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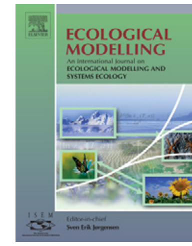

Home range dynamics and population regulation: An individual-based model of the common shrew *Sorex araneus*

Magnus Wang[a,*], *Volker Grimm*[b,1]

[a] *RIFCon GmbH, Breslauer Str. 7, 69493 Hirschberg, Germany*
[b] *UFZ, Helmholtz Centre for Environmental Research – UFZ, Department of Ecological Modelling, Permoserstr. 15, 04318 Leipzig, Germany*

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ABSTRACT

Many territorial animals show marked home range dynamics. Depending on food resources and the presence of other individuals, the size, shape and location of home ranges can change even on short time scales. Home range dynamics are thus likely to be an important aspect of population regulation. Most existing models, however, assume static home ranges. We therefore present an individual-based model that describes home range dynamics on a daily time scale. As an example organism, we focus on the common shrew (*Sorex araneus*), which shows a marked territorial behaviour. The proximate purpose of the model is to capture the relation between home range dynamics and population dynamics. The ultimate purpose is to develop a model that can be used for predicting effects of changes in agricultural practice and pesticide risk assessment. In the model, home ranges are represented by a number of cells in a landscape which are used by a particular individual. They are constantly adapted in order to provide sufficient food resources for an animal. When home ranges do not provide sufficient resources, animals disperse. The model is able to reproduce site fidelity of individuals, habitat preference, and dispersal. Population densities in a mixed habitat structure resulted in densities approximately equal to those reported from field studies. It is shown that home range size and dispersal are density-dependent and therefore likely to have a strong effect on regulation. We conclude (1) that the basic design of our model is also applicable for other species showing a marked home range behaviour, and (2) that a realistic representation of population regulation might require explicit modelling of home range behaviour.

1. Introduction

The use of home ranges and territoriality is an essential characteristic of many birds and mammals (Burt, 1943; Schoener, 1968; Ostfeld, 1990; Adams, 2001). The main purpose of maintaining a home range or territory is the acquisition of resources, basically food but also shelter or mates (Brown and Orians, 1970). Home ranges for most vertebrates increase with body mass and decrease with increased habitat productivity (e.g. Schoener, 1968; Harestad and Bunnell, 1979; Lindstedt et al., 1986), which supports the frequent function of home ranges and territoriality to ensure sufficient food resources. Home ranges, and especially defended territories, have a strong impact on population density and dynamics.

* *Corresponding author*. Tel.: +49 6221 6393361.
E-mail addresses: magnus.wang@rifcon.de (M. Wang), volker.grimm@ufz.de (V. Grimm).
[1] Tel.: +49 341 235 2903.
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Reviewing bird and mammal literature, Makarieva et al. (2005) proposed that in stable ecosystems (i.e. ecosystems which had sufficient time to reach a state of equilibrium) home range size and the inverse of population density represent one and the same measure, scaling isometrically (i.e. densities are high when home ranges are small and vice versa).

Several studies have revealed a mediator function of home ranges or territories for density dependence of demographic rates (e.g. Brown, 1969; Boutin, 1990; Grant and Kramer, 1990; Newton, 1992; Imre et al., 2004). At low density, all individuals of a population may establish territories of sufficient size and reproduce, while at high density only some individuals are able to monopolize a sufficiently large area and are able to breed (Brown, 1969). Other individuals exist as non-breeding floaters, which can buffer the population-level effects of environmental variations (Grimm et al., 2005).

Despite the importance of home ranges and territorial behaviour for ecology and population dynamics, mainly static home ranges have been considered in theoretical studies. Home range size and location are, however, dynamic, which is likely to have important consequences for the regulation of populations. Even most individual-based models (IBMs; DeAngelis and Mooij, 2005; Grimm and Railsback, 2005) ignore home range dynamics. These models simulate the behaviour of each distinct individual in a population in order to predict the development of the entire population. Individual-based models typically contain detailed submodels of various behaviours, such as mating, habitat choice, foraging, or dispersal. The lack of explicitly modelled home range behaviour is a severe limitation not only of theoretical models. Population models are being increasingly used for conservation biology and other applied problems. We are here particularly interested in using realistic population models for pesticide risk assessment (e.g. Topping et al., 2005). For such applications it is essential to model the spatial distribution of the animals and population regulation explicitly, which implies that home range dynamics have to be considered.

So far, only a few models include information about territorial behaviour or home ranges. For example, Grimm et al. (2003) distinguish territorial marmots from floaters, but without taking territory size into account. In a model by Kostova et al. (2004), home ranges of prairie voles are represented as single cells in a landscape. Similarly, Wiegand et al. (2004) model home ranges of brown bears on a grid. Their model landscape consists of cells which are characterised by a certain attractiveness. When a dispersing bear encounters nine cells whose overall attractiveness exceeds a certain threshold, these nine cells are used as a home range until the bear dies. Reuter (2000, 2005) developed a model for small mammals in which animals have the choice to establish circular territories of a constant size or disperse by random walks.

Recently, Moorcroft et al. (2006) developed a home range model based on a partial differential equation describing the movement of an individual. Numerical solutions and maximum-likelihood fittings were necessary for obtaining results from this model. The model is able to reproduce the fine scale movement of individuals in relation to scent marks, physical properties of the landscape, and prey availability. Home range dynamics and their population-level consequences, however, were not the main issue of this model, although the model could be used to predict observed shifts in coyote space-use in response to the loss of a certain pack.

The model that is most similar to our was developed by Hildenbrandt et al. (1995) and Bender et al. (1996); see also Fig. 2.3 in Grimm and Railsback (2005). It describes dynamic territories of the wall lizard. Territories consist of one to five spatial units. If a resident animal dies, neighbouring residents and floaters compete for the free units. The model mimicked observed home range dynamics, but it was designed for predicting extinction risk, not for studying the effect of home range dynamics on population regulation.

Thus, the individual-based model presented in the following pages is one of the first models explicitly describing home range dynamics and their consequences for population regulation and the spatial distribution of the animals. The model ultimately aims at the prediction of the effects of agricultural practice and risk assessment. The proximate aim, which is addressed in this article, is to present a model which realistically captures home range behaviour. As a model organism we use the common shrew (*Sorex araneus*). Home ranges in the model consist of a number of cells, each containing a fluctuating amount of food. Home ranges can change in size, depending on food availability, age, the presence of other animals, or breeding condition. Animals may leave their home ranges in order to establish new ones in other areas.

2. Biological background

The common shrew is a common insectivore in a variety of habitats, including grassland, woodland, arable land, and hedges. It feeds on various invertebrates, such as insect imagines and larvae, earthworms, or spiders (Churchfield, 1982). Animals may breed from April to September, but most young are produced in June and July (Churchfield, 1990). After a gestation period of 24–25 days five to seven young are born (Michielsen, 1966; Churchfield, 1990). Shortly after weaning (after 22–25 days) the young are completely independent and leave the territory of the mother. Mortality is high, especially during the first 2 months of life (Churchfield et al., 1995). Animals surviving until the next breeding season produce one or two litters on average before they die (Churchfield, 1990).

Common shrews are strictly territorial for most of their life, defending their territory ferociously (Michielsen, 1966; Shillito, 1963; Churchfield, 1990). During winter, animals defend relatively small territories. At the beginning of the breeding season both males and females enlarge their home ranges significantly. At this time, males stop defending territories and start to move widely around in the search for receptive females, crossing the territories of other animals (Churchfield, 1990). Apart from these seasonal dynamics, home range sizes are also habitat specific, being smaller in habitats with high-food resources than in habitats with low-food resources (Churchfield, 1990).

3. The model

The model description follows the ODD (Overview, Design concepts, and Details) protocol for describing individual- and