Journal of Applied Ecology 2002
39, 888–899

Great tits can reduce caterpillar damage in apple orchards

CHRISTEL M. M. MOLS and MARCEL E. VISSER
Netherlands Institute of Ecology (NIOO-KNAW), PO Box 40, 6666 ZG Heteren, the Netherlands

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 the 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 the autumn.
3. The longer the period of foraging by great tits, from the start of egg incubation until fledging of young, the less the overall pest 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 ($P < 0{\cdot}05$), and the yield of fruit increased significantly (from 4·7 to 7·8 kg apples per tree, $P < 0{\cdot}05$). 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 economic thresholds for other controls to be reduced. Furthermore, the contribution of natural predators to biological control of insect pests may be especially useful in orchards and in the future when a further reduction of pesticide use may be enforced.

Key-words: biological pest control, birds, damage reduction

Journal of Applied Ecology (2002) **39**, 888–899

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 (Tables 1 and 2; Kirk, Evenden & Mineau 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,

Correspondence: Ir C.M.M. Mols, Netherlands Institute of Ecology, Centre of Terrestrial Ecology, PO Box 40, 6666 ZG Heteren, the Netherlands (fax +31 26 4723227; e-mail c.mols@nioo.knaw.nl).

 Journal of Applied Ecology, **39**, 888–899

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 *c.* 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, Little & Crowe (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 corn-fields	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 density in corn rootworm	Tremblay, Mineau & Stewart (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, Schultz & Nothnagle (1979)
	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 understorey	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, Yoder & May (1999)
	Pine processionary caterpillar *Thaumetopoea pityocampa*	Hoopoes *Upupa epops*	– Removal of *c.* 70% of the pupae	Battisti, Bernardi & Ghiraldo (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	Tanhuanpää, Ruohomaki & Uuispaikka (2001)
(b) Leaf damage	Mainly larvae of geometrids, tortricids and sawflies on bilberry in five 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	Atlegrim (1989)
	Leaf-chewing insects in general in a forest dominated by white oak *Quercus alba*	Forest birds in general	– Removal of 63% of the larvae – Exclusion of birds increased leaf damage	Marquis & Whelan (1994)

especially when they are feeding their nestlings (Betts 1955; Gibb & Betts 1963; Royama 1966; van Balen 1973; Gruys 1982; Naef-Daenzer, Naef-Daenzer & Nager 2000). 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). 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. Together, these features suggest that great tits have the potential to contribute to the control of orchard 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 reduce caterpillar damage, by assessing the periods in which (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 great tits.

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 tits *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. Chaffinches, jays, chiffchaffs and willow warblers include caterpillars in their diet but numbers stay below 20% of the total diet. Only tree sparrows and blue tits are known to prey on caterpillars on leaves (Glutz von Blotzheim & Bauer 1997), but less than great tits and foraging mainly at the edges of the orchard near their nesting sites.

Four blocks were selected in the experiments: 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). 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 was never covered with nets. Great tits had access to the control trees during the whole period (i.e. the control group had 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 litre $tree^{-1}$. Caterpillars were never removed on a control group of 56 trees (i.e. the control group had Julian date 177 in the 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 randomized 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, Gruys & Vaal (1985). The other classes of caterpillar damage (July damage and late summer damage) can be distinguished easily from early spring damage, which is characterized 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 six 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 generalized 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 experiments 1 and 2. Individual trees were treated as data points in a generalized 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 GLIM).

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 percentage of apples with caterpillar damage. A generalized linear model with binomial errors was used with the number of apples per tree in June-drop

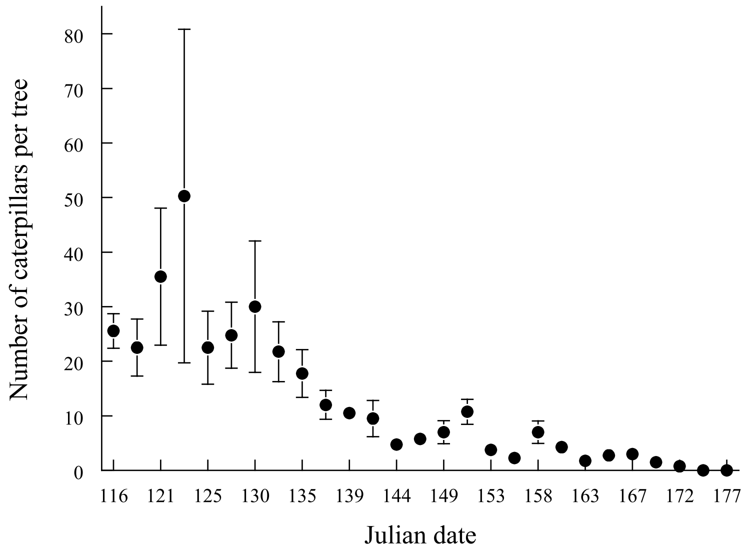

Fig. 1. Changes over time in the number of caterpillars on previously untreated trees of experiment 2 where caterpillars were removed from trees at different times during the growing season (i.e. 1 February is Julian date 32) in the experimental orchard the Schuilenburg. Each point is the average count from four trees, except for the first point which is based on 44 trees.

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 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 three 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 moths 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 (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, $F_{1,191} = 15·8$,

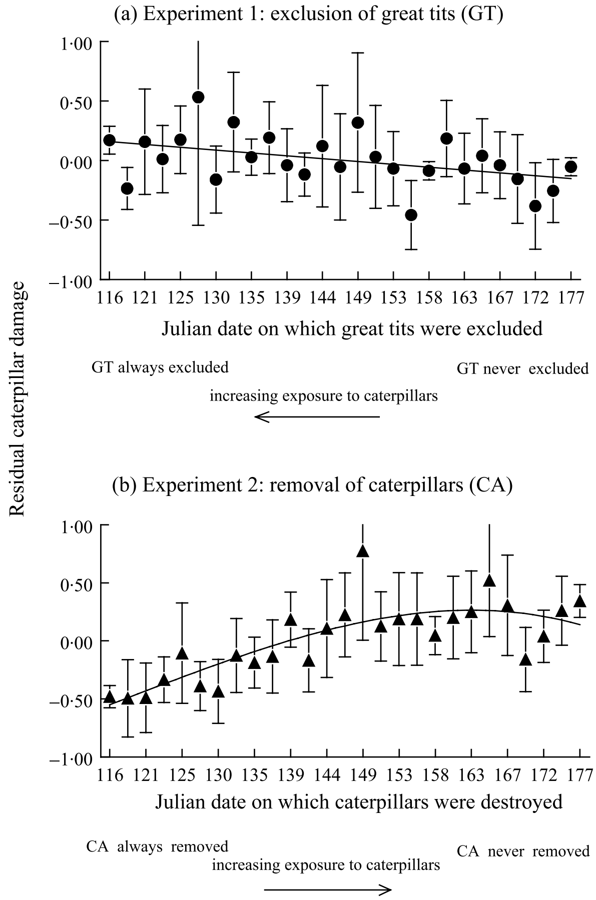

Fig. 2. (a) Experiment 1: caterpillar damage (± SE) as the residual from a model including block effect only as a result of a logistic regression of the proportion of apples per tree with caterpillar damage when great tits are excluded from trees, at different times during the growing season. A later Julian date for great tit 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. 1 February is Julian date 32).

$P < 0{\cdot}001$; date^2, $F_{1,191} = 12{\cdot}8$, $P < 0{\cdot}001$; Fig. 2b and Table 3). The percentage of caterpillar damage differed between the blocks ($F_{3,191} = 10{\cdot}8$, $P < 0{\cdot}001$), but the effect of treatment did not (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 ($F_{1,372} = 0{\cdot}73$, $P > 0{\cdot}39$). Thus the percentage of damaged apples among those harvested was not influenced by trees preferentially dropping damages 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 ($F_{1,192} = 2{\cdot}75$, $P = 0{\cdot}10$). The observed yield per tree increased from 4·65 kg (SE 0·59, $n = 44$), when great tits were excluded on Julian date 116, to 7·76 kg (SE 0·69, $n = 56$), 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 8·08 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

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. 1 February is Julian date 32) on which great tits were excluded from trees. A later Julian date means a shorter period of great tit 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

	Increase in deviance	Δ d.f.	*F*	*P*	Estimate	
Experiment 1						
Great tits excluded*						
Block	44·22	3	14·70	< 0·001	1†	−1·07
					2†	−1·42
					3†	−1·25
					4†	−1·81
Date	4·93	1	4·91	< 0·05		-3.7×10^{-3}
Experiment 2						
Caterpillars destroyed*						
Block	32·09	3	10·77	< 0·001	1†	−16·60
					2†	−17·11
					3†	−16·65
					4†	−17·30
Date	15·66	1	15·77	< 0·001		0·18
Date^2	12·45	1	12·75	< 0·001		-5.2×10^{-4}

*All interactions and variables that were not significant are not listed.
†Block number.

affects aphids, the level of aphid infestations was higher in the treatments where caterpillars were removed from the tree later in the season ($F_{1,193} = 5.42$, $P = 0.02$).

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 upon prey densities

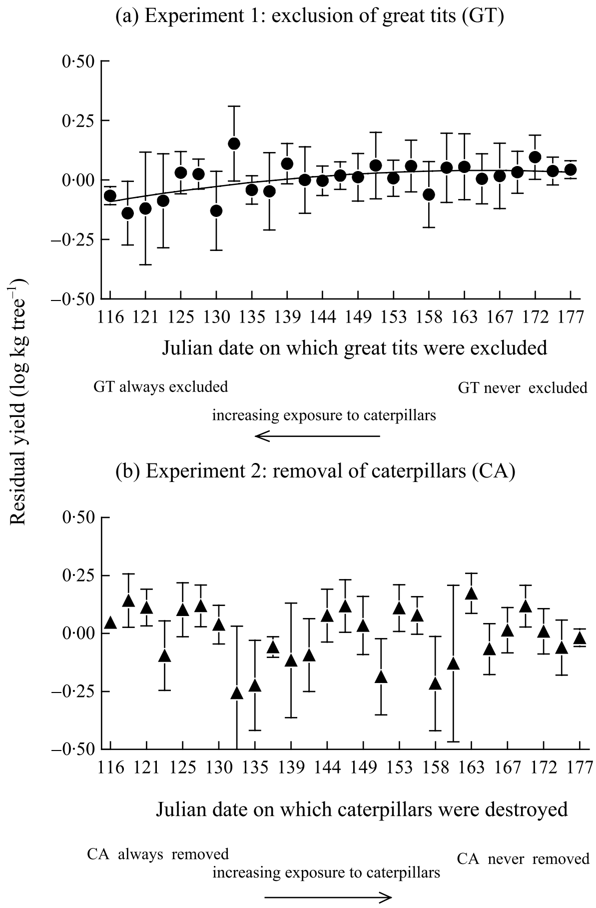

Fig. 3. (a) Experiment 1: biological (damaged and undamaged apples) yield (± SE) as the residual from a model including block effect and percentage of aphid infestation only as result of a regression of the logarithm of yield per tree when great tits are excluded from trees, at different times during the growing season. The residuals values are on a log scale because yield was log transformed. A later Julian date for great tit 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. 1 February is Julian date 32).

(Tables 1 and 2; Kirk, Evenden & Mineau 1996). Some of these other studies also concluded that birds become ineffective when densities are low (Tinbergen 1960) or above a threshold insect density (Otvos 1979 and references therein) 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 reduced.

The second experiment, together with the data on caterpillar abundance (Figs 1 and 2), showed 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; Tinbergen 1960; Gibb & Bett 1963). Naef-Daenzer, Naef-Daenzer & Nager (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 their time of appearance. At a given sample date a range of different caterpillar size classes was available to great tits, of which they prefered 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

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. 1 February is Julian date 32) on which great tits were excluded from trees. A later Julian date means a shorter period of great tit 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

	Experiment 1 great tits excluded from foraging on trees						Experiment 2 caterpillars destroyed					
Response variable	Variables in the model	Increase in deviance	Δ d.f.	*F*	*P*	Estimates	Variables in the model	Increase in deviance	Δ d.f.	*F*	*P*	Estimates
Yield*	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	$6{\cdot}9 \times 10^{-5}$	Intercept					0·83
	$Date^2$ × aphid	0·89	1	7·36	< 0·01	$1{\cdot}0 \times 10^{-5}$						
	Intercept					–1·35						
Weight per apple*	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† $9{\cdot}1 \times 10^{-5}$	Date × aphid	0·004	1	6·69	< 0·05	–0·012
						2† $13{\cdot}1 \times 10^{-5}$	$Date^2$ × aphid	0·005	1	7·86	< 0·01	$3{\cdot}6 \times 10^{-5}$
						3† $6{\cdot}9 \times 10^{-5}$	Intercept					0·12
						4† $11{\cdot}3 \times 10^{-5}$						
	Intercept					0·11						
Number of apples*	Block	8·14	3	5·47	< 0·01	1† 0·039	Block	8·32	3	4·50	< 0·05	1† 0·018
						2† 0·041						2† 0·012
						3† 0·042						3† 0·019
						4† 0·033						4[b] 0·012
	Date	6·29	1	12·68	< 0·001	$-1{\cdot}3 \times 10^{-4}$						
	Aphid	2·25	1	4·53	< 0·05	$-8{\cdot}4 \times 10^{-3}$						

*All interactions and variables that were not significant are not listed.
†Block number.

Journal of Applied Ecology, **39**, 888–899

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 can inflict the same damage as many small ones.

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 using 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.

Acknowledgements

We thank Fredy Vaal for his indispensable assistance with fieldwork, rearing and classifying caterpillars, and Leontien Witjes, Koen Pluis and Frank Mertens for assisting with the practical fieldwork. Without their help we could not have completed the study. We thank Kate Lessells, Arie van Noordwijk, Piet Drent, Leo Blommers and Herman Helsen for their comments on the manuscript and other advice. The Technology Foundation STW (code BBI. 3844), applied science division of NWO and the technology programme of the Ministry of Economic Affairs supported this research.

References

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

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

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.

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.

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

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

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.

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 Ecologists*. Blackwell Scientific Publications, Oxford, UK.

Cross, J.V., Solomon, M.G., Babandreier, D., Blommers, L., 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. II. Parasitoids. *Biocontrol Science and Technology*, **9**, 277–314.

Fleckinger, J. (1948) Les stades végétatifs des arbres fruitières en rapport avec les traitement. *Congrès pomologique de France*, pp. 81–93. Societè pomologique de France, Villefrance, France.

Fye, R.E. (1982) *The Birds and the Psyllas*. Agricultural Research No. 30. Agricultural Research Service, US Department of Agriculture, Washington, DC.

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. (1997) *Handbuch der Vögel Mittel-Europas*. Aula-Verlag, Wiesbaden, Germany.

Gradwohl, J. & Greenberg, R. (1982) The effect of a single species of avian predator on the arthropods 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.

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

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

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.

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

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

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.

Otvos, J. (1979) The effects of insectivorous bird activity in forest ecosystems: an evaluation. *The Role of Insectivorous Birds in Forest Ecosystems* (eds J. Dickson, R. Conner, R. Fleet, J. Jackson & J. Kroll), pp. 341–374. Academic Press, New York, NY.

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

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**, 263–274.

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

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

Solomon, M.E., Glen, D.M., Kendall, D.A. & Milsom, N.F. (1976) Predation of overwintering larvae of codling moth *Cydia pomonella* (L.) by birds. *Journal of Applied Ecology*, **13**, 341–352.

Solomon, M.G., Cross, J.V., Fitzgerald, J.D., Campbell, 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. III. Predators. *Biocontrol Science and Technology*, **10**, 91–128.

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

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.

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

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 *Philyctinus callosus* (Schönherr 1826), and their impact on other invertebrates in apple orchards in the Western Cape Province, South Africa. *Agriculture, Ecosystems and Environment*, **55**, 169–179.

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

Received 12 November 2001; final copy received 15 July 2002