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The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows

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Abstract The dispersal of an endangered beetle, *Osmoderma eremita*, that lives in tree hollows, was studied by mark-release-recapture with pitfall traps. As only a small proportion of all dispersals is observed by this method, a simulation model was constructed to estimate the dispersal rate per individual. The model results suggest that 15% of the adults leave the original tree for another hollow tree, and consequently most individuals remain in the same tree throughout their entire life. This suggests that each hollow tree sustains a local population with limited connection with the populations in surrounding trees. It supports the view that *O. eremita* has a metapopulation structure, with each tree possibly sustaining a local population, and with the population in an assemblage of trees forming a metapopulation. Low dispersal rate and range make the species vulnerable to habitat fragmentation, probably at a scale of only a few hundred meters.

Keywords Dispersal · Metapopulation · *Osmoderma eremita* · Population structure · Simulation

Introduction

The evolution of dispersal could in general terms be described as the result of the trade-offs between the benefits and costs of staying or moving. Theoretical models have suggested that a high frequency of local extinctions should promote dispersal, as the possible benefit of dispersal increases when there are many empty but suitable habitat patches (for a review see Johnson and Gaines 1990). Comparisons between insects living in different

habitats give support for this prediction; insects associated with an ephemeral habitat that dooms them to deterministic extinction within a few generations have a high dispersal propensity, whereas the dispersal of insects in habitats with a longer persistence is more limited (Southwood 1962; Den Boer et al. 1980; Roff 1994; Denno et al. 1996). Habitat availability and landscape pattern also influence the benefits and costs of dispersal (e.g. Gadgil 1971; Travis and Dytham 1999); however, these relationships are more complex (Davis 1986; McPeck and Holt 1992; Leimar and Norberg 1997).

The pattern of dispersal strongly influences the dynamics of metapopulations (e.g. Gilpin 1987; Stacey et al. 1997; Sutcliffe et al. 1997). Understanding the process of dispersal and the rate and distance at which dispersal occurs is therefore essential if a full and realistic picture of a working metapopulation is to be achieved. Conservation work might reduce the local extinction rate to low levels by proper management, but for long-term metapopulation survival, habitat patches must be situated close enough to permit colonization (e.g. Hanski et al. 1995; Thomas and Hanski 1997). Thus, the rate and range of dispersal are key factors when carrying out conservation plans for endangered species.

Different kinds of deadwood habitats differs widely in their persistence, and this might influence the dispersal propensity of saproxylic invertebrates associated with these habitats. Newly dead wood has a short persistence, and consequently saproxylic beetles associated with this habitat have a high dispersal propensity (e.g. Nilssen 1984; Solbreck 1980). In contrast, dead wood found in hollow trunks of living trees is a habitat that may remain for many decades, or possibly even centuries. It has therefore been suggested that beetles living in tree hollows would have a restricted dispersal propensity (McLean and Speight 1993; Nilsson and Baranowski 1997). If the rate of long-range dispersal is limited, the colonization of isolated habitat patches would rarely occur, and that might affect the spatial structure of occupancy. In concordance with this, the occurrence patterns of some species associated with tree hollows suggest that

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dispersal is a limiting factor: the frequency of occupancy is lower in sites where the density of hollow trees is lower (Ranius 2000) and where the continuity of occurrence of old trees over time seems to have been broken (Nilsson and Baranowski 1997). However, no direct assessments of the dispersal of any species dependent on tree hollows have been published.

This is a dispersal study of an endangered beetle, *Osmoderma eremita* Scopoli (Coleoptera, Scarabaeidae), that lives in tree hollows. The rate and range of inter-tree dispersals of *O. eremita* adults was assessed by a mark-release-recapture experiment. We also searched for patterns of dispersal behaviour which may affect how the metapopulation works. Dispersal which leads to aggregation in some patches has an entirely different effect on metapopulation dynamics from dispersal from dense to sparse populations: conspecific attraction lowers the proportion of occupied habitat patches within a metapopulation at equilibrium (Ray and Gilpin 1991). Only a few dispersal studies using mark-release-recapture have been carried out on beetles (Davis 1986; Herzig 1995); among insects, most studies have been performed on butterflies. Female butterflies generally show a higher between-patch dispersal rate than males (Baguette and Nève 1994; Hanski et al. 1994; Kuussaari et al. 1996). For some butterfly species individual size (Kuussaari et al. 1996) and age (Warren 1987) also affect the dispersal rate, as well as habitat size and availability of resources (Hill et al. 1996; Kuussaari et al. 1996). If *O. eremita* also shows such patterns it might affect the potential contribution to the reproductive output of colonizers in the receiving trees. Thus, we analysed the population size of trees losing dispersing beetles in relation to trees receiving dispersers, the time of dispersal events, and features of the dispersing beetles themselves.

A problem which arises in dispersal rate assessments using mark-release-recapture is that the sample of observed dispersals is usually very small, which gives an impression that dispersals are rare events. However, it is impossible to decide to what extent this impression is true, and not a reflection of technical difficulties in detecting dispersals, by pure intuition. Therefore we developed a simulation model adapted to the mark-release-recapture experiment performed. Computer simulations of dispersal have been carried out previously by Brookes and Butlin (1994), and our model is similar to theirs in that it requires data on population size and capture rate and presupposes that the species resides in, and disperses between, distinct habitat patches.

Materials and methods

The species

O. eremita larvae develop exclusively in tree hollows, in Sweden mainly in oak trees with certain characteristics which affect microclimate. The species inhabits trunk hollows containing large amounts of wood mould, which is loose, rotten wood often mixed with fungi and remains of animal nests and fragments of dead in-

sects (Ranius and Nilsson 1997). In the laboratory, the larvae normally construct a cocoon in the autumn after 2 years of development and metamorphosis takes place in the following spring. Thus, the total development time of *O. eremita* is normally 3 years, but this may depend on habitat quality (Tausin 1994). The adults occur in July to September and never hibernate (authors, personal observations). In contrast to many other saproxylic beetles they do not visit flowers or sap flows, but remain mainly in the tree hollows (Martin 1993; authors, personal observations).

The field work

This study was performed in one of the few remaining landscapes in Northern Europe with a high density of old oaks, which is situated in the province of Östergötland, southeastern Sweden (Antonsson and Wadstein 1991). In this landscape two study areas were chosen: a 1.5×2 km core with the highest density of hollow oaks (Bjärka-Säby, 58°16'N, 15°46'E), and a 0.5×0.4 km area situated 10 km southwest of this (Brokind, 58°12'N, 15°40'E). Almost all hollow oaks in these areas grow scattered in pasture woodland. We searched for tree hollows in the study areas, and classified each hollow tree into one of two categories: relatively young hollow trees with small hollows and probably small amounts of wood mould, and hollow trees in a later stage of succession with larger hollows containing large amounts of wood mould. Only the latter category was considered as possible habitat for *O. eremita* (see Ranius and Nilsson 1997), and henceforth in this paper only these trees are referred to as "hollow trees".

Inter-tree dispersal of *O. eremita* was studied in a mark-release-recapture experiment, which also aimed to assess the population size and its fluctuations (Ranius, in press). The beetles were captured with pitfall traps set in tree hollows. In 1995–1997, 26 trees were studied in Bjärka-Säby and none in Brokind, and in 1998–1999, 41 trees were studied in Bjärka-Säby and 9 in Brokind. The hollow trees were geographically concentrated, and as this may affect dispersal, the trees were divided into stands in the data treatment. A stand was defined as a cluster of hollow trees with <250 m between one tree to the next, and with <250 m between one trap to the next. In this way we identified four stands in Bjärka-Säby and one stand in Brokind (Table 1). In Bjärka-Säby there were also two solitary trees with traps, and as they did not belong to any stand, they were excluded from the statistical analyses. Traps were only set in 14–42% of the hollow oaks within the areas (Table 1), as it was impossible to set traps in the other oaks either due to the characteristics of the hollows, or because the trees were on land without public access. To be able to set a trap in a tree hollow the entrance hole must be less than 5 m from the ground (length of the ladder), and the wood mould surface not too far from the entrance hole (to be able to reach). The traps were empty jars placed with the openings level with the wood mould surface. If possible, traps with a top diameter of 7 cm were used, whereas in narrow hollows the traps were 5–6 cm wide. There was more than one entrance in some trees, but usually only one trap was set in the largest hollow in each tree. However, in three trees, two traps were set in different hollows. In Bjärka-Säby, the traps were emptied once a day and in Brokind every second day. *O. eremita* was also searched for in the hollows and on trunks. Each beetle found was given an individual number by marking on the elytra with an insect needle in a drill. Except for the first 2 weeks of the first year in Bjärka-Säby, sex was determined (according to Hansen 1925). After marking, the beetles were released on the surface of the wood mould and usually the beetles immediately dug down into the wood mould. Only once was an individual seen to fly following release, but this beetle was never recaptured. When the traps were emptied, 2.7% of the beetles were dead. The only discernible injury caused by handling was that the needle sometimes pierced the abdomen, which caused haemolymph to leak out. A study on another, smaller beetle species showed that this kind of injury has little or no effect on survival (Nilsson 1997).

Table 1 Number of hollow trees in the studied stands, the frequency of traps in these trees and the estimated population size (adults per year) totally for trees with traps

Stand	Area	Hollow trees	Frequency of traps		Population size	
			1995–1997	1998–1999	1995–1997	1998–1999
Brokind	Brokind	38	0%	24%	–	106
Bos holme	Bjärka-Säby	8	38%	38%	4	4
Bjärka äng	Bjärka-Säby	25	24%	32%	30	14
Hjorthagen	Bjärka-Säby	36	14%	42%	76	42
Kalvhagen	Bjärka-Säby	36	28%	33%	126	194

Table 2 Capture data for *Osmoderma eremita* for each year (*starting date* the date when the first adult was captured in the field work, * adults present on the first day of field work, *ending date* date when the last individual was captured, *captures* total number

of captures in the trees studied, *captured individuals* total number of captured individuals in the trees studied, *trees* number of trees with traps included in the statistical analyses)

Year	Starting date	Ending date	Captures	Captured individuals	Trees
1995	21 July*	25 August	282	164	24
1996	27 July	7 September	223	109	24
1997	14 July*	25 August	314	142	24
1998	21 July	2 September	544	205	48
1999	8 July*	15 August	377	219	48
Sum			1,740	839	

The study was performed over 5 years (Table 2). During two of the years, the trapping started before the first adults had emerged, while during the other three years adults were present on the first day of trapping. Trapping ended when the daily total capture fell below one individual, except in 1998, when the trapping ended when two captures per day were performed. When adults were present on the first day of trapping, the first adults had probably emerged 5–10 days before the field work started, and this may bias the population size and dispersal estimates. The magnitude of this bias was estimated from the data of the two years when the first days were included, by leaving out the captures on the 10 days following the emergence of the first adult. For these two years, the number of recaptures was 7.0% and 8.9% lower, the population estimate was 5.2% and 4.6% lower, and the number of observed dispersals remained the same when the captures of the first 10 days were deleted (estimated for Bjärka-Säby, males and females combined).

The mean temperature during the time of activity was higher than the long-term average in every year except 1998 (July and August; 1995: 17.0°C, 1996: 15.8°C, 1997: 18.7°C, 1998: 14.3°C, 1999: 16.8°C; mean 1961–1990: 15.8°C; data from the meteorological station at Malmslätt, 20 km from the study area).

Simulation model

Most dispersals are impossible to recognise by mark-release-recapture, as they may take place between trees that do not contain traps, or they may occur before the first or after the last capture of the individual. To be able to estimate the dispersal rate, even though many dispersals were not observed, we constructed a computer simulation model. We defined the dispersal rate as the number of individuals that disperse from one hollow tree to another divided by the total number of individuals in the trees [i.e. dispersed/(dispersed+residents)]. The simulation was based on four assumptions:

1. The tendency to leave a tree is equal for all individuals, independently of which tree they inhabit.
2. The dispersing individual could arrive at any tree within the stand (but there are never dispersals between stands), with no difference in probability between trees with and without traps.

3. The catchability is equal in all trees, but is allowed to differ between sexes.
4. Captures and dispersals occur in an order independent of each other.

The frequency of short-range dispersal was higher than long-range dispersal, and this may invalid assumption 2 if the trees with traps are not randomly placed in space. Therefore, we analysed presence/absence of traps in relation to whether there was a trap in the nearest tree, and found no significant aggregation of traps ($P=0.703$, Pearson chi-square). The large difference in catchability between sexes was taken into consideration, but we assumed the catchability to be equal for all trees (assumption 3), even though some differences in catchability have been found between trees (Ranius, in press). We analysed when dispersals occurred in relation to captures, and were not able to detect any deviation from a random distribution over time (see Results), and thus, assumption 4 was not invalidated. The model only considers those beetles that remain in the same tree or move to other hollow trees (assumption 2), but it cannot reveal how many beetles leave the habitat completely, for example, by flying to other parts of the vegetation. Telemetric studies on *O. eremita* show that such dispersals are rare in comparison to dispersals between hollow trees: among seven dispersing beetles tagged with radio transmitters, five went to other oaks with large amounts of wood mould (counted as “hollow oaks” in this study), one went to a hollow oak with a small amount of wood mould and one to the vegetation (J. Hedin and T. Ranius, unpublished work).

In the computer simulation, the numbers of beetles and captures were the input data, the number of inter-tree dispersals was a variable which was changed between runs, and the number of dispersals observed by mark-release-recapture was generated from the simulation process.

The simulation program was run as follows:

1. Individuals were distributed between hollow trees according to population sizes and number of hollow trees in field data.
2. The number of captures per year was taken from the field data. A value of the dispersal rate was arbitrarily chosen, and by multiplying this rate by the total population size per year, the number of dispersals was calculated.
3. The capture and dispersal events, one by one in a random order, were randomly distributed among the individuals. Cap-

tures were distributed between individuals inhabiting trees with traps, and dispersals between all individuals. All dispersals took place within stands, but whether or not the receiving tree contained a trap was randomly selected.

4. For every individual captured according to 3, the site of the immediately previous capture was checked. When an individual was captured in a tree different from the tree it was captured in before, it was counted as an observed dispersal.
5. The main body of the program (points 1–4) was repeated ten times (5 years×2 sexes). The number of observed dispersals of males, females and sexes combined was summed, and the SD of observed dispersals over 5 years was estimated.

For any particular combination of input values, the simulation program was repeated 1,000 times to yield a median value of the dispersals observed. Different values of the number of inter-tree dispersals were entered, until the median of observed dispersals achieved from the simulation was the same as the observed dispersals in the field data. To obtain the 95% confidence limits we also searched for the number of dispersals that generated sets of values of observed dispersals with <2.5% of the values smaller, and <2.5% larger, than the number of dispersals observed from the field data. Each simulation run consisted of a main body which was repeated ten times (5 years×2 sexes) with input values varying between the repetitions according to field data. The aim of separating male and female data was to take the difference in capture rate between sexes into account. When the observed dispersals from field data and simulation results were compared, we summed the dispersals of males and females, and for different years and areas (i.e. the ten repetitions).

Table 3 Number of captures per year of males and females combined in all trees studied

Period	Captures per year	
	Males	Females
1995–1997	259	55
1998–1999	337	76

Table 4 Dispersals of *Osmoderma eremita* observed with mark-release-recapture (*A* date of capture with dispersal observation and date of the capture immediately before, *B* whether the individual

A	B	C	D	E	
1995					
27/7–31/7	Alive	–	70 m	Trapping	
28/7–2/8	Dead	Male	30 m	Trapping	
1/8–2/8	Alive	Male	120 m	Trapping	
1/8–2/9	Dead	Female	80 m	Below a hollow tree	Excluded from analysis
1996					
19/8–30/8	Alive	Male	30 m	Trapping	
1997					
16/7–21/7	Alive	Female	70 m	Trapping	
22/7–24/7	Alive	Male	110 m	Trapping	
1998					
9/8–19/8	Dead	Male	100 m	Below a hollow tree	Excluded from analysis
13/8–20/8	Alive	Male	30 m	Without trap in a tree hollow	
1999					
15/7–25/7	Alive	Male	190 m	Trapping	
21/7–31/7	Dead	Male	100 m	Trapping	

The field data used as input values in the model were divided into four subsets: 1995–1997 and 1998–1999, with males and females separated. The reason for this division in time is that the number of trees with traps are the same within, but not between, these periods. For each subset, one average value of the number of captures was estimated from field data (Table 3). This means the catchability was regarded as equal for every tree, but possibly differing between sexes and periods.

For trees with traps, the population size was estimated with the model of Craig (1953) (Ranius, in press). The population sizes in these trees were also estimated by the Jolly-Seber model (Jolly 1965; see also Southwood 1978), which is another, independent method, and the results were consistent with Craig's model (Ranius, in press). The population sizes were divided by two to obtain the number of males and females in each tree. This was permissible since population estimates by Craig's model with sexes separated suggested that the sex ratio was 1:1 (Ranius, in press). We always chose equal dispersal rates for males and females, as we found no evidence for differences in dispersal rate between sexes (see Results). We assumed that the population size and dispersal rate were the same in trees with and without traps, even though trapping was only possible in trees with certain characteristics, which might give rise to differences in the population size. However, those trees which contained the largest number of beetles did not differ from other trees with traps with respect to those characteristics that determined whether trapping was possible or not (height of the entrance hollow, how far the wood mould surface was from the entrance, and size of the entrance; T. Ranius and J. Hedin, unpublished work).

Results

In this study, 839 individuals were captured a total of 1,740 times (Table 1). It was 377 individuals which were captured at least twice. The capture rate was considerably higher for males than for females (Table 2), and this was taken into consideration in the population estimation and the modelling of dispersal. The population size in

was dead or alive when it was recaptured, *C* sex, *D* distance, *E* circumstances of the capture with dispersal observation)

trees with traps was estimated with Craig's model (Table 3) (for details see Ranius, in press). The mean population size was 11 adults per tree per year (Ranius, in press).

The total number of recaptures was 901; 892 of these were in the same tree as the immediately previous capture, and 9 were in a different tree. The computer simulation resulted in the most likely dispersal rate being 15% (95% confidence limits: 6% and 28%). The number of observed dispersals was between one and four each year (Table 4). The difference in number of observed dispersals between years in field data was not larger than expected from sampling error for 5 years with a constant dispersal rate per year (SD of observed dispersals per year over 5 years, field data: 0.84, median SD from the simulation: 1.52).

The simulation analyses included seven males and one female and one individual not sexed. In addition, one male and one female were found dead on the ground below hollow oaks different from the original tree of capture (Table 4). Dead beetles on the ground were however excluded from the computer simulation analyses, as they were recaptured by a method which make the assumptions unlikely (the catchability was not the same for these individuals as for individuals that remained in the tree). The computer simulation showed that the most probable distribution of observed dispersals would be 8.4 males and 0.6 females, if it is assumed that the dispersal rate was 15% for both sexes, and the capture rate was the same as in the field data. This distribution is very near the observed dispersals from field data, and thus the difference in observed dispersals between sexes could be explained solely by a large difference in the probability of capture.

Among the adults with observed dispersals, five were captured more than once before the dispersal, and three were captured more than once after the dispersal. Thus, the dispersals were not found to be biased either towards the early or the late part of the adults' life-time.

During 1996–1999, the body lengths of the adults were measured. There was no difference in length between males with and without observed dispersal (mean length, dispersing: 28.9 mm, not dispersing: 29.4 mm, $P=0.597$, t -test). This was not possible to study for females, as the sample only contained one individual.

For each of the 11 dispersals recorded in Table 4, the population sizes were compared between the trees receiving and losing the individual. The population size was calculated per tree with Craig's model (for details see Ranius, in press), for the particular year when the dispersal occurred. Four of the dispersals were from a tree with a smaller population size to a tree with a larger population size, whereas seven were in the opposite direction. Among these latter dispersals, four were to trees where several other adults occurred, which had probably hatched in that tree, and three were to trees with no other adults captured in that year.

All dispersals were in a range of 30–190 m, and occurred within stands. The spatial distribution of the traps

made it possible to observe dispersals in a range of 1 km or more in Bjärka-Säby, and a few hundred meters in Brokind.

Discussion

Dispersal rate

The fraction of *O. eremita* adults that performed dispersals between trees was within a range of 6 and 28%. Theoretical studies suggest that the evolution of dispersal propensity is linked with the heterogeneity of the habitat in space and time (e.g. Gadgil 1971; Cohen and Levin 1991; Travis and Dytham 1999). A large variability in carrying capacity over time in each habitat patch increases the possible benefit of dispersal, and would therefore select for a higher degree of mobility. On the contrary, a large variability in carrying capacity in space, will select for more resident individuals, because then dispersal would on the average cause an individual to reach an environment worse than the one it was born in (Gadgil 1971; Travis and Dytham 1999). However, if the individuals are able to select favourable targets for their movements, some dispersal is selected for even in a temporally constant and spatially varying habitat (McPeck and Holt 1992). *O. eremita* is a specialized species, strictly associated with tree hollows. A study on *O. eremita* over 5 years revealed that the population fluctuations are rather narrow in each tree, whereas the variability in population size between trees was much greater (Ranius, in press). There is circumstantial evidence suggesting that a tree could be suitable for *O. eremita* for several decades (Martin 1993), and thus the species might persist for tens of generations in the same tree. In addition, *O. eremita* has probably evolved in nemoral forests dominated by deciduous trees, which are comparatively stable with a small-scaled disturbance regime (Falinski 1986). Thus, *O. eremita* is specialized for a habitat with a distinct small-scale patchiness (which increases the cost of dispersal) whereas the variability in carrying capacity is much lower over time (which decreases the possible benefit of dispersal). The low dispersal rate observed is therefore consistent with expectations from the theoretical models.

Flight behaviour of insects does not, however, only reflect the proneness to dispersal. Insect flights could have many other functions, e.g. foraging, mate location, avoidance of predators and finding oviposition sites (e.g. Hill et al. 1999). As *O. eremita* perform these activities mainly within the tree hollows (except probably feeding, as we have never seen adults feed: authors, personal observations), they have no reason to fly within habitat patches as many other insects do (e.g. Tabashnik 1980; Davis 1984).

The dispersal behaviour might differ intraspecifically as a consequence of strong selection which acts in different directions in different landscapes. For a beetle species, differences in flight behaviour between small, sparsely distributed populations and large, contiguous populations have been shown (Davis 1986). Studies on

butterflies suggest that increasing fragmentation might result in an evolutionary change in dispersal traits (Thomas et al. 1998; Hill et al. 1999). In the last 200 years, the habitat of *O. eremita* has decreased severely and been fragmented (Ranius 2000; Eliasson and Nilsson 1999), and this might have enhanced selection against migration in isolated populations of *O. eremita*. However, in the study areas the density of hollow oaks is still sufficient to allow dispersing individuals to reach suitable hollow trees. In the surroundings of the study areas, the density of old oaks is currently lower than before, but as the dispersal ranges of the beetles are small in relation to the study areas only a few migrating individuals would have suffered from this. Therefore, in this landscape, the recent changes in hollow oak density would probably have little, if any, impact on the evolution of dispersal.

Dispersal patterns

The range of the observed dispersals is in concordance with a dispersal model with a much higher frequency of short-range than long-range dispersals. A reason for not observing more very short dispersals is that the trees with traps did not occur more densely. Long-distance dispersal was not observed, probably because this occurs too rarely to be detected by mark-release-recapture. A problem which could arise in mark-release-recapture studies is that the proportion of long-distance dispersers may be underestimated, as these individuals have a lower probability of recapture and may leave the study area completely (Koenig et al. 1996). As the size of the study areas was so large relative to all observed dispersals and there was a low density of hollow trees in the surroundings of the study plots, this is probably a minor problem in the present study.

Often specific years have considerably higher dispersal rates than the average, which could be related to weather (Kindvall 1995; Nève et al. 1996). No difference in dispersal rate between years was observed in this study, but as the number of dispersals per year was small, only substantial differences between years would have been detectable. If warm weather increases dispersal, this study might overestimate the dispersal rate, as the weather was warmer than the long-term average in all years but one.

As the data from male and female captures were treated separately in the simulation and the difference in catchability was taken into account, the dispersal rate could be compared between sexes without any bias. However, as the number of female recaptures was low, the statistical power of this analysis was weak, and accordingly there was no difference in dispersal detected between sexes.

Influence on population dynamics

The low dispersal rate found in this study indicates that the populations of each tree have limited connections

with each other. The dispersal rate of *O. eremita* seems to be in the same range as for sedentary butterflies, whose populations conform to a metapopulation structure (Thomas and Hanski 1997; Thomas 2000). In *O. eremita* also, it might be possible for local populations in individual trees to become extinct, without immediate recolonization, although the tree is suitable and there are neighbouring trees with the beetle present. This is consistent with a classical metapopulation model, with each hollow tree representing a habitat patch (Hanski 1997).

The longest range of dispersal observed was 190 m. Therefore, *O. eremita* populations might have characteristics that in the long term make them vulnerable to small-scale habitat fragmentation (Fahrig 1998). On the other hand, low mobility decreases the cost of losing emigrating individuals from small stands. Therefore the extinction rate in a fragmented landscape might be lower for species like *O. eremita* than for species with higher dispersal rate (Hill et al. 1996; Thomas 2000). The occupancy pattern of *O. eremita* is consistent with this, as it indicates that the beetle is able to remain over quite long periods in small stands without connectivity, even though long term persistence might be impossible (Ranius 2000).

Direct measurements of dispersal with mark-release-recapture could not normally detect the rarity of long-term dispersal. More thorough studies on butterflies, for example, have revealed that the dispersal ranges are wider than expected from earlier studies (Hanski 1999). Therefore, if possible, other sources of evidence, like spatial patterns of occupancy and genetic differentiation, should be used to achieve several independent measures of long-distance movements (Lewis et al. 1997). For *O. eremita*, a study on the spatial pattern of occupancy supports the view of long-term dispersal and metapopulation dynamics derived from the present study: the habitat occupancy was higher in larger stands, but independent of the density of stands in the surroundings (Ranius 2000). This could be seen as a consequence of the metapopulations in small stands being too small to be able to persist in the long run, and the dispersals between stands being too rare to influence the habitat occupancy. For *O. eremita*, gene flow estimates have a major shortcoming, as such an analysis cannot distinguish between ongoing and historical gene flow (Slatkin 1987; Bossart and Pashley Prowell 1998). In Sweden, the populations of *O. eremita* have probably been reduced and isolated within the last 60 generations, as its habitat has decreased and become fragmented especially at the beginning of the 19th century (Eliasson and Nilsson 1999). Therefore we could not expect to obtain a measure of the present situation, but rather we might overestimate gene flow, due to a higher connectivity in the past.

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