

DO RESOURCES OR NATURAL ENEMIES DRIVE BEE POPULATION DYNAMICS IN FRAGMENTED HABITATS?

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Abstract. The relative importance of bottom-up or top-down forces has been mainly studied for herbivores but rarely for pollinators. Habitat fragmentation might change driving forces of population dynamics by reducing the area of resource-providing habitats, disrupting habitat connectivity, and affecting natural enemies more than their host species. We studied spatial and temporal population dynamics of the solitary bee *Osmia rufa* (Hymenoptera: Megachilidae) in 30 fragmented orchard meadows ranging in size from 0.08 to 5.8 ha in an agricultural landscape in central Germany. From 1998 to 2003, we monitored local bee population size, rate of parasitism, and rate of larval and pupal mortality in reed trap nests as an accessible and standardized nesting resource. Experimentally enhanced nest site availability resulted in a steady increase of mean local population size from 80 to 2740 brood cells between 1998 and 2002. Population size and species richness of natural enemies increased with habitat area, whereas rate of parasitism and mortality only varied among years. Inverse density-dependent parasitism in three study years with highest population size suggests rather destabilizing instead of regulating effects of top-down forces. Accordingly, an analysis of independent time series showed on average a negative impact of population size on population growth rates but provides no support for top-down regulation by natural enemies. We conclude that population dynamics of *O. rufa* are mainly driven by bottom-up forces, primarily nest site availability.

Key words: habitat fragmentation; orchard meadows; *Osmia rufa*; pollinators; population ecology; red mason bee; resource limitation; solitary bees; time series; top-down or bottom-up control.

INTRODUCTION

Population dynamics are the key for understanding the causes of a species' distribution and abundance and more generally patterns of species diversity (Kareiva 1990). Native bees are important pollinators in most terrestrial ecosystems, and therefore a better knowledge of factors driving their population dynamics is essential for future conservation of suitable habitats and ecological interactions (Kearns et al. 1998). Regulating mechanisms of population dynamics in such mutualistic plant–pollinator food webs might be different from those in antagonistic plant–herbivore food webs, but only a few studies focus on pollinators. Population dynamics can be driven by resources (bottom-up) or by natural enemies (top-down). Bottom-up factors mainly act as density-independent factors that limit population growth. In this case, dynamics of a population can be stabilized by negative feedback processes like intra- or interspecific competition resulting in reduced population growth rates (Berryman 2001, Eber 2004, Sibly et al. 2005). Top-down factors, i.e., natural enemies, can regulate population dynamics by positive density-

dependent parasitism or predation (Hassell and Wilson 1997, Berryman 2001). The relative importance of top-down or bottom-up control for population dynamics remains an open question for nearly all biological systems (Hunter et al. 1997, Ylloja et al. 1999, Hunter 2001, Freckleton et al. 2006, Moreau et al. 2006).

Population dynamics always have two dimensions: a temporal and a spatial one; thus local populations at a certain place change over time, and the dynamics of spatially separated populations might differ due to local variation in habitat conditions or interact by extinction–colonization dynamics of hosts and their natural antagonists (Eber and Brandl 1996, Hanski 1998, van Nouhuys and Hanski 2002, Cronin 2004). In the past most research has been done either on long-term time series, often including life table data of one or a few local populations (Hassell 2000, Hunter 2001, Price and Hunter 2005), or on short-term spatial colonization–extinction dynamics of metapopulations (Hanski 1998) and only few studies consider landscape scales (Solbreck 1995, Cronin and Reeve 2005, McGeoch and Price 2005).

Spatial variation of local population dynamics becomes particularly important in the context of habitat destruction and fragmentation and increasing land use intensification (Fahrig 2003). First, resource quantity is most time related to the size of a local habitat and at a

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larger scale to the quality of the surrounding landscape matrix (Vandermeer and Carvajal 2001, Krauss et al. 2004). Thus, reduced habitat area or matrix quality should increase the impact of limiting resources for population growth. Second, natural enemies are expected to respond stronger to reduced local area or increased isolation of habitats (Holt et al. 1999). Thus, top-down regulation might be disrupted by the increasing destruction and fragmentation of perennial habitats (Tscharntke and Brandl 2004, Tylianakis et al. 2006).

Bees (Hymenoptera: Apiformes) depend for reproduction on pollen, a resource that is spatially and temporally limited because it is only produced by plants as a reward to attract pollinators (Wcislo and Cane 1996, Roulston and Cane 2000). Consequently, it has been often assumed that intra- or interspecific competition for food resources plays an important role for the size of bee populations, but direct empirical evidence is still lacking (Minckley et al. 1994, Steffan-Dewenter and Tscharntke 2000, Minckley et al. 2003, Palmer et al. 2003). Nesting sites in the soil or in preexisting cavities above ground are a second key resource that potentially limits bee populations, but again experimental evidence is rare (Potts and Willmer 1997, Wuellner 1999, Potts et al. 2003, 2005).

Similarly, the knowledge about the impact of natural enemies on population dynamics of native bees is very limited, but natural enemies are hypothesized to regulate bee populations (Wcislo and Cane 1996). Rates of parasitism show great annual and regional variation (Wcislo et al. 1994, Petanidou et al. 1995, Wcislo and Cane 1996) and on average nests in natural aggregations or trap nests are more heavily parasitized than isolated ones (Wcislo and Cane 1996). Natural enemies are expected to affect common species most, because parasite loads correlate positively with the local abundance and regional distribution of their hosts (Durrer and Schmid-Hempel 1995, Steffan-Dewenter 2003). Both density-dependent and inverse density-dependent correlations between rate of parasitism and local population size have been found in the few existing case studies for solitary bees (Rosenheim 1990, Antonini et al. 2003, Bischoff 2003).

Here we present a six-year study on regional-scale population dynamics of the solitary mason bee *Osmia rufa* in a fragmented agricultural landscape. We combined observational and manipulative experimental approaches to get deeper insights into the driving forces and the relative importance of bottom-up or top-down regulation. We exposed trap nests as a standardized nesting resource in 30 orchard meadows covering an area and isolation gradient (see Plate 1). Such orchard meadows are a typical habitat for the studied species by providing pollen resources, mainly from flowering fruit trees and also from herbaceous vegetation, and nesting sites in dead wood (Steffan-Dewenter 2003). This system made it possible to annually record changes of local population size, occurrence of natural enemies, and

mortality rates (Tscharntke et al. 1998). We intended to test the following main hypotheses.

Hypothesis 1: Bee populations are limited by the quantity of nesting resources. Evidence for this hypothesis should come from an annual increase of local population size after the introduction of additional nesting resources.

Hypothesis 2: Bee populations are limited by pollen resources. Evidence for this hypothesis should come from a negative relationship between population growth rates and local population size. Further, assuming a carrying capacity due to limited resources, we expected a positive correlation between population size and habitat area as a surrogate for the quantity of pollen resources from flowering fruit trees.

Hypothesis 3: Bee populations are regulated by natural enemies. Evidence for this hypothesis should come from (1) positive density-dependent parasitism or mortality and (2) negative density-dependent regulation of population growth rates.

MATERIAL AND METHODS

The study system

The red mason bee *Osmia rufa* (Linnaeus 1758) (Hymenoptera: Megachilidae) is common throughout Germany and is widely distributed in central Europe. The males are 6–11 mm and the females 10–16 mm long. *O. rufa* is a solitary species with a univoltine life cycle. The main flight period of females lasts from mid-April until the end of June. It overlaps with the flowering time of typical orchard fruit trees like cherries and apples, which are used as major pollen sources (Westrich 1989, Seidelmann 1995). Therefore we assume that habitat area is related to pollen resource availability for *O. rufa*. Homing experiments suggest a maximum foraging distance of 800 m around the nest site (Gathmann and Tscharntke 2002). The linear brood nests are built in preexisting cavities such as hollow plant stems or beetle borings in dead wood. Females prefer as nesting substrate, holes of 5–9 mm inner diameter (Westrich 1989, Seidelmann 1995). A brood nest consists of several brood cells each provisioned with pollen as larval food and separated by loam partitions. Larvae feed on pollen provision, spin into a cocoon, pupate, and hibernate as adults in their cocoons. *O. rufa* is a polylectic species using a wide variety of pollen sources. Typical habitats are mature hedgerows, woodland edges, and old orchard meadows with dead wood (Westrich 1989). The brood cells of *O. rufa* are attacked by several brood parasitoids and cleptoparasites, which feed on larval pollen provisions (Wcislo and Cane 1996). The wasp *Monodontomerus obscurus* Westwood 1833 (Hymenoptera: Encyrtidae) is a specialist parasitoid whereas the parasitoid *Melittobia acaster* Walker 1839 (Hymenoptera: Eulophidae) and the fly *Anthrax anthrax* Schrank 1781 (Diptera: Bombyliidae) have been reared from several species of the family Megachilidae (Gathmann and Tscharntke 1999). These species develop inside the

cocoon of *O. rufa*. The most common cleptoparasite is the specialist *Cacoxenus indagator* Loew 1858 (Diptera: Drosophilidae). Female flies enter the nest and lay clutches of eggs when a female bee has departed on a foraging trip. Further cleptoparasites are the specialist mite *Chaetodactylus osmiae* (Dufour, 1839) (Acari: Chaetodactylidae) and the generalist beetle *Megatoma undata* Linnaeus 1758 (Coleoptera: Dermestidae) (Gathmann and Tscharrntke 1999).

Study region and study sites

The study was carried out in the Leine-Weser region in the vicinity of the city of Göttingen in southern Lower-Saxony, Germany, from 1998 to 2003. The study region represents a typical human-dominated central European landscape. It is characterized by a mix of annual crops, grasslands, forests, and a small fraction of seminatural habitats of high conservation value like calcareous grasslands (0.26% of the area; Krauss et al. 2003) and orchard meadows (0.7% of the area).

We selected a total of 30 orchard meadows as study sites ranging in size from 0.08 to 5.8 ha located in a region of $\sim 40 \times 35$ km. Study sites were chosen to cover the full gradient of habitat area and isolation in the region. Selection was based on a complete mapping of orchard meadows covering a total of 743 habitat fragments (Untere Naturschutzbehörde Göttingen, unpublished data).

The orchard meadows were characterized by stands of old, tall fruit trees, mainly apples, sweet cherries, and plums that provide both pollen resources and nesting sites in dead wood for the studied bee species. Management regimes (mowing, grazing, or lying fallow) varied between the study sites and partly changed over the six years. However, in an earlier study no significant effects of management regimes on trap-nesting bees were found (Steffan-Dewenter and Leschke 2003), and therefore this factor was not included in the statistical analysis.

Connectivity to other orchard meadows was quantified as $C_i = \sum e^{-d_{ij}} A_j$ where A_j is the area of neighboring orchard meadows and d_{ij} the distance (kilometers) to the study site i (Steffan-Dewenter 2003).

Trap nests

The core approach in this study was the use of trap nests in order to (1) monitor the annual change of the *O. rufa* populations and (2) to experimentally enhance the quantity of nesting resources (Tscharrntke et al. 1998). On each of the 30 study sites we exposed 12 trap nests in 1998 (a total of 360 trap nests). Four trap nests were fixed on each of three wooden posts (1.5 m in height, 5–7 cm diameter) that were placed in the center of each meadow (Steffan-Dewenter 2003). The distance between the three wooden posts per study site was 52.4 ± 18.7 m (mean $\pm$ SE) with a range between 26.3 and 114.1 m. Each trap nest consisted of 153 ± 14.3 stems of common reed, *Phragmites australis* (Cav.), with an inner diameter

of 5.4 ± 0.004 mm (mean $\pm$ SE, range, 2–10 mm; $n = 1531$ reed stems from 10 randomly selected trap nests) and a length of 20 cm. From the size distribution of the stems we calculated that on average 51.7% of the stems were within a range of 5–9 mm diameter and thus suitable nesting sites for *O. rufa*. The reed stems were placed inside plastic tubes, thus each plastic tube represents one trap nest. Four trap nests together were protected against rain by a wooden roof (50×50 cm). The trap nests were exposed at the beginning of April and removed from the sites after the end of the season between mid- and the end of September. The collected trap nests were stored at 4°C in cold storage over winter for detailed analysis of population parameters. The community structure of trap-nesting bees, wasps, and their natural enemies in orchard meadows has been described in more detail in Steffan-Dewenter (2003).

Population dynamics of O. rufa

During the winter months all reed stems containing brood cells of *O. rufa* were removed from the trap nests and opened. The brood cells in one stem from the opening to the first node were defined as one brood nest (Krombein 1967). For each brood nest we recorded the total number of brood cells, the number of dead brood cells, the number of brood cells attacked by parasitoids or cleptoparasites, and the number of fully developed cocoons. In 2001 and 2002 at nine and 17 sites, respectively, it was not possible to open and analyze all nests in detail because the numbers were too high. At these sites the number of *O. rufa* nests >300 per post were only counted but not dissected. The mean number of brood cells per nest of the dissected nests was used to calculate the total number of brood cells per site. Rate of parasitism and mortality are only based on the examined nests for these sites.

All reed stems with intact brood cells including those with natural enemies were closed and individually numbered after examination, and then stored in one plastic box per wooden post (i.e., three per study site) at 4°C until spring. The boxes (with holes) were returned to the same study site and post from which the nests had been removed the year before, together with a fresh set of empty trap nests. Thereby, hibernated *O. rufa* females could emerge, mate, and reproduce in the study sites in a natural way and, in parallel, the winter dissection allowed us to get detailed data for population parameters. The emergence boxes were collected after each field season in autumn. All numbered *O. rufa* nests were opened again to check for successful emergence of the exposed cocoons and potential additional nests that were built in the emergence boxes. From the previously described analyses we extracted the following parameters to characterize the local *O. rufa* populations:

- 1) The total number of brood cells was considered as an equivalent for variation of local population size (Steffan-Dewenter and Schiele 2004).

2) The rate of parasitism was calculated as the ratio of parasitized brood cells to the total number of brood cells.

3) The rate of larval mortality was calculated as the ratio of dead brood cells in the stage of eggs or larvae to the total number of brood cells. Responsible mortality agents for dead brood cells were presumably pathogens, but this could not be further proven.

4) The rate of pupal mortality was calculated as the number of cocoons, which did not emerge after returning them to the study sites to the total number of brood cells.

5) The annual population growth rate of local *O. rufa* populations was calculated as $r_t = \ln(N_t/N_{t-1})$, where N_t and N_{t-1} are the total number of brood cells at time t and $t - 1$ (Ylloja et al. 1999, Björkman et al. 2004).

Monitoring temporal population dynamics

From the start of the study in the spring 1998 until the end of the field season 2002 we repeated the previously described methods each year. Thus trap nests and emergence boxes (from 1999 onward) were exposed on the study sites in spring and removed for laboratory analysis in autumn. The number of trap nests was adjusted to the increasing number of *O. rufa* cocoons from 2000 onward to prevent nest site quantity from becoming a limiting resource for population growth. Thus, at posts with >100 *O. rufa* nests two additional empty trap nests were fixed in the following year. In 2003 we did not return any *O. rufa* cocoons to the study sites. Consequently, the colonization could only come from individuals that hibernated in natural nest sites on the orchard meadow or colonized from outside, thereby providing additional insights into the relative size of natural compared to experimentally enhanced *O. rufa* populations.

Statistical analysis

The statistical analyses were performed using R (R Development Core Team 2004). We used linear mixed-effect models (LMEM) to analyze the combined effects of year and habitat parameters on population parameters of *O. rufa* (Pinheiro and Bates 2000). Year, habitat area, and habitat connectivity were included as fixed factors and study site as a random factor. Thereby, our models took into account that sampling was repeated over six years on the same study sites. We used logarithmic transformation of population abundance data, habitat area, and habitat connectivity and arcsine transformation for parasitism and mortality rates. Additionally, rates of parasitism and rates of larval or pupal mortality were analyzed by fitting a generalized linear mixed model via PQL (package MASS in R) using logit transformation and assuming binomial errors. Thereby, rates estimated from small samples gave less influence (Crawley 2002). Nonsignificant interactions and parameters were removed in a stepwise approach from the model until all parameters were significant

(Crawley 2002). When year and habitat factors (or interactions with year) had significant effects on population parameters, we illustrated results in figures using simple regressions for each year independently. We always give means $\pm$ SE of untransformed data in the text and tables.

To test for density-dependent effects on annual growth rates, linear mixed effects models for year, population size at time $t - 1$, and rates of parasitism and rates of mortality at time $t - 1$ were analyzed (Hunter et al. 1997, Ylloja et al. 1999). Our data provide the potential to test for both spatial and temporal patterns of density dependence. We use the term “spatial patterns” for population data where we analyze the changes of several spatially separated local populations from one year to the next year in contrast to the classical approach of using long-term time series data of only one local population. Therefore we show spatial patterns for population growth rates against the previously mentioned variables for each study year separately. Additionally, we analyzed temporal patterns of density dependence for population size and parasitism at time $t - 1$ using time series with three or more data points. Thus, the term “temporal patterns” is used for temporal dynamics of local populations over several years. As the statistical power for each individual time series is low, we also used the distribution of correlation coefficients and tested for departure from zero (mean $\pm$ 95% confidence limits).

Spatial synchrony among local *O. rufa* populations was explored using a spatial covariance function, which describes the correlation between time series at pairs of locations as a function of the geographical distance between study sites (Bjørnstad et al. 1999, Koenig 1999). We used the R-package “NCF” to estimate the nonparametric covariance function and calculated confidence intervals for the estimated functions using bootstrap resamplings replicated 500 times (Bjørnstad and Falck 2001). Overall regional synchrony was calculated by the mean cross-correlations among all populations (Bjørnstad et al. 1999). We analyzed synchrony for annual population growth rates, population abundance, and rate of parasitism. Measures of population growth rates and parasitism did not require additional detrending, whereas abundance data showed a positive trend that might have obscured short-term spatial synchrony (Liebhold et al. 2004). Therefore residuals of a simple regression to the time series of log-abundance (1998–2002) were used for spatial covariance functions (Koenig 1999).

RESULTS

General characteristics of O. rufa populations

Altogether, we analyzed 33 959 *O. rufa* nests containing 136 664 brood cells. Each nest contained on average 4.4 ± 0.1 brood cells. We found that 17.1% of the brood cells were attacked by parasitoids or cleptoparasites, 13.6% were dead as revealed by nest dissections, and

8.2% did not emerge after they were returned to the study sites resulting in a loss of 38.9% of the provisioned brood cells.

The fraction of orchard meadows occupied by *O. rufa* was 84.4% in 1998, 88.9% in 1999, 93.4% in 2000, and 100% in 2001 and 2002 indicating that the additional nest resources promoted the establishment of new local populations. After the removal of all brood cells from 2002 the occupancy rate declined to 93.3% in 2003. The fraction of *O. rufa* populations attacked by natural enemies was extremely high and only varied between 92.5% in 1999 and 100% in 2002 suggesting that natural enemies were highly mobile and not limited by habitat connectivity.

No evidence for strong spatial synchrony of local *O. rufa* populations was found across the range of 50 km in this study (Fig. 1). Means of regional synchrony quantified by cross-correlation were 0.21 (0.09, 0.37; 95% bootstrapped confidence intervals) for population growth rates, 0.10 (0.01, 0.24) for detrended population growth rates, and 0.13 (0.01, 0.26) for rate of parasitism.

Effects of year and habitat parameters on population size

Linear mixed-effects models revealed significant effects of year and habitat area but not habitat connectivity on the number of *O. rufa* brood cells per study site (Table 1). The mean number of brood cells significantly increased from ~80 in 1998 to >2700 brood cells per site in 2002 (Appendix A). In 2003, when no brood cells of the previous year were returned to the study sites, the average number of brood cells dropped to values similar to those from the first study year (Fig. 2). Further we calculated the proportion of potentially suitable occupied reed stems with an inner diameter between 5 and 9 mm. The mean proportion of occupied reed stems was only 1.2% in 1998, steadily increased up to 26% in 2002, and then dropped back to 1% in 2003 (Appendix A). Only at one site with the highest local population size *O. rufa* used 96% of the estimated available nesting space in 2002. The proportion of brood cells of other bee species (mainly *Hylaeus*, *Chelostoma*, *Megachile*, *Heriades*, and *Osmia*) that were built in the trap nests decreased from 11.3% in 1998 to 4.0% in 2002 suggesting a higher relative performance of *O. rufa* compared to other bee species. Similarly, the proportion of brood cells from trap-nesting wasps (Eumenidae, Sphecidae, Pompilidae) declined from 52.9% in 2002 to 11.2% in 2002 (Appendix A).

Population size significantly increased with the area of orchard meadows in five out of six years (Fig. 3). The slopes of the abundance-area curves did not differ significantly between the six study years (no significant interaction between year and habitat area in Table 1).

Effects of year and habitat parameters on parasitism and mortality

Overall we found six cleptoparasites and parasitoids in nests of *O. rufa*. The most abundant species in all

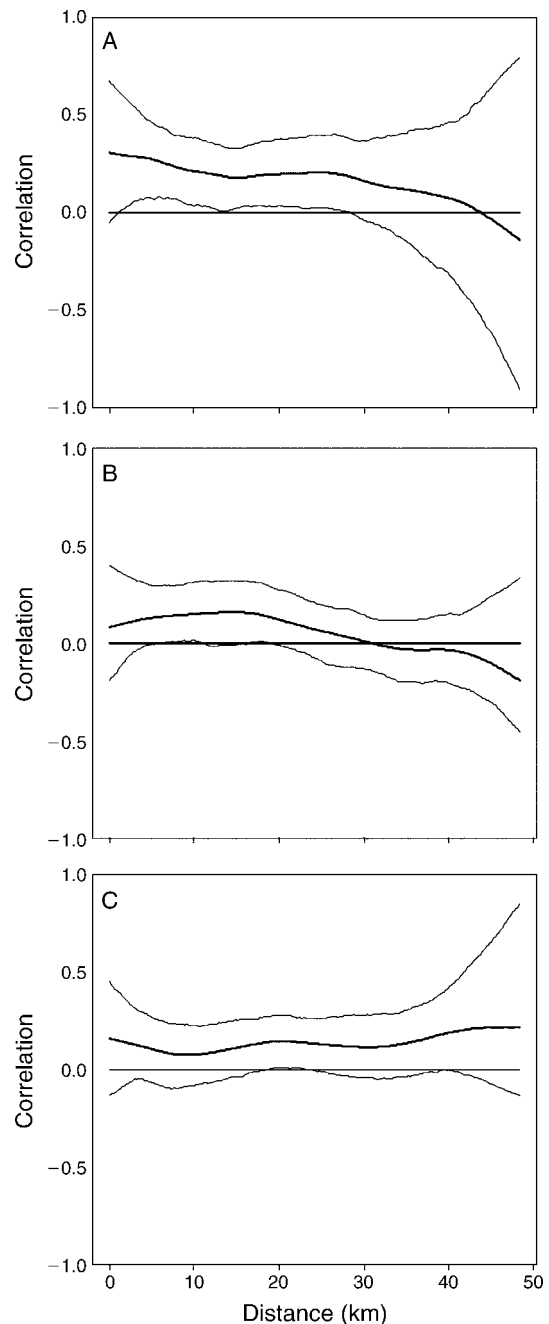


FIG. 1. Spatial covariance functions estimated for *Osmia rufa* populations: (A) annual population growth rates; (B) population size (residuals from the regression of number of brood cells against year; (C) rate of parasitism. Thin lines represent 95% bootstrapped confidence intervals.

years was the cleptoparasite *Cacoxenus indagator* attacking a total of 8537 brood cells, followed by *Megatoma undata* (642 attacked brood cells), *Monodontomerus obscurus* (407 brood cells), *Chaetodactylus osmiae* (271 brood cells), the unspecific parasitoids *Melittobia acaster* (58 brood cells), and *Anthrax anthrax* (26 brood cells).

TABLE 1. Effects of year, habitat area, and habitat connectivity on population dynamics of the solitary bee *Osmia rufa* in linear mixed-effects models.

Parameter	Source of variation	df	F	P
Number of brood cells	year	5, 145	42.43	<0.0001
	habitat area	1, 28	8.06	0.008
	habitat connectivity			ns
Annual population growth rate	year	3, 72	2.66	0.055
	habitat area			ns
	habitat connectivity			ns
Number of species (natural enemies)	year	5, 145	46.21	<0.0001
	habitat area	1, 28	7.73	0.01
	habitat connectivity			ns
Parasitism	year	5, 128	24.87	<0.0001
	habitat area			ns
	habitat connectivity			ns
Larval mortality	year	5, 129	10.29	<0.0001
	habitat area			ns
	habitat connectivity	1, 28	19.8	<0.0001
Pupal mortality	year	3, 73	3.11	<0.031
	habitat area			ns
	habitat connectivity			ns

Notes: Rates of parasitism and mortality were analyzed using logit transformation and assuming binomial errors. No significant interactions were found.

Total rates of parasitism significantly varied between years but were not affected by habitat area or habitat connectivity (Table 1). The mean rate of parasitism was lowest in 2002 and highest in 2003 (Appendix A). The percentage of unexplained larval mortality also varied significantly between years and increased with habitat connectivity (Table 1). Highest larval mortality was found in 1998 and 2003 and lowest in 1999 and 2002 (Appendix A). Pupal mortality significantly varied between years, but was not related to habitat variables (Table 1; Appendix A). Additionally, we analyzed the variation in the proportion of generalist vs. specialist natural enemies among years. We found no effect for generalists ($F_{5,145} = 1.74$, $P = 0.12$), but significant variation between years for specialist natural enemies ($F_{5,145} = 2.72$, $P = 0.02$).

Density dependence of parasitism and mortality rates

We tested whether positive density-dependent parasitism or mortality occurred in our study system. In

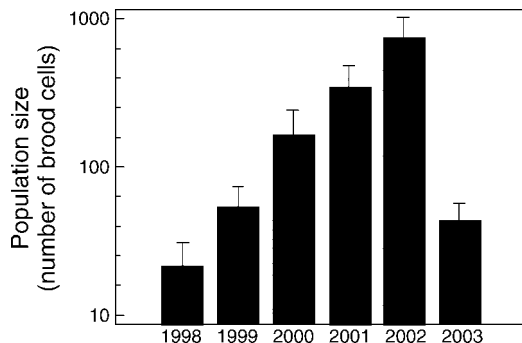


FIG. 2. Mean annual population size of *O. rufa* in trap nests in 30 orchard meadows from 1998 to 2003. Note that at the end of 2002 all brood cells were removed from the study sites, and complete recolonization from natural nesting sites took place in 2003. For statistics see Table 1.

linear mixed-effects models rate of parasitism was significantly affected by year, population size, and an interaction between year and population size (Table 2). Accordingly the direction of relationships differed among years. We found positive density-dependent

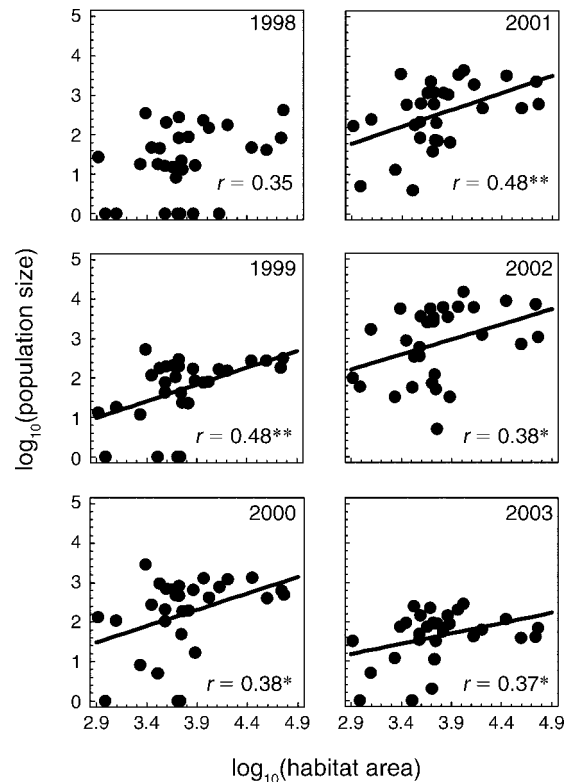


FIG. 3. Effects of habitat area on local population size of *O. rufa* during the study period (1998–2003). The correlation coefficient r and significance level ($*P < 0.05$, $**P < 0.01$), based on simple linear regression, are given in each graph. For further statistics see Table 1.

TABLE 2. Effects of year and population size on rates of parasitism and mortality of *O. rufa* populations in linear mixed-effects models.

Parameter	Source of variation	df	F	P
Parasitism	year	5, 122	32.05	<0.0001
	population size	1, 122	30.28	<0.0001
	year $\times$ population size	5, 122	3.31	0.0078
Larval mortality	year	5, 128	9.58	<0.0001
Pupal mortality	year	3, 73	3.11	0.031
	population size			ns

Notes: Rates of parasitism and mortality were analyzed using logit transformation and assuming binomial errors. Only significant interactions are shown in the table.

parasitism in 1999, but negative density dependence in the following years (2000–2003) and no relationship in 1998 (Appendix B). Larval mortality and pupal mortality were density independent (Table 2).

Evidence for regulation of population growth rates

Annual changes of *O. rufa* population size, i.e., population growth rates, were used to identify the relative importance of natural enemies or resource limitation as potential drivers of local population dynamics. In linear mixed-effects models, population size and rates of parasitism significantly affected population growth rates. The interaction among year and population size indicates annual variation in factors influencing population growth rates (Table 3). This analysis combines density-dependent effects on population growth rates in space and time. To separate these two aspects we first illustrate spatial patterns of each independent variable on population growth rates from 1999 to 2002 using simple regression analysis (Fig. 4). Density-dependent effects of population size (N_{t-1}) on population growth rates were only found in 1999, but not in the following years when local *O. rufa* populations were significantly larger. The rate of parasitism of the previous year was not correlated with population growth rate in the first three years, but showed a significant negative effect in 2002 indicating that delayed density-dependent regulation by natural enemies took place in this year (Fig. 4). Pupal mortality showed no effect on growth rates.

Second, we analyzed short time series of individual study sites each covering population dynamics for 3–4 years. In three out of 18 cases we found a significant

negative correlation between population growth rate and population size (Appendix C). The distribution of correlation coefficients for all time series indicates a general negative relationship (Fig. 5). The mean was -0.49 ± 0.19 (95% confidence intervals). In contrast no significant correlations were found for rate of parasitism ($t - 1$) in single time series; the mean of the correlation coefficients was positive, but not significantly different from zero (0.3 ± 0.48 ; 95% confidence intervals; Fig. 5), and correlation coefficients for population size and rate of parasitism were significantly different (paired t test, $t = -4.28$, $P < 0.0001$).

DISCUSSION

The main objective of our study was to evaluate the relative importance of bottom-up and top-down forces for the population dynamics of a solitary bee species in a fragmented agricultural landscape. By recording data at replicated sites on a landscape scale over six years, we got a data set that allows us to prove evidence for each of our three main hypotheses.

Evidence for bottom-up or top-down regulation

The most obvious result of our study is the marked, steady increase of population size in response to the additional nesting resources. After five years the mean population size was 35-times higher than at the beginning of the experiment. The removal of all cocoons of the previous year in 2003 required a complete recolonization of trap nests from natural nesting sites and resulted in densities as low as in the first study year. Thus, the data indicate that nesting sites are a limiting resource for local population size of *O. rufa*. Bees are known to have specific needs for nesting sites and therefore have been often assumed to be limited by this factor (e.g., Westrich 1989, Potts and Willmer 1997, Wuellner 1999). Potts et al. (2005) show that the relative abundance of dominant species is influenced by the availability of nesting sites, but we are not aware of other studies that derive evidence for nest site limitation from direct experimental manipulation of nest site quantity.

The interpretation of our data regarding bottom-up control by pollen resources is less straightforward. Considering that the analyzed populations were built up to significantly higher densities, it can be concluded

TABLE 3. Density-dependent effects on population growth rates of *O. rufa* in linear mixed-effects models.

Source of variation	df	F	P
Year	3, 63	4.22	0.009
Population size ($t - 1$)	1, 63	4.01	0.049
Parasitism ($t - 1$)	1, 63	4.59	0.036
Larval mortality ($t - 1$)			ns
Year $\times$ population size ($t - 1$)	3, 63	4.15	0.01

Notes: Only significant interactions are shown in the table. Study sites with <10 brood cells have been excluded from the analysis. For sources of variation, “($t - 1$)” indicates that the data are from the previous year.

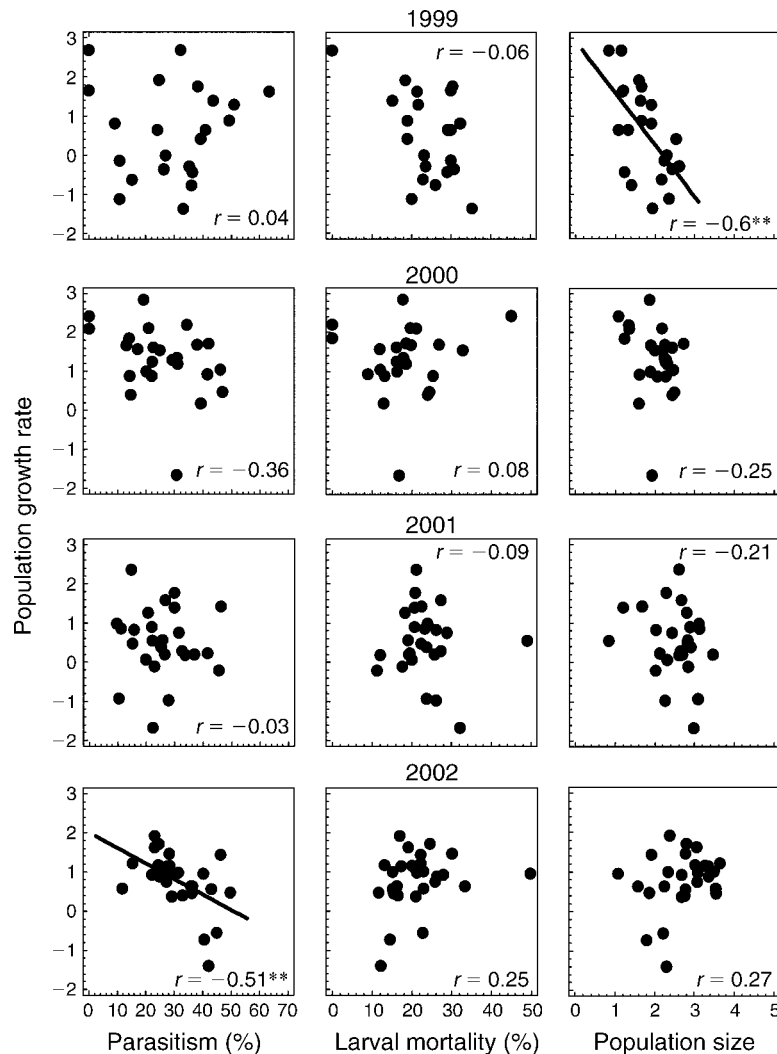


FIG. 4. Spatial density-dependent effects of parasitism rates (year $t - 1$, [no. parasitized brood cells/total no. brood cells] $\times 100$), larval mortality rates (year $t - 1$, [no. dead brood cells in larval stage/total no. brood cells] $\times 100$), and population size (year $t - 1$, total no. brood cells) on population growth rates ($\ln N_t/N_{t-1}$). The correlation coefficient r and significance level (** $P < 0.01$), based on simple linear regression, are given in each graph. Only sites with >10 brood cells were included in the analysis. For statistics see Table 3.

that pollen resource limitation is, compared to nesting sites, of minor importance as a limiting factor of *O. rufa* populations at naturally occurring densities. This conclusion is also supported by the lack of spatial patterns of density dependence of population growth rates during three years with enhanced *O. rufa* population size. On the other hand, our results from time series analysis strongly suggest a negative relationship between local population size and population growth rates. It might be that time series are more sensitive in detecting density-dependent regulation because patterns in spatial data are masked by environmental variation. For example, differences in our results for spatial and temporal patterns could possibly be explained by the annual variation in the dominance of specialist natural enemies. However,

comparable studies that could improve our understanding of how spatiotemporal dynamics might interact are lacking, despite the enormous current interest in such large-scale patterns (Freckleton et al. 2006).

A recent study by Sibly et al. (2005) suggests that many animal taxa live at densities near the carrying capacity of their environment. Similarly, it is widely expected that pollen resources are a limiting factor for bee populations and that interspecific competition for pollen resources influences fitness components (e.g., Wcislo and Cane 1996). Nonetheless, for bees there is no direct evidence for interspecific food resource competition, even for interactions between abundant and efficient foragers like social honey bees and less abundant solitary bees (Butz Huryn 1997, Steffan-Dewenter and Tscharntke 2000, Goulson 2003). The

relative abundance of other trap-nesting bee species declined parallel to the rapid increase of the *O. rufa* populations indicating that *O. rufa* might outcompete other trap-nesting bee species, but there is no evidence that interspecific competition for food resources had an effect on the population dynamics of *O. rufa*.

Indirect evidence for dependence on food resources comes from positive correlations between the abundance of mass-flowering crops and the density of social bumble bees (Westphal et al. 2003) and the variation of female reproductive success of a specialist solitary bee with pollen availability (Minckley et al. 1994). We conclude that the abundance of the studied generalist solitary bee species was not strongly limited by food resources at natural densities. However, the overall negative effect of population size on growth rates implies that the experimentally enhanced populations came closer to their carrying capacity. Similarly, the positive correlation between population size and habitat area indicates that resource quantity was relevant for population size. Generally, social bees and specialist solitary bees might be more sensitive to limitation of food resources than generalist solitary bees.

Our third hypothesis predicts bee populations to be regulated by natural enemies. To prove this hypothesis we analyzed the data for effects of direct or delayed density-dependent parasitism and mortality. Overall, natural enemies and unexplained mortality were a significant mortality factor adding up to a loss of 39% of the provisioned brood cells. The rates of larval or pupal mortality were density independent in all years; rates of parasitism were density independent in the first study year, positively density dependent in the second year, and negatively density dependent during the consecutive years. Surprising in this temporal sequence is the shift from independent to positive to negative density-dependent parasitism. This pattern might result from a combination of different processes such as functional and numerical responses, parasites being limited by handling time, or from improved defense capabilities of more aggregated hosts (Rosenheim 1990, Schenk and Bacher 2002). One precondition for regulation by natural enemies is a positive relationship between rate of parasitism and population size (Vandermeer and Goldberg 2003). In contrast, our data show strong inverse density-dependent parasitism in three years with steadily increasing local population sizes (2000–2002). An inverse density-dependent parasitism was also found by Antonini et al. (2003) for a soil-nesting solitary bee species. In another study, solitary hymenoptera parasite pressure was positively related to host densities in eight, independent in four, and inverse density dependent in four cases (Rosenheim 1990). Inverse density dependence suggests destabilizing top-down effects on population dynamics; thus the impact of natural enemies on smaller populations is stronger than on larger ones. Our data indicate that such destabilizing effects on smaller populations took place in

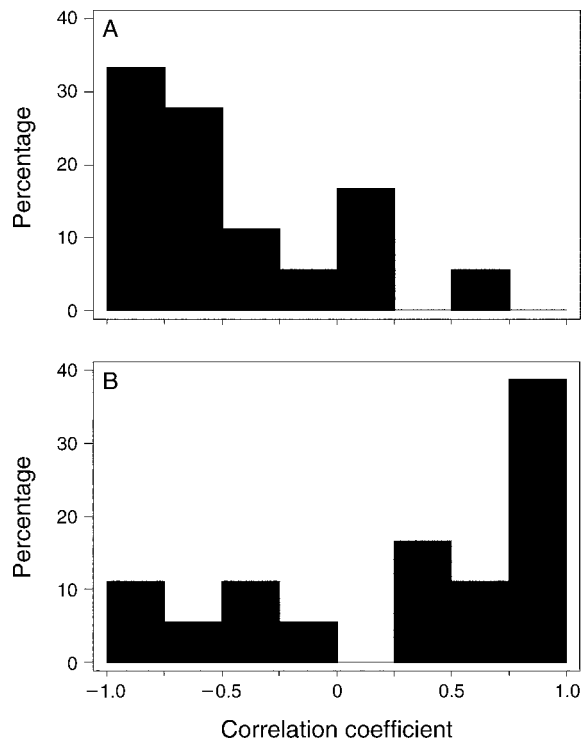


FIG. 5. Frequency histogram for correlation coefficients of 18 time series analysis: (A) population size (year $t-1$) vs. population growth rate and (B) rate of parasitism (year $t-1$) vs. population growth rate.

some years, where population growth rates were negatively correlated with rates of parasitism. Thus, inverse density-dependent effects of natural enemies presumably contributed to the discrepancies in growth rates between small and large populations and the increasing range of population sizes from 1998 to 2002. Large aggregations of *O. rufa* might represent sites with enemy free space or reduced fitness of natural enemies (e.g., Strohm et al. 2001). The most common natural enemy in our system, the drosophilid fly *Cacoxenus indagator*, is patrolling at nest entrances and uses the absence of foraging females to lay eggs on stored pollen (Westrich 1989). We assume that high densities of foraging *O. rufa* females reduced the success of *C. indagator*, thereby explaining inverse density-dependent rates of parasitism. Our results suggest that conclusions drawn from delayed density-dependent effects on population growth rates could be misinterpreted as evidence for regulation without additionally considering the direction of correlations between population size and parasitism. In conclusion, although top-down forces played a quantitative role as mortality agents, our study provides no evidence for density-dependent regulation, but in contrast suggests stronger effects of natural enemies on small populations. Thus population growth of *O. rufa* was rather limited by habitat factors such as nesting sites, pollen resources, or abiotic conditions than



PLATE 1. (Left) Orchard meadow with trap nests and (right) a red mason bee (*Osmia rufa*) at a nest entrance. Photo credits: S. Schiele.

regulated by top-down forces. For other solitary hymenoptera showing positive density-dependent parasitism (Rosenheim 1990), top-down regulation could be more important and this might partly explain the commonness of *O. rufa* in comparison to other aboveground nesting solitary bee species.

Response to spatial factors: habitat area, connectivity, and spatial synchrony

A second objective of our study was to quantify the impact of habitat fragmentation on local population dynamics. Impacts may come through limited spatial exchange by dispersal between local populations (Hanski 1998, Baguette et al. 2000, Thomas 2000), different sensitivity of trophic levels, here bees and their natural enemies, to habitat loss and isolation (Holt et al. 1999, Tschardtke and Brandl 2004), and increased importance of resource limitation due to habitat loss (Dennis et al. 2003, Krauss et al. 2004).

Spatial synchrony of growth rate, abundance, and rate of parasitism among *O. rufa* populations was low. The slightly higher spatial synchrony for population growth rates at distances up to 10 km could be a result of dispersal between neighboring populations. Although estimated foraging distances of *O. rufa* are <1 km (Gathmann and Tschardtke 2002), dispersal distances might be significantly larger. We suggest that restricted exchange between local populations is an unlikely explanation for low spatial synchrony because occupancy of orchard meadows was already high in the first study year and increased up to 100% in 2001. In total, only two local extinctions could be observed. Thus, *O. rufa* did not show a metapopulation structure and was able to colonize even the smallest and most isolated habitat patches, provided suitable nesting resources were available. Population synchrony can be based on different processes such as dispersal coupling locally regulated populations, trophic interactions, or density-independent factors that are correlated across wide

regions (Bjørnstad et al. 1999). Therefore it is not possible to identify a single cause for the lack of synchrony.

An unsolved aspect in our study is the importance of immigration and emigration rates for local population dynamics (Baguette et al. 2000). Although the evidence for high dispersal ability is obvious, we will in the following still argue that mainly local factors influenced population dynamics. First, as mentioned, we did not detect spatial autocorrelation suggesting that local *O. rufa* populations varied independently and rates of dispersal between orchard meadows were low (Björkman et al. 2004). Second, the quantitative impact of immigrating individuals from neighboring sites not involved in this study should have gone down as the local populations increased due to the reed trap nests. Third, mark-recapture experiments in five orchard meadows revealed high nest site fidelity in that 80% of reobserved females built their nests at the maternal nest site within the habitat (Steffan-Dewenter and Schiele 2004).

Our study provides no support for the hypothesis that higher trophic levels (in this case natural enemies) are more affected by habitat fragmentation than their hosts (Holt et al. 1999, Tschardtke and Brandl 2004). Natural enemies successfully colonized more or less all sites occupied by *O. rufa* and neither habitat area nor connectivity influenced rates of parasitism. Another study also found that a specific parasitoid of a restricted and rare butterfly species was not limited by dispersal (Van Nouhuys and Hanski 2002). Thus, the general hypothesis that specific natural enemies are more affected by habitat fragmentation than their hosts (e.g., Tschardtke and Brandl 2004) needs a more differentiated consideration on a single species level.

Our data suggest that the dominant effect of habitat fragmentation on this generalist mobile bee species was primarily the reduction of available nesting sites and only secondarily of food resources in small habitat

patches. Local population size in orchard meadows could be enhanced by exposing trap nests, thereby indicating that nest site limitation was mainly responsible for the absence of *O. rufa* in small habitats at the start of the experiment. The positive density–area relationship follows the predictions of the resource concentration hypothesis and might be explained by different emigration and immigration rates in small and large patches (Hambäck and Englund 2005).

Conclusions

Our study provides strong evidence for limitation of local *O. rufa* population size by nesting resources, marginal evidence for negative density-dependent bottom-up regulation of population growth rates, but no support for top-down regulation by natural enemies. Habitat area positively influenced *O. rufa* populations whereas habitat connectivity neither affected *O. rufa* nor associated natural enemies. Taking into account how few other studies on population dynamics of bees exist, it is too early to draw general conclusions for the relative importance of top-down and bottom-up forces for other more specialized solitary bees. However, it can be hypothesized that solitary species with aggregated nesting sites and inverse density-dependent parasitism may be primarily limited by food or nesting resources. It remains a challenging task to build up the data basis for a more general comparison of driving forces of population dynamics in pollinator food webs.

From an applied point of view, trap nests as additional nesting resources provide a suitable management strategy to significantly enhance solitary bee densities and to ensure pollination services for insect-pollinated perennial orchard crops (Richards 1993, Kremen et al. 2002). A detailed understanding of driving factors of pollinator population dynamics is the key for a successful implementation of such management strategies.

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APPENDIX A

Abundance and biotic interactions of *Osmia rufa* populations, and percentage brood cells of *O. rufa*, other bees, and wasps in trap nests from 1998 to 2003 (*Ecological Archives* E089-083-A1).

APPENDIX B

Effects of population size on rate of parasitism of *O. rufa* populations during the study period, 1998–2003 (*Ecological Archives* E089-083-A2).

APPENDIX C

Time series analyses of effects of population size on population growth rates (*Ecological Archives* E089-083-A3).