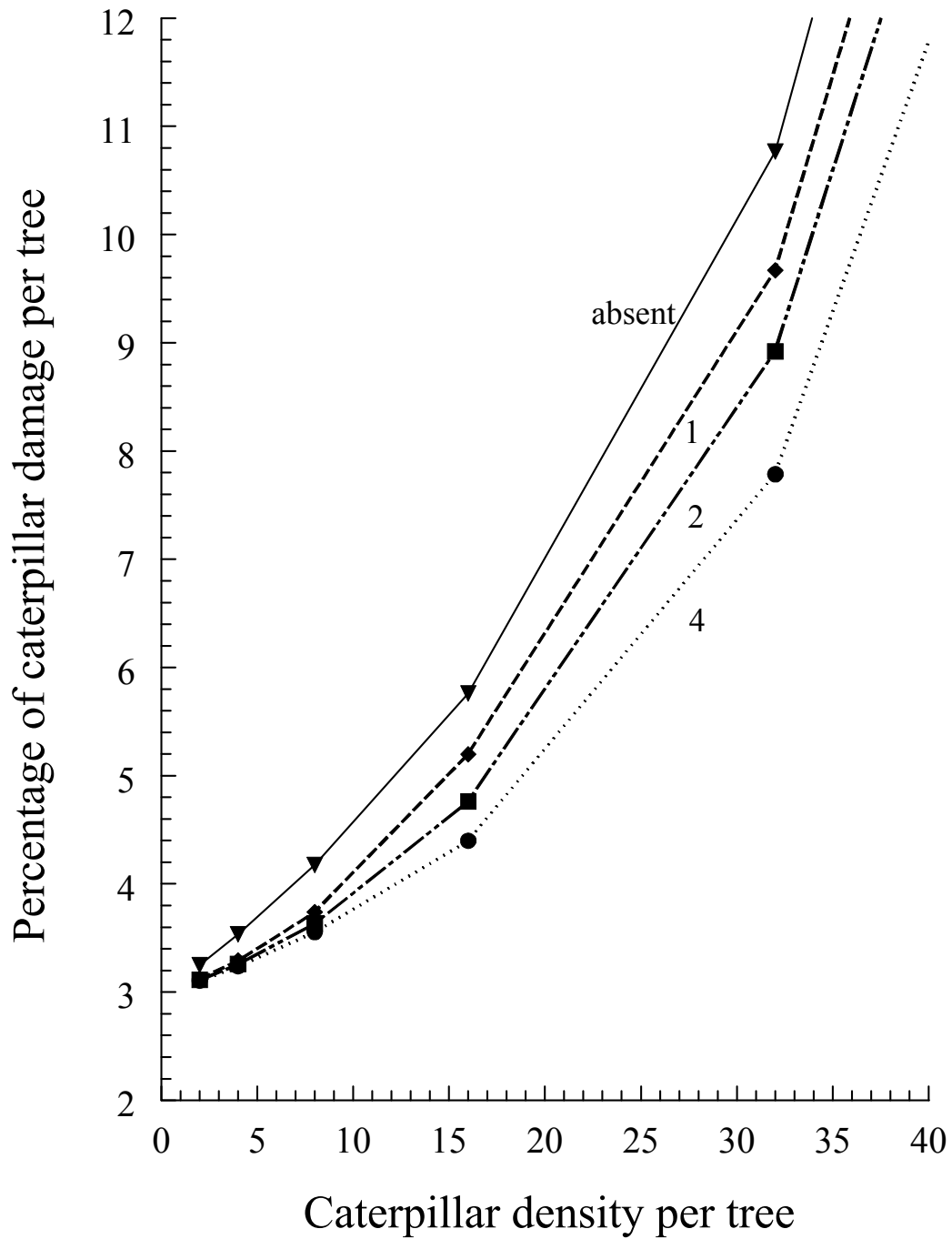
Figure 2 Variation in percentage of caterpillar damage on apples per tree predicted by the model when there are 0 (absent), 1, 2 or 4 pairs of great tits searching in the orchard.
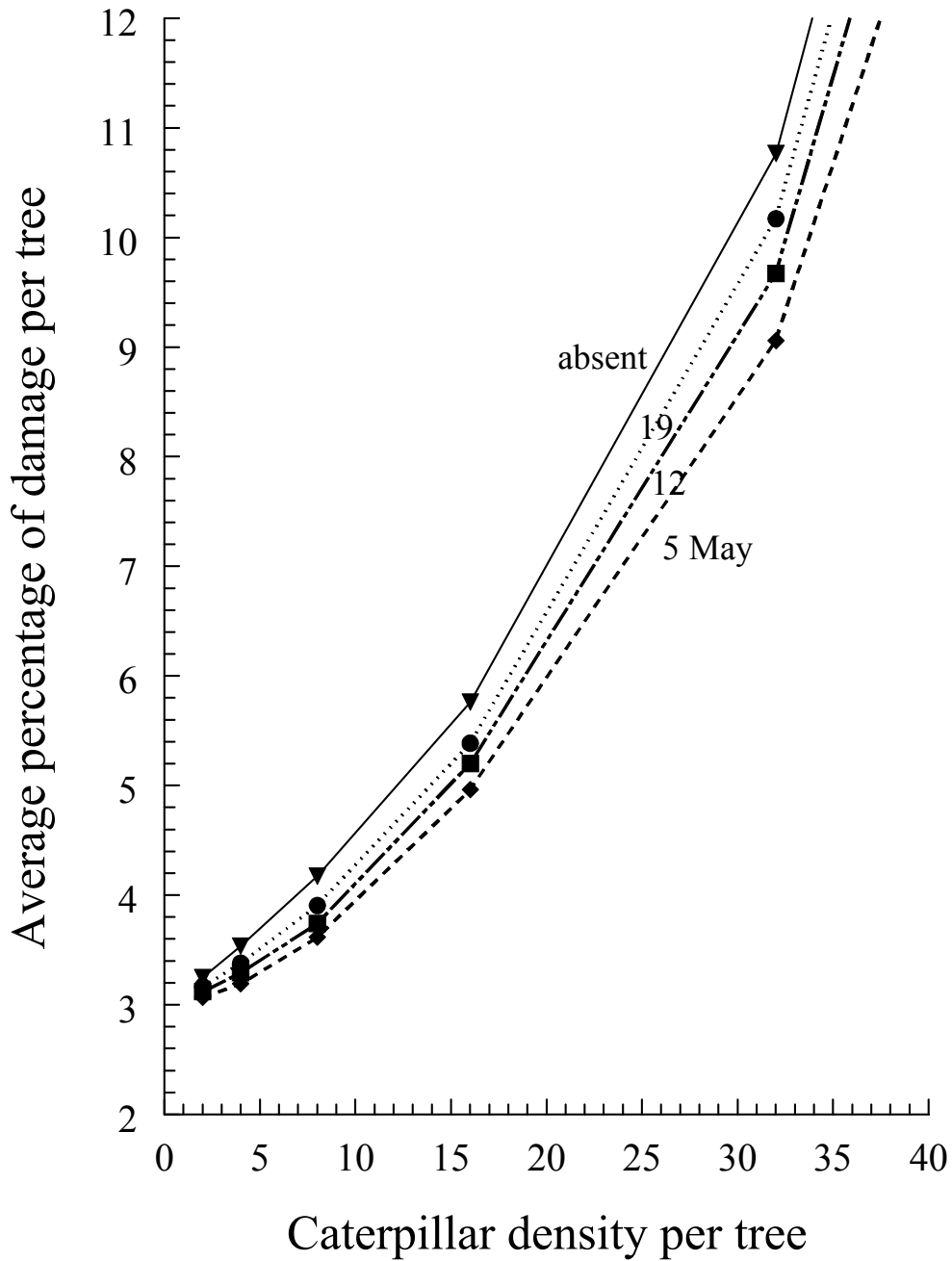
Figure 3 Variation in percentage of caterpillar damage on apples predicted by the model when young of one pair of great tits hatch 7 days earlier (5 May) or later (19 May) than the average hatching date (12 May) in orchards.

The model is insensitive for changes in the physical parameters (Table 1). The predicted caterpillar damage when these parameters are varied in a reasonable range show no or small deviations from the default prediction.

The damage predictions of the model are in the same magnitude as the field data (Fig. 4). In the experimental orchard there were no areas without great tits and thus the percentage of damage without great tits is lacking for the higher densities. For both OF and IPM orchards the damage in the area with great tits was lower than in the area without great tits. This effect seems more pronounced in IPM orchards but this was not significant ($F_{(1,14)}$=2.63, *P*=0.13).

DISCUSSION

Although some studies suggest that birds do not remove prey that occur at low densities (Bruns, 1960; Otvos, 1979; Tinbergen, 1960), our study shows that great tits are able to reduce damage at low caterpillar densities in IPM and OF orchards. Putting up nest boxes to attract great tits is a low cost measure that can reduce damage up to 1.6% i.e. an increase in yield of undamaged apples of 200 to 640 kg.ha^{-1} (assuming a production of 40.000 kg.ha^{-1} of apples). The percentage of damage reported in this paper represents the total spring caterpillar damage found when inspecting apples at harvest. This percentage is higher than the economic damage of these same apples because caterpillar damage not exceeding 0.25 cm^2 is generally considered insignificant. In our damage assessment this class of damage comprised 25% of the total damage found and would reduce the percentage of damage in Figure 1 from 6.0% to 4.5% in the absence of great tits. Analyses on economic damage between areas give similar results (one tailed paired T_{test}= -2.73, *P*<0.01, n=19).

The model that we developed predicts damage caused by caterpillars in an environment with and without great tits reasonable well. The model is robust for variation in the physical parameters and most of the biological parameters. One of the reasons that damage reduction by great tits is insensitive for these parameters in the model is that these parameters enhance the energy expenditure of the parents but do not change the number of caterpillars removed by these parents much. When energy demands of the chicks are comparatively low (i.e. early after hatching) and/or densities are equal or higher than 8 caterpillars per tree the parents can feed their chicks the maximum daily amount without reaching their energy or time limits. Furthermore, damage is calculated from the cumulative number of caterpillars and therefore the caterpillars removed in an early period put more weight to the predicted damage than those removed later in time when parents become limited in either foraging time or energy expenditure. As a result the decrease in number of caterpillars removed in the later period of chick growth do not alter the predicted damage much. For the same reason the model is insensitive to the maximum foraging time available per day. Time was not a limiting factor and thus similar numbers of caterpillars were removed for the different values of the maximum foraging time, causing almost no
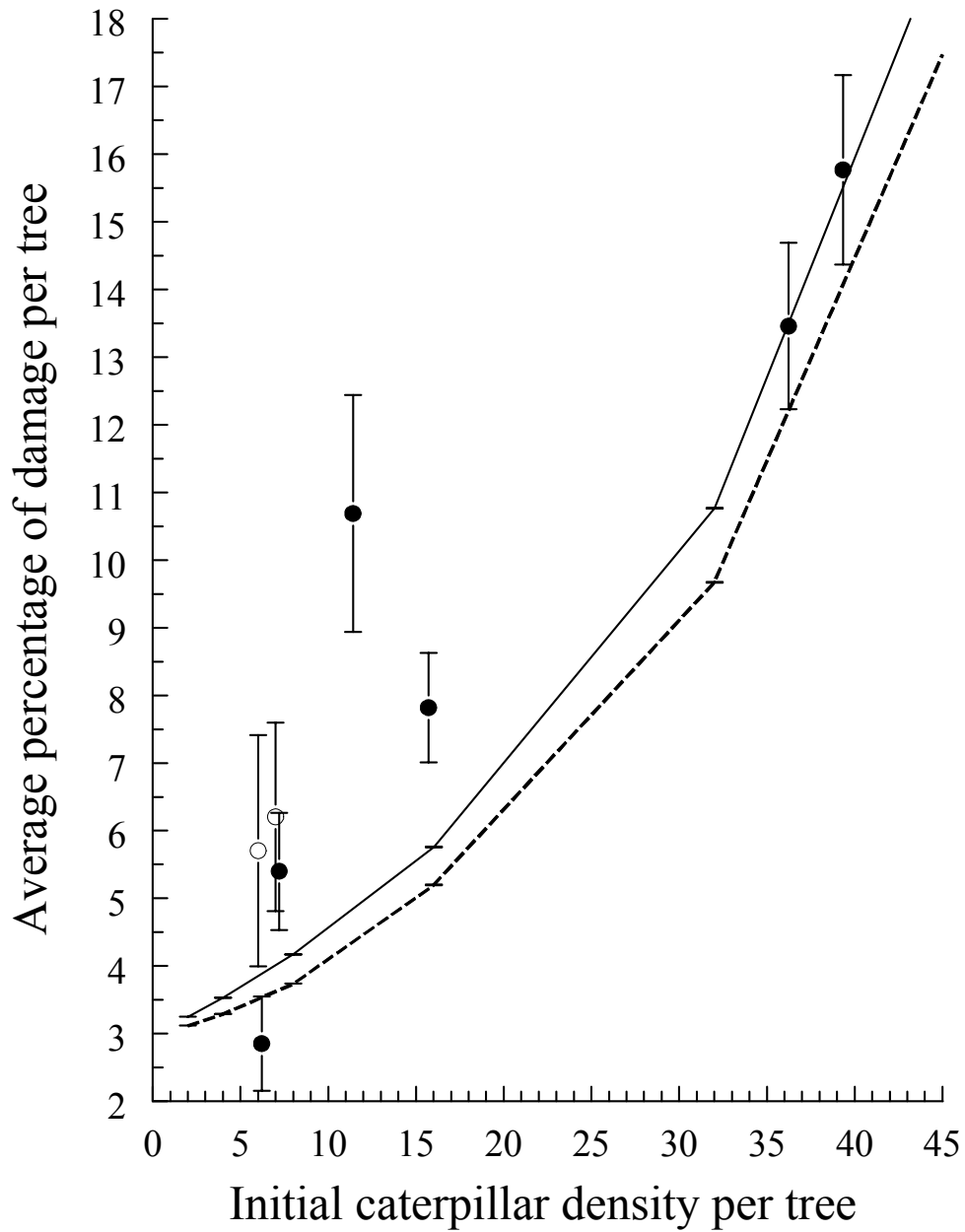
Figure 4 Predicted caterpillar damage reduction in presence (dotted line) and absence (solid line) of great tits and the average caterpillar damage (± SE) on apples found in the experimental, IPM and OF orchards with (solid circles) and without (open circles) in the IPM and OF orchards. No area without great tits was present in the experimental orchard.

difference in the cumulative number of caterpillar days and thereby predicted damage. Also nest box position had no influence on damage because great tits could only forage within the orchard. Changes in nest box position, especially the corner position, raised the energy expenditure and total foraging time of the parents i.e. they had to fly more to be able to forage in an equivalent area as the pair in the position in the centre, but not beyond the limits for the majority of simulations. The model takes only the food provisioning of the nestlings into account and is a simplification in which the self-feeding of the parents is ignored. Diet of parents is not well known and dietary needs of parents will be proportional to breeding activities.

Parameters that have an influence on the predicted damage are the number of breeding pairs in the orchard and the hatching date of the chicks. Both these factors influence the number of caterpillars removed in the orchard. When the number of breeding pairs is increased, the number of removed caterpillars also increases. When two pairs of great tits are foraging simultaneously, the number of remaining caterpillars decreased more rapidly but the time to find and get a prey item increased for all individuals. The number of caterpillars removed by two pairs is not doubled but the damage decrease is substantial. Two additive effects cause the higher damage reduction when chicks hatch earlier. Great tits not only start removing caterpillars earlier from the orchard but they also have to bring more caterpillars to the chicks to fulfil the same energy requirement as the caterpillars grow in the model and thus are smaller when chicks hatch earlier.

The difference between the percentages of damage found in the field and the predicted damage by the model can be caused by a different caterpillar species composition under field conditions. In IPM orchards the majority of caterpillars found were winter moths while in the OF orchards the majority were tortricid moths. Almost 50% of all caterpillars in the experimental orchards in the two high-density blocks were winter moths but in the other two blocks up to 86.8% of the caterpillars were tortricid moths. Variation in the probability that great tits detect winter moths and tortricid moths can occur, due to the different shelters made by the different species. The spun leaf shelters of winter moths are less tight and cryptic as those of tortricid moths (personal observation). As a consequence the search time for tortricid moths can be longer (Endler, 1991) and thus the number of tortricid moths removed per time unit will be lower than that of winter moths. When tortricid moths are the dominant species, like in OF orchards and the two low-density blocks of the experimental orchard, the model could underestimate the percentage of damage.

Our findings in the field as well as the model predictions imply that the caterpillar densities at which pesticides are applied can be raised when great tits are breeding in orchards. Depending on the number of breeding pairs and the hatching date of chicks the densities can be raised with 1 to 3 caterpillars per tree. For example when great tits are absent in the orchard a damage level of 3.5% (i.e. 2% economic caterpillar damage) is reached with 4 caterpillars per tree while the same damage occurs with 6

to 7 caterpillars per tree when 2 to 4 pairs of great tits are foraging in the orchard. To what extent the threshold caterpillar density at which pesticides are applied can be raised depends mainly on the number of breeding pairs and the hatching date of the chicks, our results clearly indicate that a shift in threshold caterpillar density at which pesticides are applied can be realised under IPM or OF management. Presence of great tits can thus lead to a more limited pesticide use in apple orchards.

ACKNOWLEDGEMENTS

APPENDIX

PARAMETERS OF AN INDIVIDUAL BASED MODEL OF GREAT TITS FORAGING

Metabolic costs of foraging

In the model the great tits forage in the grid cell with the highest net energy yield per prey. The net energy yield ($E_{grid\ cell}$) was calculated by a modified model of Kacelnic & Houston (1984):

$$E_{grid\ cell} = \frac{e_p - (t_f * M_f + t_s * M_s)}{t_f + t_s} \tag{1}$$

With e_p being the energy content of the prey, and t_f and t_s the time the great tit was respectively flying and searching to get a single prey item. M_f is the metabolic cost of flying and M_s of searching. The energy content of the prey increases with caterpillar size as described and calculated in the caterpillar dynamics section below.

Metabolic energy to fly (M_f) was calculated by multiplying the time involved in flying by the estimated energy needed to fly (Table A1). The energy needed to fly was taken from literature (Hinsley, 2000, after Masman & Klaassen, 1987; see also Norberg, 1996). The time spend flying depended on the distance between the nest box and the foraging place and the flight speed of the great tit. The distance (in m) between nest box and grid cell coordinates was calculated and multiplied by two to get the round trip distance (Table A1). The equation of Tucker (1973) was used to calculate the flight speed of great tits in the model (Table A1) and depended on body mass only. In the model all great tits had equal body mass, for which a weight of 17.5 g (SD ± 1.0, 81 female and 70 males), the mean of all great tits captured during breeding in the research period, was used. Distance was divided by flight speed to calculate round trip flying time (t_f) for every grid cell.

Metabolic energy to search (M_s) was calculated by multiplying the time involved in searching by the estimated energy needed to search (Table A1), which was estimated on the basis of literature (Holmes *et al.*, 1979a; see also Maurer, 1996). Searching behaviour is seen as a combination of hopping (5*Hdb) and perching (1.5*Hdb) (Cramp *et al.*, 1993; Holmes *et al.*, 1979a) leading to our assumed energy costs for searching (3.25*Hdb). To convert Hdb into BMR the value had to be multiplied by 1.25 (Williams & Nagy, 1984). The time involved in searching was calculated by the equation given in Table A1 and is a function of the current density and the degree of depletion in the grid cell (Mols *et al.*, this thesis, chapter 3). Therefore the current as well as initial densities of grid cells are used to calculate search time (t_s) in the equation.

Table A1 Parameters used in the model to calculate the energetic costs of foraging within the virtual orchard.

Parameter	Equation or value	Source
Metabolic costs of flying		
Metabolic energy to fly (kJ.s^{-1})	$M_f=14*BMR*T_f$	Hinsley (2000) after Masman & Klaassen (1987)
Basic Metabolic Rate (kJ.s^{-1})	$BMR=0.137+0.012*M$	Tinbergen & Dietz (1994)
Body mass (g)	$M=17.5$	Average Mols unpublished data
Round trip flying (s) per prey i[a]	$T_f = D*V^{-1}*2$	
Flight speed (m. s^{-1})[b]	$V=13.2*M^{0.20}$	Tucker (1973)
Metabolic costs of searching		
Metabolic energy to search (kJ.s^{-1})[cd]	$M_s=3.25*1.25*BMR*T_s$	
Search time[e]	$T_s=\exp(4.9-(0.11*De_{(t=t)}+0.05*De_{(t=0)}))$	(Result of experiment of Mols *et al.*, this thesis chapter 3)

[a] D distance (in m) between nest box and grid cell coordinates calculated with Pythagoras

[b] In original equation, units of V = km.hr^{-1} and M is body mass (g)

[c] Conversion factor Hdb=1.25 BMR (Williams & Nagy, 1984)

[d] Searching involves hopping, 5*Hdb and perching, 1.5*Hdb per second (Holmes *et al.*, 1979a) leading to 3.25 Hdb per second searching behaviour

[e] D is caterpillar density in the individual grid cells

Caterpillar dynamics

The 1 May was chosen as date of appearance of all caterpillars because damage by caterpillars is mainly caused after petal fall of the flowers, which varied, from the 27 April until the 5 May during the research period.

Caterpillars were given a linear decline in numbers that comprised death by predation (other than by great tits) or a-biotic factors and pupation. A linear decline is justified due to asynchrony in phenology of species, i.e. as the first species to appear decreases, the next species is still increasing in number. This leads to a more or less linear caterpillar decline over time (Mols, unpublished data). A realistic time span in which caterpillars are present in orchards is around 7 weeks. Therefore the linear decline was set over a period of 50 days.

Estimation of prey energy

The energy content of caterpillars in the model was linked to their age. Depending on age the length of the caterpillars was calculated via the relationship given in Table A2. This relationship was calculated from data collected in 8 different orchards in 1999 to avoid underestimation of average caterpillar length at the appointed date of appearance of caterpillars. In these orchards caterpillars were sampled weekly over a period of 6 weeks. The average size of all caterpillar species found in the first sample

Table A2 Caterpillar growth and energy content of prey used for calculations in the model (with sources).

Parameter	Equation or value	Source
Prey		
Energy content of prey [a] [b]	$E_p=CFW*0.175*21.35$	Bell (1990) and personal data
Caterpillar Fresh Weight (g)	$CFW=0.0025*\exp(0.1701*L)$	personal data
Length of prey (mm)	$L=0.2712*age+6.89$	personal data

[a] Conversion factor from fresh to dry weight varied in literature between 15 and 20% therefore 17.5% was chosen

[b] Energy content of caterpillars: 21.35 $kJ*g^{-1}$ dry weight (Bell, 1990 and personal data)

after bloom was set as size at appearance. The average size in the second week was seen as caterpillars of day 8, the third as day 15 etc.. This approach gave the relationship between length and age of caterpillars (length = 0.2712*age + 6.9 with R^2 = 0.98) used in the model.

The energy content of the prey at age (t) can be calculated by converting length into fresh weight and fresh weight into dry weight (see Table A2). In literature the conversion from fresh to dry weight of caterpillars varied between 15 and 20% and in the model a conversion factor of 17.5% was used. The energy content of caterpillars was 21.35 kJ per gram dry weight. This figure was composed out of literature data (Bell, 1990) and personal observations.

Nestling parameters and number of pairs

The average clutch size of great tits breeding in orchards, 8.5 (SD ± 1.5, n=81), was taken as estimate for the number of hatching chicks and hence we choose 9 chicks as the default value. To test the sensitivity of the model for this parameter this default value was raised and lowered by the natural variation in brood size, i.e. two chicks.

The average hatching date of great tits breeding in orchards was calculated from field data gathered between 1997 and 2000. The average hatching date was on 12 May (SD ± 5.5 days, n=81), which was used as the default value. To test the sensitivity of the model for this parameter the default value was raised and lowered by a week.

The energy demand of chicks increases with age (Keller & van Noordwijk, 1994) up until day 13. Royama (1966) estimated the energy brought to nests by great tits in relation to age and number of chicks. His calculations coincided with the estimation of Kluiver (1950) of the total amount of food brought to the nest during the whole nestling period. The estimates of Royama (1966) are shown in Table A3, and used in the model to calculate the age dependent energy requirements of the nestlings.

The territories of great tits may vary in size from 0.2 to 4 ha (Gosler, 1993). Numbers of pairs in the orchard (i.e. 1, 2 and 4) were chosen to fall within this size range.

Table A3 Age dependent energy requirement of one great tits' chick after Royama (1966)

Age of chick (in days)	0	1	2	3	4	5	6	7	8	9	10	11	12	13-18
Energy requirement $(kJ*day^{-1}*chick^{-1})$	1.7	2.1	3.8	7.0	8.3	10.8	12.8	14.5	16.2	17.0	17.6	18.5	18.9	19.1

There were no exact fledging ages of nestlings available from the data collected in the orchards and therefore we used the average age from literature. Depending on food abundance chicks fledge 19 to 21 days after hatching but in the last few days the food delivered to the nest is strongly reduced to force the chicks to fledge (Gosler, 1993) and hence the default fledging age was set to 18 days in the model.

Calculation of damage by the model

A relation between cumulative number of caterpillar days and damage was derived from field data of 2000. In an experiment caterpillars were counted and removed at different moments in time (Mols & Visser, 2002, this thesis chapter 2). These data were plotted in a graph and a sigmoid trend line was fitted. This function between cumulative number of caterpillars (C) and damage was used in the model to estimate the percentage of damage.

$$\text{Damage} = \frac{1}{1 + \exp{(3.479 + 0.00171 * C)}} \tag{2}$$

Conversion of caterpillar numbers of field data

In the field caterpillar numbers were determined per branch while the model worked with caterpillars per tree. Therefore the caterpillar numbers per third branch had to be converted into caterpillars per tree to be comparable with the model simulations. The numbers of caterpillars on the third branch as well as the whole tree were counted in an experimental orchard in 2000 (Mols, unpublished data). The relationship (y = 3.6*x + 5.9, R^2 = 0.49 with x is the number of caterpillars on the third branch) between these numbers was used to extrapolate caterpillar numbers to tree level.

Foraging simultaneously

When individuals are foraging simultaneously the order of individuals is determined by the time of the day i.e. the great tit which already spend 20 seconds on foraging will depart for its foraging trip before the bird that spend 22 seconds on foraging. On the first foraging trip of the day the order in which the individuals start is according to order in which the individuals are declared in the model. After the first foraging trip the time of day varies for all individuals due to differences in the time to get one prey item.

Chapter 5

Assessing the reduction of caterpillar numbers by great tits breeding in apple orchards

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ABSTRACT

Great tits can reduce damage by caterpillars in apple orchards. A model by Mols *et al.* (this thesis chapter 4) predicted that damage reduction is mainly influenced by the hatching date of the great tit nestlings and the number of breeding pairs in the orchard. The amount of damage reduction established by great tits depends on the number of caterpillars removed and the timing of their removal. Therefore, we expect that the number of caterpillars removed by great tits in orchards will be influenced by these same factors and investigate how hatching date of the great tit nestlings and the number of breeding pairs in the orchard affect the total the number of caterpillars removed from apple orchards. In the first part of the study we calculate the total number of feeding visits by great tits with two different methods, event counters and the daily weight gain of nestlings. Numbers of feeding visits are overestimated when the daily weight gain of nestlings is used without making assumptions on prey size selectivity of great tits. A reliable estimate of prey size as selected by great tits is needed before this method can be used to estimate the number of feeding visits. Using the data from the event counters we could show that the number of feeding visits increased with date and the number of nestlings. However, for the estimation of the number of caterpillars removed during the whole nesting period, no effect of hatching date could be shown with the data of the event counter. In the second part we estimated the number of caterpillars removed by varying numbers of breeding pairs and related these with the average number of caterpillars occurring in orchards under an Organic Farming regime. With the average number of 3 breeding pairs of great tits the proportion of caterpillars removed is on average 23% and can run up to 49% if all foraging takes place within the orchard.

INTRODUCTION

Great tits are insectivorous birds that feed large amounts of caterpillars to their nestlings (Betts, 1955; Gibb & Betts, 1963; Gruys, 1982; Naef-Daenzer *et al.*, 2000; Royama, 1966; van Balen, 1973). The nestling-rearing period, when the number of prey items caught is high, coincides with the period in which caterpillars of winter moths *Operophtera brumata* L. and tortricid moths are present in orchards. These caterpillars are key pests in apple orchards (Cross *et al.*, 1999; Solomon *et al.*, 2000). The great tit is a common species that breeds readily in nest boxes, and hence putting up nest boxes in orchards can easily increase the local density of great tits. Mols & Visser (2002) and Mols *et al.* (this thesis chapter 4) have shown that great tits can reduce damage to apples by removing caterpillars, but the amount of damage reduction seen in orchards with either Integrated Pest Management (IPM) or Organic Farming (OF) management is highly variable. In a model (Mols *et al.*, this thesis chapter 4) we predicted that the number of breeding pairs and hatching date have the largest influence on the level of damage reduction by great tits but that the number of

nestlings per brood had no detectable effect. To put these findings to the test we should consider in more detail the underlying processes that determine the damage reduction.

The main component of damage reduction is the number of caterpillars removed by great tits and therefore we estimate in this study, which variables determine this number of caterpillars removed in commercial orchards. We test the influence of hatching date, date and number of nestlings on the total number of feeding trips as well as on the number of caterpillars brought to nestlings. Furthermore we calculated the proportion of caterpillars removed from the orchard by estimating the number of foraging trips in- and outside the orchard. To estimate the number of caterpillars removed we used and compared two methods. In the first method, the number of visits to the nest was counted with an event counter and in the second method the growth of the nestlings was determined and the daily gain in weight was converted back into the number of prey received.

METHODS

We estimated the number of feeding visits and number of caterpillars brought to the nest by great tits in the experimental orchard "de Schuilenburg" and 6 commercial orchards (5 Integrated Pest Management (IPM) and 1 Organic Farming (OF)). Data were collected between 1998 and 2000 inclusive. In these orchards, nest boxes had been put up at least one year before the observations and the number of breeding pairs of great tits ranged from 1 to 6 per experimental plot of 2 ha. Nest boxes were checked weekly from the beginning of April onwards, to determine laying date, clutch size, hatching date and the number of fledged great tits. Around the estimated hatching date, nest boxes were checked every other day. Nestling age starts with zero on the day of hatching. To synchronise the temperature dependent developmental stages of trees and caterpillars, the dates were standardised to tree phenology, i.e. the date of the setting of fruit to remove year effects. All data were tested for remaining year effects after correction, but no effect of year was found in these analyses. The date of the setting of fruit was chosen because from this stage onwards the caterpillars inflict most damage to the apples (Mols & Visser, 2002). The dates of fruit setting were 12, 7 and 12 May for 1998, 1999 and 2000 respectively.

To obtain the number of caterpillars brought to the nest over the entire nestling-rearing period we estimated a number of parameters. First the total number of prey items fed to the nestlings was estimated, either by counting the number of visits with an event counter or by converting the daily gain in weight of nestlings into the number of prey received to realise this increase. Additionally video recordings were used to calculate the number of feeds per day. These same video recordings of parental food provisioning were used to determine the proportion of caterpillars in the diet of nestling. Multiplication of the estimated number of prey items by this proportion of caterpillars in the diet gives the number of caterpillars fed to the nestlings.
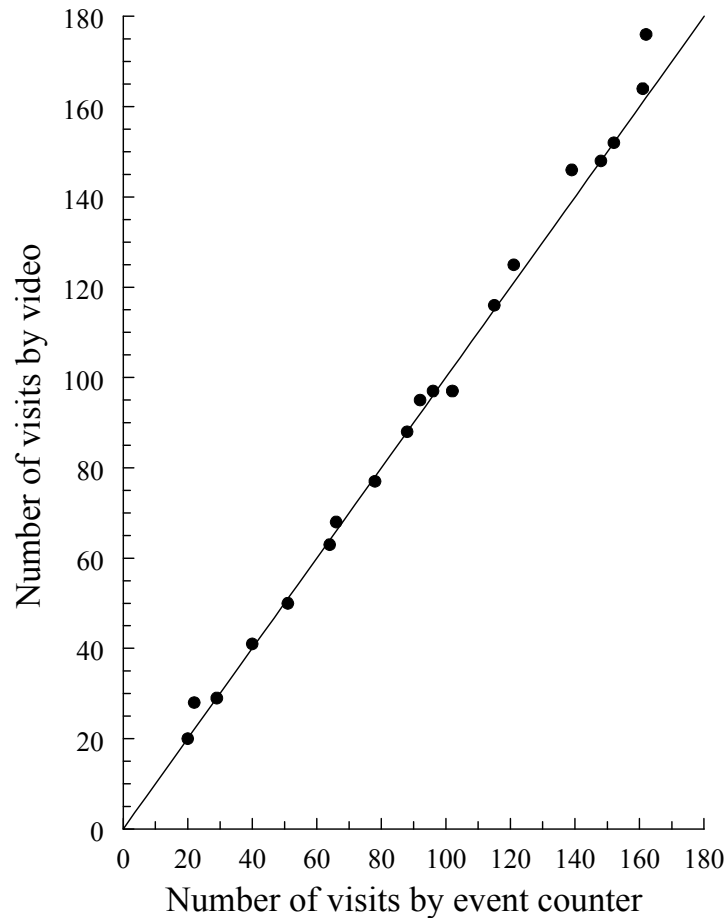
Figure 1 Correlation between the number of visits recorded by the event counters and the number of visits registered on videotapes during the same period of 1.5 (1998) and 3 (1999 and 2000) hours (Pearson correlation coefficient 0.997 (*P*<0.001).

To determine the effect of great tits on the reduction of caterpillar numbers in the orchard we calculated the proportion of caterpillars removed from the orchard by estimating the number of foraging trips in- and outside the orchard given an average caterpillar density of 7 caterpillars per tree as found in orchards with Organic Farming (see Mols *et al.*, this thesis chapter 4).

CALCULATIONS

Number of feeding visits per nest per day estimated with the event counter
We compared the number of visits recorded with the event counters with video recordings made in the experimental orchard "de Schuilenburg" in 2000. Video registrations were made in special nest boxes with the camera aimed at the nest opening. Broods were transferred from normal to video boxes when nestlings were at least 4 days of age to avoid desertion of the nests. Event counters were installed in the

video boxes one day after the nests had been transferred. The event counter was placed on the inside of the nest box entrance and contained a light sensor. Each time a bird entered or left the nest box the light beam was interrupted and a switch would either open or close. A data logger recorded the opening and closing of the switch and the point of time of the event. A 12 V battery supplied power for the light cell and the data logger and had to be swapped daily. The data logger of the event counter also had to be emptied and reset on a daily basis. Data were processed and checked with video recordings of the same period (Fig. 1). The average number of visits estimated with the counter and video were respectively, 91.9 (SD ± 47.3) and 93.7 (SD ± 48.8) visits per videotape (*T*-test, *P*=0.07, n=19). The Pearson correlation coefficient between the numbers of visits recorded on video and registered by the event counter during a 3-hour period was 0.997 (*P<0.001*).

Number of feeding visits per nest per day estimated with daily gain in weight of nestlings

Data on daily weight gain of nestlings were collected in six different commercial (five IPM and one OF) orchards and one experimental apple orchard in 1999. In the orchards, nest boxes were checked on a weekly basis from half April until all clutches had hatched to determine the breeding parameters of great tits, such as laying date, clutch size and hatching date. Around the hatching date, nest boxes were checked more frequently to assess the exact hatching date. In the period that the nestlings were 4 to 12 days of age they were weighed every other day and their fledging weight (*Mf* in g) was determined on day 15. Nestlings were not weighed before day 4 to reduce the chance of nest desertion caused by disturbance in the period that the female is still brooding the nestlings regularly and not after day 15 to prevent premature fledging of the young.

Winkler and Adler (1996) developed an energy-based model that predicts the mass of developing passerine nestlings. The model is based on assumptions about the amount of food obtained by the nestlings and published estimates of their metabolic costs, efficiencies and requirements as functions of nestling mass and/or age. Their general submodel of growth as a function of age is:

$$M_{(t + 1)} = M_{(t)} + (\alpha(H (M_{(t)})) - C (M_{(t)})) / E_{(t)} \tag{1}$$

where $M_{(t)}$ is the nestling's mass (in g) at the beginning of day *t*, *H* is food processed (in kJ) with an assimilation efficiency α, *C* is the 24-hour metabolic requirement for nestlings (in kJ), and *E* is the energy density (in kJ/g wet mass) of the growing bird. The assimilation efficiency of 0.71 was used and the metabolic costs (*C*) were calculated as:

$$C = 24\rho R \tag{2}$$

with ρ as the resting metabolic rate (in kJ/h) and R as the ratio of field to resting metabolic rate. The nestling's resting metabolic rate increases with their mass and therefore ρ is given as a function of its mass:

$$\rho = \beta M_{(t)}^{\gamma} = 0.03 M_{(t)}^{1.04} \tag{3}$$

β and γ were calculated with the equations given by Winkler and Adler (1996) and depended on the mass of an adult of the species being modelled. We used the average weight of all great tits found in winter roosting inspections in the orchards between 1998 and 2000 as mass of the adult. The average weight was 17.9 g (SD ± 1.1, n=362).

Winkler and Adler (1996) give the ratio between field and resting metabolic rate (R) as a function of the proportional age (A) by dividing ages by the age of fledging (i.e. 18 days was chosen as fledging age for great tits):

$$R = 1.667 - 0.845A + 0.893A^2 \tag{4}$$

Finally the energy density (E in kJ.g^{-1} wet weight) is calculated as a function of the proportional mass, defined as $M_{(t)}/M_f$

$$E = 3.51 + 4.82(M_{(t)}/M_f) \tag{5}$$

where M_f is the mass of the nestling at fledging. For justifications and explanations of the calculation see Winkler & Adler (1996). The food processed (H in kJ) by the nestlings can be calculated with this model and our weight measurements. The model defines growth as the daily gain in weight of the nestlings. Because we measured the weights of the nestlings every two (or three) days, the daily gain in weight was not known. We assumed that growth was linear between two consecutive measurements to estimate the weight for the missing data points.

We calculated the amount of food processed per day, i.e. the energy received, for each nestling separately. We checked (Table 1) if our calculations were in the same range as the values derived from a graph of Royama (1966). The age dependent average per nest was calculated and subsequently the average among nests.

We converted the received energy into number of prey items consumed per day for each nestling using prey size information for that date. The number of prey items brought to the nest was multiplied with the proportion of caterpillars in the diet to estimate the number of removed caterpillars. Finally the numbers of caterpillars removed per nestling per day were added together per nest per day and for the period of nestling ages between 4 and 15 days inclusive.

Table 1 Age dependent energy need per chick (with SE) estimated by converting the chicks weight gain per day into total energy intake to accomplish this growth according to the model of Winkler and Adler (1996). For comparison the estimated energy by Royama (1966) is given in the right column. Age zero is the day of hatching.

Nestling age	Average estimated energy per nestling (kJ.g^{-1} dry weight)	SE	Royama (1966) estimated energy per nestling (kJ.g^{-1} dry weight)
0	--	--	1.7
1	--	--	2.1
2	--	--	3.8
3	--	--	6.0
4	9.5	0.2	8.3
5	11.0	0.3	10.8
6	12.2	0.3	12.8
7	13.9	0.3	14.5
8	14.9	0.4	16.2
9	16.2	0.4	17.0
10	16.4	0.7	17.6
11	17.7	0.4	18.5
12	18.1	0.5	18.9
13	19.0	0.5	19.1
14	19.7	0.5	19.1
15	19.7	0.5	19.1

To calculate the total number of feeds per nestling, the energy received per day was divided by the estimated energy content of a prey item. Due to the changing ratio between caterpillars and arthropods in the diet and the growth of caterpillars with time the energy content of a prey item was date dependent, with date expressed in days after the setting of fruit. For each date the weight of caterpillars was calculated as a function of length (with a maximum of 30 mm) and length as a function of age and converted to dry weight as described in Mols *et al.* (this thesis chapter 4). The average length (9.7 mm, SD ± 4.6, n=30) of caterpillars in branch samples around the same date as the date of the setting of fruit was used to synchronise the age of caterpillars with date. For each date the estimated dry weight per caterpillar was multiplied by the energy content of caterpillars and the proportion of caterpillars in the diet. The energy content of caterpillars was 21.4 kJ.g^{-1} dry weight, composed out of literature data (Bell, 1990) and personal observations. All other prey items were termed arthropods (thus defined as all arthropods with exception of lepidopteran larvae). The weight of arthropods was assumed to be constant over time. The average length of arthropods on video recordings (6.9 mm, SD ± 2.8, n=1191) was used in the equation of Hódar (1996) to estimate the dry weight of arthropods. For each date, the estimated dry weight per arthropod was multiplied by the energy content of arthropods and the proportion of arthropods in the diet. The energy content for arthropods was 24.4 kJ.g^{-1} dry weight (Gibb, 1957). The sum of the energy content of one caterpillar and one arthropod each multiplied by their proportion in the diet per date was taken as the

energy content of an average prey item. The energy content of prey items was subsequently described as a function of date. The energy content of average prey without size selectivity of foraging great tits was:

$$E_{prey} = -5*10^{-6}D^2 + 0.0021D + 0.0592 \tag{6a}$$

and, in addition, the energy content of average prey with size selectivity of foraging great tits, as given in Cramps *et al*. (1993 and references therein), was:

$$E_{prey} = -9*10^{-5}D^2 + 0.0042D + 0.1143 \tag{6b}$$

where *D* is date in days after the setting of fruit.

Estimated number of feeding visits and caterpillars for nestling age between 4 and 15 days inclusive

To calculate the total number of feeding visits and caterpillars for the nestling ages between 4 and 15 days inclusive by the event counter, some missing values (i.e. day 4 until installation of event counter) had to be estimated. We performed a regression analysis (see statistical analysis) on the available data of the event counter to determine the predictive parameters for the number of feeding visits per day (Table 2). Date squared and number of nestlings had an effect on the number of feeds per day and therefore the relationship between these parameters and the number of feeds was used to estimate the missing values. Subsequently, the estimated number of feeding visits per day was added together per nest for the nestling ages between 4 and 15 days inclusive to derive the total number of feeds per nestling period. The total number of caterpillars was calculated in a similar manner. First the number of prey items per day was multiplied by the proportion of caterpillars in the diet of the nestlings and then added together.

Proportion of caterpillars in diet

To estimate the proportion of caterpillars in the diet of the nestlings of great tits breeding in orchards, video recordings of parental food provisioning were made over a period of 3 years (1998-2000). Video cameras (Sony CCD-TR825E) were placed into a special nest box such that they were facing the nest box entrance. Two small light bulbs (12 V) provided sufficient light to record inside the nest box. Nests with nestlings of at least 4 days of age were transferred from their regular nest box into a video nest box to avoid abandoning of the nests by the parents. Video recordings were made in all 3 types of orchards (IPM, OF and experimental). Video recordings of 90 minutes in 1998 and 180 minutes in 1999 and 2000 were made in the morning between 8 and 12 a.m. (n=67), the afternoon between 1 and 4 p.m. (n=48) and in the evening between 5 and 9 p.m. (n=9). Hi8 tapes were copied to VHS tapes and

Table 2 Results of the regression analysis of the number of feeds per nest per day. In method 1, the number of feeds were estimated using event counters, in method 2 using the daily gain in weight of the nestlings, and additional the comparison with video recordings. Date and hatching date in the analysis are expressed in number of days after the setting of fruit and number of nestlings is the number of nestlings at hatching.

		sample size (no. of nests)	increase in deviance	df	*F*	*P*	estimate
Method 1:	event counter[ab]	81 (10)					
	date^2		$2.8\ 10^5$	1	10.2	<0.01	0.9
	number of nestlings		$1.4\ 10^5$	1	5.3	0.02	24.3
	intercept						127.4
	date		$0.4\ 10^5$	1	1.7	0.20	
	hatching date		$0.6\ 10^5$	1	2.1	0.16	
Method 2:	gain in weight of the nestlings[a]	324 (27)					
	date*hatching date		$1.0\ 10^6$	1	22.9	<0.001	9.6
	hatching date* number of nestlings		$0.3\ 10^6$	1	7.3	<0.01	7.8
	date		$5.8\ 10^6$	1	127.0	<0.001	177.7
	date^2		$4.7\ 10^6$	1	103.8	<0.001	-7.4
	hatching date		$2.8\ 10^6$	1	61.5	<0.001	-138.1
	number of nestlings		$19.9\ 10^6$	1	435.6	<0.001	187.2
	intercept						-866.8
	management type[c]		$0.1\ 10^6$	2	2.2	0.12	
Additional:	video recordings	89 (27)					
	date		$3.7\ 10^5$	1	10.8	<0.01	29.1
	hatching date		$4.5\ 10^5$	1	12.8	<0.001	-27.6
	number of nestlings		$4.9\ 10^5$	1	14.2	<0.001	44.5
	intercept						- 191.0
	date^2		$0.1\ 10^5$	1	0.6	0.56	
	management type[c]		$1.3\ 10^5$	2	1.9	0.15	

a All interactions and variables that were not significant are not listed
b The event recorder was only used in the experimental orchard thus type cannot be tested
c Initial caterpillar densities for the three management types were 6, 7 and 28 caterpillars per tree (Mols *et al.*, this thesis chapter 4; Mols & Visser, 2002, this thesis chapter 2)

analysed. For each visit, we recorded the time of day, the sex of the parent and classified the prey item brought to the nest. Prey items were classified into caterpillars, other insect larvae, spiders, other arthropods and unidentified items. For the analyses in this paper we only consider two prey types, caterpillars or other arthropods.

Proportion of foraging trips within the orchard

We estimated the proportion of caterpillars removed (as estimated from the event counter data) for the average caterpillar density in OF orchards (Mols *et al.*, this thesis chapter 4). As this depends on whether the birds forage within or outside the orchard, we calculated the number of caterpillars removed for the whole range from when all

prey items are removed from within the orchard to the when all prey items are gathered outside the orchard. The variation in the proportion of prey obtained within the orchard is illustrated by field observations of 1998 and 1999 in IPM and OF orchards. Observations were performed with two observers, one observer on a scaffold (4 m high) near the nest box and one other observer strategically positioned outside the orchard to register if the birds were leaving the orchard. The observers communicated by radio. Nine nests were observed for a period of 3 hours, once or twice a day on 2 to 6 days. During these observations the time of arrival and sex of the parent were noted and the direction in which it departed and from which it returned. Furthermore, we noted whether the bird stayed within the orchard or went outside.

Proportion of caterpillars removed from an orchard

The total number of caterpillars removed by one pair of great tits was estimated to be 2950 (Table 3). This number was derived from the total number of visits measured by the event counter in the experimental orchard, given the date dependent proportion of caterpillars in the diet. The proportion of caterpillars in the diet was derived from video recordings made in the IPM, OF and experimental orchard. To calculate the total effect, we used the density of 7 caterpillars per tree (average caterpillar density in OF orchards (see Mols *et al.*, this thesis chapter 4) and there were 2666 apple trees per ha, the most common number of trees in IPM and OF orchards. We calculated the proportion of caterpillars removed by multiplying the number of caterpillars removed by the proportion of foraging visits within the orchard (data of IPM and OF orchards) and the number of breeding pairs and dividing this by the total number of caterpillars in the orchard.

STATISTICAL ANALYSIS

We tested number of feeding visits per day per nest, number of feeding visits and number of caterpillars per nestling period between 4 and 15 days, as response variables. These variables were estimated by two different methods, i.e. the event counter and the daily weight gain of nestlings. Additionally, the number of feeding visits was also estimated with video recordings. Due to the large amount of missing values in the video data, the number of feeding visits and number of caterpillars per nestling period between 4 and 15 days could not be calculated. We analysed the same video data to obtain the proportion of caterpillars in the diet of the nestlings. The relationship found in this analysis was used to transform the number of feeding visits per day into number of caterpillars per day.

Number of feeding visits per day per nest

To investigate whether the number of feeding visits was influenced by hatching date, date and number of nestlings at hatching, we tested the number of feeding visits per

nest per day as a response variable. For the analysis of the estimates for number of feeding visits by both methods (event counter and daily weight gain) and the video recording, we used generalised linear models (GLIM4) with normal errors. We tested hatching date, date and number of nestlings at hatching, as continuous variables. Date squared was included in the model to test for non-linear effects. Hatching date and date were expressed in days after the setting of fruit. Type of orchard (Integrated Pest Management, Organic or experimental) was included as a factor in the analysis of number of feeding visits estimated by daily weight gain of the nestlings and video recordings, to control for possible differences between management types. For the event counter only data of the experimental orchard were available and type could not be tested. All two-way interactions were fitted with the exception of type, which was fitted as a main effect only. Non-significant terms were dropped from the model starting with the highest order interaction (stepwise backward procedure).

Estimated number of feeding visits and caterpillars for nestling age between 4 and 15 days inclusive

For variation in the total number of feeding visits and number of caterpillars for nestling ages between 4 and 15 days, we used generalised linear models (GLIM4) with normal errors for estimates of both methods (event counter and daily weight gain). We used either the number of feeding visits or the number of caterpillars as the response variable. We included hatching date and number of nestlings at hatching as continuous parameters and hatching date squared was added to the model to test for non-linear relationships. Type of orchard (Integrated Pest Management, Organic or experimental) was included as a factor in the analysis of number of feeding visits estimated by daily weight gain of the nestlings, to control for possible differences between management types. This factor could not be included in the analysis of the estimates of the event counter because these data were only available for the experimental orchard.

Proportion of caterpillars in the diet

To analyse the proportion of caterpillars brought to the nest we used generalised linear models with binomial errors (the prey item brought to the nest was either or not a caterpillar; binary data). We used the number of caterpillars as the response variable, with the total number of identified prey items per videotape as the binomial denominator (effectively weighting data points by the number of prey items brought to the nest).

We tested hatching date, date and number of nestlings at hatching, as continuous variables, and also date squared to test for non-linear effects. Hatching date and date were expressed in days after the setting of fruit. Type of orchard (Integrated Pest Management, Organic or experimental) was included as a factor. All two-way interactions were fitted. Non-significant terms were dropped from the model starting

with the highest order interaction (stepwise backward procedure). Because the residual deviance was substantially larger than the residual degrees of freedom, Williams' adjustment for overdispersion was applied (Crawley, 1993), and hence the significance of terms in the model was assessed using an *F*-test (Crawley, 1993).

RESULTS

Estimated number of feeding visits per day per nest

We estimated the number of feeding visits ($nest^{-1}.day^{-1}$) with the event counter, the gain in weight of the nestlings and the video data, and plotted them against the number of days after the setting of fruit to correct for difference between years (Fig. 2a). The estimated number of feeding visits by the event counter and the video data are in the same order of magnitude but the estimated number of caterpillars removed by the gain in weight of the nestlings is much higher (Fig. 2a). This discrepancy is probably caused by the difference between the average prey size in the environment and the actual prey size great tits feed to their nestlings. Betts (1955) and Royama (1966; 1970) found that adult birds ate small food items themselves and carried larger items to the nest. Cramps *et al*. (1993 and references therein) state that the average prey size brought to the nest was 4.9 mm larger than the average prey size available in the environment. The effect of the underestimation of prey size is shown in Figure 2b. We assumed prey size to be 4.9 mm larger than average due to the selectivity of great tits and recalculated the estimated number of feeds (Fig. 2b). The estimated numbers of feeds per day are almost halved and are in about the same range as the data of the event counters.

We investigated whether date, hatching date and number of nestlings at hatching had a significant influence on the number of feeding visits to the nest per day. Date squared was also tested to check for non-linear relationships. All three methods to estimate the number of feeding visits per day per nest (i.e. event counter, daily gain in weight of nestlings and video recordings) show an increase in the number of feeding visits with a higher number of nestlings at hatching (Table 2). Furthermore the number of feeds per day changes non-linearly with date when estimated with the event counter (accelerating) and daily weight gain of the nestlings (decelerating) and linearly with date when estimated with the video recordings (Table 2). The number of feeding visits, when estimated by weight gain and video recordings, was negatively influenced by the date of hatching. There was no effect of hatching date in the estimated number of feeding visits of the event counter data (Table 2).

Estimated number of feeding visits for nestling age between 4 and 15 days inclusive

We tested the influence of hatching date and number of nestlings at hatching on the number of feeding visits and number of caterpillars for nestling age between 4 and 15 days inclusive for data gathered with the event counter and calculated with the daily

Table 3. Results of the regression analysis of the number of feeds per nest for the period of nestling ages between 4 and 15 days inclusive. In method 1, the number of feeds were estimated using event counters, and in method 2 using the gain in weight of the nestlings. Hatching date in the analysis is expressed in number of days after the setting of fruit and number of nestlings is the number of nestlings at hatching.
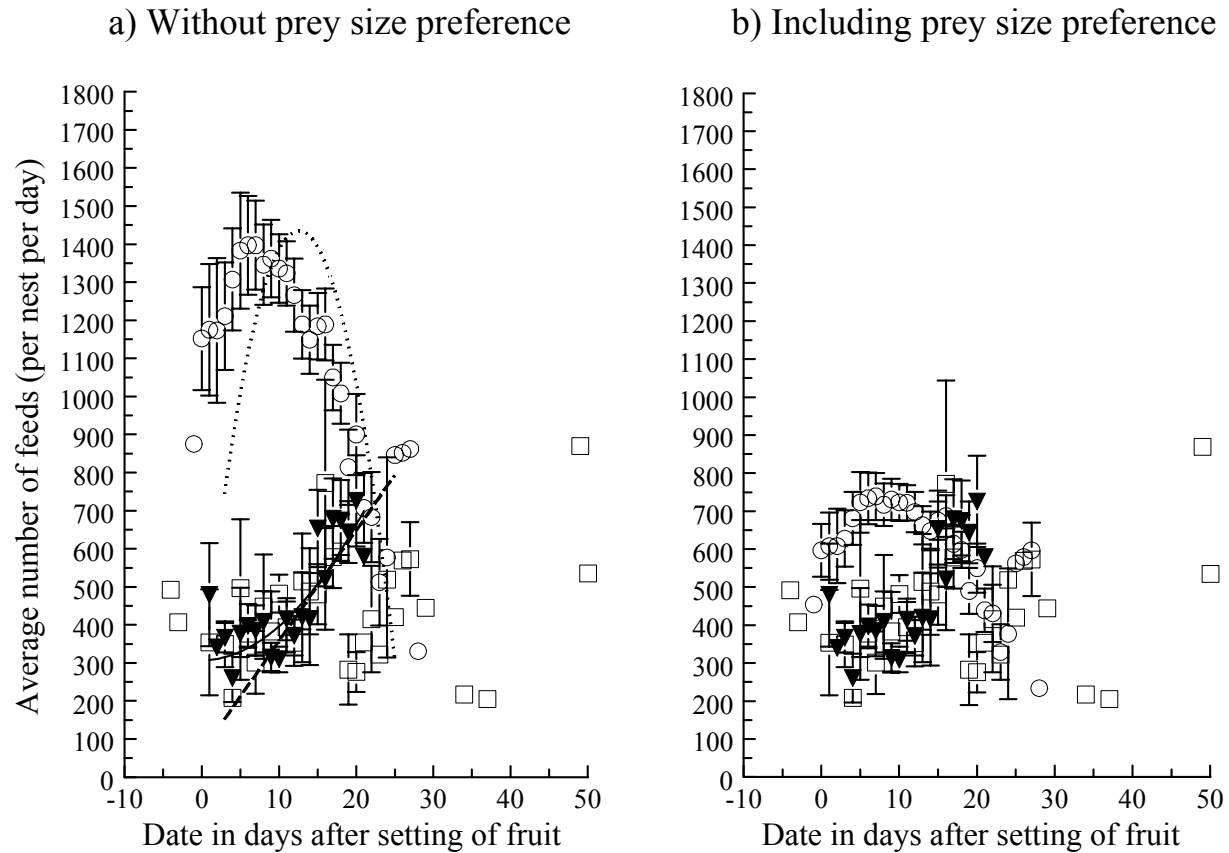
	response variable number of feeds (including caterpillars)					response variable number of caterpillars					
	variables in the model	increase in deviance	df	F	P	estimates	variables in the model	increase in deviance	df	F	P	estimates
Method 1:	*event counter[abc]*						*event counter[abc]*					
	intercept					5338	intercept					2950
	hatching date	$6.4\ 10^6$	1	3.9	0.10		hatching date	$0.3\ 10^6$	1	0.76	0.42	
	hatching date^2	$2.7\ 10^6$	1	1.6	0.25		hatching date^2	$1.0\ 10^6$	1	2.27	0.18	
	number of nestlings	$2.8\ 10^6$	1	1.7	0.24		number of nestlings	$0.5\ 10^2$	1	$0.1\ 10^{-3}$	0.99	
Method 2:	*gain in weight of the nestlings[a]*						*gain in weight of the nestlings[a]*					
	hatching date	$58.4\ 10^6$	1	8.2	<0.01	-643.9	hatching date	$56.3\ 10^6$	1	21.9	<0.001	-561.8
	number of nestlings	$144.8\ 10^6$	1	20.2	<0.001	1560	number of nestlings	$5.5\ 10^6$	1	21.4	<0.001	931.0
	intercept					4997	intercept					3450
	hatching date^2	$0.03\ 10^6$	1	$0.4\ 10^{-2}$	0.95		hatching date^2	$0.6\ 10^6$	1	0.2	0.64	
	management type^d	$4.5\ 10^6$	2	0.3	0.58		management type^d	$1.7\ 10^6$	2	0.3	0.72	

[a] All interactions that were not significant are not listed

[b] The event recorder was only used in the experimental orchard thus type cannot be tested

[c] For sample size of number of nests see Table 2

[d] Initial caterpillar densities for the three management types were 6, 7 and 28 caterpillars per tree (Mols et al., this thesis chapter 4; Mols & Visser, 2002, this thesis chapter 2)

a) Without prey size preference **b) Including prey size preference**

Average number of feeds (per nest per day)

Date in days after setting of fruit

Figure 2 Average numbers of feeds per nest per day (± SE) estimated by three different methods. Total numbers of visits per day were estimated using (1) event counters (closed triangles), (2) the gain in weight of the nestlings transferred via energy intake to number of feeds (open circles) and (3) video recordings (open squares). Video recordings were made for 1.5 or 3 hours periods and this number was extrapolated to cover the whole day. The fitted lines show the relationship found by regression in GLIM4 between all significant variables (see Table 2) and the average number of feeds per nest per day. The average hatching date and number of nestlings were used in the equations of the lines. In a) the weight gain was transferred to number of visits on the basis of the average prey size of that date in the orchard and in b) we used an increased prey size to correct for prey size selection of birds.
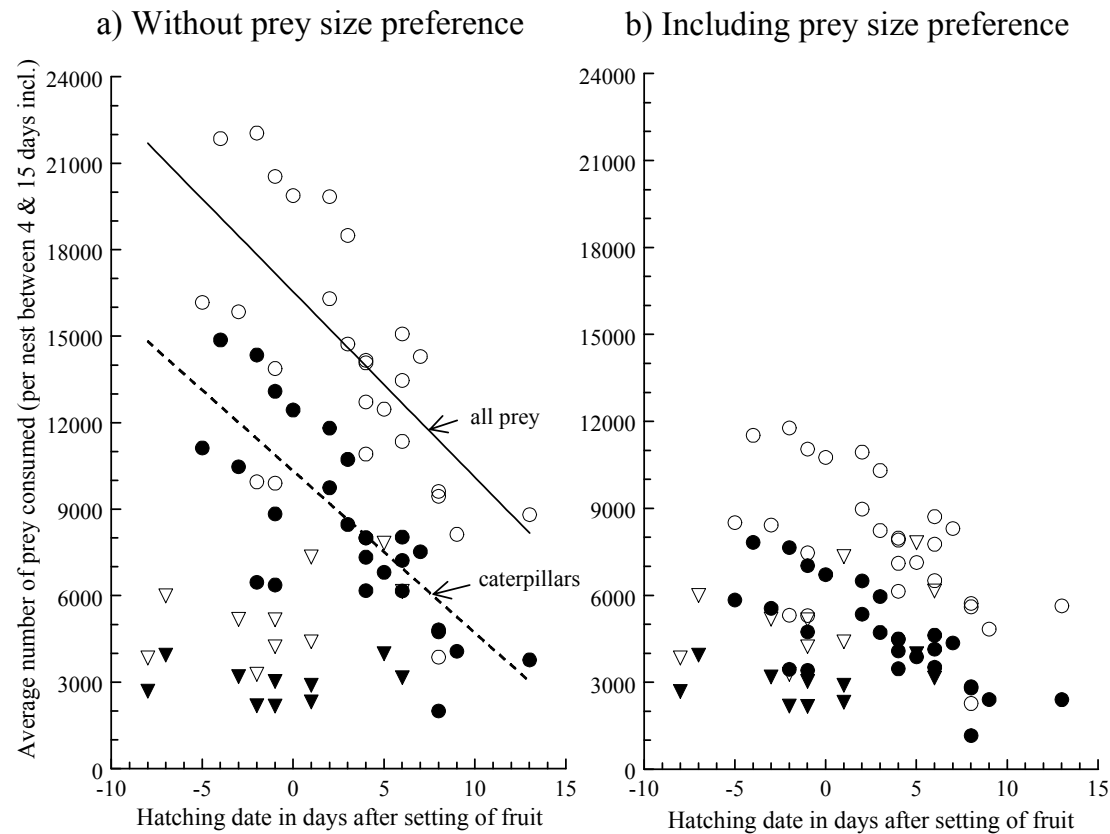
Figure 3 Total numbers of feeds (open symbols) and caterpillars (closed symbols), fed to nestlings against hatching date (in days after setting of fruit). Total numbers of feeds per day per nest were estimated using (1) event counters (triangles) and (2) the gain in weight of the nestlings transferred via energy intake to number of feeds per day (circles). Next, these numbers of visits per nest were added up to obtain the total number of feeds per nest and hatching date. To estimate the total number of caterpillars per nest against hatching date the total number of feeds per day were multiplied with the date dependent percentage of caterpillars in the diet and then added up. The fitted lines show the relationship found by regression in GLIM4 between all significant variables (see Table 4) and the total number of feeds and caterpillars per nest. In a) the weight gain was transferred to number of visits on the basis of the average prey size of that date in the orchard and in b) we used an increased prey size to correct for prey size selection of birds.

gain in weight of nestlings. The number of feeding visits estimated with the event counter showed no effect of hatching date or the number of nestlings at hatching (Fig. 3a, Table 3). The number of visits calculated with the daily weight gain of nestlings is much higher then counted by the event counter and showed a linear decrease with increasing hatching date (Fig. 3a, Table 3). When correcting for prey selectivity of great tits (as described in the previous section) the number of feeds per day estimated by the daily weight gain of nestlings are reduced and in the same range as the data of the event counter (Fig. 3b). The number of nestlings had also an influence on the number of feeding visits. The total number of feeding trips increased with increasing number of nestlings at hatching (Table 3).

Proportion of caterpillars in the diet

We found a decreasing proportion of caterpillars in the diet of nestlings with increasing date and number of nestlings (Table 4 and Fig. 4). The estimates in Table 4 were used to compose the formula to estimate the proportion of caterpillars in the diet that is used to derive the number of caterpillars from the total number of feeds ($nest^{-1}.day^{-1}$). Between 0 and 50 days after the setting of fruit the proportion of caterpillars in the diet of nestlings dropped from 78.3% to 14.4% for the average brood size (7.4 ± 1.6) of all video recordings (Fig. 4). There was no effect of type of orchard on the proportion of caterpillars in the diet (Table 4).

Estimated number of caterpillars for nestling age between 4 and 15 days inclusive

We calculated the total number of caterpillars removed per nest as the sum of all caterpillars removed per nest in the period of nestling ages between 4 and 15 days inclusive. The number of feeding visits was calculated and multiplied by the proportion of caterpillars in the diet. Data from the event counter and the gain in weight of the nestlings were available. The number of caterpillars brought to the nest declined linearly with increasing hatching date (Table 4, Fig. 4) when estimated with the daily weight gain of the nestlings and the number of caterpillars was higher with increasing number of nestlings at the moment of hatching (Table 4, Fig. 4). Hatching date and number of chicks had no influence on the number of caterpillars brought to the nest when estimated with the event recorder. As expected these results do not deviate from the results of the total number of feeding visits.

## *Justification of comparison of data of different years and orchard types*

The different years of data collection and the different management types of the orchard have not led to the differences between the methods. There was no effect of year ($F_{(2,118)}$ =1.9, P=0.17) nor orchard type (Table 4) in the proportion of caterpillars in the diet that was estimated with data from all years and orchard types. Furthermore,

Table 4 Logistic regression analysis of the proportion of feeding visits of which the prey was a caterpillar. Date and hatching date are expressed as the number of days after the setting of fruit, and number of nestlings is the number of nestlings at hatching.

	sample size (no. of nests)	increase in deviance	df	*F*	*P*	estimate
	89 (27)					
date [ab]		7.10	1	6.24	0.01	-0.22
number of nestlings		14.63	1	12.85	< 0.001	-0.06
intercept						2.72
hatching date		0.65	1	0.57	0.45	
management type		6.77	2	2.97	0.06	

[a] All interactions that were not significant are not listed.

[b] Initial caterpillar densities for the tree management types were 6, 7 and 28 caterpillars per tree (Mols *et al.*, this thesis chapter 4; Mols & Visser, 2002, this thesis chapter 2).
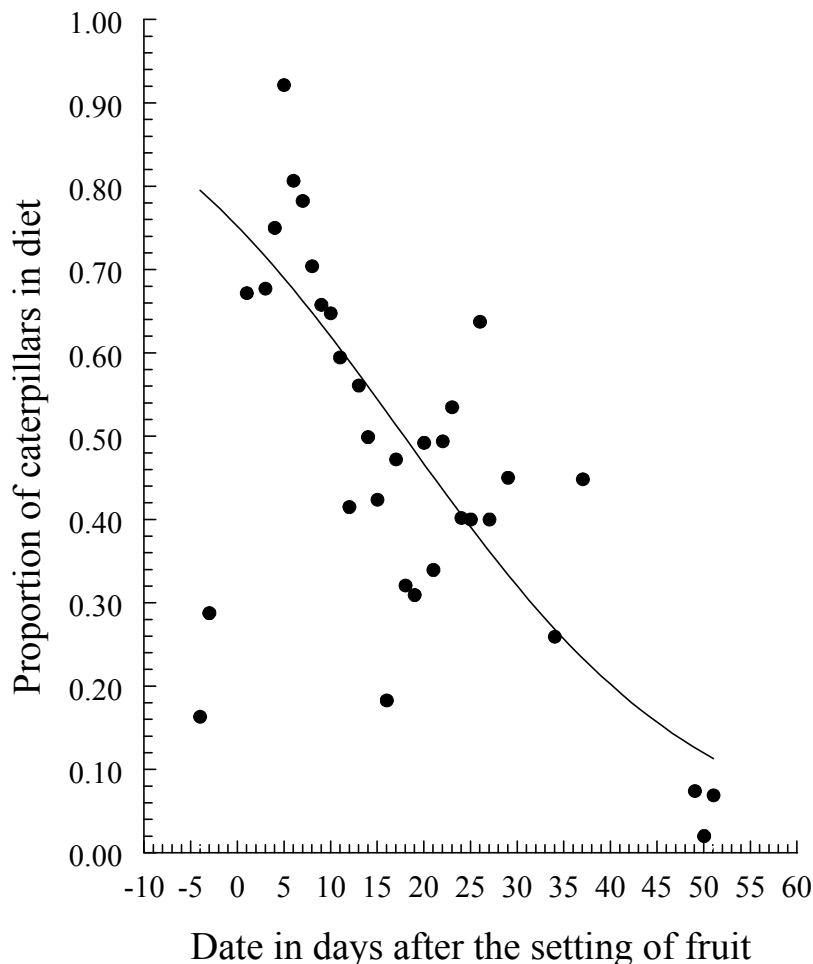

Figure 4 Changes over time in the proportion of caterpillars in the diet of nestlings determined by video recordings made of several nests on various dates in 1998, 1999 and 2000. Videos were made in three orchard types (i.e. Integrated Pest Management, Organic Farming and experimental). The fitted line shows the relationship found by logistic regression in GLIM4 between date and the number of chicks and proportion of caterpillars in the diet.

the overlap of the estimated number of feeding visits with video recordings and event counters (Fig. 2a) also indicates no change in feeding patterns over the years. The estimated number of feeding visits per nest per day with the event recordings as found in this study are also in the same range as found by Kluiver (1950), Gibb (1955) and Verhulst & Tinbergen (1997). Grieco & van Noordwijk (2001) also did not find difference in provisioning rates of blue tits between two subsequent years.

Proportion of feeding trips within the orchard
We observed great tits foraging and determined if the place of foraging was in or outside the orchard. There were large differences in the average proportion of foraging trips within the orchard between individual nests (Fig. 5). The average proportion of feeding visits in the orchard varied between 34 and 100% for nests in a central position and between 6 and 71% for nests closer to the border of the orchard.
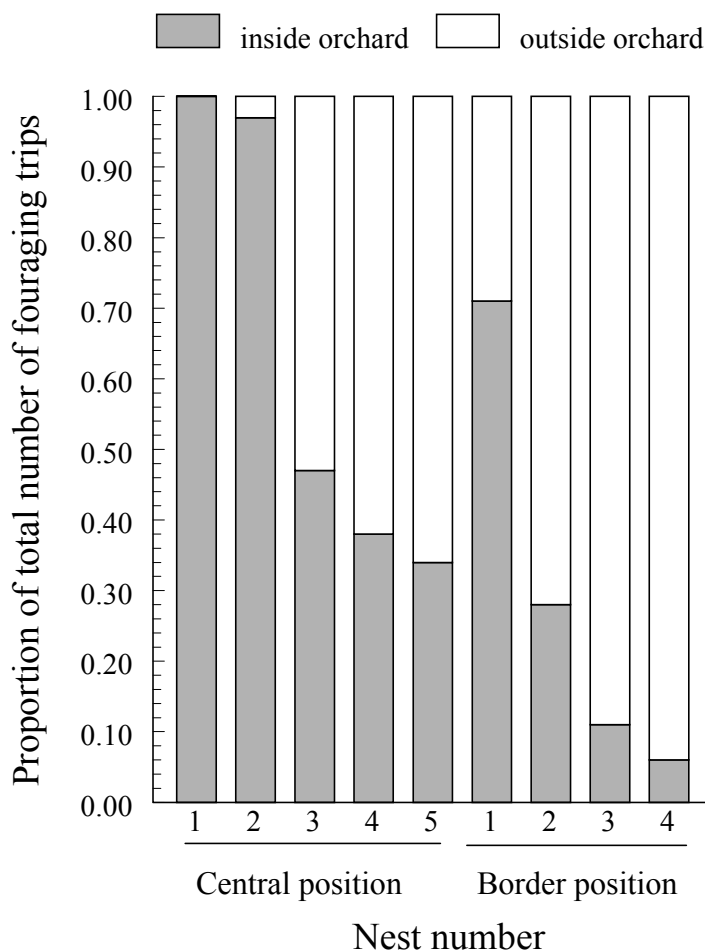
Figure 5 Proportion of foraging trips in Integrated Pest Management and Organic Farming orchards for nest boxes close to the border of the orchard and further from the centre of the orchard.
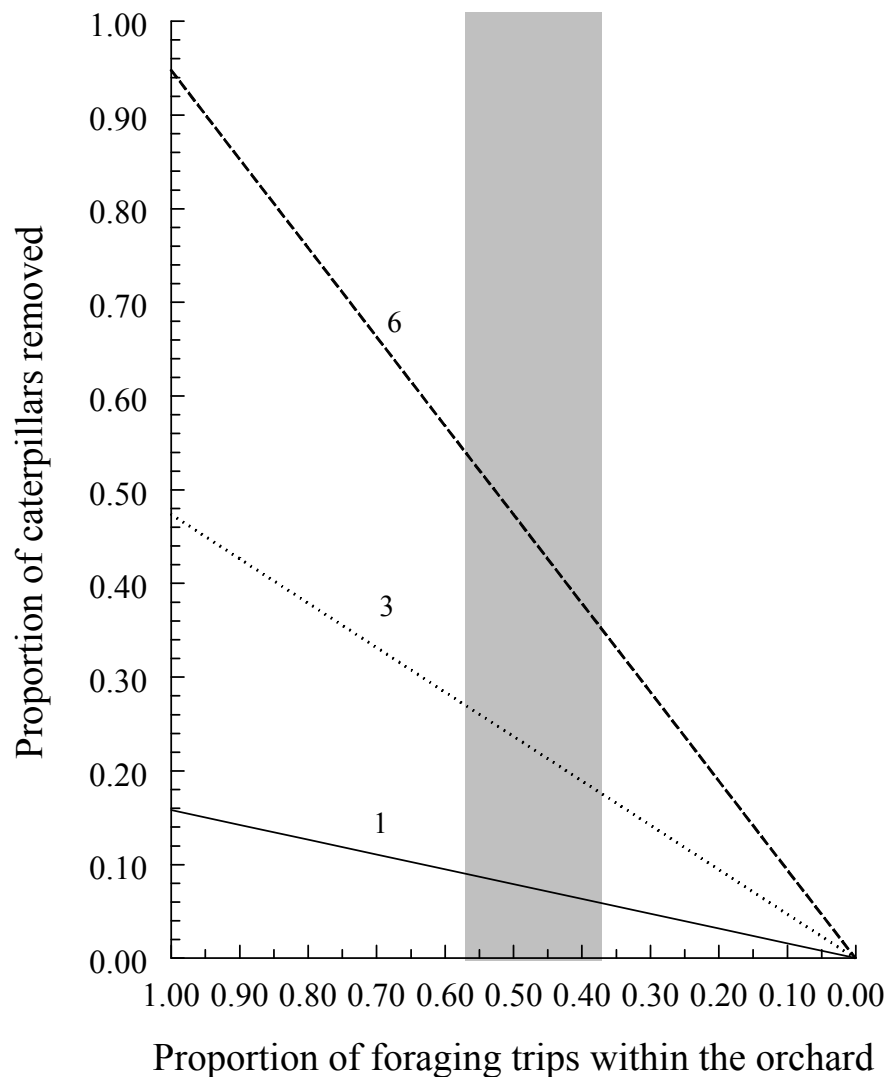
Figure 6 Proportion of the caterpillars removed in an orchard of 1 ha with an average density of 7 caterpillars per tree (=average number of caterpillars found in commercial orchards) in relation to the proportion of foraging trips in the orchard for one (solid line), three (dotted line) or six (dashed line) breeding pairs of great tits. The grey bar represents the observed average proportion of visits within the orchard with its standard error.

Proportion of caterpillars removed from the orchard

The proportion of caterpillars removed from the orchard was calculated for the situations in which the proportion of feeding visits within the orchard ranged from 0 to 100%. In the research period the number of breeding pairs ranged from 1 to 6 with an average of 3.5 (SD ± 1.3) nests. Therefore we presented the number of caterpillars removed in Figure 6 for 1, 3 and 6 breeding pairs of great tits. The grey bar shows the average number of feeding visits within the orchard with its standard error (48 ± 11%) from the nine nests shown in Figure 5. For the average proportion of feeding visits within the orchard, the expected proportion of caterpillars removed was 7.6%, 22.8% and 45.5% for respectively one, three and six breeding pairs of great tits.

DISCUSSION

We tested the effect of hatching date, date and number of nestlings on the number of caterpillars removed with two different methods and had additional video data for comparison. Data gathered with the event counters are actual counts of visits to the nest box and comparison with video recordings from the same date and time gave the same results (Fig. 1). Therefore these data are reliable. However, the data gathered with the daily gain in weight of the nestlings gave an overestimation of the number of prey items. Especially in the beginning of the breeding season the number of feeding visits is overestimated while in the end of the season a steep decline is shown. The overestimation is probably caused by an underestimation of the energy content of the prey. Additionally, the tendency of higher mortality rate of nestlings with higher hatching dates ($F_{(1,26)}$=3.95, P=0.06) may have contributed to the decline in estimated number of visits for nests with higher hatching dates.

The function of the energy of the prey was based on an increasing energy content of caterpillars as a function of their length and a constant energy content for prey items other than caterpillars, both multiplied by their proportion in the diet. As an estimate for the length of caterpillars at a certain time we used the average length of caterpillars occurring in the orchards. However, great tits have a preference to feed larger prey to their nestlings (Betts, 1955; Royama, 1966, 1970). When making the assumption that great tits select larger prey than the average prey size occurring in the environment, the estimated number of feeding visits comes much closer to the number of visits estimated with the event counter (Fig 2b & 3b). A further refinement could probably be made on the basis of actual sizes brought to the nest estimated from video. We felt that our data on prey size collected from the video were too unreliable to do so.

Mortality of nestlings in a later stage of the nestling period may explain the steep decline in the number of feeding visits. In the nests where the daily weight gain of nestlings was measured, the average age at which nestlings died was 8.3 days (SD ± 2.7). Judging from Table 1 the average energy need of a nestling of 8 days or older received on average 14.9 kJ of food representing 149 to 186 feeding visits which is about the drop between two consecutive points in Figure 2a. Because the mortality was higher in nests with later hatching dates and the age of death was on average 8 days this decrease in numbers merely becomes apparent in later dates after the setting of fruit (Fig. 2a) and later hatching dates (Fig. 3a). The reason why this effect of higher mortality in nests with higher hatching dates is less apparent in the data of the event counter is due to the much smaller ranges of hatching dates and lower mortality in these nests. The average hatching date in the nests of the event counter was -0.9 (SD ± 4.5) days after the setting of fruit and the average proportions of nestling survival of nests before and after this average hatching date, i.e. 1.0 (SD ± 0) and 0.9 (SD ± 0.1) respectively, was lower. Furthermore, the nestlings that died in between two weight measurements had still received food between the last measurement and their death. This received energy is totally discarded in the weight gain method and

causes an underestimation of the number of feeds while in the event counter data these number of feeding visits are not lost.

We can conclude that the gain in weight of the nestlings can be reliable converted into the energy received by the nestlings (Table 1) with the model of Winkler and Adler (1996). However the method will overestimate the number of caterpillars per nest in the early stage of the breeding season due to the discrepancy between the estimated energy of an average prey item and the real energy value of the selected prey items by the great tits. Therefore, the method can only be used with a reliable estimate of prey size or weight of prey items selected by great tits. Additionally, taking weight measurements at a daily basis may reduce the underestimation of the number of prey due to chick mortality especially for nests with later hatching date.

Numbers of caterpillars removed
Due to the uncertainties in the data of the daily weight gain we will further only discuss the effect of hatching date, date and number of nestlings considering the results from the event counters. We found an effect of date but not of hatching date or the interaction between hatching date and date. The interaction between hatching date and date can be seen as the age of the nestlings. Due to the increase of the energy need of older nestlings we would have expected to find an effect of hatching date in interaction with date. The absence of this finding is probably caused by the fact that data of the event counter only start at the nestling being 6 to 7 days of age. The day-to-day increase in energy demand of older nestlings is much smaller than the increase for nestlings at younger age (Table 1) and therefore the effect of nestling age could not be shown. Furthermore, the small range of hatching dates (see Fig. 3a) and the small sample size (n=11) of the event counter data may have caused the absence of an effect of hatching date in these data. The decreasing proportion of caterpillars in the diet probably causes the significant non-linear increase of the number of feeding visists in time. Caterpillars have a higher energy content than other prey items and when the proportion of caterpillars in the diet is decreasing the great tits have to feed more prey, other than caterpillars, to compensate for this loss in energy. We would expect a plateau in the number of feeding visits when great tits have reached their maximum feeding rate per day but this did not happen within the range of our data.

In accordance with Gibb (1955), Wright *et al.* (1998) and Naef-Danzer *et al.* (2000) we found an increase in the number of feeding visits with an increasing number of nestlings. However this increase was not linear because the visiting rates per chick decrease with increasing brood size (Wright *et al.*, 1998). Gibb and Betts (1963) found that nestlings of a brood of 7 each received 7.3 g (wet weight) of food per nestling per day (averaged over days 12-19) whereas nestlings of a brood of 9 each received 4.7 g (averaged over days 13-18). In addition, food requirements per nestling are greater in a small brood than in a large brood because of greater heat loss (Royama, 1966), and the food requirements decline as air temperature rises (Mertens, 1969). Therefore, the food requirement per chick in later broods need not be the same

as that of early broods. This could explain why there was no effect of number of nestlings on the number of feeding visits and caterpillars when for the whole period of nestling ages between 4 and 15 days inclusive was considered.

We found a negative effect of the number of nestlings on the proportion of caterpillars in the diet (Table 4) with increasing number of nestlings. The diet choice model of Lessells & Stephens (1983) explains this negative effect, which was also found by Wright *et al.* (1998). The diet choice model shows that the prey value is related to search time, i.e. the more selective the forager the longer it will have to search until an acceptable item is found. Great tits with larger broods have a higher provisioning rate to supply their nestlings with enough food to survive. Therefore they have less time to search for the most preferred prey, i.e. caterpillars, and this causes the proportion of caterpillars to drop with higher brood sizes.

There was no effect of hatching date on the total number of feeding visits or on the number of caterpillars fed to the nestlings. We had expected that nests with earlier hatching dates would have had higher feeding rates than later nest because caterpillars are small in the beginning of the season and thus the average energy of the prey is smaller than later in the season when large caterpillars are available. Consequently the number of caterpillars was also expected to be higher not only because of these higher feeding rates but also because the proportion of caterpillars in the diet is higher early in the breeding season. There are two reasons that can explain why feeding rates were not affected by hatching date. The first reason is the selection of larger prey by great tits (Betts, 1955; Gibb & Betts, 1963; Naef-Daenzer *et al.*, 2000; Tinbergen, 1960). Due to this preference the average size of caterpillars brought to the nest was probably fairly constant and therefore no effect on feeding rate would occur. Prey size is found generally to follow the nestling growth curve, increasing rapidly from day 1-6, then changing little (Kluijver, 1950; Royama, 1966, 1970; van Balen, 1973). Because the measurements with the event counters were mostly taken from day 6 onwards, we probably missed the period in which an effect of prey size on feeding rates could have been detected. The second cause is probably the decreasing proportion of caterpillars in the diet later in the season. Great tits have to compensate the lower energy value of prey other than caterpillars by increasing their feeding rates. However, if this is the case a higher feeding rate is expected for later hatching dates. The lack of this increase may have been the small range of hatching dates in our data and the small sample size. Furthermore, the absence of an effect of hatching date on the number of caterpillars removed may also be caused by this lack of variation in hatching dates.

We wanted to test whether the important components for damage reduction predicted by the model of Mols *et al.* (this thesis chapter 4), i.e. number of breeding pairs and hatching date, also influence the number of caterpillars removed (the main component of damage reduction) by great tits in orchards. We focussed on hatching date because it is obvious that an increase in the number of breeding pairs will increase the number of caterpillars removed. The model of Mols *et al.* (this thesis chapter 4) predicted that two additive effects cause the higher percentage of damage reduction for earlier hatching date. Caterpillars would not only be removed earlier and

thereby have less time to inflict damage (Mols *et al.*, this thesis chapter 4; Mols & Visser, 2002) but also the number of caterpillars removed would be higher. However our data do not support this last effect. Therefore, the influence of hatching date on the amount of damage reduction must be only caused by the earlier removal of caterpillars.

Besides the testing of the effect of hatching date and number of breeding pairs on the number of feeds and caterpillars per nest of great tits, we illustrated their effect on the number of caterpillars removed within an orchard with field data. The proportion of foraging trips within the orchard is highly variable and nest box position seems to be a main factor influencing this proportion (Fig. 5). Central place foraging theory predicts that central place foragers such as the great tit will maximize the net energetic gain per foraging effort (Kacelnik, 1984). This is achieved by selecting the best (i.e. the nearest and most profitable) foraging patches and exploiting the most energetically efficient prey types (Wright *et al.*, 1998 and references therein). Positioning the nest box further away from the border of the orchard will therefore reduce the profitability of foraging outside the orchard and therewith increase the foraging visits within the orchard. In an orchard with number of caterpillars as found in IPM and OF orchards and an average proportion of foraging trips, we predict that on average around 6% of the caterpillars in the orchard will be removed by one pair of great tits when about half of the foraging trips are within the orchard. With an increasing number of breeding pairs this percentage will increase but probably not totally proportional as illustrated by Figure 6 due to interactions among breeding pairs. In these calculations the number of caterpillars removed for self-feeding of the parents is totally disregarded and therefore these numbers give an underestimation of the number of caterpillars removed in the field. If we assume that these effects cancel each other out, we still expect that the average number of 3 breeding pairs of great tits per ha as found in IPM and OF orchards to remove on average 23% of the caterpillars present in the orchard and this can run up to 49% if all foraging trips take place within the orchard.

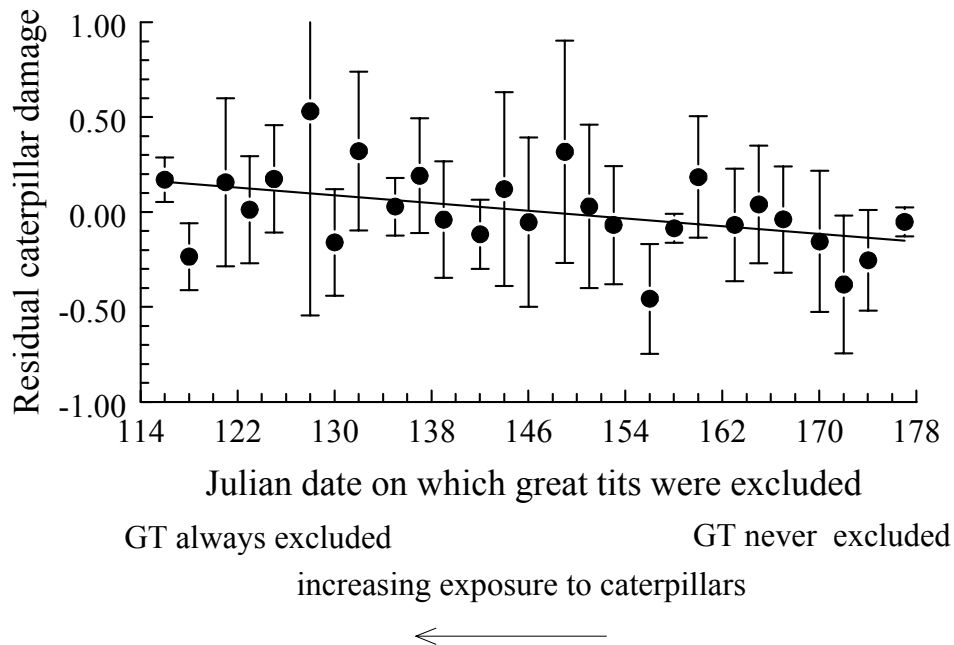# Chapter 6

Summarising discussion

The interest in biological control of pests in apple orchard systems has increased in recent years as: legislation increasingly restricts the use of pesticides, resistance of harmful insects to pesticides is a problem that persists and the adverse public attitudes to pesticides have intensified. Great tits are known predators of caterpillars and therefore might reduce damage inflicted to apples by caterpillars. Whether and how great tits can contribute to reducing caterpillar numbers and hence reduce damage to apples was investigated in this study.
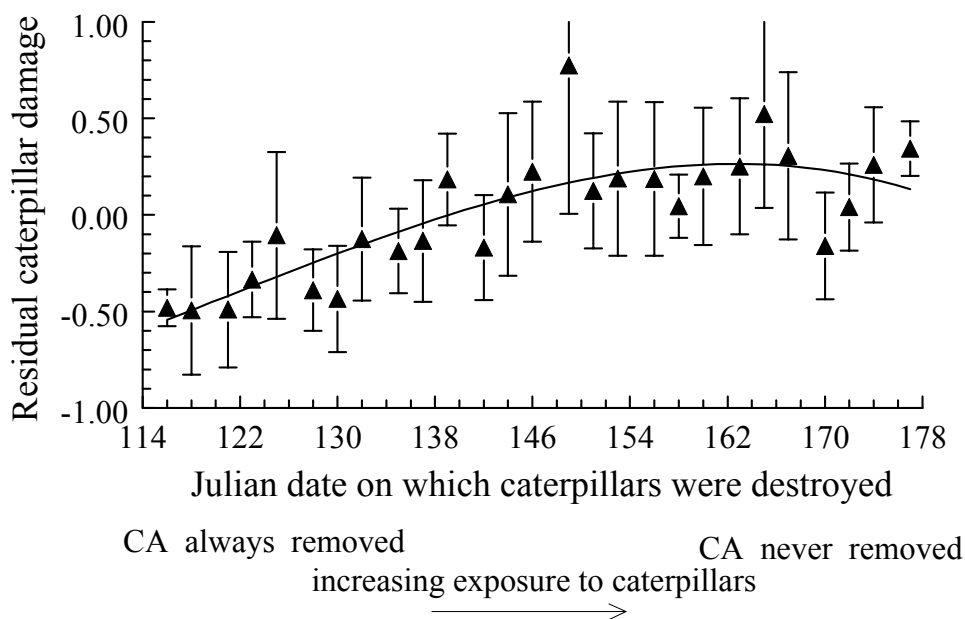
Damage reduction in the field

Birds have largely been ignored in the search for new biological pest control agents in orchards, even though several studies have reported high predation rates of insect pests by birds in agricultural systems and forests. In general, insect populations may be limited by predation if predators remove a greater proportion of the population when prey densities increase (Solomon, 1949). A density dependent response may result either from a functional response, in which the predator changes its feeding action, or by a numeric response, involving a change in the number of predators (Crawford & Jennings, 1989; Solomon, 1949). Great tits can show a limited numeric response before nest building starts in spring. In years or areas with higher food abundance the breeding densities of great tits increase (Gosler, 1993; van Balen, 1973). Spatial redistribution may lead to more birds in areas with relatively higher prey densities. After the establishment of the numbers of breeding pairs no numeric response in the sense of number of breeding pairs can occur within the season as great tits are territorial birds. However, there is still scope of a different type of numeric response as with higher caterpillar density the birds increase their clutch size (Perrins, 1991) and therewith their food requirement in the nestling rearing period. Food requirement is also higher in years with higher food abundance because the mortality of nestlings is lower and thus more nestlings survive and have to be fed. Additional to these numerical responses, the birds show a functional response in diet composition by increasing the proportion of caterpillars in their diet when caterpillar numbers are higher. On the other hand, in times of low caterpillar density they survive by feeding on other prey but will take all caterpillars encountered, as caterpillars are their preferred prey. The question is however whether this behaviour is sufficient to reduce caterpillar numbers and thereby reduce damage to apples in orchards with varying densities. Furthermore, the time at which caterpillars actually inflict damage was not clearly known and therefore I assessed the effect of time of caterpillar removal on the magnitude of damage reduction. I have shown in chapter 2 that foraging by great tits in the period from the start of great tit egg incubation until fledging of their young reduced caterpillar damage (Fig. 1a). This reduction was not only due to a lower percentage of damaged apples but also to a higher yield when trees were accessible to foraging great tits. Yield increases mainly in the first treatments that great tits were excluded until the end of bloom and flattened out thereafter. The effect on yield seems therefore to be mainly caused by a reduction of the number of flowers by caterpillars.

a) Experiment 1: exclusion of great tits (GT)

Julian date on which great tits were excluded

GT always excluded   GT never excluded

increasing exposure to caterpillars

b) Experiment 2: removal of caterpillars (CA)

Julian date on which caterpillars were destroyed

CA always removed   CA never removed

increasing exposure to caterpillars

Figure 1 (a) Experiment 1: Caterpillar damage (± SE) as the residual from a model including block effect only as result of a logistic regression of the proportion of apples per tree with caterpillar damage when great tits are excluded from trees, at different times during the growing season. A later Julian date for great tits exclusion implies a longer period of great tit predation and hence a lower exposure to caterpillars (indicated by arrow). (b) Experiment 2: Caterpillar damage (± SE) as the residual from a model including block effect only as result of a logistic regression of the proportion of apples per tree with caterpillar damage when caterpillars were removed from trees, at different times during the growing season. A later Julian date for caterpillar destruction implies a higher exposure to caterpillars (indicated by arrow). Julian date is the date according to the Julian calendar (i.e. the 1st of February is Julian date 32)

The compound buds, with flowers and leaves, are the first buds that open on apple trees in spring. Therefore early caterpillars feed on these buds and can decrease the number of flowers that can be fertilised and should develop into an apple and thereby reduce yield. However, care should be taken in interpreting this yield increase. We experimentally excluded great tits using nets and although mesh size was large enough to allow access by bees, we cannot exclude that the nets might have reduced pollination. However, since an effect on the number of apples was also found when caterpillars were destroyed, we are confident that the effect on yield is due to the exclusion of great tits and not to side effects of the nets. Moreover, June-drop appears to increase with damage, explaining part of the variation in the numbers of apples. Fruit growers are more interested in damage reduction than changes in yield because normally in IPM and OF orchards, respectively, chemical and manual thinning of apples is applied to get a more regular yield over years. Under these circumstances effects on yield cannot be investigated. Furthermore, there is large variation in the number of flowers per tree and the total production of trees between areas and years. The areas with and without great tits were as far apart as possible. This introduces environmental variation that makes the detection of differences in yield quite difficult.

The experiment in which caterpillars were removed at different times shows that caterpillar damage to apples increased when caterpillars stayed on the trees for longer periods. This increase in damage continued until the time that caterpillars pupated (Fig. 1b). These results clearly show that great tits achieve the largest reduction of caterpillar damage when they remove caterpillars as early as possible. Consequently nests with earlier hatching dates will cause a higher damage reduction than nests with later hatching dates (chapter 4) simply because parents need to forage for caterpillars earlier in the season to feed their nestlings and damage is already inflicted from the onset of fruit onwards. Furthermore, the proportion of caterpillars in the diet is higher earlier in the growing season (chapter 5), which presumably leads to a higher number of caterpillars removed for earlier hatched nests. The great tits' ability to remove caterpillars as early as possible can be reduced by their preference to bring larger prey to their nestlings. Given an age dependent maximum energy requirement of the nestlings, this maximum is reached with lower numbers of caterpillars when caterpillars are larger.

The caterpillar species occurring in the orchard differed in full-grown size as well as in their time of appearance. At a given sample date a range of different caterpillar size classes is available to great tits of which they select the larger ones for their nestlings. However, the minimum size of caterpillars may be over-estimated when self-feeding of the parents is not included in the observed size of removed caterpillars. Betts (1955) and Royama (1966; 1970) found that adult birds ate small food items themselves and carried larger items to the nest. In addition, the relationship between time of removal by great tits and caterpillar damage was linear and thereby indicated that a few large caterpillars inflicted the same damage as many small ones. Despite their preference to feed larger prey to their nestlings, birds are able to reduce caterpillar damage to apples.

Commercial orchards

The experiment in chapter 2, which shows that great tits reduced caterpillar damage to apples, was carried out in an experimental orchard. There, the caterpillar density was high and thus the remaining caterpillar damage was much higher than in IPM and OF orchards. To assess the potential of great tits under commercial management, great tits should also be able to reduce caterpillar damage at lower caterpillar densities, as typical for IPM and OF orchards. For this, great tits need to remove proportionally more caterpillars at low caterpillar densities (although the total number of removed caterpillars will be smaller). Crawford and Jennings (1989) give an example of this effect in a study of the predation of birds on budworms in Spruce-fir stands. At low densities of budworm, birds removed 84 000 larvae or pupae of 100 000 larvae.ha^{-1} (84%) and 110 000 of 500 000 larvae.ha^{-1} (22%) where budworm densities began transition from low to high densities. Thus, although the number removed at high densities is higher, the proportion removed is lower. Depending on the great tits' functional response, the total number of removed caterpillars can be smaller in IPM and OF orchards but the total proportion of caterpillars removed may be higher, and thereby the total damage reduction might be greater than in the experimental orchard. On the other hand if caterpillar densities in the orchards are below the threshold density, that is the probability to find a prey becomes too low, great tits will forage for other prey items or outside the orchard. Under this latter scenario there will be no effect of the presence of breeding great tits on caterpillar damage to apples.

In IPM and OF orchards two equivalent areas of 2 ha were chosen and nest boxes were put up in one of the two areas to attract great tits. Farmers had no restrictions in the research areas and performed their normal management. In autumn caterpillar damage to apples was assessed and compared between the area with and without breeding great tits. The results in Figure 2a show the effect of great tits at low caterpillar densities of these IPM and OF orchards and this reduction, relative to the total amount of damage, is higher than in the experimental orchards. In the experimental orchard damage was reduced by 18.8% from 13.8% to 11.2% (chapter 2) and in the IPM and OF orchards by 25.0% from 6% to 4.5% (chapter 4).

The resulting 4.5 % of caterpillar damage is still higher than the percentages of damage reported by fruit growers. This is because in this study the total amount of damage caused by caterpillars includes the damage class of scars with an area of less than 0.25 cm^2. Fruit growers do not take this class into account. Additionally, in my analysis each apple is screened carefully whereas fruit growers grade apples simultaneously into classes for the market and therewith the chances of missing smaller spots of caterpillar damage is higher.

To partly compare my data with theirs I also show the damage as measured by fruit growers in Figure 2b. This damage was reduced by 27.3% from 4.4% to 3.2%. Thus, whether this class is in- or excluded does not change the results of this study.

(a) Total damage   (b) Economic damage
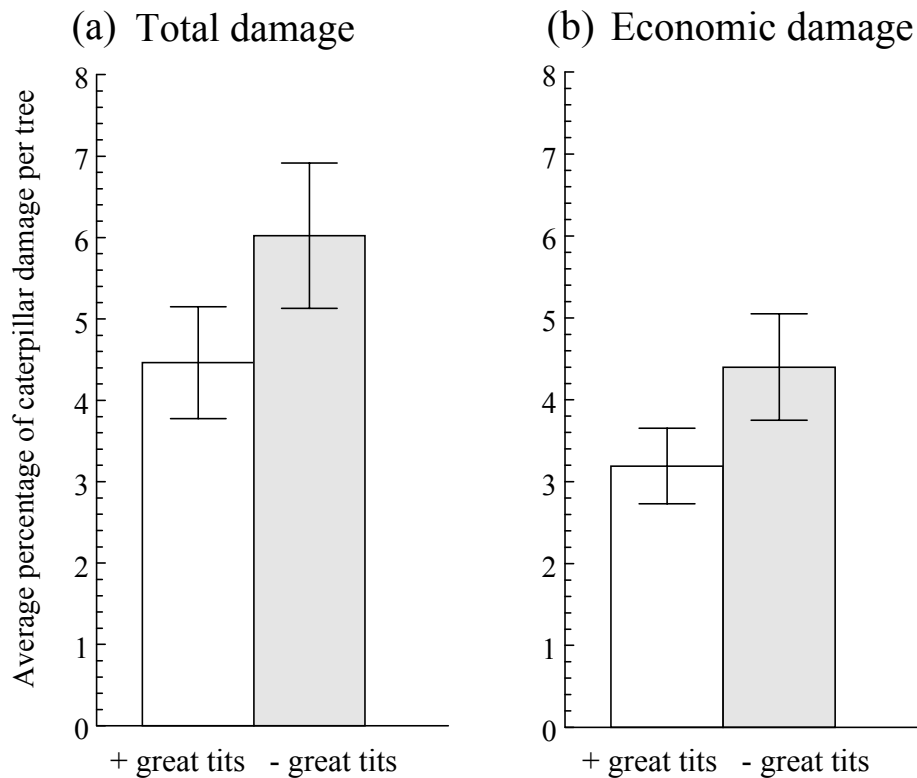
Figure 2 (a) Average percentage of damage (±SE) to apples in pairs of 2 ha areas with and without breeding great tits in 6 IPM and 6 OF orchards (Chapter 4). (b) Average percentage of damage to apples in a 2 ha area with and without breeding great tits in 12 commercially managed orchards when only economic damage is taken in account. Economic damage is caterpillar damage with an area greater than 0.25 cm^2.

MODELLING FORAGING BEHAVIOUR AND THEREBY DAMAGE REDUCTION

In chapters 2 and 4, I showed that great tits could reduce caterpillar damage both under high and low caterpillar densities. What is still missing is information about the impact of the birds at intermediate densities. These densities are of interest because in the near future caterpillar densities in IPM and OF orchards are expected to increase due to new legislation which increasingly restricts the use of pesticides (Anonymous, 2001). Moreover, in the presence of breeding great tits, these intermediate densities may result in the same percentage of damage to the crop than the lower densities in the absence of great tits. If so, a shift in control threshold numbers can be established (see next section). During the study period these densities did not occur in the field. Therefore damage reduction by great tits was modelled for the whole range of densities from high to low (chapter 4).

   Two important relationships are incorporated in the model to predict the number of caterpillars removed by great tits and thereby the amount of damage reduction. The

first relationship links caterpillar density to the time a great tit needs to find a caterpillar and thereby determines the time it takes to remove the caterpillars and the number of caterpillars removed. The second relationship links the cumulative number of caterpillar-days to the percentage of damage to the apples. It was therefore crucial to have good data on the resulting damage when different densities of caterpillars were present on apple trees for different periods of time. The cumulative number of caterpillar days was chosen because the results of the experiment where caterpillars were left longer on the trees (chapter 2) showed that not only caterpillar density but also the period that caterpillars were present determined the amount of damage in the harvest.
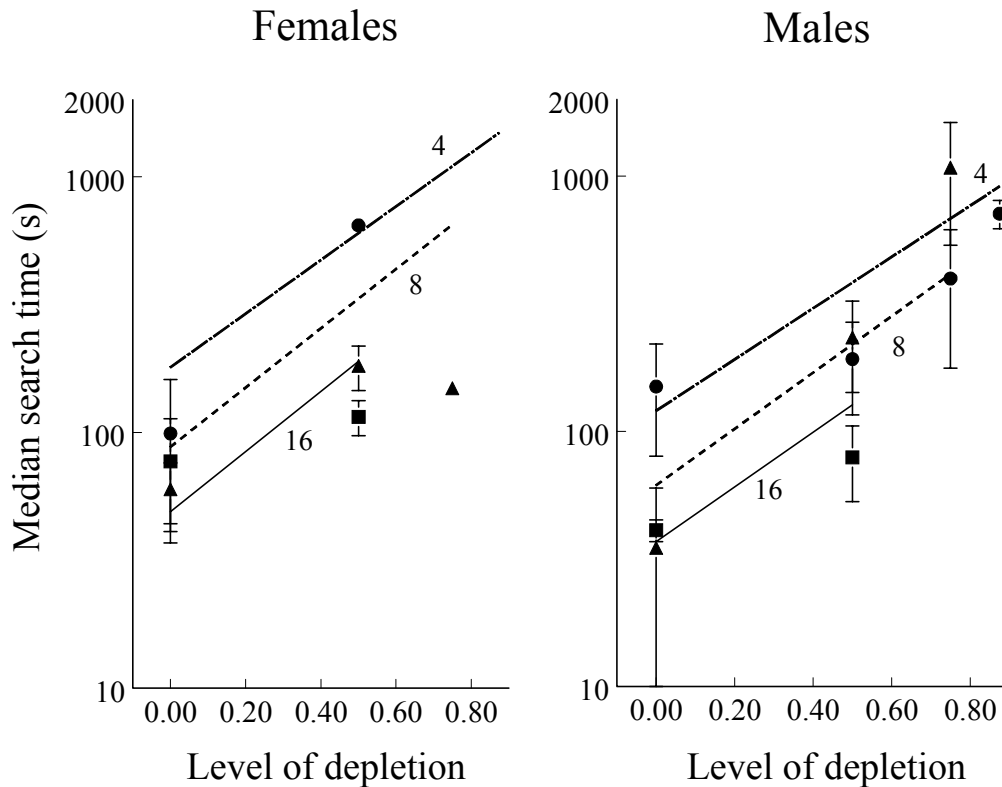
1. Search time and density

As there was no good relationship known between caterpillar density and search time we carried out an experiment to determine search time in relation to density in a semi-natural environment (chapter 3). The experiment showed that encounter rate increased less than directly proportionally with prey density and decreases dramatically with increasing levels of depletion (Fig. 3). Thus, when density decreases due to exploitation by other predators, encounter rate decreases much more than expected from the decrease in density alone. This effect of depletion was stronger at higher current prey densities. Ignoring depletion of caterpillars in the model of great tits foraging within an orchard would therefore have led to an overestimation of the number of caterpillars removed and thereby would over-estimate the amount of damage reduction by great tits. To avoid this, search time was calculated as a function of the current density and the degree of depletion in the model.

The incorporation of the level of depletion in the foraging model to predict foraging behaviour of great tits is new. Depletion has often been ignored and decreases in capture rate (assuming random search) within a patch have been attributed to decreased in prey abundance only (Cowie & Krebs, 1979).

The effect of depletion on prey availability has been addressed by Charnov *et al.* (1976) who give three explanations, behavioural depression, microhabitat depression, or the prey that is easiest to find are taken first because of heterogeneity in either the prey or environment (see chapter 3). In the experiment reported on in this study the effect of depletion can be attributed to the heterogeneity in encounter rates, with the easiest prey to find being removed first, leading to a decrease in the average encounter rate of the individual remaining prey.

The effects found in our experiment can lead to a paradoxical situation in partly depleted environments, where patches with a relatively low current density, but little previous exploitation, may offer the best foraging opportunities. Depletion of foraging patches in natural environments may therefore be one of the reasons why predators deviate from the foraging sites predicted by classic foraging models.

Figure 3 Median time to find the first prey ('search time'; Kaplan-Meier estimate with s.e.) in relation to the level of depletion for 3 current prey densities (dots = 4, triangles = 8, squares = 16 prey) for male and female Great Tits foraging for caterpillars the two sexes. Lines are calculated from the proportional hazard model (see Table 1b chapter 3 for co-variates and their estimated coefficients).

The reduced encounter rate in partially exploited patches will also effectively create refugia from predation, and hence may profoundly influence population dynamics. Some recent models of predator-prey interactions do take into account heterogeneity in encounter rates between prey (Anderson & May, 1991; Sibly *et al.*, 2002). However, this is often limited to easily recognisable classes of prey such as age, size or sex. A strong effect of previous exploitation was found when both the prey size distribution and environment are more homogeneous than in most natural situations, and that an unexplained departure from direct proportionality between encounter rate and the density of previously unexploited prey was found. This means that caution must be taken with assumptions of classical predator-prey models, even in seemingly uniform environments.

2. Caterpillars and damage
The second relationship was derived from field data from chapter 2 and linked the cumulative number of caterpillar-days to the resulting damage in harvest. Caterpillar densities on trees were measured at different times in the growing season. It was assumed that all caterpillars had been present from the start of apple bloom. The cumulative number of caterpillar-days for each tree was calculated and linked to the

damage to apples in autumn. Due to mortality of caterpillars and possible sampling errors, some trees were found to have no caterpillars but did have caterpillar damage. Because of this effect, the relation between the cumulative number of caterpillar-days and damage does not go through the origin (i.e. zero caterpillars does not result in zero damage).

In addition to these field data I carried out an experiment to get a better estimate of the relationship between the cumulative number of caterpillar-days and damage but this turned out to be rather complicated. Establishing the relationship between the cumulative number of caterpillar-days and damage would be relatively easy if caterpillar densities can be determined at time zero and then removed after a given time period. However, sampling caterpillar densities is a destructive procedure. Some caterpillars build multiple shelters and therefore shelters have to be opened to check for caterpillar presence. In addition, caterpillars, particularly those of tortricid moths, drop to the ground as a defence mechanism against predation. This leads to the situation that after sampling almost none of the counted caterpillars stay on the inspected branch. To overcome this problem I put out first larval stage of two species of caterpillars, winter moth and *Orthosia incerta,* on branches to obtain a known initial density. Two species were chosen to investigate whether different species cause different amounts of damage. When tracing them back at given time intervals almost none of the caterpillars were recovered (i.e. 18.2% of winter moths and 6.7% of *Orthosia incerta*). Mortality, but in particular their mobility, are likely causes for the absence of caterpillars on the sampled branches. Trees are planted close together in orchards and branches of different trees touch each other. Caterpillars can therefore move within and between trees. Due to the low recovery of caterpillars, the density and period that caterpillars were on the sampling branches was not accurate and the experiment failed in the sense that an improved relationship between the cumulative number of caterpillar-days and damage could not be established. A better way of putting out caterpillars has to be found and the whole tree has to be taken as a sampling unit to link cumulative number of caterpillar-days to damage. Moreover, the individual trees should be isolated to avoid crossing over of caterpillars between trees.

In the model I used the relation determined from field data from chapter 2. This relationship over-estimates damage for low cumulative number of caterpillar-days, but can well be used in the model, as I was interested in the difference between the situation with and without great tits. Therefore any inaccuracy in the estimated relationship equally holds for both situations and does not change the relative difference in damage.

3. The model
The model was developed to predict damage in areas with and without great tits for other densities than currently present in the field. The expected damage reduction for low to high caterpillar densities was modelled. Furthermore, the influence of number of breeding pairs and their nest box positions, breeding parameters of great tits and physical parameters in the model on the estimated damage was tested. The model

ignores self-feeding of the parents and foraging outside the nestling period. Furthermore great tits in the model can only forage within the orchard. Despite these assumptions the model is still useful to compare damage levels in the presence and absence of great tits.

The model was not sensitive for changes in the estimated physical parameters, such as, metabolic costs of searching and flying. One of the reasons that damage reduction by great tits is insensitive to these parameters in the model, is that these parameters enhance the energy expenditure of the parents which is only included in the model as a switch to prevent exceeding the maximum Daily Energy Expenditure and hence do not change the number of caterpillars removed by these parents much. When energy demands of the chicks are comparatively low (i.e. early after hatching) and/or densities are equal or higher than 8 caterpillars per tree the parents can feed their chicks the maximum daily amount without reaching their energy or time limits.

In the model the amount of damage reduction by great tits depended mainly on the number of breeding pairs in the orchard (Fig. 4) and on the hatching date of the nestlings of great tits (chapter 4).

For low, intermediate and high caterpillar densities the predicted damage by the model when zero, one, two or four pairs of great tits are present are shown in Figure 3. The amount of damage reduction is given by the difference between the lines showing the damage for a situation without great tits and the lines for one, two, and four pairs of great tits respectively. The relative damage reduction (i.e. the amount of damage reduction divided by the total amount of damage) is highest for densities in the range between 16 and 32 caterpillars per tree (Fig. 4).

When the number of breeding pairs increased, the numbers of caterpillars removed also increased. This increase is less than proportional due to an increase in foraging time per prey item caused by the steeper decline in caterpillar density and the increasing level of depletion.

Hatching date had also an effect on the level of damage reduction by great tits. When chicks hatch earlier in the season great tits have to start removing caterpillars earlier from the orchard and thereby caterpillars have less time to inflict damage. Furthermore, caterpillars are smaller early in the season and therefore great tits are presumed to bring more caterpillars to the chicks to fulfil the same energy requirement.

Given the predictions of the model, that the damage reduction was mainly influenced by the number of breeding pairs and the hatching date of the chicks, I investigated how these same factors influenced the total number of caterpillars removed from apple orchards (Mols *et al.*, this thesis chapter 5). This gives an important validation of the model because the number of caterpillars removed and the timing of their removal determine the amount of damage reduction established by great tits. Given the average density of 3 pairs of breeding great tits per ha in Integrated Pest management and Organic Farming orchards, the total number of caterpillars removed was 23% of the caterpillars present in the orchard and could run up to 49% when all foraging takes place inside the orchard.
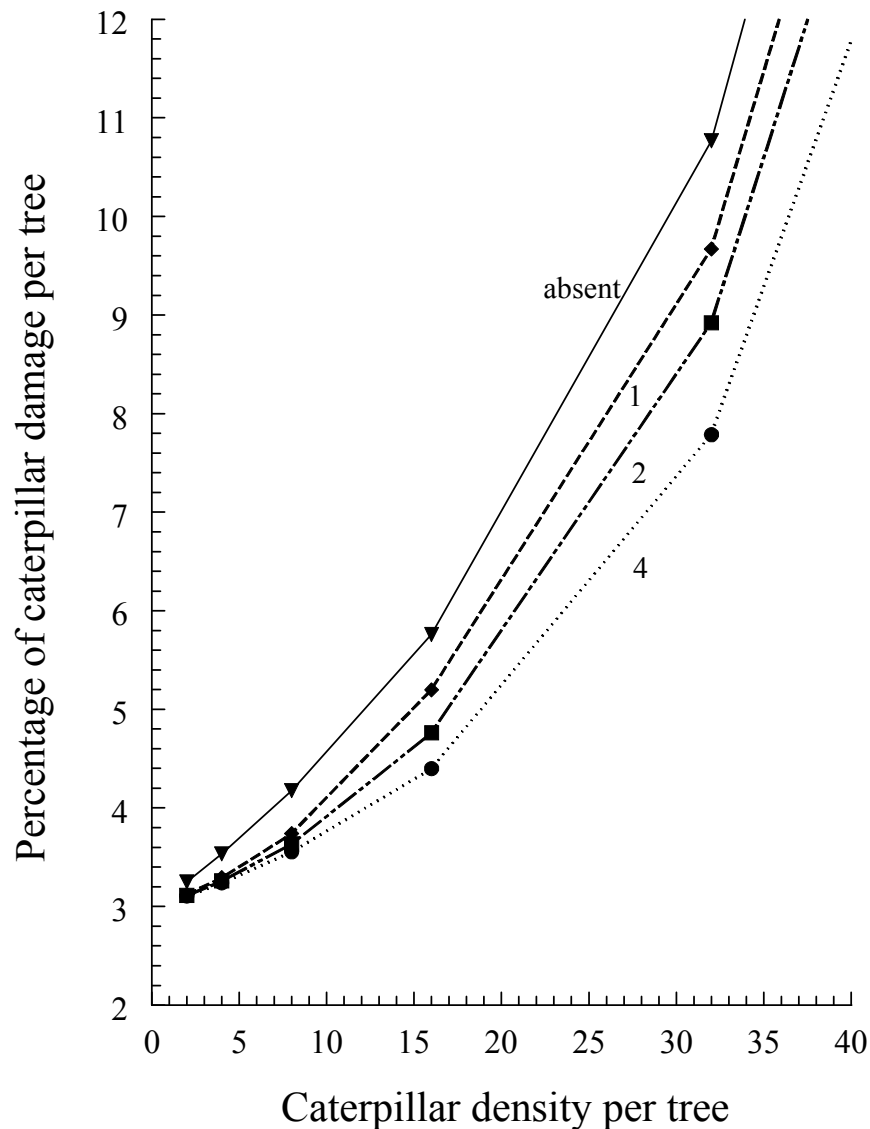
Figure 2 Variation in percentage of caterpillar damage on apples per tree predicted by the model when there are 0 (absent), 1, 2 or 4 pairs of great tits searching in the orchard.

SHIFTING CONTROL THRESHOLDS

The findings in this study imply that the caterpillar densities at which pesticides are applied can be raised when great tits are breeding in orchards. Field data and the model show that for equal numbers of caterpillars the resulting damage in the presence of great tits is lower and thereby for a fixed damage threshold more caterpillars can be allowed.

Use of an insecticide is recommended when the control threshold of 8 to 10 caterpillars per 100 flower clusters in the green bud stage is reached (Asselbergs *et al.*, 1996). In 1999 the average number of flower buds per apple tree was 159 (s.d. ± 146) in four IPM and four OF orchards. This leads to a control threshold of 13 to 16

caterpillars per tree for an average tree. If we take an initial density of 14 caterpillars per tree as control threshold, the predicted damage is 5.1% (or 4.5% when not counting the minor damage as fruit growers do) without great tits present (see Fig. 4). When one, two or four pairs of great tits are present, the same percentage of damage occurs with an initial density of 16, 18 and 21 respectively. Depending on the number of breeding pairs and the hatching date of chicks the control thresholds can be raised with 2 to 7 caterpillars per tree. The damage reduction of 25 % (from 6% to 4.5%) in the IPM and OF orchards was established on average by 3.5 (SD± 1.3) pairs of great tit. These effects concern the damage reduction only. The possible positive effects on yield will even increase the profitability of great tits.

PRACTICAL IMPLICATIONS AND BEYOND

As suggested by this study the current control thresholds can be altered in the presence of great tits. However, for a successful implementation in the current management systems some work still needs to be done. As discussed above, the current control threshold is 8 to 10 caterpillar per 100 clusters before bloom but fruit growers consider the resulting damage of 5 percent too high. The current control thresholds have not been changed since they where established in the nineteen-seventies. In addition, they were not experimentally established but were derived from trial and error by cooperating fruit growers. When the damage exceeded the acceptable level, the thresholds were adjusted and tested again. The control thresholds have not changed but the requirements for apples to meet the highest quality standard have increased. This led to the situation that fruit growers use lower control threshold than have been established and therefore the control threshold, even in the absence of great tits, has to be re-established.

For the implementation of great tits into the management system of apple orchards, fruit growers have to be convinced of the reliability of the effect of great tits. When they are confident that the raised threshold numbers in the presence of great tits will not cause more damage than the current control thresholds without great tits, the fruit growers will change their management and thus reduce the use of insecticides. Especially because the only cost to the fruit growers is that of putting up nest boxes (*c.* 2 ha^{-1}) to allow great tits to breed in the orchards.

The process described above to adjust control thresholds in the presence of great tits will take some time. However, an alternative way to implement great tits into the management systems is more direct. The results of Figure 2 show that when fruit growers put up nest boxes in addition to their regular management there will already be damage reduction. When fruit growers detect fewer caterpillars in spring due to predation of great tits or empirically discover over the years that higher caterpillar numbers can be allowed for in the presence of great tits, a reduction in pesticide use can occur. In this manner great tits can already cause a reduction in the use of pesticides even though new control thresholds have not been established.

Despite these apparent advantages, some fruit growers are reluctant to encourage great tits or birds in general to breed in their orchards. They fear that great tits themselves inflict damage to the fruit. In none of the participating orchards I have found great tit damage on apples when assessing damage levels during harvest, but damage does occur in pears. In a mixed orchard with apple and pears during a period of 6 weeks I tried to observe which bird species caused the damage to pears. Observations were performed on three mornings of each week and lasted 2 hours. During these observations I saw two blue tits and one unringed great tit inflicting damage. No blue tits had been breeding in the part of the orchard with apple trees and all breeding great tits and their nestlings had been ringed. Although there may not be a direct relation between the number of great tits in spring and autumn in the orchard, it needs further investigation whether mixed orchards with apple and pear have more bird damage in pears when great tits have been breeding in the orchard in spring. If bird damage in pears of mixed orchards increases when great tits have been breeding in the apple part of the orchard the advantages and disadvantages of great tits should be compared. If the damage to pears exceed the positive effects in apples, great tits can only be useful in orchards that cultivate apples only.

Although several studies, including this one, have shown that natural enemies reduce damage, they cannot prevent damage fully and reliably alone (Solomon *et al.*, 2000). Thus if one really wants to test whether biological control can regulate pest insects to an economically acceptable level under field conditions, the joint forces of a complex of natural enemies should be tested.

This thesis and other studies (see review by Cross *et al.*, 1999; Solomon *et al.*, 2000) show the possibility that a complex of natural enemies can work, and that birds can contribute to pest control. If fruit growers are compensated either by government or other organisations to sustain their livelihood during the period in which natural enemy populations build up, an orchard system with natural enemies can build up and it can be tested whether a complex of interacting natural enemies can keep pests densities at an economically acceptable level.

REFERENCES

Anonymous (2001). Zicht op gezonde teelt, gewasbeschermingsbeleid tot 2010. Den Haag, Nederland, Ministerie van Landbouw, Natuurbeheer en Visserij.

Anonymous (2002). Voorkomen van ziekten en plagen: over gewasbescherming in de landbouw. Den Haag, Netherland, Ministerie van Landbouw, Natuurbeheer en Visserij.

Anderson, R.M. & May, R.M. (1991). Infectious diseases of humans, dynamics and control. Oxford, Oxford University Press.

Asselbergs, D.J.M., van Nierop, S., Oomen, P.A. & Oostelbos, P.F.J. (1996). Gewasbeschermingsgids: handboek voor de bestrijding van ziekten, plagenen onkruiden en de toepassing van groeiregulatoren in de land- en tuinbouwen het openbaar groen. Wageningen, Plantenziektenkundige Dienst.

Atlegrim, O. (1989). Exclusion of birds from bilberry stands: impact on insect larval density and damage to the bilberry. Oecologia, 79, 136-139.

Battisti, A., Bernardi, M. & Ghiraldo, C. (2000). Predation by the hoopoe (*Upupa epops*) on pupae of *Thaumetopoea pityocampa* and the likely influence on other natural enemies. Biocontrol, 45, 311-323.

Bell, G.P. (1990). Birds and mammals on an insect diet: a primer on diet composition analysis in relation to ecological energetics. Studies in Avian Biology, 13, 416-422.

Bendell, B.E., Weatherhead, P.J. & Stewart, E.K. (1981). The impact of predation by red-winged blackbirds in European corn borer populations. Canadian Journal of Zoology, 59, 1535-1538.

Betts, M.M. (1955). The food of the titmice in oak woodland. Journal of Animal Ecology, 24, 282-323.

Blommers, L.H.M. (1994). Integrated pest management in European apple orchards. Annual Review of Entomology, 39, 213-241.

Bruns, H. (1960). The economic importance of birds in forests. Bird Study, 7 (4), 193-208.

Buckner, C.H. & Turnock, W.J. (1965). Avian predation on the larch sawfly, *Pristiphora erichsonii* (Hymenoptera: Tenthredinidae). Ecology, 46, 223-236.

Carson, R. (1962). Silent spring. New York, Fawcett Crest.

Charnov, E.L., Orians, G.H. & Hyatt, K. (1976). Ecological implications of resource depression. American Naturalist, 110, 247-259.

Conner, E.F., Yoder, J.M. & May, J.A. (1999). Density-related predation by the Carolina chickadee, *Poecile carolinensis*, on the leaf-mining moth, *Cameraria hamadryadella* at three spatial scales. Oikos, 87, 105-112.

Cowie, R.J & Krebs, J.R. (1979). Optimal foraging in patchy environment. (R. M. Anderson, B. D. Turner & L. R. Taylor Ed.) *The British Ecological Society Symposium, Population Dynamics*. Oxford, Blackwell Scientific Publications. 20, 183-205.

Cramp, S., Perrins, C.M., Brooks, J.D., Dunn, E., Gillmor, R., Hall-Craggs, J., Hillcoat, B., Hollom, P.A.D., Nicholson, E.M., Roselaar, R.S., Seale, W.T.C., Sellar, P.J., Simmons, K.E.L., Snow, D.W., Vincent, D., Voous, K.H., Wallace, D.I.M. & Wilson, M.G. (1993). *Parus major*, Great Tit. (C. M. Perrins & J. D. Brooks Ed.) *Handbook of the Birds of Europe the Middle East and North Africa. The birds of the western Paleartic VII : Flycatchers to Shrikes*. New York, Oxford University Press, 255-269.

Crawford, H.S. & Jennings, D.T. (1989). Predation on spruce budworm *Choristoneura fumifera*: Functional, numerical and total response. Ecology, 70, 152-163.

Crawley, M.J. (1993). GLIM for ecologist. Oxford, Blackwell Scientific Publications.

Cross, J.V., Solomon, M.G., Babandreier, D., Blommers, L.H.M., Easterbrook, M.A., Jay, C.N., Jenser, G., Jolly, R.L., Kuhlmann, U., Lilley, R., Olivella, E., Toepfer, S. & Vidal S (1999). Biocontrol of pests of apples and pears in Northern and Central Europe. 2. Pasitoids. Biocontrol Science and Technology, 9, 277-314.

de Reede, R.H., Gruys, P. & Vaal, F. (1985). Leafrollers in apple IPM under regimes based on *Bacillus thuringiensis*, on diflubenzuron, or on epofenonane. Entomologia Experimentalis et Applicata, 37, 263-247.

Endler, J.A. (1991). Interaction between predators and prey. (Ed. J. R. Krebs & N. B. Davies) *Behavioural Ecology*. London, England, Blackwell Scientific. Third Edition, 169-196.

Fye, R.E. (1982). The bird and the Psyllas. Agricultural Research, 30 (12), 15.

Gibb, J.A. (1955). Feeding rates of Great Tits. British Birds, XLVIII, 49-58.

Gibb, J.A. (1957). Food requirements and other observations on captive tits. Bird Study, 4, 207-215.

Gibb, J.A. (1958). Predation by tits and squirrels on the eucosmid *Ernarmonia conicolana* (Heyl.). Journal of Animal Ecology, 27, 375-396.

Gibb, J.A. & Betts, M.M. (1963). Food and food supply of nestling Tits (*Paridae*) in Breckland Pine. Journal of Animal Ecology, 32, 489-533.

Glen, D.M. & Milsom, N.F. (1978). Survival of mature larvae of codling moth (*Cydia pomonella*) on apple trees and ground. Annals of Applied Biology, 90, 133-146.

Glutz von Blotzheim, U.N. & Bauer, K.M. (eds) (1988). Handbuch der Vögel Mittel-Europas 11-2 Passeriformes (teil 2). Wiesbaden, Aula-Verlag.

Glutz von Blotzheim, U.N. & Bauer, K.M. (eds) (1991). Handbuch der Vögel Mittel-Europas 12-2 Passeriformes (teil 3). Wiesbaden, Aula-Verlag.

Glutz von Blotzheim, U.N. & Bauer, K.M. (eds) (1993a). Handbuch der Vögel Mittel-Europas 13-1 Passeriformes (teil 4). Wiesbaden, Aula-Verlag.

Glutz von Blotzheim, U.N. & Bauer, K.M. (eds) (1993b). Handbuch der Vögel Mittel-Europas 13-3 Passeriformes (teil 4). Wiesbaden, Aula-Verlag.

Glutz von Blotzheim, U.N. & Bauer, K.M. (eds) (1997). Handbuch der Vögel Mittel-Europas 14-2 Passeriformes (teil 5). Wiesbaden, Aula-Verlag.

Gosler, A.G. (1993). The great tit. London, Hamlyn Limited.

Gradwohl, J. & Greenberg, R. (1982). The effect of a single species of avian predator on the athropods of aerial leaf litter. Ecology, 63, 581-583.

Greenberg, R., Bichier, P., Angon, A.C., MacVean, C., Perez, R. & Cano, E. (2000). The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. Ecology, 81, 1750-1755.

Grieco, F. & van Noordwijk, A.J. (2001). The trade-off between provisonings rate and prey size in breeding blue tits (Parus caeruleus): effects of an additional feeding experiment. Ph D thesis. Wageningen, the Netherlands, Ponsen & Looijen B.V.

Gruys, P. (1982). Hits and misses. The ecological approach to pest control in orchards. Entomologia Experimentalis et Applicata, 31, 70-87.

Hinsley, S.A. (2000). The costs of multiple patch use by birds. Landscape Ecology, 15, 765-775.

Hódar, J.A. (1996). The use of regression equations for estimation of arthropod biomass in ecological studies. Acta Oecologica, 17, 421-433.

Holmes, R.T., Black, C.P. & Sherry, T.W. (1979a). Comparative population bioenergetics of three insectivorous passerines in a deciduous forest. Condor, 81, 9-20.

Holmes, R.T., Schultz, J.C. & Nothnagle, P. (1979b). Bird predation on forest insects: an exclosure experiment. Science, 206, 462-463.

Houston, A.I. (1987). Optimal foraging by parent birds feeding dependent young. Journal of Theoretical Biology, 124, 251-274.

Houston, A.I. & McNamara, J.M. (1985). A general theory of central place foraging for single-prey loaders. Theoretical Population Biology, 28, 233-262.

Kacelnik, A. (1984). Central place foraging in starlings (Sturnus vulgaris) I. Patch residence time. Journal of Animal Ecology, 53, 283-299.

Kacelnik, A. & Houston, A.I. (1984). Some effects of energy costs on foraging strategies. Animal Behaviour, 32, 609-614.

Kalbfleisch, J.D. & Prentice, R.L. (1980). The statistical analysis of failure time data. New York, John Wiley.

Keller, L.F. & van Noordwijk, A.J. (1994). Effects of local environmental conditions on nestling growth in the great tit *Parus major* L. Ardea, 82, 349-362.

Kirk, D.A., Evenden, M.D. & Mineau, P. (1996). Past and current attempts to evaluate the role of birds as predators of insect pests in temperate agriculture. Current Ornithology, 13, 175-269.

Kluijver, H.N. (1950). Daily routines of the Great Tit: *Parus major* (L.). Ardea, 38, 99-135.

Lessells, C.M. & Stephens, D.W. (1983). Central Place Foraging: Single-prey loaders again. Animal Behaviour, 31, 238-243.

Lotka, A.J. (1925). Elements of physical biology. Baltimore, Williams & Wilkins.

MacLellan, C.R. (1958). Role of woodpeckers in control of the codling moth in Novia Scotia. Canadian Entomologist, 90, 18-22.

MacLellan, C.R. (1959). Woodpeckers as predators of the codling moth in Novia Scotia. Canadian Entomologist, 91, 673-680.

Marchetti, C. & Drent, P.J. (2000). Individual differences in the use of social information in foraging by captive great tits. Animal Behaviour, 60, 131-140.

Marquis, R.J. & Whelan, C.J. (1994). Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology, 75, 2007-2014.

Masman, D. & Klaassen, M. (1987). Energy expenditure during free flight in trained and free-living Eurasian kestrels (*Falco tinnunculus*). Auk, 104, 603-616.

Maurer, B.A. (1996). Energetics of avian foraging. (Ed. C. Carey) *Avian energetics and nutritional ecology*. New York, Chapman & Hall, 250-279.

Mertens, J.A.L. (1969). The influence of brood size on the energy metabolism and water loss of nestling Great tits *Parus major major*. Ibis, 111, 11-16.

Mols, C.M.M., Mooij, W.M., Blommers, L.H.M. & Visser, M.E. (this thesis chapter 4). Reduction of caterpillar damage in apple orchards by great tits (*Parus major*).

Mols, C.M.M., van Oers, K., Witjes, L.M.A., Lessells, C.M., Drent, P.J. & Visser, M.E. (this thesis chapter 3). Central assumptions of predator-prey models fail in a semi-natural experimental system.

Mols, C.M.M. & Visser, M.E. (2002). Great tits can reduce caterpillar damage in apple orchards. Journal of Applied Ecology. 39 (6), 888-899.

Mooij, W.M. & Boersma, M. (1996). An object-oriented simulation framework for individual-based simulations (OSIRIS): Daphnia population dynamics as an example. Ecological Modelling, 93 (1-3), 139-153.

Naef-Daenzer, L., Naef-Daenzer, B. & Nager, R.G. (2000). Prey selection and foraging performance of breeding Great Tits *Parus major* in relation to food availability. Journal of Avian Biology, 31, 206-214.

Nicholson, A.J. (1933). The balance of animal populations. Journal of Animal Ecology, 2, 131-178.

Norberg, U.M. (1996). Energetics of flight. (C. Carey Ed.) *Avian energetics and nutritional ecology*. New York, Chapman & Hall, 199-247.

Orians, G.H. & Pearson, N.E. (1979). On the theory of central place foraging. (Ed. D. J. Horn, R. D. Mitchell & G. R. Stairs) *Analysis of ecological systems.* Columbus, Ohio, Ohio State University Press, 155-177.

Otvos, J. (1979). The effects of insectivorous bird activity in forest ecosystems: an evaluation. (Ed. J. Dickson, R. Conner, R. Fleet, J. Jackson & J. Kroll) *The role of insectovorous birds in forest ecosystems*. New York, Academic press, 341-374.

Perrins, C.M. (1991). Tits and their caterpillar food supply. Ibis, 133, 49-54.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977). Optimal Foraging: a selective review of theory and tests. Quarterly Review of Biology, 52 (2).

Quiring, D.T. & Timmins, P.R. (1988). Predation by American crows reduces overwintering European corn-borer populations in southwestern Ontario. Canadian Journal of Zoology, 66, 2143-2145.

Royama, T. (1966). Factors governing feeding rate, food requirement and broodsize of nestling great tits *Parus major*. Ibis, 108, 313-347.

Royama, T. (1970). Factors governing the hunting behaviour and the selection of food by the great tit (*Parus major* L.). Journal of Animal Ecology, 39, 619-668.

Sibly, R.M., Hone, J. & Clutton-Brock, T.H. (2002). Population growth rate: determining factors and role in population regulation. Philosophical Transactions Royal Society of London B., 357, 1149-1151.

Solomon, M.E. (1949). The natural control of animal populations. Journal of Animal Ecology, 18, 1-35.

Solomon, M.E. & Glen, D.M. (1979). Prey density and rates of predation by tits (*Parus* spp.) on the larvae of the codling moth (*Cydia pomonella*) under bark. Journal of Applied Ecology, 16, 49-59.

Solomon, M.E., Glen, D.M., Kendall, D.A. & Milson, N.F. (1976). Predation of the overwintering larvae of the codling moth (*Cydia pomonella*) by birds. Journal of Animal Ecology, 13, 341-352.

Solomon, M.G., Cross, J.V., Fitzgerald, J.D., Cambell, C.A.M., Jolly, R.L., Olszak, R.W., Niemczyk, E. & Vogt, H. (2000). Biocontrol of pests of apples and pears in Northern and Central Europe. 3. Predators. Biocontrol Science and Technology, 10, 91-128.

Spiller, D.A. & Schoener, T.W. (1990). A terrestrial field experiment showing the impact of eliminating top predators on foliage damage. Nature, 347, 469-472.

Stephens, D.W. & Krebs, J.R. (1986). Foraging Theory (monographs in behavior and ecology). New Jersey, Princeton University Press.

Strong, A.M., Sherry, T.W. & R.T., H. (2000). Bird predation on herbivorous insects: indirect effects on sugar maple saplings. Oecologia, 125, 370-379.

Subinprasert, S. (1987). Natural enemies and their impact on overwintering codling moth populations (*Laspeyresia pomonella* L.) (Lep.Tortricidae) in South Sweden. Journal of Applied Entomology, 103, 46-55.

Sutherland, W.J. (1996). From individual to population ecology. Oxford, Oxford University Press.

Tanhuanpää, M., Ruohomaki, K. & Uuispaikka, E. (2001). High larval predation rate in non-outbreaking populations of a geometrid moth. Ecology, 82, 281-289.

Tinbergen, J.M. & Dietz, M.W. (1994). Parental energy expenditure during brood rearing in the Great Tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. Functional Ecology, 8, 563-572.

Tinbergen, L. (1960). The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. Archives Néerlandaises de Zoologie, 13, 265-343.

Tremblay, A., Mineau, P. & Stewart, R.K. (2001). Effects of bird predation on some pest insect populations in corn. Agriculture Ecosystems and Environment, 83, 143-152.

Tucker, V.A. (1973). Bird metabolism during flight: evaluation of a theory. Journal of Experimental Biology, 48, 67-87.

van Balen, J.H. (1973). A comparative study of the breeding ecology of the Great Tit *Parus major* in different habitats. Ardea, 61, 1-93.

van den Ende, E., Blommers, L.H.M. & Trapman, M. (1996). Gaby: a computer-based decision support system for intergrated pest mamagement in Dutch apple orchards. Integrated Pest Management Reviews, 1, 147-162.

Verbeek, M.E.M., Drent, P.J. & Wiepkema, P.R. (1994). Consistent individual-differences in early exploratory-behavior of male great tits. Animal Behaviour, 48, 1113-1121.

Verhulst, S. & Tinbergen, J.M. (1997). Clutch size and parental effort in the Great Tit *Parus major*. Ardea, 85, 111-126.

Wearing, C.H. & McCarthy, K. (1992). Predation of codling moth *Cydia pomonella* L. by the silvereye *Zosterops lateralis* Latham. Biocontrol Science and Technology, 2, 285-295.

Williams, J.B. & Nagy, K.A. (1984). Daily energy expenditure of savannah sparrows: comparison of time-energy budget and Doubly-Labeled water estimates. Auk, 101, 221-229.

Winkler, D.W. & Adler, F.R. (1996). Dynamic state variable models for parental care. 1. a submodel for the growth of the chicks of passerine birds. Journal of Avian Biology, 27, 343-353.

Witt, A.B.R., Little, R.M. & Crowe, T.M. (1995). The effectiveness of helmeted guineafowl *Numida meleagris* (Linnaeus 1766) in controlling the banded fruit weevil *Phlyctinus callosus* (Schonherr 1826), and their impact on other invertebrates in apple orchards in the Western Cape Province, South Africa. Agriculture Ecosystems and Environment, 55 (3), 169-179.

Wright, J., Both, C., Cotton, P.A. & Bryant, D. (1998). Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. Journal of Animal Ecology, 67, 620-634.

Zajac, R. (1979). The influence of bird feeding on the number of overwinterng larvae of codling moth, *Laspeyresia pomonella* L., in orchards of central Poland. Ekologia Polska, 27, 571-580.

Samenvatting

Achtergrond van het onderzoek

Plaaginsekten kunnen in (fruit)boomgaarden veel schade veroorzaken. Vaak wordt het optreden van plaaginsekten in boomgaarden tegengegaan door meer of minder intensief gebruik van insecticiden. In Nederland wordt door een grote meerderheid van fruittelers, de zogenaamde *geïntegreerde bestrijding* (IPM) toegepast. Bij deze vorm van gewasbescherming wordt gebruik gemaakt van bestrijdingsdrempels. Dit betekent dat er geen bestrijding wordt toegepast tenzij het aantal plaaginsekten van een bepaalde soort boven een vastgestelde drempelwaarde uitstijgt. Daarnaast worden voornamelijk selectieve bestrijdingsmiddelen gebruikt, die alleen het plaaginsekt aanpakken en andere organismen zoals de natuurlijke vijanden van plagen niet doden.

Sinds de zeventiger jaren wordt ook steeds meer aandacht besteed aan het gebruik van biologische bestrijdingsmiddelen, zoals bestanddelen uit planten, natuurlijke vijanden (waaronder virussen en bacteria) en feromoonverwarring. De laatste jaren is de belangstelling voor biologische bestrijding verder toegenomen. De strengere regelgeving omtrent de toelating en het gebruik van bestrijdingsmiddelen, maar ook de ontwikkeling van resistentie van plagen voor veel gebruikte bestrijdingsmiddelen maken alternatieve methoden noodzakelijk. Verder heeft de consument steeds meer aandacht voor milieu en voedselveiligheid. Consumenten willen steeds vaker producten, die niet alleen goed smaken en er mooi uitzien, maar die tegelijkertijd op een veilige en milieuvriendelijk manier geteeld zijn. In ongeveer 10 procent van de appelboomgaarden vindt op dit moment *biologische bestrijding* (EKO) plaats. Bij deze vorm van gewasbescherming mogen geen synthetische pesticiden of herbiciden gebruikt worden.

Eén van de hoofdplagen in zowel IPM als EKO appelboomgaarden zijn rupsen. Door natuurlijke vijanden van rupsen in de boomgaard te stimuleren, zou een fruitteler het gebruik van insecticiden (biologisch dan wel conventioneel) verder kunnen beperken. Insekten-etende vogels, zoals koolmezen, zouden hiervoor in aanmerking kunnen komen. Uit onderzoek is bekend dat koolmezen in hun broedperiode grote hoeveelheden rupsen aan hun jongen voeren en daardoor zijn koolmezen voor rupsen een natuurlijke vijand bij uitstek. Bovendien kunnen koolmezen, door het ophangen van nestkasten, relatief eenvoudig gestimuleerd worden om in de boomgaard te broeden.

Het onderzoek

De vraagstelling in dit onderzoek is of koolmezen de schade die door rupsen aan appels wordt veroorzaakt, zodanig kunnen verminderen dat hierdoor de huidige bestrijdingsdrempel verhoogd kan worden. Dit betekent dat de teler minder vaak bestrijdingsmiddelen hoeft te gebruiken. Deze vraagstelling is op drie, elkaar aanvullende, manieren onderzocht. Aan de hand van experimenteel werk in proefboomgaard "de Schuilenburg" is bij een relatief hoge rupsendichtheid bepaald of en gedurende welke periode koolmezen rupsenschade kunnen verminderen. Daarnaast is in een aantal IPM en EKO boomgaarden het aantalsverloop van ruspen gedurende het

broedseizoen en het percentage rupsenschade in de oogst bepaald op percelen met en zonder broedende koolmezen bij relatief lage rupsendichtheden. Omdat de onderzochte situaties in de experimentele boomgaard en de IPM en EKO boomgaarden slechts informatie geven over schadevermindering door koolmezen voor de gevonden hoge en lage dichtheden, is tevens een theoretisch model ontwikkeld om de effecten voor de tussenliggende dichtheden te berekenen. Ook is het model gebruikt om te bepalen of de huidige bestrijdingsdrempel verhoogd kan worden in de aanwezigheid van koolmezen. In de ontwikkeling van het model bleek dat essentiële informatie over het zoekgedrag niet bekend was. De relatie tussen zoektijd en rupsendichtheid werd daarom in een experiment gemeten.

Experimentele boomgaard

De vraag of koolmezen, door het verwijderen van rupsen, schade aan appels kunnen verminderen is onderzocht met behulp van een experiment in proefboomgaard "de Schuilenburg". In dit experiment is bepaald gedurende welke periode koolmezen schade kunnen verminderen. Op verschillende tijdstippen in het groeiseizoen zijn bomen afgedekt met netten, waardoor koolmezen buitengesloten werden (hoofdstuk 2). Zo is er aangetoond, dat koolmezen schade kunnen verminderen vanaf het moment waarop zij beginnen met het bebroeden van hun eieren tot het moment waarop de jongen het nest verlaten. Gedurende deze periode werd niet alleen de rupsenschade aan appels verminderd, maar werd ook de opbrengst per boom vergroot. Dit opbrengst effect moet echter nog onder normale productie omstandigheden (IPM en EKO) onderzocht worden.

Koolmezen kunnen rupsenschade alleen verminderen als de periode waarin koolmezen hun jongen voeren en dus de meeste rupsen weghalen, samenvalt met de periode dat rupsen schade aan appels toebrengen. In het experiment in de proefboomgaard is daarom bekeken in welke periode rupsen schade aan appels toe-brengen. Hiervoor zijn op verschillende tijdstippen in het groeiseizoen alle rupsen van de betreffende appelbomen verwijderd (hoofdstuk 2). Dit experiment laat zien, dat naarmate rupsen langer op de boom blijven, er meer schade aan appels wordt toegebracht. De schade aan appels neemt toe vanaf het moment, waarop de appels gaan zetten, totdat de rupsen zich verpoppen. Deze resultaten tonen duidelijk aan, dat de vermindering van rupsenschade door koolmezen, het grootste zal zijn wanneer koolmezen de rupsen zo vroeg mogelijk in het seizoen verwijderen. Als gevolg hiervan zullen nesten, waarvan de eieren vroeg uitkomen ten opzichte van het verschijnen van de rupsen in de boomgaard, meer schade kunnen voorkomen dan nesten met eieren, die laat uitkomen (hoofdstuk 4). Koolmezen, die vroeg in het seizoen al jongen hebben, beginnen eerder met het zoeken en verwijderen van rupsen uit de boomgaard, waardoor rupsen minder tijd hebben schade toe te brengen aan het fruit. Daarnaast is het aandeel rupsen in het dieet van jonge koolmezen hoger in het begin van het groeiseizoen (hoofdstuk 5), waardoor er per nest waarschijnlijk meer rupsen verwijderd worden door koolmezen met vroeg uitgekomen jongen.

IPM en EKO boomgaarden

Dat koolmezen rupsenschade kunnen verminderen is aangetoond in een proefboomgaard met hoge rupsendichtheden. Deze dichtheden waren veel hoger dan de dichtheden, die in commerciële IPM en EKO boomgaarden gevonden zijn. De resterende rupsenschade aan appels was in de proefboomgaard, vanuit een economisch standpunt bekeken, te hoog. Om bij te dragen aan biologische bestrijding moeten koolmezen ook bij lagere rupsendichtheden schade aan appels kunnen verminderen. De bijdrage van koolmezen wordt met name belangrijk als de rupsendichtheid in de buurt ligt van de huidige spuitdrempel, dus het moment waarop de teler besluit om bestrijdingsmiddelen te gaan gebruiken.

Er is daarom ook bij bedrijven naar de vermindering van rupsenschade aan appels door koolmezen gekeken. In zowel IPM als EKO boomgaarden zijn 2 gelijkwaardige percelen van 2 ha uitgezocht. In één van deze 2 percelen zijn nestkasten opgehangen om koolmezen aan te trekken, het andere fungeerde als controle perceel. De fruittelers voerden hun normale werkzaamheden uit zonder beperkingen in de onderzoekspercelen. In de herfst is het percentage rupsenschade in de oogst bepaald op de percelen met en zonder broedende koolmezen. Op de percelen met broedende koolmezen was het percentage rupsenschade gemiddeld 25% lager, een vermindering van 6% naar 4.5% (hoofdstuk 4).

Theoretisch model

Er is zowel voor de hoge dichtheden in de experimentele boomgaard (hoofdstuk 2) als voor de lagere dichtheden in de IPM en EKO boomgaarden (hoofdstuk 4) aangetoond dat koolmezen rupsenschade kunnen verminderen. De informatie, die nog ontbreekt, is hoeveel rupsenschade koolmezen kunnen verminderen voor de tussenliggende dichtheden. Voorspellingen over de mate van schade vermindering voor deze tussenliggende dichtheden kunnen belangrijk worden, omdat rupsendichtheden in de toekomst wellicht gaan toenemen, doordat steeds meer insecticiden verboden worden (Anonymous, 2001). Daarnaast kan het schade percentage bij deze tussenliggende rupsendichtheden in de aanwezigheid van koolmezen resulteren in eenzelfde schade percentage in de oogst als bij lagere dichtheden zonder koolmezen. Wanneer dit het geval is, kan de huidige bestrijdingsdrempel in de aanwezigheid van koolmezen verhoogd worden. Omdat deze dichtheden niet voorkwamen tijdens de onderzoeksperiode is de vermindering van rupsenschade door koolmezen in een theoretisch model berekend (hoofdstuk 4).

Het model voorspelde hoeveel rupsen koolmezen verwijderen uit de boomgaard voor verschillende rupsendichtheden en koppelde deze gegevens aan de uiteindelijke schade in de appel-oogst. In het model werden verschillende waarden ingevoerd voor een aantal factoren, zodat het effect op de appelschade kon worden bepaald. De mate waarin rupsenschade verminderd werd, was met name afhankelijk van het aantal broedparen koolmezen en het moment waarop de jongen uit het ei kwamen (hoofdstuk 4). Meer broedparen in de boomgaard betekent dat er meer rupsen worden

verwijderd. De toename van het aantal verwijderde rupsen is niet in dezelfde verhouding als de toename van het aantal nesten, want koolmezen moeten steeds langer zoeken naarmate er meer rupsen uit de boomgaard verwijderd zijn. Als de jongen eerder uit het ei komen, zullen de koolmezen vroeger rupsen uit de boomgaard verwijderen. De periode, dat rupsen schade kunnen toebrengen aan appels, is daardoor korter. Daarnaast zijn de rupsen in het begin van het groeiseizoen kleiner. Koolmezen moeten dan meer rupsen aan de jongen voeren om in hun voedselbehoefte te voorzien.

Om in het model uit te kunnen rekenen hoeveel rupsen door koolmezen verwijderd worden, moeten een aantal factoren bekend zijn. Zo kon uit de literatuur worden gehaald wat de energie behoefte per dag is van koolmeesjongen. Ook kon worden berekend hoeveel meer energie een gemiddelde rups bevat bij elke mm die een rups in het seizoen groeit. Verder moest aangegeven worden hoeveel tijd een koolmees nodig heeft om een rups te vinden afhankelijk van de rupsendichtheid. Dit was nog niet eerder onderzocht en daarom is er een experiment uitgevoerd waarin de relatie tussen zoektijd en rupsendichtheid is bepaald (hoofdstuk 3).

Het experiment toonde aan dat de zoektijd, om één rups te vinden, toeneemt naarmate de dichtheid aan rupsen afneemt. Tevens is de toename in zoektijd sterker naarmate de begin-dichtheid verder afneemt, doordat er al rupsen zijn weggegeten. Dit wijst op een verschil in vindbaarheid van rupsen op een boom. De rupsen, die gemakkelijk te vinden zijn, worden als eerste weggegeten en daardoor neemt de zoektijd van koolmezen toe, naarmate er meer ruspen verwijderd zijn. Dit leidt tot de paradoxale situatie dat koolmezen eerder een rups kunnen vinden in een boom met een lage dichtheid die nog niet eerder door koolmezen is bezocht, dan in bomen met een hogere rupsendichtheid waar de gemakkelijk vindbare rupsen al zijn verwijderd.

Omdat zoektijd niet alleen bepaald wordt door de heersende rupsendichtheid in een boom, maar ook door het aantal rupsen dat al weggegeten is, zijn deze beide factoren in het model verwerkt.

Controle van het model met praktijk gegevens

Het model voorspelt dat de vermindering van rupsenschade hoofdzakelijk beïnvloed wordt door het aantal broedparen en het tijdstip waarop de jongen uit het ei komen. Daarom is er in hoofdstuk 5 gekeken of deze factoren ook bepalend zijn voor het aantal verwijderde rupsen in de praktijk situatie. Dit is een manier om de voorspellingen van het model te controleren, omdat het aantal verwijderde rupsen en het tijdstip waarop de rupsen verwijderd worden de mate van schade vermindering bepalen. Er is met video camera's bekeken hoeveel rupsen, ten opzichte van andere insekten, een paartje koolmezen aan hun jongen voeren. Vroeg in het seizoen werden er naar verhouding meer rupsen aan de jongen gevoerd. Later in het seizoen nam de verhouding rupsen in het dieet van de jongen af en werden er meer andere insekten gevoerd. Met tellers is gekeken hoe vaak per uur de koolmezen een prooi binnenbrengen. Door de jongen om de dag te wegen is bepaald hoeveel prooien de koolmezen binnengebracht moeten hebben om deze groei te bewerkstelligen. Met deze

gegevens hebben we niet aan kunnen tonen dat de vroege nesten meer rupsen naar het nest brachten dan de late nesten (zoals voorspeld door het model in hoofdstuk 4). Hierbij speelt mee dat het verschil in het uitkomen van de jongen tussen vroege en late nesten niet meer dan een week betrof. Daarnaast selecteren koolmezen in het begin van het seizoen rupsen die groter zijn dan de gemiddelde grootte van alle rupsen die in de boomgaard zijn. Hierdoor is het verschil in energie-opbrengst tussen de gevoerde rupsen vroeg en later in het broedseizoen waarschijnlijk kleiner dan verwacht.

Met behulp van deze gegevens is er wel aangetoond dat bij een gemiddelde dichtheid van 3 broedparen koolmezen per hectare in boomgaarden, 23 % van de rupsen uit de boomgaard werd verwijderd en dit percentage kan toenemen tot 49%, wanneer koolmezen alleen in de boomgaard en niet daarbuiten naar voedsel zouden zoeken.

Praktische toepassing

De resultaten uit dit onderzoek geven aan dat de huidige bestrijdingsdrempel voor rupsen verhoogd kan worden, wanneer er broedende koolmezen in de boomgaard aanwezig zijn. Zowel de gegevens, die zijn verzameld in de IPM en EKO boomgaarden, als de voorspellingen van het model geven aan dat voor gelijke rupsendichtheden de uiteindelijke rupsenschade in de oogst lager is als er koolmezen aanwezig zijn. Bij een vaste schadedrempel voor rupsen kunnen er in de aanwezigheid van koolmezen dus hogere dichtheden toegestaan worden voordat bespuitingen uitgevoerd dienen te worden.

Op dit moment wordt geadviseerd om rupsen te bestrijden als er voor de bloei meer dan 8 tot 10 rupsen per 100 bloemclusters gevonden worden. In 4 IPM en 4 EKO boomgaarden zijn in 1999 het aantal bloemclusters per boom geteld. Het gemiddeld aantal bloemknoppen per boom was 159 (s.d. $\pm$ 146). Dit betekent dat er op een gemiddelde boom 13 tot 16 rupsen gevonden kunnen worden, voordat er een bespuiting uitgevoerd hoeft te worden. Wanneer we uitgaan van een spuitdrempel van 14 rupsen per boom voor de bloei dan is de voorspelde schade door het model 5.1% (inclusief ruspenschade kleiner dan 0.25 cm^2) in afwezigheid van koolmezen. Echter, wanneer er een, twee of vier paartjes koolmezen in de boomgaard broeden, wordt dit schade percentage pas bereikt wanneer de begindichtheid van rupsen respectievelijk 16, 18 en 21 rupsen per boom bedraagt. Afhankelijk van het aantal broedparen en de uitkomst-datum van de jongen kan de spuitdrempel verhoogd worden met 2 to 7 rupsen per boom. De schade reductie van 25% (van 6% naar 4.5%) in IPM en EKO werd waargenomen met een gemiddeld aantal broedparen van 3.5 (SD$\pm$ 1.3) zonder dat de fruittelers hun normale bedrijfsvoering hebben aangepast in de onderzochte gebieden.

Fruittelers moeten vertrouwen hebben in de vermindering van rupsenschade door koolmezen, voordat zij koolmezen zullen opnemen in hun bedrijfsvoering. Wanneer zij overtuigd zijn van het feit, dat het verhogen van de bestrijdingsdrempel voor ruspen als er broedende koolmezen in de boomgaard voorkomen niet leidt tot een

verhoging van de rupsenschade aan de oogst, dan zullen zij hun bedrijfsvoering aanpassen en daarmee het gebruik van insecticiden verminderen. Met name omdat het ophangen van nestkasten (minimaal 2 per ha) een goedkope en arbeids-extensive maatregel is in vergelijking met het uitvoeren van bespuitingen.

Nawoord

Na vier en een half jaar is het dan zover, het proefschrift is klaar. Na het uitpuffen van de laatste stressvolle weken, is het ophalen van herinneringen begonnen. Er is veel gebeurd in deze afgelopen jaren, waarin ik een resultaat heb neer kunnen zetten, tegen de verwachting in van de sceptici op het NIOO. Mijn onderzoek heeft me veel over mezelf geleerd en ik heb ook zeker mijn grenzen leren kennen. Het is me duidelijk geworden dat je met hulp van anderen boven jezelf uit kunt stijgen.

Het project had niet kunnen bestaan zonder de medewerking van de fruittelers waar ik de afgelopen jaren meer of minder vaak de deur heb plat gelopen. Ze hebben me veel over de fruitteelt geleerd. Ik wil met name Harmen Peters, Henry Albers, Hans Poley en Wim Stoker bedanken voor hun gastvrijheid, de medewerking gedurende het hele onderzoek en het geduld om dit "broekkie" in de fruitteelt uitleg te geven over hun vak. Ook wil ik Jan van Erp, vader en zoon van de Bosch, Rob Janssen en Philip de Groen bedanken voor de toestemming voor een proef en het extra werk dat zij daarmee voor mij verricht hebben. Robin Kars, Rein Mantel, Wil Sturkenboom, Hans Damen, Jaap Flikweert, Louis Ruissen en Jack Stoop hebben het samen met de andere EKO bedrijven mogelijk gemaakt om in een jaar genoeg oogst-analyses te kunnen uitvoeren om de monstergrootte voor een goede uitspraak over het effect van koolmezen in productie boomgaarden over het kritieke minimum te tillen. Tenslotte wil ik dhr. van Ingen, dhr. van Beusichem en dhr. Lutterveld bedanken voor de mogelijkheid broed- en groeigegevens van koolmezen te verzamelen.

Naast de commerciële bedrijven hebben 2 proefboomgaarden, De Schuilenburg en de boomgaard van het vroegere fruitteelt praktijkonderzoek (FPO) in Randwijk, gezorgd voor de ideale onderzoeksfaciliteiten. Ik wil Leo en Herman hartelijk danken voor het geduld en de gesprekken, die me wegwijs hebben gemaakt in de appelteelt en het goede advies bij de opzet van proeven. Bart Heijne wil ik bedanken voor de mogelijkheid mijn onderzoek voort te zetten in Randwijk na de sluiting van de Schuilenburg. Veel dank ben ik aan Fredy verschuldigd, door jouw inzet zijn er bergen determinatiewerk verzet, kweken verzorgd, rupsen gezocht op hele bomen en ben ik niet wanhopig geworden tijdens het beoordelen van de duizenden appels tijdens alle oogstanalyses, die we in de loop der jaren samen gedaan hebben. Fredy je was en bent een juweeltje als vakman en collega.

Toen ik aan het project begon wist ik niet dat er in de loop der jaren meer dan 4.880 takken en 400 bomen afgezocht zouden worden naar rupsen, er 2.962 rupsen gedetermineerd moesten worden, er 8.200 bloemknoppen op buis werden gezet, er 73.634 appels zouden worden beoordeeld en tenminste 2.314 volgroeide wintervlindersrupsen zouden worden gekweekt, om over de uren video's uitwerken maar niet te spreken. Deze bult werk heb ik natuurlijk niet alleen kunnen verzetten. Toen ik in 1998 net voor het veldseizoen begon, heeft Connie me op de rails gezet en gehouden. Connie, ik heb van je droge humor tijdens ons veldwerk genoten. In de laatste anderhalf jaar kwam Leontien het project versterken. Het werk dat wij met zijn tweeën verzet hebben, doet me achteraf verbazen. Je inzet was formidabel. Tijdens de slopende oogstanalyses van 2000 hielden we elkaars motivatie om de beurt omhoog. Het woordje "gaaf" zal nooit meer hetzelfde zijn. Je vrolijke aard zorgde voor leven in

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CURRICULUM VITAE

Christine Michaela Maria Mols werd op 15 april 1971 in Tilburg geboren. Van 1983 tot 1989 bezocht zij het Mill Hill College te Goirle en behaalde haar Atheneum diploma in juni 1989. Aansluitend ging zij naar de Landbouwuniversiteit in Wageningen om biologie te studeren.

Het afstudeervak bij de vakgroep Natuurbeheer resulteerde in de scriptie: "Voedselkeuze en terreingebruik van Konik paarden in de winter". Via de vakgroep dieroecologie heeft zij op Oost Java in Indonesië onderzoek verricht naar de verspreiding van wilde zwijnen. In opdracht van de Koninklijke Nederlandse Jagers Vereniging (K.N.J.V). heeft zij een literatuurstudie verricht naar het Viraal Hemorragisch Syndroom bij konijnen en een beheersplan opgesteld voor de wildbeheereenheid de "Utrechtse en Gelderse Vallei". In maart 1996 studeerde zij af met de specialisatie populatie/oecosysteem.

Vervolgens heeft zij anderhalf jaar bij de leerstoelgroep Veevoeding gewerkt. Hier werd onderzoek verricht naar het gebruik van de alkanen in de waslaag van verschillende plantensoorten om dit als merker te gebruiken in de stofwisseling bij herbivoren. In april 1998 begon zij op het toenmalige Nederlands Instituut voor Oecologie (nu Ecologie) als Onderzoeker in Opleiding aan een promotie onderzoek dat door NWO-STW werd gesubsidieerd en waarvan de resultaten in dit proefschrift staan beschreven.