Linking pesticide exposure and spatial dynamics: An individual-based model of wood mouse (*Apodemus sylvaticus*) populations in agricultural landscapes

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A B S T R A C T

The wood mouse is a common and abundant species in agricultural landscape and is a focal species in pesticide risk assessment. Empirical studies on the ecology of the wood mouse have provided sufficient information for the species to be modelled mechanistically. An individual-based model was constructed to explicitly represent the locations and movement patterns of individual mice. This together with the schedule of pesticide application allows prediction of the risk to the population from pesticide exposure. The model included life-history traits of wood mice as well as typical landscape dynamics in agricultural farmland in the UK. The model obtains a good fit to the available population data and is fit for risk assessment purposes. It can help identify spatio-temporal situations with the largest potential risk of exposure and enables extrapolation from individual-level endpoints to population-level effects. Largest risk of exposure to pesticides was found when good crop growth in the "sink" fields coincided with high "source" population densities in the hedgerows.

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1. Introduction

In Europe, wood mice (*Apodemus sylvaticus*) are used as a generic focal non-target species in regulatory risk assessments of pesticides (EFSA, 2009). They are the most widespread rodent in the UK and many other EU member states (Pelz, 1989; Johnson et al., 1992). They are omnivorous (Watts, 1968; Wolton, 1985) and can therefore easily adapt to various habitats. Other small mammals require more specific diets and habitats. Voles (*Microtus agrestis*), for example, are herbivores (Pollard and Relton, 1970), and shrews mainly feed on insects and earthworms (Rudge, 1967). Such species thus occur less commonly in cultivated crop fields (Barber et al., 2003). Moreover, wood mice construct extended burrow systems which allow them to spend their entire life cycle in crop fields (Loman, 1991). Consequently, wood mice are likely to be more exposed to and potentially affected by pesticides than other small rodents. In particular, since they prefer grains in their diet (Watts, 1968; Green, 1979; Tattersall and Macdonald, 2003), they can be at risk from seed treatment (Barber et al., 2003), which is a key challenge in risk assessment for birds and mammals.

In current pesticide risk assessment, the ratio of toxicity to exposure (TER) is used to quantify risk. Toxicity is quantified via lethal or harmful concentrations of the pesticide whereas exposure is quantified via the expected concentration in the field. The smaller the TER, the higher the risk, which can be caused by low lethal concentrations, high exposure, or a combination of both. Currently most risk assessment schemes focus on effects on individuals, but the protection goal in most regulations is the population (EFSA PPR, 2010; Streissl, 2010). How effects on individuals, usually determined in the laboratory, extrapolate to effects on population abundance, structure, distribution, and resilience is unknown. Therefore, population models are increasingly used for this extrapolation (Grimm et al., 2009; Galic et al., 2010; Schmolke et al., 2010; Thorbek et al., 2010).

However, so far most population models for pesticide risk assessments in terrestrial habitats do not sufficiently include the ecology and behaviour of organisms when they give estimates of exposure, which can easily lead to unrealistic or even incorrect assessments. Risk will be lower if non-target animals are not present in the field when pesticides are applied, simply because they will be less exposed. Risk will be higher if pesticides are applied at a time when there are more animals in the field. For robust risk assessments, it is therefore important to explicitly represent spatial and temporal variation in habitat type and quality as well

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as animals' spatial behaviour including habitat choice, response to conspecifics, and recolonisation of disturbed habitats. We here present such a model for wood mice.

Our model is partly derived from existing models of small mammals that were designed for pesticide risk assessment. Wang and Grimm (2007) developed an individual-based model of the common shrew with a special focus on the resource-driven home range dynamics and population regulation. The model was applied to hypothetical exposure scenarios to compare the sensitivity and relevance of different population-level metrics, or endpoints, or risk, for example population growth rate, abundance, extinction risk, and recovery time (Wang and Grimm, 2010). Topping et al. (2003) developed a very detailed individual-based model for voles in a typical agricultural landscape in Denmark, using the ALMaSS modelling framework. They showed that landscape characteristics and agricultural practice can have larger effects on population-level risk than differences in individual-level toxicity (see also Dalkvist et al., 2009). Loos et al. (2010) modelled a food web comprising three small rodents (wood mouse; common vole, *Microtus arvalis*; and European mole, *Talpa europea*) and a predator (little owl, *Athene noctua*) to assess the risk of multiple environmental stressors. Their model provided important insights, but food web models go beyond current risk assessment schemes of terrestrial organisms which focus on single species instead of communities.

Our model is, like the common shrew and vole model referred to above, individual-based, i.e. represents individual organisms, their life cycle, and their interaction with their habitat and conspecifics (Grimm and Railsback, 2005; Railsback and Grimm, 2012). We chose this model type because for realistic estimates of exposure we need to represent the exact location of individuals, using a not too coarse temporal resolution so that the spatial dynamics of mice and their surroundings are captured as well as the timing of pesticide exposures and other agricultural practices. To establish location, movement patterns among feeding and nesting sites are modelled in detail. The model uses basic ecological knowledge of wood mice available in the literature. It includes a stylised landscape with crop rotation. Since quantitative data on the spatial behaviour of wood mice are scarce, we use qualitative patterns to ensure biological realism. This has the consequence, though, that the model aims at qualitative, comparative risk assessments rather than precise, quantitative predictions.

In the following, we describe model design and evaluate the model by comparing its outputs with the existing relevant field data. To demonstrate the potential use of the model we consider the following questions: how are the population dynamics of the wood mouse in arable fields affected by (1) application patterns (where and when) of the pesticides, (2) landscape settings in the fields (e.g. rotation scheme) and (3) effects of agricultural practices?

2. Materials and methods

2.1. Species studied

The wood mouse is known as an opportunist and has a broad diet (Watts, 1968; Wolton, 1985). It can adapt to a wide variety of habitats including woodlands, arable fields, semi-natural grasslands, heath and semi-deserts (Green, 1979; Rogers and Gorman, 1995). It largely prefers to inhabit nest sites with well grown plants so as to get protection against predators such as owls, cats and foxes (Kikkawa, 1964; Wilson et al., 1993; Fitzgibbon, 1997; Jacob, 2008). It has a maximum life span of 18–20 months, but most mice do not survive till the second summer (Macdonald and Barrett, 2005). The breeding system is to a large extent promiscuous and generally reproduction is not limited by the number of male mice in the population (Tew and Macdonald, 1994). Female mice can produce up to six litters each year (generally 1–2 litters) (Corbet and Harris, 1996) and average litter size is 4–7, with peak in June–August (Corbet and Harris, 1996). The gestation period is usually 19–29 days (Ashby, 1967; Macdonald and Barrett, 2005). Newborn mice reach independence about three weeks after birth and become sexually mature two months after birth (Corbet and Harris, 1996).

2.2. Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual-based models (Grimm et al., 2006, 2010). The model is implemented in NetLogo 4.1 (Wilensky, 1999). The NetLogo implementation of the model is available in Supplementary package.

2.2.1. Purpose

The purpose of the model is to simulate population dynamics of the wood mouse in arable fields with a focus on spatial dynamics in order to obtain realistic estimates of exposure to pesticides.

2.2.2. Entities, state variables, and scales

The entities in the model are the spatial units (patches in NetLogo terminology) comprising the landscape and female wood mice. Additionally, the overall environment is characterised by whether or not mice are in the breeding season, which is the same for all mice.

Each patch in the landscape represents a square of 5 m × 5 m and is characterised by the following state variables: (1) *location* (*x*- and *y*-coordinate); (2) *habitat type*: hedgerows, spring barley, winter oil seed rape, winter wheat, potatoes, stubble (after harvest) and fallow (between rotations; Table 1). The seven habitat types differ in quality of vegetation cover as well as farming practices; (3) *rotation order*: determines current crop type in the rotation scheme; (4) *time and current farming activity* (Table 1), which brings different levels of physical disturbance to the mice and their burrow systems (see Supplementary materials for more details); (5) *habitat quality* (*plant cover*): Boolean, good when plant is higher than 30 cm and cover is larger than 50%; otherwise bad quality; (6) *status of burrow system*: Boolean, whether or not the patch has an existing burrow system. Mice prefer to use an existing burrow system than digging their own; Montgomery and Gurnell (1985) and (7) *host*: the mouse which owns the patch as part of its home range; a patch can be owned by more than one mouse.

In our model, only female wood mice are represented (justification see Section 2.1 Species studied). The female mice are distinguished into three life stages: infants, which are not weaned yet and dependent on their mother; juveniles, which are weaned and independent, but not yet sexually mature; and adult mice, which are sexually mature. Each individual mouse is characterised by: (1) *identity number*; (2) *age*; (3) *previous nest site*; (4) *current nest site*; (5) *position*: Boolean, whether or not at the current time step the mouse goes out of its normal home range to forage; (6) *potential home range*: the set of patches that can be potentially used by the mouse as home ranges. The home ranges of different mice can overlap; (7) *daily foraging sites* (*actual home range*): the set of patches that the mouse actually visits to forage within its potential home range plus the excursion sites (i.e. if a mouse visits any sites farther afield outside its normal home range area).

Adult females are also characterised by reproductive traits (values see Table 2): (1) *status of pregnancy*: Boolean, pregnant or not; (2) *status of lactation*: Boolean; (3) *litter size*; (4) *litters per year* and (5) *time of first reproduction*.

The model can represent any kind of landscape consisting of the habitat types described above, but in the simulations presented here, the landscape consists of four 10-ha crop fields and 5-m wide hedgerows surrounding the crop fields. The total size of the

Table 1
External file used to assign environment data to the four crop fields. e.g. in the spring barley field, after sowing on February 25, the crop experiences early-stage growing (February 25–May 04). Cover for wood mice is poor and so is habitat quality. After May 05, the crop is maturing and provides good cover; after harvest on August 10, the field becomes stubble, thus bad cover again. For simplicity, the model assumes 30 days in each month and 360 days every year. The last column visualises the landscape setting, how rotation is realised and in what order; numbers in the grey cells correspond to the rotation order in the 1st column.

| Rotation order	Start	Finish	Habitat/crop type	Habitat quality	Farming date	Farming practice	Year and rotation
1	01-January	24-February	Fallow	Bad	15-February	Plough	Year 1
	25-February	04-May	Spring barley	Bad	24-February	Harrow	
	05-May	10-August	Spring barley	Good	25-February	Sow	
	11-August	24-August	Stubble	Bad	10-August	Harvest	
	25-August	30-December	Winter rape	Bad	23-August	Cultivate	
	N.A.	N.A.	N.A.	N.A.	24-August	Harrow	
	N.A.	N.A.	N.A.	N.A.	25-August	Sow	
2	01-January	14-February	Winter rape	Bad	15-July	Harvest	Year 2
	15-February	15-July	Winter rape	Good	25-September	Cultivate	
	16-July	04-October	Stubble	Bad	04-October	Harrow	
	05-October	30-December	Winter wheat	Bad	05-October	Sow	
3	01-January	14-April	Winter wheat	Bad	25-August	Harvest	Year 3
	15-April	25-August	Winter wheat	Good	01-November	Cultivate	
	26-August	30-October	Stubble	Bad	N.A.	N.A.	
	01-November	30-December	Fallow	Bad	N.A.	N.A.	
4	01-January	04-April	Fallow	Bad	04-April	Plant	Year 4
	05-April	14-June	Potatoes	Bad	15-October	Dig	
	15-June	15-October	Potatoes	Good	N.A.	N.A.	
	16-October	30-December	Fallow	Bad	N.A.	N.A.	

landscape is therefore 41.41 ha, which was represented as 202×82 square patches. The spatial scale and settings are designed to represent a typical British farmland.

To avoid edge effects, the landscape is designed as a torus: the patches on the leftmost and the rightmost side of the landscape are direct neighbours, as well as the patches in the top and bottom row. A time step in the model corresponds to one day and the model can be run for a flexible number of years, however, in the following, the stabilised annual population dynamics will be of main interest.

2.2.3. Process overview and scheduling

Every time step, the processes below are executed in order (underlines denote submodels; overview see Fig. 1). Entities like patches and mice are processed in a randomised sequence, if not stated otherwise, and state variables are updated
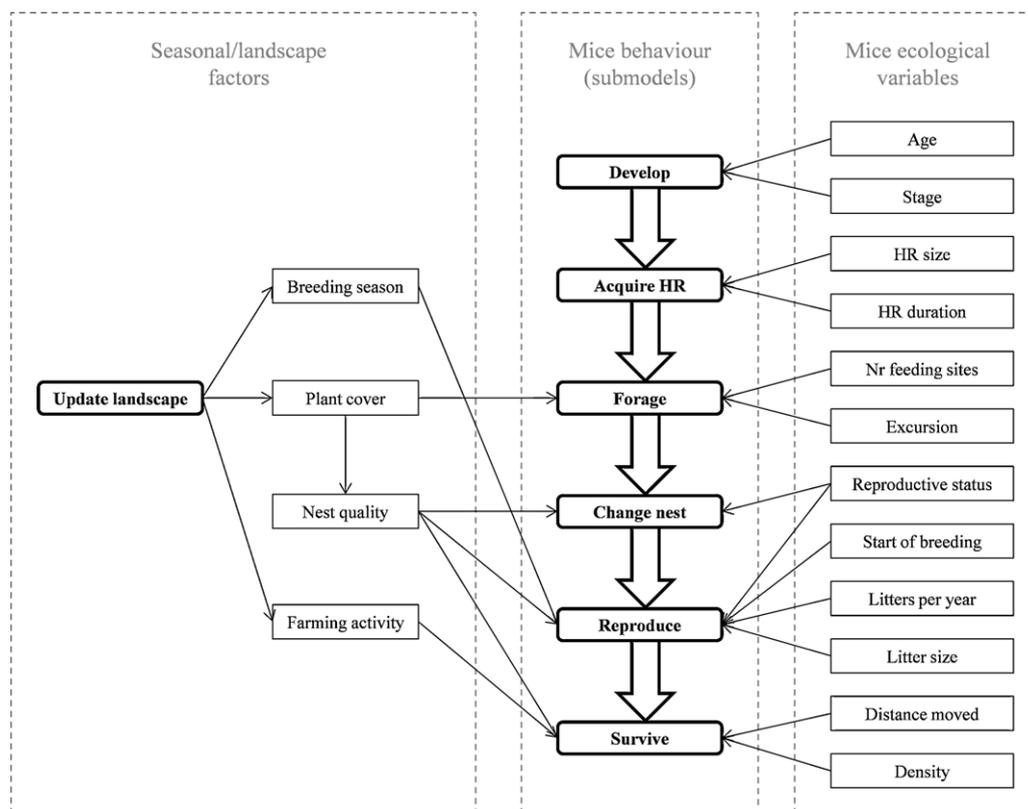
Fig. 1. Overview of model processes (bold boxes) and key variables (normal boxes). Fat arrows indicate the order of processes and thin arrows indicate influences. HR: home range; Nr: number.

Table 2
Key parameters, values and references.

Category	Name/meaning (notes)	Unit	Range/default value	Reference
Home range and feeding	Habitat quality (= plant cover)[a]		Good (when plant height $\geq$ 30 cm and cover $\geq$ 50%) Bad (when plant height < 30 cm or cover < 50%)	Ouin et al. (2000)
	Home range size	m^2	1424	Wolton (1985)
	Home range duration[b]	days	[10,30]	Wolton (1985)
	Nr-feeding-sites (daily)[c]		10 (breeding season) [3,5] (non-breeding season)	Jealott's Hill (unpublished data) Wolton (1985)
	Max nr of mice in one nest		1 (breeding season) 3 (non-breeding season)	Wolton (1985)
	Excursion-distance	m	>25 m	Wolton (1985)
	Daily excursion probability		2% (adults breeding season) 4% (juveniles breeding season) 5% (adults non-breeding season) 10% (juveniles non-breeding-season)	Wolton (1985)
Reproduction	Breeding-season[d]		[March, November]	Flowerdew and Tattersall (2008)
	Date of first reproduction[e]	day	[01-March, 30-April]	Tattersall and Macdonald (2003) Green (1979)
	Wean-age	day	20	Flowerdew and Tattersall (2008)
	Mature-age	day	60	Macdonald and Barrett (2005)
	Max litters-per-year[f]		6	Macdonald and Barrett (2005)
	Litter-size[g]		Base line 2 or 3, in June and July: +1, in August: +2	Flowerdew and Tattersall (2008), Macdonald and Barrett (2005) and Smyth (1966)
	Pregnancy-duration	days	25	Ashby (1967)
	Lactation-duration	days	20	
Survival	Age	days	[1,600]	Macdonald and Barrett (2005)
	$d = \Sigma c_i$: daily mortality rate:			
	c_1: increased mortality caused by movements in nest changing[h]		$0.001 \times$ distance	Calibrated
	c_2: increased mortality caused by excursion		0.05	Calibrated
	c_3: global density-dependent mortality[i]		When pop. size > 1600: 0.0006 per surplus mouse i.e. $0.0006 \times$ (pop size − 1600)	
	c_4: increased mortality caused by poor nest[j]		0.1	
	c_5: local density- dependent mortality for mice in different life stages[k]		During [February, May]: $0.005 \times$ local MICE pop size (for infants and juveniles) $0.005 \times$ local ADULT pop size (for adults) During other months: no density-dependent mortality	Macdonald and Barrett (2005)
	c_6: increased mortality caused by farming practices		0.04 (plough; dig) 0.02 (harrow; sow; cultivate; plant) 0.1 (harvest)	Calibrated Calibrated Tew and Macdonald (1993)

Notes:
[a] In this model, food abundance is not considered.
[b] Time duration of how long a home range remains the same.
[c] Dependent on active hours in different season.
[d] Typical breeding season is March–October, but sometimes can continue throughout the winter.
[e] Breeding females starts to appear in February/March time and all females are in reproductive status before May. Onset of breeding varies between years; therefore we assume there is no clear pattern for the time of first reproduction, thus a uniform distribution within the reported range of dates.
[f] Number of litters a mouse can produce during one year. Max of six successive pregnancies recorded in wild.
[g] Mean size 4–7, halved as only females are modelled. Litter size peaks in June–August. Winter litters are usually small.
[h] When a mouse moves longer than 50 m, otherwise $c_1 = 0$.
[i] See Section 2.2.3 for justification.
[j] Assume same as harvest effect.
[k] Density dependence is strong during population increase but is not acting during decrease. Spatial density-dependent female reproductive activity and territoriality limits the peak numbers. Local: within 50 m radius; infants and juveniles are not competent enough to affect adult survival, so adults only count other *adults* as density whilst infants and juveniles have to count *all* stage groups.

immediately after each action. If the population goes extinct, the model stops. Note that most spatial processes are mainly included to obtain realistic estimates of pesticide exposure, not for the purpose of investigating the mechanisms of home range behaviour. For details of how the processes are represented, see Section 2.2.7 submodels and the Supplementary materials.

Time and landscape are updated – Date and breeding season are updated; the landscape's patches update their habitat type, rotation order, habitat quality, farming activity and status of burrows.

Mice ageing/development – Mice age and change life stages. Weaned juveniles leave the parental nests.

Acquire home range – Every N days, with N being a random number between 10 and 30 (days), all adult and juvenile mice

re-acquire their home range, which is believed to remain stable within such time period (after Wolton, 1985). Note that this process is modelled phenomenologically, i.e. in order to reproduce the shape and size of home range reported by Wolton (1985).

Forage – Every day, adult and juvenile mice forage at selected sites with good cover within their home ranges; sometimes they forage further afield at excursion sites.

Go back home – Mice go back to their nests after foraging.

Change nest – When juveniles and non-lactating adults are in poorly covered nests (i.e. sites with bad habitat quality, see Section 2.2.2. Entities, state variables, and scales and Table 2), they move to better covered nests if available.

Reproduce – In breeding season, adult mice reproduce if they acquire good nest sites (i.e. with good habitat quality).

Survive – Individual-specific daily mortality rate (Table 2) is affected by a mouse's daily activity such as distance it moved, protection it got from the plant cover above its nest, disturbance by farming activities, and number of conspecifics in the local environment (local density dependence). At exceptionally high population density, all individuals have higher mortality (global density dependence) to represent factors such as disease or aggregation of predators.

2.2.4. Design concepts

2.2.4.1. Basic principles.
The key processes in the model are those that determine mice movement patterns and those that determine farming practices. Habitat selection strongly affects population dynamics of some small mammals (e.g. common shrew, Wang and Grimm, 2007). Wood mouse movement patterns are largely based on plant cover and food availability (Kikkawa, 1964; Montgomery and Dowie, 1993; Wilson et al., 1993; Fitzgibbon, 1997; Jacob, 2008). Food is assumed not to be limiting in the current model because hedgerows act as permanent habitat which save the mice from food shortage, especially in winter. To this end, only plant cover, which here equals to habitat quality (Table 2), is represented and food availability (or mouse energetics) is not included in this model (see Section 4 for justification). Plant cover in the fields is modelled based on the standard agronomic phenological development stages of the crops (following the "BBCH code", Hess et al., 1997). Rotation scheme and farming activities are modelled according to farming practices in the UK.

2.2.4.2. Emergence.
Population dynamics, stage/age structure, and spatial distribution emerge from the individuals' behaviour and interactions with other mice and the dynamic landscape. When the pesticide scenarios are introduced, the individuals' exposure emerges from their distribution and movement.

2.2.4.3. Adaptation.
There is implicit adaptation in the way that mice always try to nest and forage in places with good cover, which optimises survival. The mice also avoid being in crowded sites, which minimises competition.

2.2.4.4. Prediction.
There is indirect prediction that plant cover is related with predation risk (mortality rate).

2.2.4.5. Sensing.
Mice can sense (1) the habitat quality (plant cover) of the environment within their home ranges, but they cannot sense the quality of excursion sites before they actually visit them (Wolton, 1985), (2) the presence of other mice in the local environment or in the potential nest site and (3) presence of infant offspring in the nest.

2.2.4.6. Interaction.
Mice avoid nesting or foraging in crowded sites with consequent local density-dependent mortality.

2.2.4.7. Stochasticity.
In order to identify the forces driving the population dynamics, stochasticity is reduced to a reasonable minimum wherever possible. Habitat quality is modelled deterministically. Biological features of the mice such as maximum life span, gestation and lactation duration are set to constant values. Reproductive stochasticity in terms of litter size and time of first reproduction are drawn from certain random distributions. When a mouse makes a spatial choice, if there are more suitable sites than are needed, it chooses randomly. Environmental fluctuations such as in weather and climate are not included.

2.2.4.8. Collectives.
Patches that belong to the same individual mouse are grouped to aid exposure assessments.

2.2.4.9. Observation.
The distribution of utilised home range/nest sites and movement patterns can be observed from the model. The movement routes of individuals can be tracked. Other features observed are listed under Section 2.2.4.2.

2.2.5. Initialisation

The start date in the model is 1st January. We used the complete rotation scheme "four crops in four fields" for all simulations underlying the results, but also used simpler schemes for model testing (see Supplementary materials). The landscape is initially set as four crop fields surrounded by hedgerows. Crop information is read from an external file (the crop files need to be saved in a same folder as the NetLogo model for the model to run correctly).

On 1st January, habitat quality in the crop fields is generally poor whilst hedgerows remain permanent good habitat with good plant cover and no rotation or farming. So the model is initiated with 30 nests in hedgerows, each hosting two mature mice (in January, the population comprises only mature adults). Except for the initial nest sites, there is no existing burrow system.

2.2.6. Input data

The scheme for crop rotation is read from external files (Table 1). Four different schemes were available (also see Supplementary materials).

2.2.7. Submodels

For reasons of space limitation, we here only provide factual descriptions of the processes which are essential for understanding the movement patterns that determine exposure to pesticides. For a detailed description of all processes, including the submodels' rationale and biological justifications, see Supplementary materials.

2.2.7.1. Define-home-range.
Infant mice stay within parental nests and do not have home ranges. For juvenile and adult mice, if an individual's home range is out of date according to the 10–30 day stable period, it acquires a new one according to the algorithm in Fig. 2. It starts with the nest site and moves to each of the eight patches surrounding the nest in a random sequence and assigns them to its home range. When it reaches the last square it repeats the process until it has acquired 57 patches, i.e. a home range of 1425 m^2. If at any point it owns all eight neighbouring patches, it jumps for once a maximum of three patches to reach a patch it does not own and then continues as before. In such way, a home range of random but not extreme shape is created and most patches within the range are connected with others. The movements in this submodel are only "pseudo" and do not reflect real movement; neither do they affect the calculation of daily mortality rates. Not all patches in the home range are actually visited, only those selected as foraging sites are (see "forage" below). A mouse does not check whether other individuals own the patches, so home ranges can overlap.
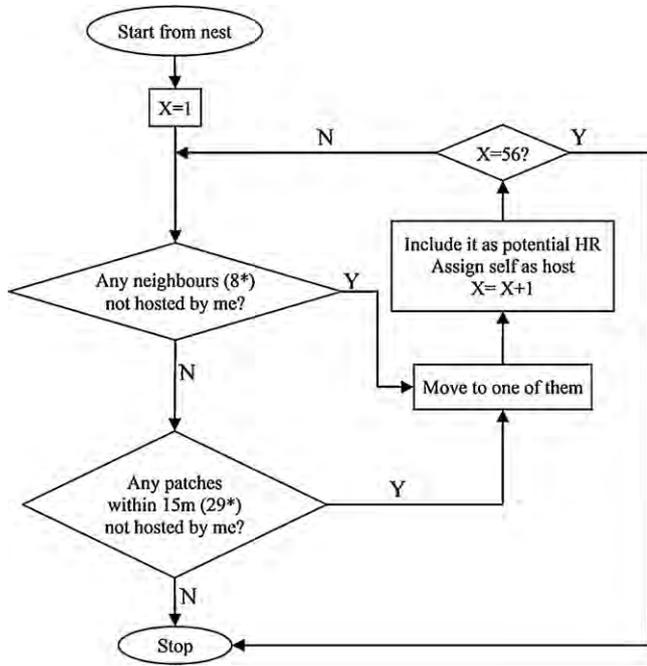
Fig. 2. Flow chart of how a mouse defines its potential home range (HR) in the model (for details see Section 2.2.7). *In the grid settings in the model landscapes, each patch has eight immediate neighbours and 29 neighbouring patches within a distance of three patches (15 m). "X" is used for the counting of repeating times until a mouse has acquire a home range of 1425 m².

This submodel is motivated by observations of Wolton (1985) who distinguished between home range (after Burt, 1943) and occasional excursion sites. Home ranges of female wood mice showed slight overlap but no consistent shapes were identified, nor did location of nests within home ranges show any clear patterns (Wolton, 1985). Based on Wolton's study (1985), we assume home ranges of the wood mice remain relatively constant within each 10–30 days' period.

In our model, a potential home range is a group of local patches of which the wood mouse has good knowledge, and from which it selects foraging sites.

2.2.7.2. Forage (choose-feeding-sites). Each juvenile and adult chooses a certain number (see Table 2) of places (preferably with
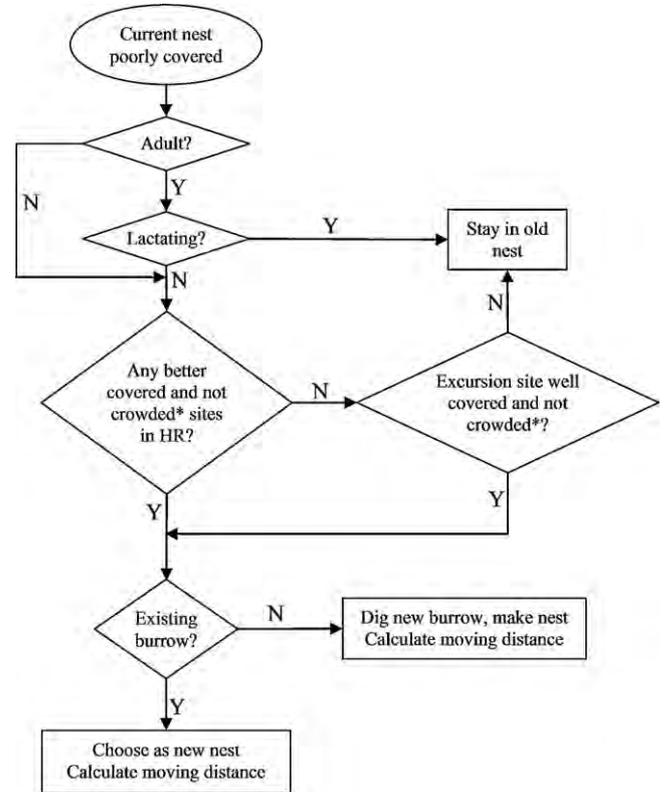
Fig. 4. Flow chart of how an individual changes nest sites. HR: home range. *In breeding season mice have exclusive nests and in non-breeding season up to three individuals can share one nest.

good plant cover) from its home range as foraging sites using the algorithm in Fig. 3. In addition, they will occasionally visit excursion sites outside the home range. Each mouse keeps a record of all the foraging sites it has ever chosen so that the time spent in different habitats can be tracked and exposure can be assessed.

2.2.7.3. Change-nest. When juveniles and non-lactating adults are in poorly covered nests and other sites with better quality (preferably with existing burrows) are available within their home range or excursion sites, they change to one of these better nest sites using the algorithm in Fig. 4. The distance between the new nest
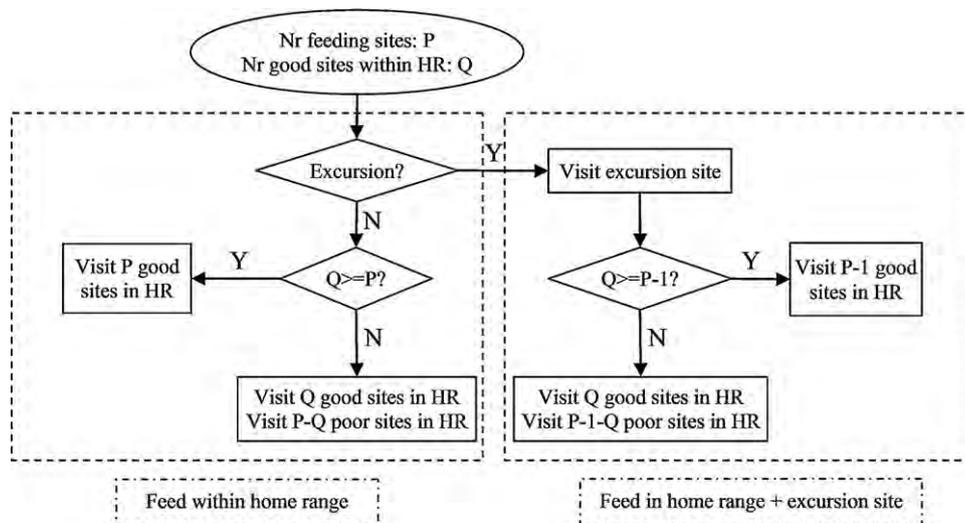
Fig. 3. Flow chart of how adult and juvenile mice choose foraging sites from potential home range (HR). Whether a mouse goes on excursion is dependent on the excursion probability. For an individual mouse in the breeding season P = 10; in the non-breeding season P = 3–5 (see Table 2).

and the old one is calculated and used in the calculation of daily mortality rate (see Section 2.2.7.4). If a mature mouse is in breeding condition, reproduction takes place in the new nest. If there are not any qualified new sites (Fig. 4), the mouse has to stay in the poor one and consequently will have a higher daily mortality rate. In our model each mouse always has a nest site, be it good or bad.

2.2.7.4. Survive. Daily survival is determined by a Bernoulli process with the daily mortality rate for each mouse calculated as a result of the six processes listed in Table 2, assumed to act independently, so the total is the sum of the component mortality rates. Two of the processes result from movement, it being known that the longer a wood mouse moves, the higher the predation risk (Tew and Macdonald, 1993; Ouin et al., 2000). The density-dependent processes could be the result of competition for resources such as food, mating partners or space (Begon et al., 2006). Farming activities are also known to kill wood mice in arable landscapes (Tew and Macdonald, 1993). When a lactating mother dies her dependent offspring also die.

2.3. Model testing and simulations

The model has been thoroughly tested and sensitivity analyses have been conducted (both documented in Supplementary materials). The population reaches a stable structure after four to eight years; accordingly, all analyses reported are based on model years 9–12. All simulations were conducted with 15 replicates (details see Supplementary materials).

2.4. Validation

We conducted pattern-oriented validation (Railsback and Grimm, 2012) on three separate patterns: population dynamics, habitat usage and proportion breeding. The population dynamics with default parameter values and no pesticide exposure were compared with data from field experiments (Green, 1979; Wilson et al., 1993), where the traps were located in the middle of the field and new born and young mice were not heavy enough to be caught in the traps (Green, 1979). So in the comparisons we only used model adult mice appearing in the crop fields. Todd et al. (2000) studied habitat use of wood mouse in an agricultural area with winter rape, winter barley and winter wheat fields surrounded by hedgerows. Accordingly, the model landscape was modified to three fields and hedgerows (Table S4 in Supplementary materials) for comparison. We also compared the proportion of the populations that was breeding in the model with observations from field studies of Elton et al. (1931) and Tattersall et al. (2004). We used the following criteria for comparing model outputs with field data: since the model does not include environmental variation across years, we looked for general patterns in peak to trough, overall levels and seasonal differences rather than precise matches.

2.5. Model application: predicting potential exposure to pesticides

The greatest risk of exposure to pesticides comes from wood mice foraging in fields during or shortly after pesticide treatment. Therefore, we calculated the proportion of different habitat types in the foraging sites (PF) over the year. First, we did the analysis excluding mice that only foraged in the hedgerows in order to match current guidance (EFSA, 2009) and get protective (conservative) estimates. Next, all mice in the population were included in the analysis to explore how such skewed sampling may affect the PF.
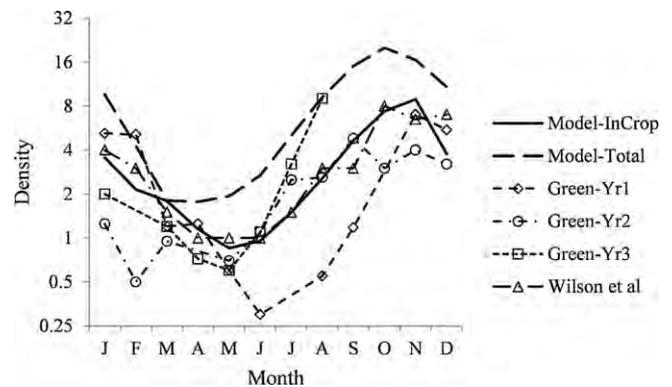

Fig. 5. Density index (number of mice per *ha*): model output (both the "in crop" population and the total including hedgerow population are shown) compared with field data reported from the literature (after Green, 1979; Wilson et al., 1993).

3. Results

3.1. Validation results

3.1.1. Population dynamics and seasonal pattern

Using the default settings, the model predicted densities and seasonal population dynamics similar to field data (Fig. 5, "Model-InCrop", i.e. the subpopulation which make use of crop field as either foraging or nesting site), with the population starting to increase in early summer, peaking in autumn and decreasing over winter (Miller, 1958; Ashby, 1967; Green, 1979; Bengtson et al., 1989; Wilson et al., 1993). In the model, the total population contained many more individuals and started increasing earlier than the crop population, which was mainly caused by the "hedgerow population", as shown in the comparison with "InCrop" population in Fig. 5. Later when mouse density in the hedge reached higher levels, flow from this source population (hedge) started to colonise sinks in the fields. This matches well with the conclusion by Barber et al. (2003) about the importance of hedgerow habitats and the fact that the majority (>60%) of the population rarely visit crop fields. The model does not reflect the differences between years seen in the field studies (Green, 1979; Wilson et al., 1993) but this is because it did not include variation in weather and other environmental conditions. In all settings, the model produced long-term stable population dynamics (i.e. variation of annual population size < 5% in different years) over 200 years.

#### 3.1.2. Home range and habitat usage

The shape and size of actual home ranges (foraging sites) in the model were similar to field tracking results (Fig. 6). The model mice preferred hedgerows in winter, whilst in summer all habitat types were more evenly used, with preference for wheat (Fig. 7), consistent with reported habitat preferences (Todd et al., 2000). They have found a higher preference for winter rape than what was predicted by our model, however, they assume such exceptional preference in that particular year to be caused by specific study conditions (more cover and higher food availability than usual) thus not a general pattern (Todd et al., 2000).

#### 3.1.3. Proportion of breeding individuals

Both the proportion of pregnant mice and the proportion breeding showed a good fit with field studies (Fig. 8).

3.2. Sensitivity

Overall the model was robust to changes in mortality related parameters, but sensitive to changes in parameters related to reproduction (see Supplementary materials).
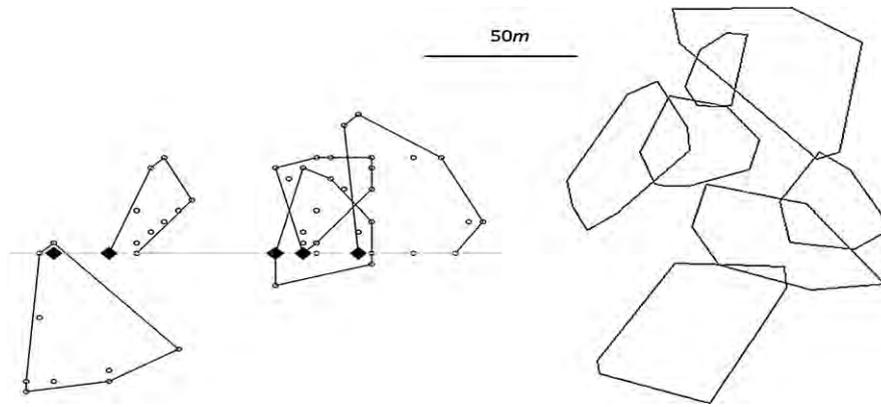
Fig. 6. Left: minimum convex polygons (MCPs) of the home ranges of five female mice in the model. The grey line denotes the hedgerow, winter rape field to the north and winter wheat field to the south; hollow dots denote actual foraging sites and solid diamonds denote nest sites. Right: home range distribution of seven female wood mice in a field study (after Wolton, 1985).
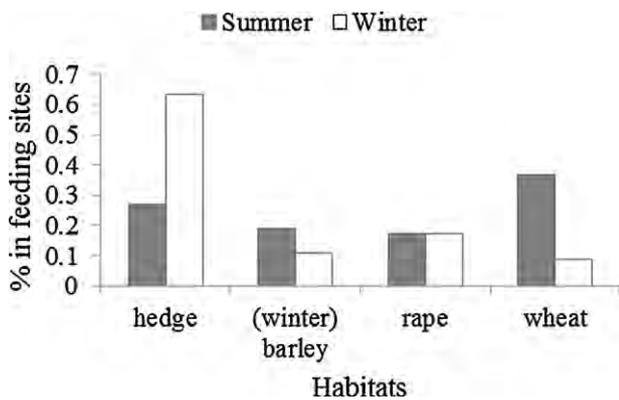
Fig. 7. Predicted proportion of different habitats in the foraging sites of adult wood mice from the model in summer (June–August) and winter (November–March).

3.3. Spatial distribution and exposure

Because the spatial choice of each mouse is explicitly modelled, the model can predict potential exposure to pesticides. By assuming diet obtained from treated areas is related to the proportion of such habitat in the foraging sites (PF), Fig. 9 gives quantitative predictions of PF and potential exposure in each of the four crops (with hedgerow as reference) throughout the year, indicating that the relative preferences for the different habitats change across the year, e.g. in August PF is lower in oil seed rape and barley than in wheat and potatoes. In winter, PF is much higher in hedgerows than in any of the crops, whereas in summer PF is higher in crops. Thus, overall exposure is potentially higher after summer than after winter applications, but there are differences between the individual crops (Fig. 9).

3.4. Farming and rotation effects

Including direct (i.e. mortality) and indirect (e.g. destruction of burrows) effects of mechanical farming activities such as ploughing leads to a reduction of overall population size by 5%. For the individual crops farming activities significantly reduced the number of nests in wheat, barley and oil seed rape (Table 3).

When running the model with the most realistic full rotation scheme (Table 1) but without hedgerows, which was the only off-crop habitat in our extreme landscape, the population went extinct (data not presented). In the presence of hedgerows, the type of rotation scheme had some impact on the overall population density. The lowest densities were found in mono-cultures of winter wheat (Table 4, scenario I) and the highest were found when there were four crops in the landscape but no rotation (Table 4, scenario II). The most realistic scheme gave intermediate densities (Table 4, scenario IV).

4. Discussion

Overall the model achieved a good fit to the data available from the literature (Figs. 5 and 6), and predictions of habitat use also accord well with available data (Figs. 7 and 9). The model represented phenomenological movements, life-history traits and
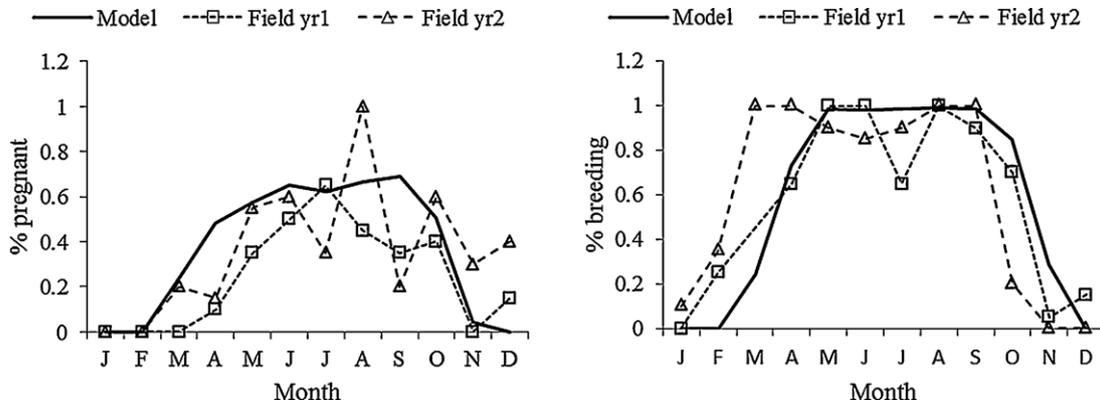
Fig. 8. Comparison of model output and field data. Left: proportion of pregnant mice in adults, field data from Elton et al. (1931); right: proportion of mice in breeding status (i.e. pregnant or lactating) in adults, field data from Tattersall et al. (2004).

Table 3
Number of nests in each habitat depending on effects of farming activities destroying burrows (BUR) and killing mice (KILL). Annual sums of daily numbers are presented. WW, winter wheat; SB, spring barley; OSR, winter rape; PO, potatoes. Fallow and stubble are phases outside crop growth, therefore are not of interest here.

BUR	KILL	Cumulative number of nests in each habitat				
		WW	SB	OSR	PO	Hedge
On	On	217	11	184	31,583	339,565
On	Off	172	8	171	32,101	340,975
Off	On	9291	3399	4972	23,349	354,586
Off	Off	9211	3366	5146	22,697	358,594

Table 4
Average population size in different rotation schemes, for details see: scenario I (no rotation, winter wheat in all fields) – Table S1; scenario II (no rotation, four different crops) – Table S2; scenario III (four-year rotation, same crop on all fields at a time) – Table S3 and scenario IV (full four-year rotation) – Table 1. (Tables S1–S3 are in Supplementary materials).

Scenarios	Average population size
I	283
II	338
III	297
IV	334

the landscape in detail, but food availability was not represented explicitly. Despite this lack the model provides credible population predictions including reported daily spatial distribution of individuals (Figs. 6, 7 and 9), and can thus identify individuals at risk of exposure to pesticides, whether the route is oral or dermal. In so doing it fulfils the purpose for which it was designed (Schmolke et al., 2010). Similar approach of estimating exposure based on individual spatial patterns has been proved to be useful in a conceptual framework in personalised exposure assessments of farmworkers (Leyk et al., 2009).

Food availability or territoriality have been included as drivers for home range choices in other models of small mammals that can be used for risk assessment purposes: in the ALMaSS vole model of Topping et al. (2003), habitat quality is assessed based on crop cover and height, number of mates and the level of territory overlap, scaled by the local population density; as a result, the population dynamics is significantly influenced by changing landscape structure and management. In the common shrew model of Wang and Grimm (2007), a dynamic home range results from food resources and the presence of other individuals; home range size, habitat preference, dispersal and finally the population dynamics are thus related through habitat productivity and density-dependence. We believe changes in food availability are broadly synchronised with plant cover, especially for green plant materials, which may explain why our model generally performs well without

implementing food explicitly, though there are cases such as when unusually high seed availabilities attract more mice whereas the model under-predicted foraging in winter rape (see Table 1 in Todd et al., 2000). However, since the purpose of the study is to support pesticide risk assessment with a generic model in a worst-case landscape, it is the model's ability to capture general trends rather than special conditions (e.g. weather) that matters. This also holds for the prediction of population dynamics and timing of breeding (Figs. 5 and 8): the model captures the general patterns well, but not the differences between years (e.g. Green data year 1–3 in Fig. 5).

Analyses of the model showed that the potential for exposure to pesticides is mainly driven by two factors: crop cover and density of the wood mice in the hedgerows. Hence, when the increase in density and the search for new habitats coincide with sufficient plant cover in the crops, the risk of exposure increases. It is mainly the populations overflowing from off-crop habitat to the arable fields that are potentially at risk to pesticides. The simulations therefore indicated that landscape structure may be important not only in terms of source-sink dynamics (Tattersall et al., 2004) between undisturbed habitats and arable fields, but also in terms of the overall population size in landscapes of different structure. For instance, when there were no off-crop habitats (e.g. hedgerows) in the landscape, there was no risk of exposure to pesticides simply because the population had gone extinct even in the absence of pesticide applications. In this sense, we arrive at the paradoxical conclusion that when the probability of extinction is decreased, by adding hedgerows, the risk of exposure to pesticides actually increases. Exposure and changes in landscape structure thus have to be considered together. The model focused on identifying the subgroups of the population that are potentially at risk, with a conservative assumption about food intake. To calculate the real exposure in these individuals, the amount of food consumed and the concentration of pesticide on different food items need to be taken into account. The latter is likely to have an inverse relationship with plant cover if contamination of insects and seeds is considered. This is another reason why a future model version, which considers the
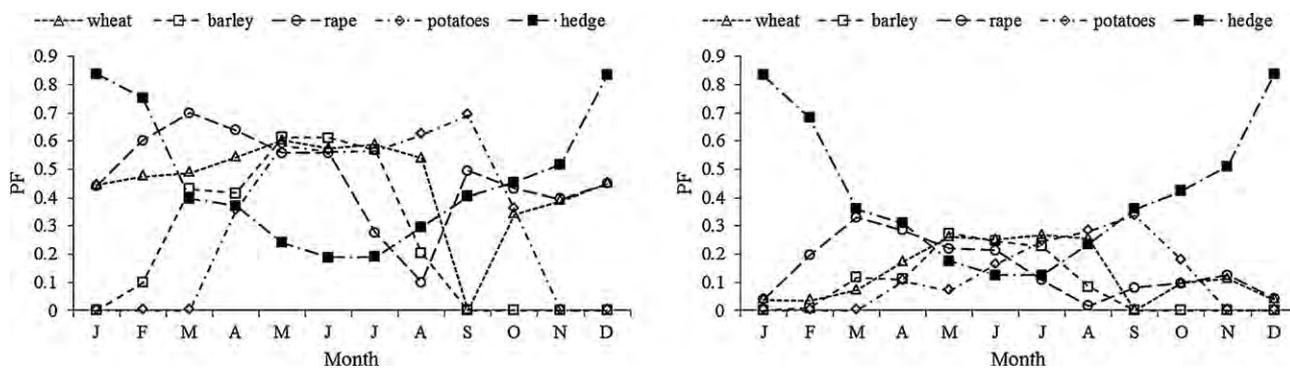
Fig. 9. Seasonal variation of proportion of different habitats in foraging sites (PF) including burrow (nest) sites for "consumers" (left) and the whole population (right). In the left panel, PF is calculated by averaging over the individuals that have visited the type of habitat in question (the so-called "consumers") at the current time step; this implies looking at different sample sizes depending on habitat type, thus PFs do not add up to 1; in the right panel, the whole population including those that have only stayed in hedgerows and never visited crop fields are included, thus PFs add up to 1.

wood mouse food directly, would be desirable, but this will require collecting new data in targeted experiments.

Rotation scheme also had some influence on overall population density: generally a diverse landscape benefits the mice more than mono-cultures, because different crops are preferred at different times of the year. Similarly, Topping et al. (2003) demonstrated that landscape structure, together with weather, farming activities and vegetation growth strongly affects the population dynamics of the field voles. Nevertheless, the more heterogeneous the landscape, the fewer voles in the population (Topping et al., 2003). This is because field voles are habitat-specialists in nature whilst wood mice are opportunists.

When we first compared our model output to field data, we found that the model over-predicted winter densities. However, a closer inspection disclosed that it was mainly an artefact of the field trials trapping in the arable field and us using the model outputs from the whole landscape including hedgerows, where most mice will spend the winter. When we corrected for this by looking at mice simulated in the fields, the fit was much better (Fig. 5). This addresses the importance of "comparing like with like" in model evaluations. Another issue comes from the focus and design of field studies. The studies to assess proportion of time spent in treated crops (PT) for use in regulatory risk assessments are required to follow mice that spend time in the relevant crop fields, referred to as "consumers" and hence these studies focus on a highly skewed sample of the population. In the case of studies in cereals, wood mice showed slight avoidance of cereal fields and were more attracted by the surrounding habitats (e.g. wood/forest and hedgerows) despite the fact that the study fields had minimum cultivation (i.e. no ploughing) to improve attractiveness to mice (unpublished data). So existing studies of PT are not ideal for model validation, better would be population data from a larger landscape. It would be interesting to see whether unbiased tracking/trapping data would lead to improved fits with the model.

This model can be used in risk assessments in two ways. It can be used to indicate situations that are likely to be more at risk, where field studies focusing on particular seasons (e.g. typical sensitive time window) and crop types/landscape settings will be most important. The model can also be used to refine risk assessments by predicting population level effects. Using the simplistic assumption that time spent in different crops is proportional to the composition of habitats in the foraging sites, the model can predict how much of a mouse's diet comes from the treated areas, so if pesticide residue concentrations are known or can be estimated, the model can predict the daily dose for each mouse. It is worth noting that in our PF analyses (Fig. 9), we included the time spent in burrow (nest) as well as foraging sites, which is slightly different with PT which focuses on active foraging time only. Ideally other food types such as invertebrates or weed seed should also be taken into account for a realistic diet composition, but for reasons explained above, food was not explicitly implemented in our model. By combining the daily diet estimates with knowledge of the ecotoxicological profile (e.g. dose–response curve, LD_{50}, NOEC, etc.) of the pesticide in question, the effect on each individual can be calculated. The model can then be used to test a range of endpoints such as survival, time for first reproduction, litter size, etc., potentially combined with other stressors such as mechanical farming activities, and finally predict whether observed individual-level effects have implications at the population level regarding population size, density, structure or time to recovery.

To conclude, our model represents natural population dynamics and spatial locations of wood mice with sufficient realism to be useful for the evaluation of relative impact by farming activities including pesticide use. The level of flexibility and model performance provide a good match with the purpose of the model: to link spatial dynamics of arable wood mice to the potential level of exposure to pesticides in risk assessments. The model helps identify conditions (i.e. landscape settings) and stressors (e.g. tillage, pesticide use) in treated fields and the surrounding environment which pose risks to wood mice populations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2012.09.016.

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