REVIEW

Thomas Ranius

Measuring the dispersal of saproxylic insects: a key characteristic for their conservation

Abstract In the discipline of nature conservation it is important to understand under which circumstances populations can survive by compensating local extinctions with colonizations. Many saproxylic (= wood-dwelling) insect species have declining populations and are regarded as threatened due to low habitat availability in managed forests. Several methods have been used to better understand the dispersal biology and colonization ability of saproxylic insects with declining populations. The present article summarizes and compares the results of such studies. When the same species have been studied using several methods, the results are consistent, but different aspects of dispersal biology are revealed with different methods. Capture-recapture and telemetry are direct methods that can be used to quantify dispersal rate and range in the field. Studies of genetic structure and occupancy patterns are complementary, as they reveal the consequences of dispersals that have taken place over a larger spatial and temporal scale than is possible to study with direct methods. Because colonization, rather than dispersal, is important for population persistence, colonization experiments provide useful information. To obtain information relevant for conservation work, dispersal studies should be conducted on model species that are representative of threatened species. Colonization ability probability differs between common and rare species, and therefore it is important to also study the dispersal of rare species, even if it is more difficult.

Keywords Capture-recapture · Colonization · Dead wood · *Osmoderma eremita* · Telemetry · Tethered flight

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Introduction

In order to understand population dynamics and assess extinction risks, it is important to obtain knowledge on a species' dispersal rate and range. Dispersal is necessary for gene flow (Slatkin 1987) and the colonization of empty habitat patches (Hanski et al. 1994), and may also affect the population dynamics (Pulliam 1988) and extinction risks of local populations (Brown and Kodrick-Brown 1977). Therefore, dispersal affects how the populations are able to cope with changes in the environment, such as habitat loss and fragmentation (Thomas 2000). Models that do not explicitly involve costs for dispersal, such as Levins' (1969, 1970) metapopulation model, suggest that dispersal is always beneficial. If the dispersal rate is high, however, an increased local extinction risk may make species with high dispersal rates more vulnerable in fragmented landscapes (Hanski and Zhang 1993).

Empirical data support the view that there is no simple positive relationship between dispersal and population persistence in fragmented landscapes; Thomas (2000) related the recent decline of British butterfly species with their proneness for dispersal and found that species in the intermediate category had experienced the most serious declines, while both more mobile and more sedentary species had persisted better. This pattern is dependent on the degree of fragmentation; at a later stage in the fragmentation process, we should expect the sedentary species to be the most affected, while the most mobile species would, to a high extent, still persist (Thomas 2000). The strategy for nature conservation should take into consideration the colonization ability of the target species. For species with a limited colonization ability, it is important to maintain and improve habitat quality within, or nearby, localities where they exist (Huxel and Hastings 1999). For the conservation of species with a high capacity for long-distance colonization, other criteria should be used for cost-efficient conservation efforts. For example, priority should be

given to localities with a high possibility for quick improvement of habitat quality (Ranius and Kindvall 2006).

A large proportion of forest insects are saproxylic, i.e. dependent on dead wood directly, or dependent on other saproxylic organisms (Speight 1989). Because there is little dead wood in intensively managed forests, the populations of many saproxylic insects have decreased in size and are now regarded as threatened (Siitonen 2001). This paper reviews the literature on the dispersal of saproxylic insects, with a focus on species that may be targets for conservation efforts. The aim of this article is to compare the conclusions that are possible to draw dependent on the method that is used. Also presented are new analyses on previously published data collected on beetles inhabiting tree hollows, in particular, *Osmoderma eremita*.

Capture-recapture

The capture-recapture technique is useful when assessing population sizes, but it also enables the researcher to observe directly a marked individual's movements. Information on dispersal has also been obtained by the recapture of individuals released from certain dispersal sources (Togashi 1990). Although models have been developed to estimate dispersal parameters from capture-recapture studies (Hanski et al. 2000; Ovaskainen 2004), to date, when dispersal rate and the range of saproxylic insects have been studied, these models have not been applied. The reason for this is that saproxylic insects have not been captured in every habitat patch in an entire landscape and, at least in one case, the number of observed migrations have been too small.

Capture-recapture has been used in metapopulation studies of three beetle species: *Osmoderma eremita* (Ranius and Hedin 2001), *Bolitotherus cornutus* (Whitlock 1992; Starzomski and Bondrup-Nielsen 2002), and *Bolitophagus reticulatus* (Nilsson 1997). Larvae of *O. eremita* develop in hollow trees, which also form the main habitat of the adults (Fig. 1). The adults survive for a month and do usually not feed. Larvae of *Bolitophagus reticulatus* and *Bolitotherus cornutus* develop in sporocarps of a bracket fungus that frequently occur in dead wood (Fig. 2). The adults, which may have a life span of up to 3 years, also feed on the sporocarps. Hollow oaks provide a more permanent habitat than sporocarps. Consequently, we expect species residing in hollow oaks to be generally more sedentary than those in sporocarps. The reason for this expectation is based on both theoretical analyses and a number of empirical studies which suggest that species in long-lived (= more permanent) habitats have a more limited dispersal than those in short-lived habitats (Southwood 1962; Johnson and Gaines 1990; Roff 1994).

Among the 377 *Osmoderma eremita* individuals that were captured at least twice by Ranius and Hedin (2001), 2.4% were observed to move from one tree to

Fig. 1 a In Sweden, *Osmoderma eremita* and other beetles associated with tree hollows predominantly occur in oak (*Quercus robur*) pastures grazed by cattle. Photo: Jens Johannesson. **b** Pitfall trap set in a trunk hollow, used in a capture-recapture study of *O. eremita*. Photo: Niklas Jönsson

another. In Whitlock's (1992) study of *B. cornutus*, movements between logs were observed for 14.6% of the 288 adult beetles captured at least twice. For *B. reticulatus*, 932 individuals were captured at least twice, and movements between logs were observed in 30.3% of these individuals (Nilsson 1997). These figures are underestimates of the dispersal rate, because many
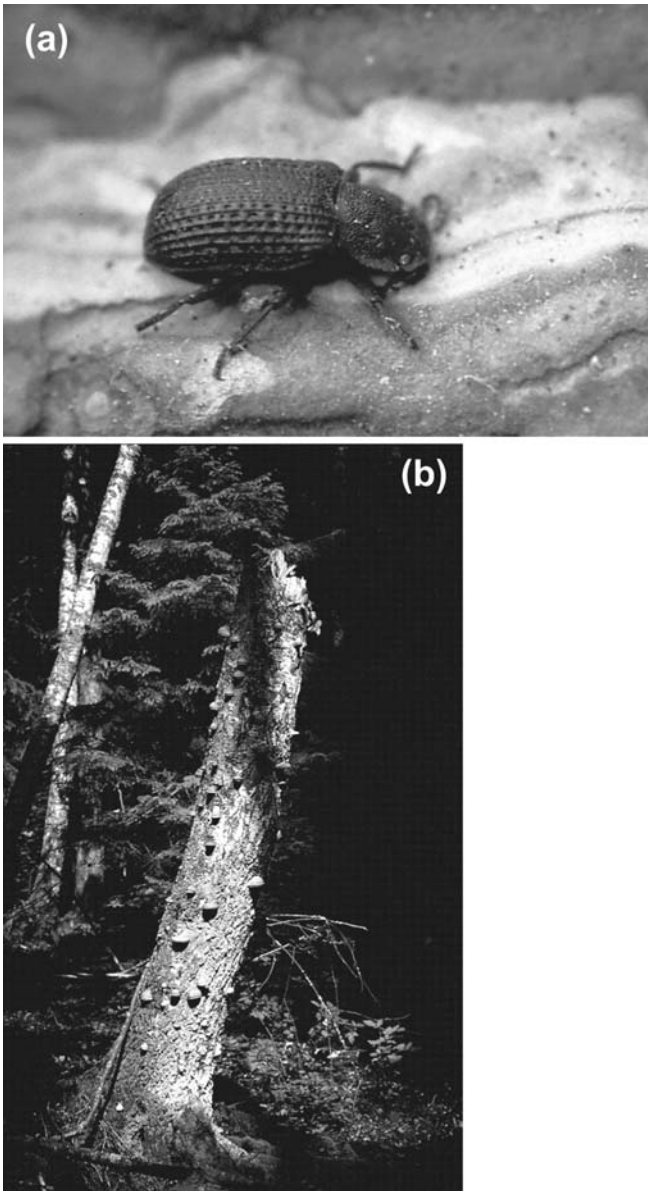
Fig. 2 a The black tinder fungus beetle *Bolitophagus reticulatus* is a 5- to 8-mm-long beetle. **b** *B. reticulatus* is associated with sporocarps of the tinder fungus, *Fomes fomentarius*. Photo: Mats Jonsell

In a metapopulation in equilibrium, the local extinction rate is equal to the colonization rate. *O. eremita* was studied for 5 years, but this period was clearly too short for being observing colonizations and local extinctions. For *B. cornutus*, the disappearance rate was calculated to be 0.10 per log and year (equal to the disappearance rate of habitat patches). This means that the mean longevity of a local population is 9 years (Whitlock 1992). For *B. reticulatus*, Nilsson (1997) reported that the species disappeared from logs at a rate of 38% per year, indicating that the mean longevity would be 2 years. Given that for *B. reticulatus*, the larval development takes 1 year and the adult beetles survive 1-3 years, the reported longevity in a log is of the same magnitude as the life-time of an individual.

Based on the dispersal rate, *O. eremita* has been described as a metapopulation (Ranius and Hedin 2001), with each tree regarded as a habitat patch that potentially hosts local populations. These local populations are partly independent and, therefore, there is an asynchrony in the population fluctuations (Ranius 2001). In contrast, for *B. cornutus*, Starzomski and Bondrup-Nielsen (2002) concluded that a local population potentially covers an area encompassing a group of logs rather than an individual log with sporocarps. With respect to *B. reticulatus*, it is even more obvious that the dispersal between logs is so extensive, and the individuals arrive and disappear so often, that it makes no sense to describe the beetles found in an individual log as a local population. Despite this, Nilsson's study has been used as an argument for assuming a metapopulation structure of *B. reticulatus* with individual logs harboring local populations (Nilsson 1997; Rukke and Midtgaard 1998).

The dispersal rate of *O. eremita* has also been studied with telemetry, and the rates obtained with this method were found to be similar to those estimated in the capture-recapture study (Hedin et al. 2003). The dispersal rates of *B. cornutus* and *B. reticulatus* have not been estimated with any other method. However, dispersal rate and colonization-extinction-dynamics affect the genetic structure of a population, which for these species has been found to be consistent with an extensive turnover of populations in individual logs (*B. cornutus*: Whitlock 1992; *B. reticulatus*: Jonsson et al. 2003).

It is difficult to assess dispersal ranges from capture-recapture studies (Schneider 2003). As Nilsson's (1997) study was conducted in an area less than 1 ha, it was impossible to draw conclusions about dispersal for distances greater than some tens of metres, which explains why no dispersal ranges were presented. Whitlock's (1992) study was carried out over a 50×600-m area, and the mean observed movement distance was 27 m. *O. eremita* has been studied in two areas (400×500 m, and 1,500×2,000 m, respectively). The observed dispersals were within a range of 30–190 m. In a telemetric study carried out in the same study area, dispersals of 10–180 m were observed.

individuals disperse to trees or logs not included in the study, or they disperse before their first capture of after their last recapture. In the *O. eremita* study, this was adjusted using a computer simulation model, which suggested that 15% of the *O. eremita* individuals moved to other trees during their life-time (Ranius and Hedin 2001). Whitlock (1992) estimated the dispersal rate to be 31%, taking into account immigration from the surroundings and the time period between captures in relation to the adult beetles' life-span. No similar analysis has been conducted for *B. reticulatus*, but it is likely that for this species also, the actual dispersal rate is considerably higher than that which has been observed (30.3%).

The dispersal distance distribution of *O. eremita* obtained by the capture-recapture method and telemetry was compared with the prediction from a power function, $P = aD^{-n}$, and a negative exponential function, $P = \exp(-D/k)$, where P is the probability that an individual moves the distance D or farther, and a, n, and k are constants. The negative exponential function has been used in metapopulation models (Hanski et al. 2000), but in several empirical studies the power function has fitted better with field data (Hill et al. 1996; Baguette et al. 2000; Roslin 2000). However, in *O. eremita*, the negative exponential curve fitted best with field data (Fig. 3, for logarithmic values: Pearson correlation coefficient (negative exponential function) = 0.97; Pearson correlation coefficient (power function) = 0.88). The value of k is equal to the mean dispersal distance, and was found to be 60 m. For distances > 200 m, the negative exponential function predicts that less than one movement would be observed in the two studies totally. Thus, there is no reason to believe that the distance of the longest observed dispersal (190 m) represents any maximum limit for dispersal; dispersal over longer distances is predicted to be so rare that it could easily remain unobserved in field studies. Because no physiological limit in the dispersal range of *O. eremita* is known, we should leave the negative exponential function untruncated. This means that the dispersal range might be infinite; however, the probability for such a range tends towards zero. By the function it could be predicted that 1.6% of the dispersing individuals move > 250 m. Given that the number of adult beetles emerging each year in an area with a high density of suitable trees (Bjärka-Säby, Sweden) has been estimated to be 1300 (Ranius 2001), and the dispersal rate is estimated to 15%, it can be expected that each year about three adult beetles move more than 250 m. If the same function is used in small stands of hollow trees inhabited by *O. eremita* (with some tens of beetles emerging every year; Ranius 2000), there would be about one beetle moving more than 250 m every 10 years. Most likely, the probability of such dispersal events varies between years and is dependent on weather (Kindvall 1995; Nève et al. 1996); however, for *O. eremita*, no such relationship has been shown to date (Ranius and Hedin 2001).

Because the *O. eremita* beetles move from one suitable tree to another (Hedin et al. 2003), their dispersal range is not only a function of the species' biology; to some extent it is also affected by the spatial structure of the trees. The dispersal range of *O. eremita* beetles has only been studied at two localities where the density of suitable trees is high. Consequently, it is not known how the dispersal rate and range will differ in a landscape with a lower density of hollow trees (cf. Mennechez et al. 2003). However, in a landscape with many small stands of hollow oaks, single suitable trees remained unoccupied if situated only a few hundred meters from occupied stands (Ranius 2000). Thus, the dispersal range does not seem to be much larger when the stands of hollow trees are small.

Telemetry

The only other method which can be used to obtain direct measures of field dispersal – apart from the mark-recapture techniques – is telemetry. Telemetry can be used on larger insects and to follow flying individuals. This method has been applied in studies of the saproxylic beetles *Lucanus cervus* (Sprecher-Uebersax and Durrer 2001) and *O. eremita* (Fig. 4; Hedin and Ranius 2002; Hedin et al. 2003) and on the beetle *Scapanes scapanes* that bores in wood of living coconut palms (Beaudoin-Ollivier et al. 2003). The radio transmitters
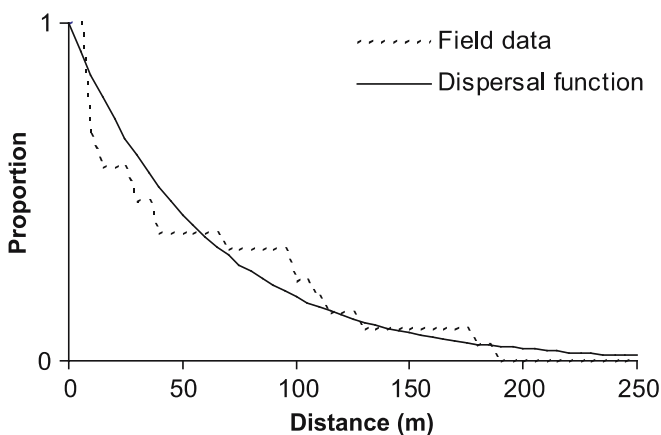

Fig. 3 Proportion of dispersing *O. eremita* individuals with dispersal ranges exceeding certain distances. Pooled data from capture-recapture (Ranius and Hedin 2001) and telemetry (Hedin et al. 2003) ($n = 21$) are compared with a negative exponential function [$P = \exp(-D/60)$, where P is probability that a dispersing individual exceeds the distance D (in meters)]

Fig. 4 *Osmoderma eremita* is a 30-mm-long beetle, here tagged with a radio transmitter. Photo: Jonas Hedin. Reprinted from Hedin and Ranius (2002) with permission from Elsevier

used weigh 0.4–0.52 g, which corresponds to 12–20% of an individual beetle's weight for *L. cervus*, 20–25% for *O. eremita*, and 5–7% for *S. scapanes*.

A great advantage with telemetry is that it is also possible to observe those movements that end in unexpected habitats; this is in contrast with the capture-recapture method by which the only individuals that are recaptured are those that move to habitats where the species is searched for. A possible disadvantage of telemetry is that the radio transmitters may affect the behavior of the individuals. However, when the method has been used, there have been no obvious signs of changed behavior, even for the smallest species (Hedin and Ranius 2002). In the study on *O. eremita*, the beetles were tracked every day, and if a beetle disappeared from the location where it was found at the last observation, it was searched for within a radius of 800 m from that point. Thus, it was not possible to observe movements exceeding 800 m. However, given the results presented in Fig. 3, such movements were probably very rare, if they existed at all. For several *O. eremita* beetles tagged with radio transmitters, contact was lost before the batteries were expected to run out of charge. In some cases this was a result of the transmitters being damaged as a consequence of moisture seeping into them (Hedin and Ranius 2002), but for several individuals it was impossible to rule out the possibility that they had moved too far away to be tracked.

Hedin et al. (2003) observed that 3 of 26 (12%) transmitter-tagged females dispersed, while 5 of 39 (13%) males showed the same behavior. Thus, there was no difference in dispersal rate between males and female beetles. Better data were obtained on the males than on the females because contact was lost for higher proportion of the females. Between 82 and 88% of the adults remained in their natal trees. All observed movements ended up in hollow oaks regarded as suitable habitats for the species that were situated less than 200 m from the natal tree. Only one male was observed to show more than one dispersal (160 m + 20 m) between trees.

Sprecher-Uebersax and Durrer (2001) studied four females and four males of *L. cervus*. They observed several movements for every individual. On the contrary to *O. eremita*, there was a clear difference between sexes: males flew longer distances (often about 200 m per flight), while females only dispersed shorter distances by walking.

Occurrence patterns

A species' occurrence patterns may be the result of colonizations and extinctions in individual habitat patches (Peltonen and Hanski 1991; Thomas et al. 1992) and, as such, these patterns could be used as an indirect measure of colonization rates. The present occurrence patterns, however, are not only dependent on the size of the current habitat and its structure but may also reflect the

situation historically (Hanski and Ovaskainen 2002). Research on nature conservation often focuses on declining habitats. Therefore, the habitat density has often been historically higher than that measured at the time of the study. Because the occurrence pattern results both from the colonization rate and the extinction risk, and is affected both by present and historical characteristics of the landscape (with the latter being more or less unknown), it is often difficult to draw firm conclusions about dispersal from occurrence patterns alone. However, because direct studies of dispersal are usually conducted on a limited area over only a few years, studies of occurrence patterns could constitute a valuable complement, as they reflect the long-term effects of the colonization ability over a larger area.

The relationship between species occupancy and habitat density is dependent on the spatial scale. Thus, several different spatial scales should be considered (as in Rukke and Midtgaard 1998; Kehler and Bondrup-Nielsen 1999). A method has been developed that can be used to compare the strength of the relationship at different spatial scales (Holland et al. 2004). The spatial scale of the colonizations is commonly interpreted from the relationship between occupancy and habitat patch connectivity or isolation. As a measure of isolation, the most commonly used parameter has been the distance to a limited number of neighboring habitat patches that are the closest to each habitat patch (Nilsson 1997; Rukke and Midtgaard 1998; Sverdrup-Thygeson and Midtgaard 1998; Kehler and Bondrup-Nielsen 1999). Information is lost with this measure, however, because it assumes that only a very limited number of habitat patches may be relevant as dispersal sources, while all other habitat patches are irrelevant. Ranius (2000) used the number of hollow trees per stand as a measure of connectivity. This was possible because the hollow trees were clustered into stands. Also in that study the hollow trees were regarded as either relevant (within the stand) or irrelevant (belonging to another stand) with respect to their function as dispersal sources. In many cases it may be more appropriate to use a connectivity measure developed by Hanski (1999), which takes into account all habitat patches that could possibly act as dispersal sources. These patches are weighted in relation to the distance and the expected mean dispersal distance of the study species.

Ranius (2000) found that the occupancy of *O. eremita* per tree was positively correlated with stand size (Fig. 5), but the occupancy per stand was not related to the number and size of the surrounding stands. Combined with data from capture-recapture (Ranius and Hedin 2001), this suggests that dispersal within stands affects the current occupancy pattern, while dispersal between stands is so rare that it does not influence the species' occupancy. Instead, at the larger scale, the occurrence pattern mainly reflects the extinction risk in the stands. For the beetles *Elater ferrugineus* and *Tenebrio opacus* (Ranius 2002a) and the pseudoscorpion *Larca lata* (Ranius and Wilander 2000), which are species
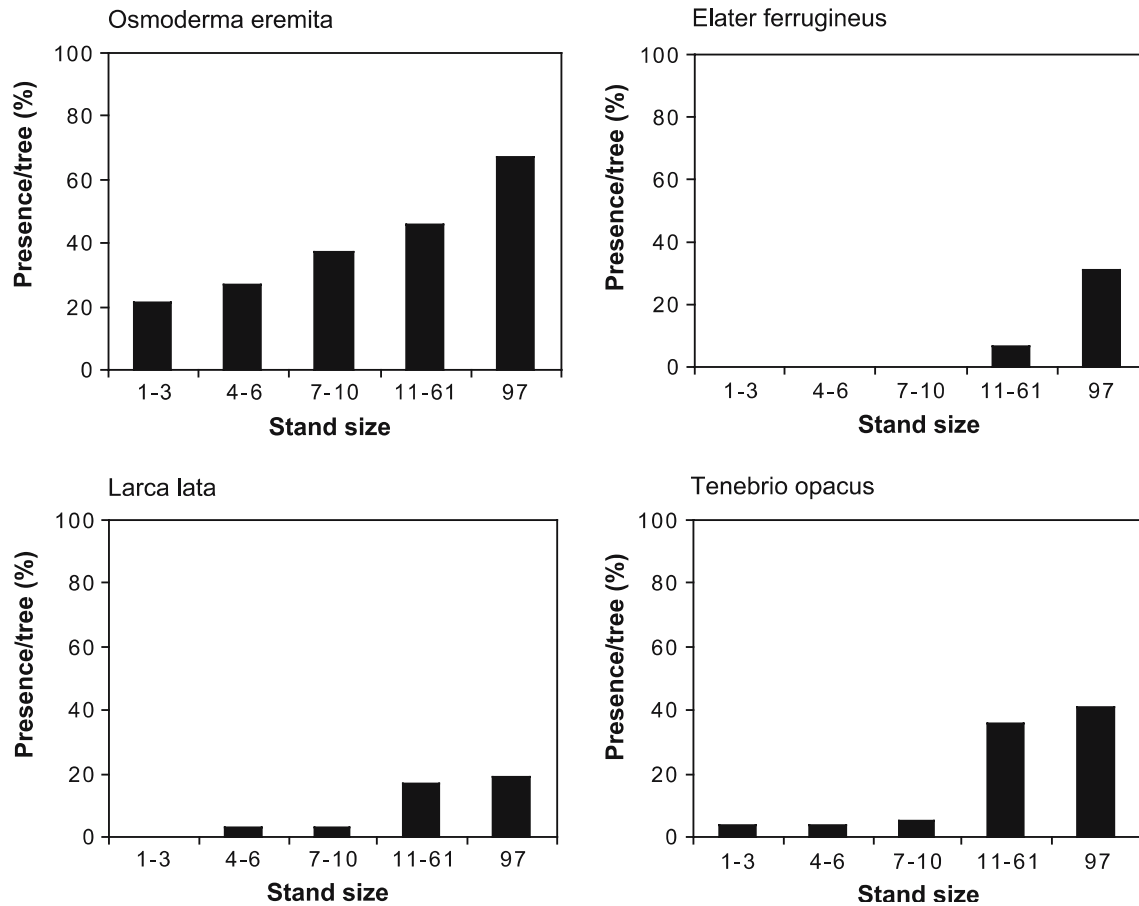
Fig. 5 Frequency of occurrence per tree in relation to stand size for the beetles *Osmoderma eremita*, *Elater ferrugineus*, and *Tenebrio opacus* and the pseudoscorpion *Larca lata* (redrawn from Ranius 2002b). Only species with a significant relationship with stand size are presented here. Stand size is defined as the number of suitable trees within a cluster with a distance of < 250 m from one suitable tree to another

belonging to the same community, a positive relationship between occupancy per tree and stand size was also found (Fig. 5). Because there are no studies on the dispersal or population dynamics of these species, it was more difficult to determine whether this relationship resulted from their limited dispersal between stands or from a higher extinction rate per stand, relative to those species without this pattern (Ranius 2002a). However, an analysis presented below (Table 1) lends some support to the view that *E. ferrugineus* and *T. opacus* have a lower dispersal rate than many other beetle species associated with tree hollows.

In a study of *B. cornutus*, a negative relationship between occupancy and isolation was found at all three spatial scales considered (Kehler and Bondrup-Nielsen 1999). Kehler and Bondrup-Nielsen (1999) suggest that the small-scale pattern may arise from dispersal patterns by walking, while the large-scale pattern arises from dispersal patterns by flying.

Also for *B. reticulatus*, a negative relationship between occupancy and isolation has been observed at a per log scale (Rukke and Midtgaard 1998; Sverdrup-Thygeson and Midtgaard 1998). As previously suggested for *B. cornutus*, this might be a result of dispersal by walking between closely situated logs (Jonsell et al. 2003). However, the effect of isolation was not significant at a larger scale (Rukke and Midtgaard 1998), probably because the beetles tend to fly frequently over long distances (Jonsson 2003) and, consequently, the occupancy per forest island was not restricted by limited colonization.

Thus, for both *B. reticulatus* (Rukke and Midtgaard 1998) and *O. eremita* (Ranius 2000) there was no relationship between occurrence per stand and stand isolation, but different conclusions are drawn. This is because for *O. eremita*, the occupancy per tree was systematically lower in smaller stands (and thus, the species was absent in many of the smallest stands), which would not be the case if the beetles readily moved between trees belonging to different stands. For *B. reticulatus* no similar analysis was conducted by Rukke and Midtgaard (1998), but Jonsell et al. (2003) found no relationship between the species' occupancy per sporocarp and habitat density per forest.

Table 1 Beetle species associated with tree hollows that have been captured in pitfall traps and window traps (Fig. 8) set in the same oak trees ($n = 90$) in south-eastern Sweden

Species[a]	Number of captured individuals[b]	Proportion of individuals captured in window traps (%)[c]	Relationship between proportion present with stand size[d]
Elater ferrugineus	9	0	0.37***
Plegaderus caesus	15	0	–
Tenebrio opacus	37	0	0.32***
Osmoderma eremita	87	1	0.39*
Cryptophagus quercinus	71	1	–
Euplectus karsteni	16	6	–
Dendrophilus corticalis	223	12	–
Ampedus cardinalis	28	14	0.20
Euplectus nanus	6	17	–
Prionychus ater	88	26	−0.03
Ampedus hjorti	39	28	0.18
Procraerus tibialis	16	31	0.17
Pseudocistela ceramboides	56	46	0.22
Allecula morio	151	54	0.17
Cryptophagus populi	5	80	–
Mycetochara humeralis	45	89	–
Pentaphyllus testaceus	11	91	–

[a]Only species present in $> 2.5\%$ of the traps are included
[b]Total number of individuals captured by window traps and pitfall traps
[c]Proportion of these individuals that were captured by window traps (from Ranius and Jansson 2002)
[d]Coefficient and statistical significance (Kendall's tau-*b*; *$P < 0.05$, ***$P < 0.001$) of the relationship between proportion of hollow trees occupied by the species and stand size (from Ranius 2002a)

Genetic studies

Similar to studies of occurrence patterns, genetic studies are useful when assessing the long-term effect of dispersal, also at a larger spatial scale. In a few genetic studies the dispersal of saproxylic invertebrate species have been considered. Jonsson et al. (2003) compared the genetic structure of a common (*B. reticulatus*) and a rare beetle (*O. haemorrhoidalis*) living in sporocarps of a bracket fungi. The genetic differentiation between sites was larger in *O. haemorrhoidalis*, and gene flow seemed to have declined as an effect of recent fragmentation. In contrast, *B. reticulatus* likely moves over large areas and has higher gene flow (Jonsson et al. 2003). Knutsen et al. (2000) also studied *B. reticulatus* and found only – at a larger geographical scale – a very small genetic differentiation between their two study areas. However, they did find a significant genetic differentiation between trees, probably due to a founder effect (Jonsson et al. 2003). For *B. cornutus* also, an increased genetic variance between different logs was found to be an effect of the extinction-colonization process at the log level (Whitlock 1992). Ranius and Douwes (2002) studied the genetic structure of two pseudoscorpion species. These species could obviously not fly between localities, and phoretic dispersal has only occasionally been observed. Despite this, the genetic differentiation was low for the species, both between trees and between sites situated 4–900 km from each other.

Although genetic studies on saproxylic organisms have provided hints about the dispersal rate, there may be alternative explanations for the observed patterns because the observed genetic differentiation not only reflects the current dispersal rate but also bottlenecks in the local populations, extinction-colonization events, historical dispersal rates, among others (Slatkin 1987; Bossart and Pashley Prowell 1998). Another problem with genetic studies is that when rare saproxylic invertebrates are studied, it is often difficult to have a large enough sample size. To date, allozymes and random amplified polymorphic DNA (RAPD) analyses with a limited number of marker loci have been used. Modern molecular techniques [such as amplified fragment length polymorphism (AFLP) genotyping: Mueller and Wolfenbarger 1999] will improve the possibilities to obtain enough resolution even when a small number of individuals is used.
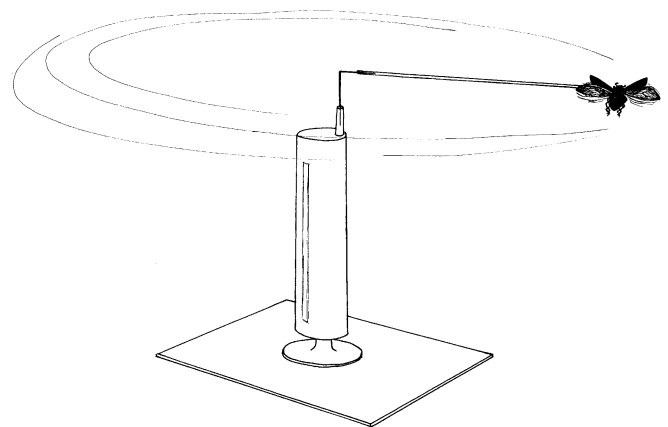

Fig. 6 Principal sketch of a flight-mill that has been used to measure the flight ability of insects (from Jonsson 2005)

Tethered flight

In the laboratory, it is possible to assess the tethered flight of insects in flight-mills (Fig. 6). This method has been used to study the flight capacity and propensity especially for pest species. Forsse (1991) used tethered flight to study how migratory behavior varies among geographic populations of *Ips typographus*. Jonsson (2003) has used tethered flight to compare the flight distance of one rare (*Oplocaphala haemorrhoidalis*) and one common (*B. reticulatus*) beetle species inhabiting sporocarps of a bracket fungus. He found that both species were able to fly for very long time periods, which can be assumed to be translated into long distances. *B. reticulatus* carried out more but shorter flights in comparison to *O. haemorrhoidalis* (Fig. 7).

Because it is not known how much of the flight potential expressed in the laboratory is actually used under field conditions (Forsse and Solbreck 1985), the absolute measures from tethered flight studies may be less informative. However, this method is obviously useful for comparisons of the dispersal biology between populations and species. Moreover, it can be used to understand whether a dispersal range function should be truncated because of physiological limits, or if the maximum possible dispersal range is so large that the function should have no truncation (as supposed in Fig. 3). Tethered flight could provide information on differences in dispersal biology between sexes, and between periods of an individual's life-time (Humphry and Linit 1989), both of which might be useful for interpreting dispersal data obtained by other methods.

Observations of flying individuals

In some cases, observations on flying insects (or the absence of them) have been used to approximate dispersal behavior (Nilsson and Baranowski 1994). The willingness to fly could be studied in a more systematic way in experiments i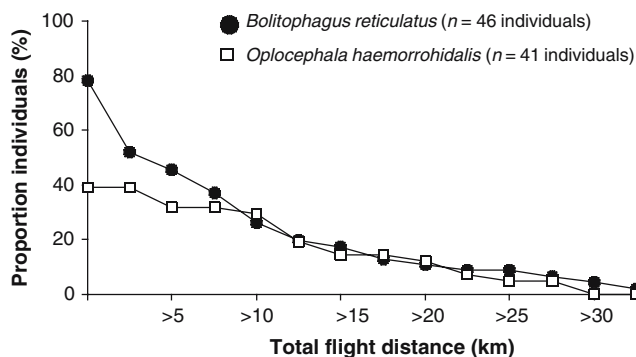n which attempts to take off are registered (Jonsson 2003). Another method to estimate insect flight is to use window traps, which sample flying individuals. However, many other behavioral differences between the species will obviously also influence this estimate.

Ranius and Jansson (2002) compared the results from window traps and pitfall traps set in the same trees (Fig. 8). The pitfall traps were set in tree hollows, and only species associated with that microhabitat (Ranius and Jansson 2002) were considered. By comparing the number of individuals captured by window traps with the number of individuals captured in the same trees by pitfall traps, an estimate is obtained that is related to the species' proneness to fly. The outcome was compared with the relationship between occupancy per tree and stand size observed in another independent survey (Table 1). The strong correlation between the results (Table 1) from these two independent studies supports the view that a low tendency to be captured in window traps did indeed reflect a low dispersal proneness.

Colonization experiments

When metapopulation survival is predicted, it is the colonization rate that is relevant rather than dispersal. A restricted capacity to colonize suitable habitat patches may be the result of a small population size, low dispersal rate, low dispersal range, high dispersal mortality, or a low ability to establish a new population (e.g., due to a limited fecundity or ability to compete with other species).
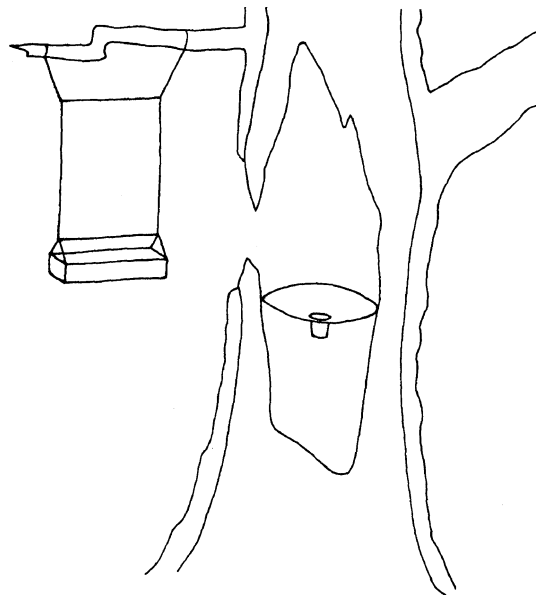

Fig. 7 Proportion of beetle individuals flying as far or further than certain distances. Redrawn from a flight-mill study on *Bolitophagus reticulatus* and *Oplocephala haemorrhoidalis* by Jonsson (2003)

Fig. 8 Two kinds of traps used to collect beetles in the same hollow trees. Pitfall traps were plastic cups placed in the tree hollows. Window traps consisted of a 30×40-cm² (surface area) transparent plastic plate with a tray underneath (figure from Ranius 2002b)

Fig. 9 Sporocarp set out for the purpose of studying the extent at which it becomes colonized by beetles. The sporocarp was collected alive and frozen to ensure that no insects were present at the starting point of the experiment. Photo: Mats Jonsell

Fig. 10 Proportion of sporocarps colonized by *Cis quadridens* (**a**) and *C. glabratus* (**b**) inside (−80 m) and at different distances from the border of an old-growth forest. Redrawn from Jonsson and Nordlander (2006)

Colonization has been studied directly by experimentally arranging empty habitat patches. Whitlock (1992), Jonsell et al. (1999), and Jonsson and Nordlander (2006) used sporocarps of bracket fungi that were collected alive and then frozen in order to kill the insects (Fig. 9). Whitlock (1992) assessed the colonization rate of *B. cornutus*. Jonsell et al. (1999) compared the colonization patterns between species, and found that *Dorcatoma* spp. were better colonizers than *Cis* spp. and that parasitoids appeared to be more affected by distance than their hosts. The colonization rate is a function of the size of the dispersal source, but these authors failed to present any information on habitat amount or population size. Thus, general conclusions cannot be drawn on the colonization rate under different circumstances. Jonsson and Nordlander (2006) studied the steepness of the decline in colonization rate with distance from an old-growth forest. One of their main results was that colonization decreased with distance for *Cis quadridens*, while there was no such trend for *C. glabratus* (Fig. 10). This difference in colonization ability may explain why *C. glabratus* occurs even in managed forests with a low habitat density, while *C. quadridens* rarely appears under similar conditions (Jonsell and Nordlander 2002). Nilssen (1984) conducted a study on a much larger spatial scale. He placed recently cut logs of
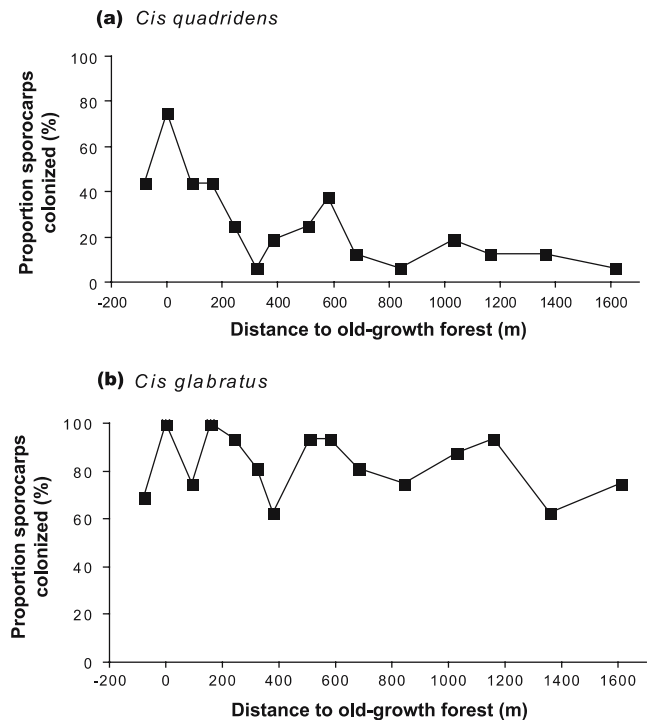
Norway spruce at different distances from the northernmost spruce forest and found that some bark beetles colonized logs situated as far as 171 km from the nearest spruce forests.

Interpretation of dispersal data: combining methods and extrapolating between species and spatial scales

No method provides a complete picture of a species' dispersal biology. Consequently, a combination of several different methods to study dispersal is often useful. One example of a fruitful approach has been the combination of the telemetric and capture-recapture study on *O. eremita*. In the interpretation of telemetry data, the adult life-time obtained from the capture-recapture study was essential (Hedin et al. 2003), while for the interpretation of the capture-recapture study, information about the end-point of dispersals obtained in the telemetry study was required (Ranius and Hedin 2001). Combinations of direct and indirect methods are also productive in that they reveal different aspects of the dispersal biology.

Independent of the method used, the spatial scale of the study may affect the outcome. For instance, in capture-recapture studies, movements over longer distances than the study area will obviously never be detected; instead the migrating individuals just 'disappear' (Koenig et al. 1996). Another example is from the ge-

netic studies of *B. reticulatus*, where Knutsen et al. (2000) found the dispersal to be limited, while Jonsson et al. (2003) concluded that the dispersal was relatively more extensive. To some extent this difference was based on the choice of Jonsson et al. (2003) to also include larger scales in their study. Usually, it is much easier to obtain data from a smaller spatial scale. However, the rare long-distance dispersals are the most important for species persistence at a landscape level.

It might be tempting to extrapolate the results obtained from a small scale design to a larger scale. One example is the conclusion by Jonsell et al. (1999) that "it is reasonable to assume that most of the insects included in this study can colonize substrate within 1 km of their point of origin, and the *Dorcatoma* species should be able to cover even longer distances", even though these researchers had only studied colonizations 0–500 m from the potential dispersal sources. Another example is given in this paper. I estimate the expected number of *O. eremita* dispersing more than 250 m using a dispersal model, even though no such dispersal has been observed. This may be acceptable since information on the dispersal of threatened organisms is urgently needed for nature conservation and, hence, it is better to use preliminary information on dispersal from extrapolations than to provide no estimate at all. However, it is important to point out which information is supported by data from empirical studies and what reasoning is that underpins any extrapolation from such data.

It is impossible to study the dispersal biology of all species because dispersal studies are very time-consuming. Furthermore, it is easier to study dispersal for some species than for others because of the available methods of capture and of systematic survey in a landscape, or available genetic markers. Therefore, dispersal may be studied in some model species, assuming that they are good representatives for whole assemblages of species. This approach involves an extrapolation from a few model species to other similar species.

Extrapolations to other spatial scales and to other species may generate pitfalls that should be avoided. First, because it is often difficult to observe dispersal, early studies tend to suggest low dispersal. When an appropriate method and an appropriate spatial scale has been used, more dispersal is observed (Schneider 2003). This sequence of events has been the case for many butterfly species (Hanski 1999). The second pitfall arises when inappropriate model species are used. In general, it is easier to study common species instead of rare ones. However, we should expect non-threatened species, on average, to be stronger colonizers than threatened species (Kotiaho et al. 2005). Consequently, if studies of non-threatened species are used to understand the dispersal biology of threatened species that have been difficult to study, there is a risk that dispersal would be overestimated. The conclusion "insects are generally characterized by high motility" (Hansson et al. 1992, in a textbook on nature conser-

vation) is logical, if based on those many dispersal studies that have been conducted on pest species and other model species that have been easy to study. However, it could obviously be deleterious for nature conservation if it is also used as a general rule-of-thumb for threatened species with unknown dispersal biology.

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