ORIGINAL PAPER

Small local population sizes and high habitat patch fidelity in a specialised solitary bee

Markus Franzén · Magnus Larsson ·
Sven G. Nilsson

Abstract *Andrena hattorfiana* is a rare solitary bee which has declined during the last decades throughout western Europe. It is specialised to forage pollen from plants of the family Dipsacaceae. Knowledge of distribution, dispersal propensity, and local population sizes is essential for successful conservation of *A. hattorfiana*. The investigated local bee populations ($n = 78$) were dominated by small local populations and 60% were smaller than 10 female individuals and 80% were smaller than 50 female individuals. The area of the median occupied habitat patch was 1.25 hectare and harboured 7 female bees. Mark-release-recapture studies of female *A. hattorfiana* revealed a sedentary behaviour. Among pollen-foraging female bees the average registered distance moved was 46 m. The patch emigration rate was about 2%, with an observed maximum colonization distance of 900 m. Only 10% of the individuals crossed areas without the pollen plant within grassland patches, such as unpaved roads, stone walls and small tree-stands, even if these areas were less than 10 m wide. This study shows that solitary bees can occur in local populations of extremely small size and they have a sedentary behaviour. These are features that usually increase the risk of local population extinction.

M. Franzén (✉) · S. G. Nilsson
Department of Animal Ecology, Ecology Building, Lund University, Sölvegatan 37, 223 62 Lund, Sweden
e-mail: Markus.Franzen@zooekol.lu.se

S. G. Nilsson
e-mail: Sven.Nilsson@zooekol.lu.se

M. Larsson
Department of Plant Ecology, Evolutionary Biology Centre, Uppsala University, Villavägen 14, 752 36 Uppsala, Sweden
e-mail: Magnus.Larsson@ebc.uu.se

Introduction

Temperate European agricultural landscapes changes dramatically, and require distinct and appropriate management to prevent further impoverishment of the flora and fauna. This is especially urgent for solitary bees and other pollinating insects that provide important ecosystem services (Kremen et al. 2007). Many endangered species occur in metapopulations in highly fragmented habitats (Hanski and Gaggiotti 2004). The between habitat patch dispersal propensity and the size of the local populations are key parameters to determine the viability of metapopulations (Lamont and Klinkhamer 1993; Hanski et al. 1996). Often local populations are distributed with few small, many medium and few large sized populations (Thomas and Harrison 1992; Hanski 1994). However, many small local populations and few large ones can be found among some threatened species (Harrison et al. 1988; Pimm et al. 1988; Hanski et al. 1995; Stith et al. 1996; Carlson and Edenhamn 2000). Extinction risk is usually associated with population size or its surrogate patch size (Harrison 1991; Hanski and Singer 2001; Abrams 2002). Until now, these patterns and processes have mainly been examined for species from a few well known taxonomic groups, e.g., plants, birds and butterflies (Thomas et al. 2004).

Some specialised solitary bees may occur in very small local populations (Oertli et al. 2005; Müller et al. 2006; Larsson and Franzén 2007), and forage over a few hundred metres only (Kapyla 1978; Eickwort and Ginsberg 1980; Gathmann and Tscharntke 2002). These bees can

remember floral resources and the flight distance is often related to the density of the pollen plant (Levin and Kerster 1969), but flower availability can change rapidly due to management of their grassland habitats. This pattern of short local movements of solitary bees is contrary to the social bumblebees and honeybees, where workers can forage over several kilometres (Goulson and Stout 2001). For metapopulation modelling it is important to know when, how often and why dispersal occurs, but this is often unknown and difficult to study, especially in small populations (Koenig et al. 1996; Franzén and Nilsson 2007). The aim of this study was to describe the population structure and movement patterns for females of the declining solitary bee *Andrena hattorfiana* by estimating the size of local populations, and examining within-population movements and dispersal patterns between local populations.

Methods

Study species

Andrena hattorfiana (Fabricius) is highly specialized and its main pollen source in north-western and central Europe is *Knautia arvensis* (Dipsacaceae) (L.) Coult. (Westrich 1990; Müller et al. 1997; Pekkarinen 1998). *A. hattorfiana* is a large and conspicuous solitary bee with a size similar to the honey-bee (female body length is 13–16 mm). The bee is active in our study area from mid June to August and across the whole day (ca. 09:00–18:00), and is easily recognisable in the field from a distance of up to 5 m due to its distinctive coloration with no other similar species. Females forage for pollen during the daytime between ca. 10 and 17 (Larsson and Franzén 2007). Each female constructs a nest in the ground and produces five to ten broodcells, each with one egg and pollen for its development, in her life-time (Larsson and Franzén 2007). This bee species has declined and is currently red-listed in several countries in north-western Europe, including Sweden (Gärdenfors 2005). This decline is suggested to be the result of a reduced abundance of the pollenplant due to the development towards intensively managed larger farm units and abandonment of traditionally managed hay meadows during the past 50 years (Westrich 1990; Falk 1991). Mining bees (*Andrena* spp.) are often parasitized by host specific cleptoparasitic bee species of *Nomada* spp., which can parasitize a large proportion of brood cells in local populations (Linsley and MacSwain 1955). *Nomada armata* Herrich-Schäffer, which occurs in the study areas, is a cleptoparasite on its single host-species *A. hattorfiana*.

The pollen plant *K. arvensis* is perennial and gynodioecious, i.e., populations are composed of individuals having female flowers that only produce nectar, and individuals having hermaphroditic flowers that produce both nectar and pollen. The inflorescences attract a broad spectrum of nectar-feeding, pollen-feeding and pollen-collecting flower-visitors (Knuth 1899; Larsson 2005). The herb is common throughout southern Sweden in pastures, road-sides, edges of ditches, meadows and forest edges, but varies temporally and spatially in abundance between years (Tyler and Olsson 1997).

Study-area

We studied the solitary bee *A. hattorfiana* in two separate study-areas in southern Sweden. The study-area in Småland, the central part of Stenbrohult parish in southern Sweden (56°37′N, 14°11′E), covers 80 km² including some lakes and borders the large Lake Möckeln in the west and forest-dominated land to the south, east and north. Numerous small farms occur throughout the region, but only a low proportion of our study-area consists of agriculturally intensively managed fields (1%). There are some substantial areas of semi-natural grassland habitats (3.5% of land cover), which include pastures mainly grazed by cattle and recently abandoned pastures. Such grassland habitats are centred around the small farms, providing small habitat islands in a dense forest matrix, mainly dominated by spruce *Picea abies*. The distances between the farms are often about 1 km. Two nature reserves with traditionally managed hay meadows with late harvest, each with about 5 hectare of hay meadow, are situated in the study-area, and these meadows have a rich associated flora (Nilsson and Nilsson 2004). The study-area on the central parts of the Baltic island of Öland (56°40′N, 16°36′E) covers approximately 200 km² and is dominated by arable fields and pastures, while forest patches are mainly deciduous.

Definition of local populations

We define a habitat patch as the local plant-population of *K. arvensis* with 20 flowers or more (the bee was never found in smaller patches that were searched in other studies in Småland; Franzén and Nilsson 2007). A habitat patch was regarded as distinct if groups of the pollen plant were separated by more than 100 m. Plant patches separated by tall tree stands that provided an additional barrier were regarded as separate if the distance between them were 75 m or more. The bees foraging in a habitat patch were defined as a local *A. hattorfiana* population. We define dispersal as a movement between habitat patches by one individual.

Survey-walks

The total number of habitat patches occupied by *A. hattorfiana* was 78, 13 on Öland and 65 in Småland. Survey-walks were performed on all potential habitat patch with the pollen plant ≥3 times per mid-season, during at least one of the years 2003–2005. In this study we only used survey-walks from mid-season to reduce the variance in the number of bees recorded. Mid-season started in the end of June or beginning of July depending on local weather conditions and lasted approximately one month. Mid-season starts when the day-to-day new bee individual emergence increases rapidly and stops when number of foraging bee individuals decreases rapidly. The mid-season was 23 June to 2 August 2003, 25 June to 5 August 2004 and 19 June to 29 July 2005. Survey-walks were performed by observing foraging bees on the pollen plant *K. arvensis*. During each survey-walk, the total number of observations of female *A. hattorfiana* was recorded. The mean number of bees per survey-walk and season at each patch was calculated. The mean number of observations per survey-walk was correlated with the estimated local population size obtained from mark-recapture ($r = 0.99$, $P < 0.001$) (see Larsson and Franzén in press). An estimation of the local bee population size in each patch was made from the mean number of observed bees per survey-walk in mid-season using the equation $R = e^{0.642 + 1.61 \cdot \text{Ln}(T)}$ where, T is the number of observed *A. hattorfiana* per average survey-walk and R is the predicted bee population size (Larsson and Franzén in press). For patches studied more than one year (three on Öland and 42 in Småland) an annual mean number of bees per patch were calculated to avoid pseudoreplication (for primary data see Franzén 2007). Each survey-walk started at a random spot within a patch and included the entire patch. The observer walked slowly (ca 1.5 km/h) and surveyed flowering inflorescences of *K. arvensis* within a radius of approximately 5 m. During each survey-walk each inflorescence in the process of flowering was examined once and the bees were counted. Survey-walks required from 20 to 55 min at each patch depending on patch size and the density of the pollen plant *K. arvensis*.

The survey-walks were only performed between 10:00 and 17:00 local time, but not in unfavourable weather conditions such as rain (and within 1 h after rainfall) temperatures lower than 17°C, or winds stronger than approximately 4 m/s.

Mark-release-recapture

Mark-release-recapture (MRR) was performed to study local movements and dispersal patterns of the bees. Female bees were caught by a hand-held butterfly net and marked with a day and patch specific colour or combination of colours (12 colours manufactured by Humbrol Ltd.) on the thorax by the use of an insect pin. All marking was performed immediately after catching and the bee then was released. Capture, marking and release of one bee individual required approximately 11 s. Re-sighting was often made without capturing individuals as the colours were recognised by eye or by using a short-distance binocular.

Within-patch movements

To study movements within local bee populations, MRR studies were performed at two localities with large bee populations. Each patch was divided into sub-areas where the pollen plant-population was separated by a road, wall, trees or a field-strip. This part of the study took place in 2003 at Arontorp (Öland) and in 2004 and 2005 at Höö (Småland). Bees were marked with sub-area specific colours to detect movements, and populations were studied in suitable weather conditions as stated above. Arontorp was visited 12 times in 2003 (22 June–20 July). The locality at Höö was visited 12 times in 2004 (28 June–6 August) and 9 times in 2005 (1 July–27 July). The two localities consisted of five sub-areas each, where the pollen plant occurred.

Between-patch dispersal

To detect dispersal (movements) between patches MRR studies were performed in all potential habitat patches in the Stenbrohult study-area. This included all patches with more than 20 flowers of the pollen plant *K. arvensis*, since all potential sites were searched for this species. The bees were marked as described above. All habitat patches with bees and the pollen plant were visited regularly, each second or third day during suitable weather conditions in 2004 (23 June–9 August) and 2005 (28 June–28 July). In Småland, every day with suitable weather, all semi-natural grasslands were extensively surveyed for other pollinating insects, but *A. hattorfiana* was never seen outside patches with the pollen plant *K. arvensis* (unpublished data).

Analysis

Rates of movement and dispersal were calculated as the number of individuals transferring between habitat patches divided by the sum of the number of recaptured individuals in all patches. The marking procedure limited the possibility to know the exact number of individuals recaptured

in the same patch as where marked. When the exact number of recaptured individuals was not known, because markings were specific only to day and individual patch/sub-area, we use the minimum number of individuals. Mean values are given with ± one standard error (SE).
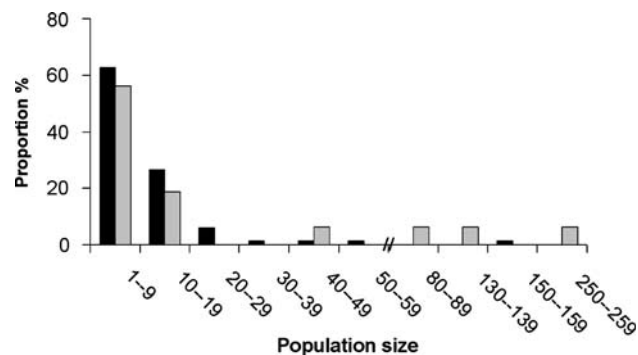
Results

Local bee population sizes

In both regions over 80% of the local populations were estimated to contain less than 50 female individuals (Fig. 1). The arithmetic mean local female bee population size in Småland was 11.3 ± 1.99 and the median population was 7 individuals ($n = 65$) and on Öland the mean local female bee population was 35.3 ± 17.5 and the median population was 4 individuals ($n = 13$). The population sizes were not normally distributed (K-S, Småland, d = 0.30, $P < 0.001$ and Öland, d = 0.38, $P < 0.001$ and Fig. 1).

Within patch movements

Andrena hattorfiana movements were restricted to certain sub-areas within habitat patches as defined above (Fig. 2). At Höö (Småland) 80 female bees were marked in 2004 and 43 recaptures were made. In 2005, 104 females were marked and 52 recaptures were made (Fig. 2). The mean distance of movements was 33 m (median 52 m, min. 10 and max. 83). At Arontorp (Öland) 171 females were marked and 57 recaptures made. The mean distance moved was 58 m (median 76 m, min. 10 and max. 130). There were only a few short movements of individuals between closely situated sub-areas with the plant *K. arvensis* and 11% ($n = 9$, 2004; $n = 6$, 2005) were found to move

between different sub-areas with pollen plants at Höö and at least 7% at Arontorp ($n = 8$, 2003). In Arontorp and Höö only one individual moved between sub-areas with pollen plants located over 50 m from each other (120 m) (Fig. 2). Small areas without pollen plant (less than 10 m wide) as unpaved roads, stone-walls, and small tree stands we interpret as barriers and prevented local movements.
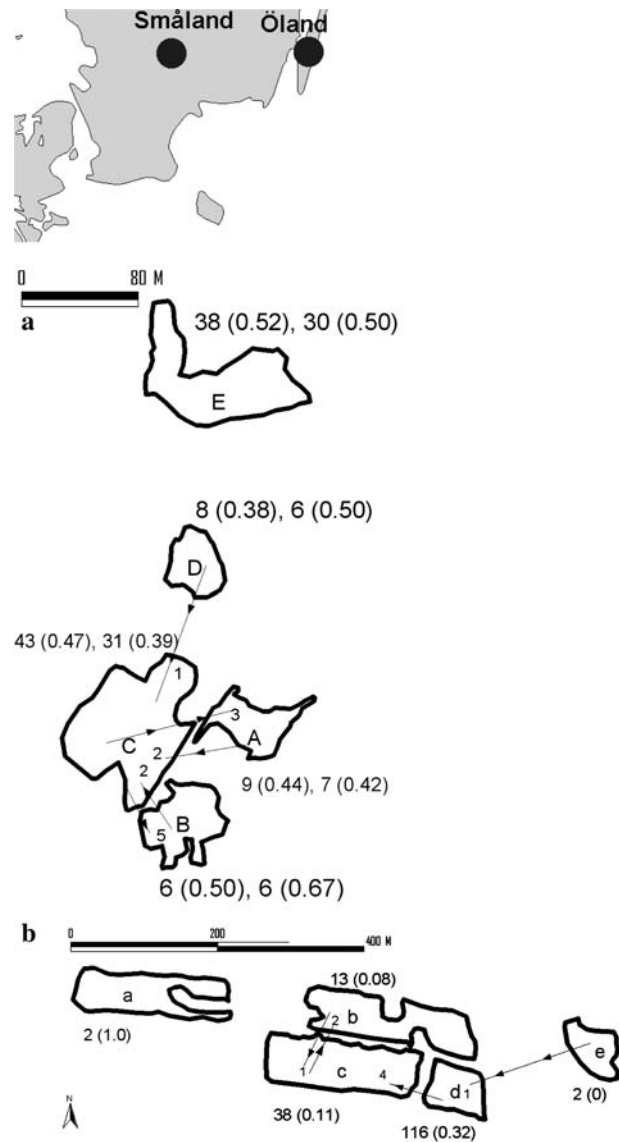
Fig. 2 The two study sites in southern Sweden divided into sub-areas, with presence of the pollen plant *Knautia arvensis*, shown in detail and surrounded by lines. The number of marked female *Andrena hattorfiana* individuals, the proportion of recaptured individuals (in brackets), the location and direction of the movements at (**a**) Småland Höö, in 2004 followed by data for 2005. (**b**) Öland Arontorp, in 2003. The numbers inside each sub-area denote the number of individuals arriving to the sub-area

Fig. 1 The distribution of local bee population size classes of female *Andrena hattorfiana* in Småland (black bars, $n = 65$) and Öland (grey bars, $n = 13$). Note that >80% of the local populations consisted of <50 individuals

Between-patch dispersal

In the Stenbrohult area 327 females of *A. hattorfiana* were marked and 153 recaptures made in 33 habitat patches in 2004 whereas 393 females were marked and 117 recaptures made in 38 patches in 2005. In total 720 females were marked and 270 recaptures made in 43 local populations. The mean habitat patch size was 1.25 ± 0.17 hectare with a mean edge to edge within patch distance of 113 ± 7.9 m. The distance to the nearest other habitat patch was on average 325 m (min. 100, max. 1500). The mean distance moved by *A. hattorfiana* females was 119 m (median 131), using the patch edge to edge distance as the movement distance for recaptures within the patch and the distance between patches for dispersal between them. The emigration rate was 2%; only two females transferred between two patches, both with a distance travelled of at least 900 m. These two between patch dispersal events took place when the original habitat patch was mown late in July 2004 and all floral resources were removed.

Discussion

The majority (>80%) of all local bee populations were smaller than 50 females (Fig. 1). The low reproductive rate of *A. hattorfiana* (one offspring produced per day in weather suitable for foraging and five to ten offspring per life-time) (Larsson and Franzén 2007) might be representative for most specialised solitary bees. This results in extremely small population sizes that probably involves frequent events of extinction (cf. Michener and Rettenmeyer 1956; Giovanetti and Lasso 2005). When the local pollen plant resource becomes inadequate, *A. hattorfiana* and other specialised bees must forage over larger distances, even if it is energetically more expensive to do so (Stephens and Krebs 1986). Being specialised to limited pollen resources of one plant species may cause increased costs when foraging, and thus reduce local bee population size.

Small local populations influence population processes, notably the risk that populations become extinct (Pimm et al. 1988; Schoener and Spiller 1992; Hanski et al. 1994). In species where most local populations consist of a few individuals, as we found in *A. hattorfiana*, the extinction risk is substantial from stochastic, demographic and genetic reasons. Stochastic events such as extreme weather situations can destroy nests (Michener and Rettenmayer 1956), and in small solitary bee populations a high frequency of parasitism and male biased sex ratio can eliminate whole local populations (Bischoff 2003). Population bottlenecks can also increase extinction risk (Frankham et al. 1999; Zayed et al. 2004). In contrast, *Andrena vaga* among other

bee species, can nest in colonies consisting of thousands female individuals (Bischoff 2003).

The fidelity of foraging *A. hattorfiana* to a suitable habitat patch was very high and the movements within and dispersal between the patches were low. A foraging range of <130 m and generally below 50 m was found in this study. This is similar to other studies where foraging has been limited to <300 m among solitary bee species (Kapyla 1978; Gathmann and Tscharntke 2002). Bees acquire and possess a general landscape memory (Gathmann and Tscharntke 2002) and thus foraging can be limited to suitable floral resources close to their nest. A positive relationship between average foraging distances and the body size of the bee species has been suggested for solitary bees (Gathmann and Tscharntke 2002; Greenleaf et al. 2007). *A. hattorfiana* (one of the largest solitary bee species) might be less mobile than its body size predicts because of the high degree of specialisation (cf. Westrich 1990). Female individuals may disperse over some distance, at least over 1 km, suggesting that isolated patches can be (re)colonised. A longer possible dispersal event of an unmarked bee was observed in Stenbrohult out on a peninsular in a large lake to a previously unoccupied patch over 2 km from the nearest local *A. hattorfiana* population (S.G. Nilsson personal observation). This, together with indirect observations during 2003–2006 (occupancy patterns, personal observation), suggests that the bee can disperse over a few kilometres, although we only documented movements of up to 900 m.

In this case it is not obvious how to separate natal dispersal (permanent movement from its birth site) from breeding dispersal (movement of adults between breeding attempts) (Paradis et al. 1998). The bees were marked when they searched for pollen indicating a reproducing population in the area. The nests are extremely difficult to find but the results for local movements suggest that the females only search for pollen close to their nest. It is not known if one female bee can construct more than one nest in a life-time.

Habitat requirements of solitary bees include nesting sites, food resources and nesting material. The few nests of *A. hattorfiana* we have found suggests relatively unspecialized demands on the nest site, with scarce vegetation with a warm microclimate (unpublished data). Foraging distances among solitary bees and potentially increased mortality of reproductive females may have fatal consequences for population persistence. Between 15% and 35% of individuals in some butterfly metapopulations are estimated to die when moving between patches (Thomas and Kunin 1999; Hanski et al. 2000), and survival consequences are also expected among solitary bees. Increased habitat fragmentation is likely to increase mortality rate during dispersal. This may select for a low dispersal

propensity if pollen plants are available nearby. The relative costs and benefits of dispersal, at the level of the individual, will be determined by the size, spacing, quantity, quality and temporal variability of the habitat within particular landscapes (Thomas 2000).

Dispersal is no constant feature, and may vary with weather conditions (Walls et al. 2005), density and resource availability (Kuussaari et al. 1996). Increased dispersal rates when resources become disturbed (removed) are expected (Stephens and Krebs 1986). In the Småland study-area several patches were disturbed and floral resources removed in the middle of the flowering season due to varying activities (mowing, grazing and storage of wood etc.), possibly increasing the between patch dispersal rate and colonisation frequency. Genes associated with dispersal can be lost from isolated populations (Saccheri et al. 1998), which may lead to non-random extinction of populations and species characterised by different levels of dispersal (Thomas 2000). However, if and how males (which we did not study due to difficulties of detection) contribute to gene flow (dispersal and multiple matings) require further studies.

The study design implies that larger patches and patches with more flowers were surveyed for longer time. Because bee population size is positively related to plant population size (Larsson and Franzén 2007), it is necessary to have this design when estimating total local population sizes. Even if the same individual is more likely to be found and/or double-counted in a large patch it was not the case in this study. The bees were extremely sedentary when foraging for pollen within patches, which reduces bias from double-counting and in fact it seems that it is a higher probability of detection in small patches (unpublished data).

Implications for conservation

Energy budgets of female bees provisioning brood is likely to be an extremely important factor in reproductive success and needs to be carefully considered when designing conservation programs for endangered bee species (i.e., each foraging female bee needs to have enough energy to get to the pollen plant and then back to the nest). The other important factor in bee conservation is that many bees have very specialized nesting requirements. Some bees prefer to nest in wood, stalks of certain plants or in exposed sand of a certain grain size and compaction. Other bees seem to have less strict preferences and can nest in a variety of soil types, as seems likely in *A. hattorfiana*. These factors combine to make the conservation of solitary bee species a degree more difficult than many other invertebrates.

Our results highlight the fact that local populations of solitary bees may consist of very few individuals and therefore are at risk of extinction. The conclusion is that it is crucial to maintain large populations that can act as sources for the surrounding landscape, resembling a mainland-island situation (MacArthur and Wilson 1967; With 2004). Great concern should therefore be raised towards the conservation and re-introduction of solitary bee populations, since they may face high extinction risks.

References

Abrams PA (2002) Will small population sizes warn us of impending extinctions? Am Nat 160:293–305

Bischoff I (2003) Population dynamics of the solitary digger bee *Andrena vaga* Panzer (Hymenoptera, Andrenidae) studied using mark-recapture and nest counts. Popul Ecol 45:197–204

Carlson A, Edenhamn P (2000) Extinction dynamics and the regional persistence of a tree frog metapopulation. Proc R Soc Biol Sci Ser B 267:1311–1313

Eickwort GC, Ginsberg HS (1980) Foraging and mating behaviour in Apoidea. Annu Rev Entomol 25:421–446

Falk S (1991) A review of the scarce and threatened bees, wasps and ants of Great Britain. Nature Conservancy Council, Peterborough

Frankham R, Lees K, Montgomery ME, England PR, Lowe EH, Briscoe DA (1999) Do population size bottlenecks reduce evolutionary potential? Anim Conserv 2:255–260

Franzén M (2007) Insect diversity in changing landscapes. Ecology Building, Department of animal ecology, Lund University, Lund

Franzén M, Nilsson SG (2007) What is the required minimum landscape size for dispersal studies? J Anim Ecol 76:1224–1230

Gärdenfors U (2005) The 2005 redlist of Swedish species. Swedish Species Information Centre, Uppsala

Gathmann A, Tscharntke T (2002) Foraging ranges of solitary bees. J Anim Ecol 71:757–764

Giovanetti M, Lasso E (2005) Body size, loading capacity and rate of reproduction in the communal bee *Andrena agilissima* (Hymenoptera; Andrenidae). Apidologie 36:439–447

Goulson D, Stout JC (2001) Homing ability of the bumblebee *Bombus terrestris* (Hymenoptera : Apidae). Apidologie 32:105–111

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153:589–596

Hanski I (1994) A practical model of metapopulation dynamics. J Anim Ecol 63:151–162

Hanski I, Gaggiotti O (2004) Ecology, genetics and evolution of metapopulations. Elsevier Academic Press, Amsterdam

Hanski I, Singer MC (2001) Extinction-colonization dynamics and host-plant choice in butterfly metapopulations. Am Nat 158:341–353

Hanski I, Alho J, Moilanen A (2000) Estimating the parameters of survival and migration of individuals in metapopulations. Ecology 81:239–251

Hanski I, Kuussaari M, Nieminen M (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia*. Ecology 75:747–762

Hanski I, Moilanen A, Gyllenberg M (1996) Minimum viable metapopulation size. Am Nat 147:527–541

Hanski I, Pakkala T, Kuussaari M, Lei G (1995) Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos 72:21–28

Harrison S (1991) Local extinction in a metapopulation context—An empirical evaluation. Biol J Linn Soc 42:73–88

Harrison S, Murphy DD, Ehrlich PR (1988) Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis*—evidence for a metapopulation model. Am Nat 132:360–382

Kapyla M (1978) Foraging distance of small solitary bee, *Chelostoma maxillosum* (Hym., Megachilidae). Annales Entomologici Fennici 44:63–64

Knuth P (1899) Handbuch der Blütenbiologie. Engelmann, Leipzig

Koenig WD, van Vuren D, Hooge PN (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends Ecol Evol 11:514–517

Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, LeBuhn G, Minckley R, Packer L, Potts SG, Roulston T, Steffan-Dewenter I, Vázquez DP, Winfree R, Adams L, Crone EE, Greenleaf SS, Keitt TH, Klein A, Regetz J, Ricketts TH (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol Lett 10:299–314

Kuussaari M, Nieminen M, Hanski I (1996) An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. J Anim Ecol 65:791–801

Lamont BB, Klinkhamer PGL (1993) Population size and viability. Nature 362:211

Larsson M (2005) Higher pollinator effectiveness by specialist than generalist flower-visitors of unspecialized *Knautia arvensis* (Dipsacaceae). Oecologia 146:394–403

Larsson M, Franzén M (2007) Critical resource levels of pollen for the declining bee *Andrena hattorfiana* (Hymenoptera, Andrenidae). Biol Conserv 134:405–414

Larsson M, Franzén M Estimating the population size of specialized solitary bees. Ecol Ent (in press)

Levin DA, Kerster HW (1969) Dependence of bee-mediated pollen and gene dispersal upon plant density. Evolution 23:560–571

Linsley EG, MacSwain JW (1955) Observations on the nesting habitats and flower relationships of some species of Melandrena (Hymenoptera). Pan-Pac Entomol 31:178–185

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA

Michener CD, Rettenmeyer CW (1956) The ethology of *Andrena erythronii* with comparative data on other species (Hymenoptera, Andrenidae). Univ Kans Sci Bull 16:645–684

Müller A, Krebs A, Amiet F (1997) Bienen. Naturbuch Verlag, München

Müller A, Diener S, Schnyder S, Stutz K, Sedivy C, Dorn S (2006) Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee-flower relationships. Biol Conserv 130:604–615

Nilsson SG, Nilsson IN (2004) Biodiversity at Linnaeuśs birthplace in Stenbrohult, southern Sweden 4. The vascular plant flora and its changes. Sv Bot Tidskr 98:65–160

Oertli S, Müller A, Dorn S (2005) Ecological and seasonal patterns in the diversity of a species-rich bee assemblage (Hymenoptera: Apoidea: Apiformes). Eur J Entomol 102:53–63

Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. J Anim Ecol 67:518–536

Pekkarinen A (1998) Oligolectic bee species in Northern Europe (Hymenoptera, Apoidea). Entomologica Fennica 8:205–214

Pimm SL, Lee HJ, Diamond J (1988) On the risk of extinction. Am Nat 132:757–785

Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W, Hanski I (1998) Inbreeding and extinction in a butterfly metapopulation. Nature 392:491–494

Schoener TW, Spiller DA (1992) Is extinction rate related to temporal variability in population size? An empirical answer for orb spiders. Am Nat 139:1176–1207

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, New Jersey, USA

Stith BM, Fitzpatrick JW, Woolfenden GE, Pranty B (1996) Classification and conservation of metapopulations: a case study of the Florida Scrub Jay. In: McCullough DR, Covelo CA (eds) Metapopulations and wildlife conservation. Island Press, Washington, pp 187–215

Thomas CD (2000) Dispersal and extinction in fragmented landscapes. Proc R Soc Biol Sci Ser B 267:139–145

Thomas CD, Harrison S (1992) Spatial dynamics of a patchily distributed butterfly species. J Anim Ecol 61:437–446

Thomas CD, Kunin WE (1999) The spatial structure of populations. J Anim Ecol 68:647–657

Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, Asher J, Fox R, Clarke RT, Lawton JH (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303:1879–1881

Tyler T, Olsson KA (1997) Förändringar i Skånes flora under perioden 1938–1996—statistisk analys av resultat från två inventeringar: rapport från Projekt Skånes flora. Sv Bot Tidskr 3:143–185

Walls SS, Kenward RE, Holloway GJ (2005) Weather to disperse? Evidence that climate conditions influence vertebrate dispersal. J Anim Ecol 74:190–197

Westrich P (1990) Die wildbienen Baden-Württembergs. Eugen Ulmer, Hohenheim

With KA (2004) Metapopulation dynamics: perspective from landscape ecology. In: Hanski I, Gaggiotti O (eds) Ecology, genetics, and evolution in metapopulations. Academic Press, London, pp 23–44

Zayed A, Roubik DW, Packer L (2004) Use of diploid male frequency data as an indicator of pollinator decline. Proc R Soc Biol Sci Ser B 271:9–12