Both population size and patch quality affect local extinctions and colonizations

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Currently, the habitat of many species is fragmented, resulting in small local populations with individuals occasionally dispersing between the remaining habitat patches. In a solitary bee metapopulation, extinction probability was related to both local bee population sizes and pollen resources measured as host plant population size. Patch size, on the other hand, had no additional predictive power. The turnover rate of local bee populations in 63 habitat patches over 4 years was high, with 72 extinction events and 31 colonization events, but the pollen plant population was stable with no extinctions or colonizations. Both pollen resources and bee populations had strong and independent effects on extinction probability, but connectivity was not of importance. Colonizations occurred more frequently within larger host plant populations. For metapopulation survival of the bee, large pollen plant populations are essential, independent of current bee population size.

Keywords: metapopulation; connectivity; area; pollination; solitary bee; Andrena hattorfiana

1. INTRODUCTION

Currently, the habitat of many species is fragmented, resulting in small local populations with individuals occasionally dispersing between the remaining habitat patches (Thomas & Kunin 1999). During the last two decades, the dynamics of such populations have been studied within the metapopulation concept (Hanski & Gaggiotti 2004). Metapopulations survive when local population extinctions are balanced by recolonizations, but there are few studies of these essential processes. Most studies use habitat patch area and isolation in conjunction with occupancy when modelling population viability. Based on general principles, colonization rate is expected to decline with distance to source populations, whereas extinction rate is assumed to increase with declining habitat patch size. Patch size is often used as an easily measured surrogate of habitat quality (available resources) and local population sizes.

Many models have recently been developed to assess the survival of metapopulations, most often based on occupancy patterns of local habitat patches on at least two occasions (Hanski & Gaggiotti 2004). These models have been used in nature conservation, but few studies have examined the basic assumption that habitat patch size is a good surrogate for local population size (cf. Talley 2007). Critics have argued that habitat quality of the patch is as important as patch size per se (Thomas et al. 2001). This relates to sink–source dynamics, similar to metapopulation dynamics. In sink–source models, some habitats are of lower quality with a low reproductive success, while other habitats are of better quality with higher reproduction success (Pulliam 1988; Pulliam & Danielson 1991).

In a recent study, extinction patterns were predicted more effectively by local population size than by patch area (Pellet et al. 2007). However, local population size in a patch may vary strongly between years, even in a stable habitat patch network, especially over many generations (Thomas et al. 2002). In years when relatively few individuals inhabit a large patch, the resources per capita are larger and may positively influence reproductive success and/or survival for the next generation. Thus, extinction probability may decrease in patches of high habitat quality, patches with large local population sizes and patches of large size. Similarly, when dispersing individuals encounter an empty large or high-quality patch, their propensity to stay and reproduce may be higher than in a small or low-quality patch. Even with random dispersal, a large habitat patch will be colonized by chance more often by dispersing individuals than a small patch. Thus, colonization probability can increase with patch size and/or quality.

As pollinators, solitary bees are key components in terrestrial ecosystems, and they are essential for economic as well as ecological reasons (Matheson et al. 1996; Murren 2002; Westphal et al. 2003). Recent studies demonstrate that specialized haplodiploid solitary bee species may have high turnover rates for genetic reasons (Zayed & Packer 2005). Here, we explore whether extinction and colonization patterns in a solitary bee metapopulation are related to habitat quality, local bee population size, habitat patch size and isolation over 4 years.

2. MATERIAL AND METHODS

(a) Study area

The study area in Stenbrohult parish in southern Sweden (56° 37’ N, 14° 11’ E) is forest-dominated with agricultural land occupying 5 per cent of the study area, mainly consisting of seminatural grasslands. Local bee populations were investigated in all suitable habitats over 4 years in an area of 80 km². The study area is adjacent to the large lake Möckeln in the West and built-up areas and an exploited bog in the

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South. Coniferous forests dominate to the North and East. Thus, the landscape surrounding the study area has a low proportion of agricultural land.

(b) Studied species

We studied the specialized bee *Andrena hattorfiana* (Fabricius) for which the main pollen source in Northwest and Central Europe is *Knautia arvensis* (L.) Cault. (Dipsacaceae). In the study area, the bee only collects pollen from *K. arvensis*. The bee species is large with a length of approximately 14 mm and easily identified in the field. Females differ from males in both appearance and behaviour and can easily be sex determined in the field. *Andrena hattorfiana* has declined in several European countries and a pollen budget has been described (Larsson & Franzen 2007a). The ecology of *A. hattorfiana* is relatively well known and the bee is active foraging for pollen from mid-June until mid-August and has one generation per year. The pollen plant and bee phenology are well synchronized. The average active foraging span has been estimated at 14.2 days, and the longest recorded foraging span was 44 days (Larsson & Franzen 2007b). In a plant population exposed to other flower visitors, *A. hattorfiana* required on average 47 *K. arvensis* stalks (= 16 plant individuals) to produce one offspring (Larsson & Franzen 2007a). The reproductive rate is low and one *A. hattorfiana* female produces only five to 10 brood cells each with one egg. It is not known whether a female can make more than one nest in a lifetime. The bee has a sedentary behaviour with short foraging ranges around the pollen resource, usually within 50 m, and only 2 per cent of marked bees dispersing between habitat patches as defined below (Franzen et al. 2009). Thus, in the study area, the majority of the bee individuals forage for pollen, mate and nest in the same patch. The males fly around inflorescences of *K. arvensis* in a typical mating flight, searching for females to mate with. Mating takes place on the inflorescence or in the air and lasts only up to a few seconds (M. Franzen 2004, unpublished data). The males hatch some days before the females, are less easy to find and probably have a shorter lifespan compared with the females.

The study species is an example of a highly specialized haplodiploid species with an expected high turnover rate compared with diploid species (Zayed & Packer 2005; Zayed et al. 2005). Haplodiploid organisms have been considered immune to genetic load impacts because deleterious alleles are readily purged in haploid males. However, single-locus complementary sex determination ancestral to the haplodiploid solitary bees imposes a substantial genetic load through homzygosity at the sex locus that results in the production of non-viable or sterile diploid males. This increases the risk of inbreeding depression. Thus, haplodiploids are more, rather than less, prone to extinction for genetic reasons.

The pollen resource (plant population size) was estimated by counting all *K. arvensis* stalks with flowers or flower buds at each patch once per season. The plants are at the same phenological stage with new flower heads appearing regularly in the study area from June to August. The number of flower stalks in each habitats defined above was used to estimate the number of bees in the surrounding area. Connectivity was also analysed with radii of 300–500 m around each patch, but this did not change the result (results not presented). Further, a connectivity measure that includes the distance to the nearest occupied patch was tested with a similar result.
distance to all other patches, which is 1200 m (table S1, electronic supplementary material). The distances between the habitat patches were 100–9300 m. In an extensive mark–release–recapture study in the study area, the mean movement distance was less than 100 m and the maximum observed dispersal distance was 1 km (Franzén et al. 2009).

(c) Spatial autocorrelation
The non-independence of data caused by spatial structure can cause analyses to be generous, and even weakly correlated variables may appear to yield significant coefficients owing to the confounding effects of space. The level of significance is important when trying to understand the effect of different predictors on a response variable, such as whether population size will explain spatial variation in the number of transect counts performed in mid-season at each patch using the t-test. Colonizations and extinctions occurred independent of the number of transect counts performed in mid-season (colonizations; \( t = -0.55, p = 0.59, d.f. = 71 \) and extinctions; \( t = 0.93, p = 0.35, d.f. = 114 \)). To test whether there is a higher probability of detection at intensively visited patches, extinctions and colonizations were related to intensively visited (3–6 transect surveys in mid-season) habitat patches. No such effect was found (colonizations; \( t = 0.75, p = 0.27, d.f. = 71 \) and extinctions; \( t = 0.43, p = 0.65, d.f. = 114 \)). All statistical analyses were performed in SPSS 14.0. Means are presented with ±1 s.e.

3. RESULTS
The pollen plant *K. arvensis* occurred at 63 patches, covering 1.83 per cent of the total study area, with a mean patch area of 1.28 ± 0.19 hectares (figure 1). In 2003–2006 the bee occurred at 54 (totally 1266 individuals), 24 (313 individuals), 40 (568 individuals) and 13 (75 individuals) habitat patches. The bee occupied 10 (16%) of the 63 habitat patches all 4 consecutive years (2003–2006) (figure 2, table S2, electronic supplementary material). The largest local population was the one consisting of more than 20 female individuals all 4 years (334, 132, 233 and 23 individuals). In total,
Table 1. Colonizations and extinctions was analysed against patch characteristics using the listed variables and years. Variables in brackets (x) analysed as alternatives to the connectivity measure (bees in surrounding 3 km² year t) and were included in the same model instead of another connectivity measure.

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<tr>
<td>year</td>
<td>t</td>
<td>t – t – 1</td>
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<tr>
<td>patch area (log 10-transformed)</td>
<td>x</td>
<td>x</td>
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<tr>
<td>bee population size (log 10-transformed)</td>
<td>x</td>
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<td>plant population size (log 10-transformed)</td>
<td>x</td>
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<td>bees in surrounding (3 km²)</td>
<td>x</td>
<td>(x)</td>
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<tr>
<td>bees in surrounding (12 km²)</td>
<td>(x)</td>
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Table 2. Correlation matrices presenting significance levels (p-value) and correlation coefficients (slope) between the independent variables. Correlation based on data from 2004 for all 63 patches.

<table>
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<th>patch area</th>
<th>host plant population size</th>
<th>connectivity (3 km)</th>
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<tbody>
<tr>
<td>host plant population size</td>
<td>slope 0.259</td>
<td>p-value 0.038</td>
<td>—</td>
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<tr>
<td>connectivity (3 km)</td>
<td>slope −0.187</td>
<td>p-value 0.246</td>
<td>−0.246</td>
</tr>
<tr>
<td>bee population size</td>
<td>slope 0.212</td>
<td>p-value 0.093</td>
<td>0.613</td>
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4. DISCUSSION

Both the size of the local pollen plant population and the local bee population had strong and independent effects on the local extinction probability of the solitary bee (figure 3). Solitary bees provide the opportunity to explore the interacting effects on extinction risks of patch area, population size and resource availability that are impossible to explore in most other insects. For metapopulation survival of the bee, large host plant populations are essential. These results are important since a general decline of both bees and insect-pollinated plants has been found (Biesmeijer et al. 2006). For the integrity of ecosystems and survival of both bees and plants, attention should be given to crucial factors for viable metapopulations of bees. Our results emphasize the importance of large local populations of those plant species on which specialized pollinators depend. Further, our results carry a general message to metapopulation studies: patch quality and local population sizes are not surrogates for each other, but both may be important factors in metapopulation dynamics.

Other studies separating the effects of habitat patch size and local population size on colonization and extinction probabilities are few (cf. Talley 2007). Our results stress that the factors generating population turnover can be additive and complex. Patch area might be more important than population size (or vice versa) for extinction and colonization patterns in different situations and species. Between-patch dispersal could balance local extinctions by colonizations. In our study area, no evidence for a rescue effect sensu (Brown & Kodric-Brown 1977) was evident.

The mechanism of a higher bee extinction risk in small host plant populations, even when bee population size has been accounted for, could be that bees are pollen-limited in small host plant K. arvensis populations to a much larger extent compared with larger host plant populations. Other pollen-foraging flower visitors might have a higher visitation frequency in small plant populations. This has been found in the plant Viscaria vulgaris, also visited by a diverse insect fauna (Jennersten & Nilsson 1993). Additionally, a possible high visitation frequency of other flower visitors in small K. arvensis populations may induce bee dispersal. We suggest that relatively low pollen availability in small K. arvensis populations could be the determining factor influencing both extinction and colonization processes in A. hattorfiana.
Colonization probability increased with pollen resources measured as host plant population size. It is more probable that large patches become colonized by chance (Simberloff 1978) and large plant populations might be found more easily if dispersal is non-random (Thomas 1994; Conradt et al. 2000). We did not find any effect of connectivity on colonization probability. The lack of connectivity effects suggest that the bees are relatively good at finding suitable patches over the distances covered in this study (Moilanen & Hanski 2001; Moilanen & Nieminen 2002; With 2004). However, connectivity measures used in models might not reflect how the species perceive connectivity. Patch area, population size and matrix influence real connectivity (Moilanen & Hanski 2001; Ricketts 2001; Fleishman et al. 2003; Sutcliffe et al. 2003). A tendency towards a more frequent extinction occurring at patches surrounded by many bees was observed, suggesting that the bees temporarily colonize patches with low habitat quality (figure 3). It is possible that the bee has a source–sink dynamic where some patches are of lower quality with a high turnover rate and other source populations have a high quality with high reproductive success (Pulliam 1988; Pulliam & Danielson 1991). In fact, the 10 local populations that occupied 4 consecutive years (2003–2006) might represent source populations. The temporary use of low-quality habitats are important to consider when assessing the conservation status and modelling population persistence. More studies are required to understand whether and how connectivity and source–sink dynamics influence the studied population.

Extinctions and colonizations showed no evidence of spatial synchrony (table S1, electronic supplementary material). The connectivity measure was spatially structured with a significant spatial autocorrelation. This was expected because areas surrounding the patches are considered in the connectivity measure. This procedure increases the spatial correlations and is similar to the reducing degrees of freedom, since the patches depend on each other (Moilanen & Nieminen 2002; Brooks 2003). We judged it unnecessary to integrate the spatial information into the regression models because the patches were spatially independent of each other (table S1, electronic supplementary material).

The probability of detection is crucial in metapopulation studies (e.g. Moilanen 2002). In species with a low probability of detection, apparent extinction and colonization patterns can be an effect of pseudoturnover (Nilsson & Nilsson 1985; Moilanen 2002), i.e. small populations still occur at a patch but are not detected. Even small A. hattorfiana populations appear to be easily detected, and our data suggest a high probability of detection. The discrepancy between different surveyors was very low. Comparing the occupancy pattern of bees in habitat patches between two different independent surveyors reveal that within 40 visited patches with three or more mid-season visits by two independent surveyors, only six patches (15%) differed in occupancy between the surveyors. These were observations of single bee females and thus detection error is low.
the model: patch area: $B = -0.24, p = 0.82$; bee population size: $B = -2.99, p = 0.035$, plant population size: $B = -4.58, p = 0.003$; bees in surrounding 3 km$^2$ in 2005: $B = -0.009, p = 0.24$. Logistic regression 2005–2006, all variables included in the model: patch area: $B = -2.87, p = 0.15$; bee population size: $B = -5.39, p = 0.009$; plant population size: $B = -5.83, p = 0.044$; bees in surrounding 3 km$^2$ in 2005: $B = -0.06, p = 0.34$. Extinctions in 2005 were not analysed statistically owing to few observations.

5. CONCLUSION

Determining the factors influencing local extinction and colonization events are of crucial importance to understanding the regional dynamics of populations as well as developing sound conservation measures. Indeed, many rare and endangered species occur in small local populations in highly fragmented habitats. Our study highlights that in a species where only 1.8 per cent of the landscape consists of suitable habitat patches, patch quality and local population size were important factors independent of each other, influencing metapopulation dynamics. On the other hand, habitat patch size had no additional predictive power. We, therefore, suggest metapopulation studies to explore these three important potential factors for extinction and colonization probabilities.

We tentatively suggest that the extinction risk of local populations of solitary bees may be high compared with many other taxa. In the German region studied in detail, Baden-Württemberg, 57 per cent of the recorded 429 bee species are endangered or close to extinction (Westrich 1990). Over 5 per cent (15 species) in Sweden of the Apoidea fauna have become extinct, with similar or higher values in several other countries (Matheson et al. 1996). The indicated elevated extinction proneness of solitary bees, combined with the keystone pollinator services that they provide, makes them valuable when assessing the health of natural and agricultural ecosystems. For metapopulation survival of bees, large pollen plant populations appear to be essential.

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