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Development of tree hollows in pedunculate oak (*Quercus robur*)

Thomas Ranius [a,*], Mats Niklasson [b], Niclas Berg [a]

[a] Swedish University of Agricultural Sciences, Department of Ecology, P.O. Box 7044, SE-750 07 Uppsala, Sweden
[b] Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, P.O. Box 49, SE-230 53 Alnarp, Sweden

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ABSTRACT

Many invertebrates, birds and mammals are dependent on hollow trees. For landscape planning that aims at persistence of species inhabiting hollow trees it is crucial to understand the development of such trees. In this study we constructed an individual-based simulation model to predict diameter distribution and formation of hollows in oak tree populations. Based on tree ring data from individual trees, we estimated the ages when hollow formation commences for pedunculate oak (*Quercus robur*) in southeast Sweden. At ages of about 200–300 years, 50% of the trees had hollows. Among trees <100 years old, less than 1% had hollows, while all >400-year-old trees had hollows. Hollows formed at earlier ages in fast-growing trees than in slow-growing trees, which may be because hollows are formed when big branches shed, and branches are thicker on fast-growing trees in comparison to slow-growing trees of the same age. The simulation model was evaluated by predicting the frequency of presence of hollows in relation to tree size in seven oak stands in the study area. The evaluation suggested that future studies should focus on tree mortality at different conditions. Tree ring methods on individual trees are useful in studies on development of hollow trees as they allow analysis of the variability in time for hollow formation among trees.

1. Introduction

Tree hollows provide important habitats for a wide range of invertebrates, birds and mammals (Gibbons and Lindenmayer, 2002; Kosinski, 2006; Ranius et al., 2005). Species dependent on tree hollows are facing decreasing habitat availability because ancient trees have declined both in forests and agricultural landscapes (Kirby and Watkins, 1998; Nilsson, 1997). For this reason, an urgent task for conservationists is to ensure that sufficient numbers of hollow trees are maintained continuously in the future. Because hollow trees do not persist forever, it is essential to ensure that new hollow trees are generated if a given number of hollow trees is to be maintained. Furthermore, many sites have so few hollow trees that there are considerable risks of the extinction of threatened species (Ranius et al., 2005). At such sites the number of hollow trees should not only be maintained, but also be increased as quickly as possible. Thus, for long-term conservation planning, knowledge about the rates of formation and deterioration of hollow trees is required. Simulation models have been used to predict long-term changes in the abundance of hollow trees in forests (Ball et al., 1999; Fan et al., 2004); Fan et al. (2004) parameterised such a model based on simple statistical relationships derived from stand level data from a forest landscape in the USA, while Ball et al. (1999) focused on one eucalypt species in Australia. The latter model was parameterised inter alia from changes in trees observed through repeated measurements (Lindenmayer et al., 1997). This approach should yield reliable data. However, because the dynamics of tree hollows are slow, there may be long delays before meaningful results based on direct observations of formation and deterioration of hollow trees can be obtained. An alternative is to parameterise a model of hollow dynamics by interpreting patterns observed in snapshot studies of trees, using tree ring-based assessments of their ages.

In this study, we constructed and parameterised a dynamic model that predicted size distribution and formation of hollows in trees. In contrast to attempts to model hollow tree dynamics in Northern America and Australia, we used an individual-based model, taking into account the variability in growth rate and hollow formation among trees. This was possible because we used tree rings of individual trees to estimate the ages of trees when hollow formation commences. Our study was conducted on pedunculate oaks *Quercus robur* L. in southeast Sweden at sites largely consisting of pasture land. In Europe, pedunculate oak is the most important tree species for invertebrates associated with tree hollows (e.g. Palm, 1959; Ranius et al., 2005). Our main objective

* Corresponding author. Tel.: +46 18 67 23 34; fax: +46 18 67 28 90.
E-mail addresses: thomas.ranius@ekol.slu.se (T. Ranius), mats.niklasson@ess.slu.se (M. Niklasson), bergovic@gmail.com (N. Berg).

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was to estimate at which age hollows are formed in trees with different growth rate. The simulation model required growth rate data, so we analysed variations in growth rate among trees and during the ageing of individual trees. By comparing model predictions with field data on tree size distribution and incidence of tree hollows at seven sites, we evaluated the model and identified gaps in our knowledge that should be filled in by future field studies.

2. Methods

2.1. Study sites and study trees

We conducted this study in an area south from Linköping, southeast Sweden, with one of the highest concentrations of old oaks in Northern Europe (around 58°15′N, 15°45′E; Antonsson and Wadstein, 1991). This was because samples from a large number of hollow trees are required, and for some of the analyses it was required that the trees have been growing under similar conditions, while for others a variability in e.g. growth rate was desirable. We studied seven sites with a high density of hollow oaks, situated 0.5–25 km from each other. The variability among these sites is representative for oak localities with high conservation value in Sweden. Five of these sites (Brokind, Kalvhagen, Orräng, Storängen, and Sundsbro) are currently grazed by cattle and situated on fertile soils dominated by deep clay soils (Johansson and Gorbatschev, 1973). At the two other sites, Långvassudde and Sturefors, there is no grazing and shallow soils are dominating. Levels of sun-exposure differ both among and within sites, but due to grazing or to the shallowness of the soils only a few trees are found in very dense situations (Fig. 1). Previously, the land was used for hay-making, which also inhibited the development of dense vegetation.

In surveys of all sites, for all trees with dbh >10 cm we recorded circumference, whether the tree was alive or dead, and whether or not the tree had a hollow. Hollows were defined as cavities in which the inner space was wider than the entrance, and the diameter of the entrance was >3 cm. To obtain data on the age and growth rates, sets of ten oaks per site were selected for ring sampling. The oaks were selected to match the mean diameter and proportion of hollow trees in the entire oak population at the respective sites (Tables 1 and 2).

We also needed a data set from trees that have grown under similar conditions. Therefore we selected sites with similar tree growth rates (Sundsbro, Brokind, Storängen, and Kalvhagen; Table 2) and extended the tree ring sample to 53–57 trees per site (three sites: Brokind, Sundsbro, and Bjärka Säby; Bjärka Säby consists of three subsites: Storängen, Kalvhagen, and Bjärka äng) for a more detailed analysis of the among-tree-variability in age at which hollow development commences (Table 3). Thus, in total we had tree ring samples from 195 trees (53 + 55 + 57 + 10 + 10 + 10; two of the seven study sites were included in the Bjärka Säby site). All trees were alive except two, which had died recently. We attempted to select approximately equal numbers of trees from each of the following categories: (i) young trees without hollows, (ii) older trees without hollows, and hollow trees with (iii) small entrances, (iv) intermediately sized entrances and (v) large entrances.

Fig. 1. Oaks (*Quercus robur*) at one of the study sites – Storängen – which is grazed by cattle.

2.2. Model outline and tree mortality

The destiny of each tree was determined by stochastic equations that predicted tree growth, formation of hollows and tree mortality. For each simulated year, we summed the number of trees present categorised according to different tree characteristics. As we assumed the recruitment and mortality of trees and formation of hollows to occur with the same probability every

Table 1
Frequencies of trees and characteristics of pedunculate oaks (*Quercus robur*) at the seven study sites in southeast Sweden

	Area (ha)	Trees/ha[a]	Percentage oaks	Percentage of oaks which had hollows	Percentage of oaks which were dead	Closeness (mean)[b]	Mean diameter of hollow oaks (cm)[a]	Mean diameter of oaks with no hollows (cm)[a]
Brokind	15.5	18	52	17	1	0.89	101	59
Kalvhagen	9.5	60	46	22	2	1.00	99	74
Långvassudde	2.9	226	47	27	12	1.88	56	52
Orräng	4.8	78	66	24	2	0.85	88	74
Storängen	5.2	84	70	17	3	1.08	96	50
Sturefors	2.6	173	48	21	0	1.36	51	40
Sundsbro	7.1	69	63	19	2	0.80	104	62

[a] Including all trees with a diameter at breast height >10 cm.
[b] Closeness of the surrounding canopy was estimated for each tree as free-standing (=0), half-open (=1) or closed (=2).