Nest-Site Fidelity, Body Weight and Population Size of the Red Mason Bee, Osmia rufa (Hymenoptera: Megachilidae), Evaluated by Mark-Recapture Experiments

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Mark-recapture experiments were used to examine nest-site fidelity, natural local population size and effects of body weight on dispersal strategies in the solitary bee *Osmia rufa* Linnaeus 1758. A total of 974 hibernated ♀♀ was individually marked and weighed inside their cocoons and then released in five orchard meadows for emergence. In May 2002, colonisation of three spatially separated trap nest locations on each study site (mean distance 52 m) by marked and unmarked ♀♀ of *O. rufa* was monitored. Only 222 (22.8 %) of all marked ♀♀ (3–108 per site) were re-observed. Mortality rates varied between 2.2 and 26.4 % between study sites. Thus estimated 74 % of emerged ♀♀ left the parental nest-site. The number of observed unmarked ♀♀ varied between 9 and 16 per site resulting in an estimated natural population size between 48 and 258 individuals or 15 ♀♀ per 1000 m² on average. The mean body weight of marked recaptured ♀♀ (113.0 ± 14.9 mg) was significantly higher than the body weight of marked but not recaptured ♀♀(107.3 ± 19.0 mg). The results give new insights into the possible densities of natural populations of a solitary bee species, its nest-site fidelity and the potential role of body weight for dispersal strategies.

Key words: *Osmia rufa* Linnaeus 1758 – dispersal – orchard meadows – population dynamics – trap nests

1   Introduction

Native bees are key pollinators in most terrestrial ecosystems, and therefore a better understanding of their ecology is essential for future conservation of suitable habitats and ecological interactions [KEARNS et al 1998]. Up to now, only a few studies deal with spatial population dynamics in European bees [STEFFAN-DEWENTER 2003].

A key parameter is the size of a population that is affected by local reproductive success and mortality and the proportion of immigrating or emigrating individuals between regional populations [HANSKI 1998].

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The knowledge of bee populations is limited, because nest-sites are inconspicuous, local populations of most species are small, and quantitative data on adult bee densities and dispersal distances are difficult to obtain [POTTS & WILLMER 1997, MICHENER 2000, KELLS & GOULSON 2003]. Several studies have shown high nest-site fidelity [WESTRICH 1989, POTTS & WILLMER 1997, MICHENER 2000], whereas others indicate high colonisation ability [STEFFAN-DEWENTER 2002]. Such dispersal after emergence may significantly differ from foraging distances of nest-provisioning species, derived from homing experiments or harmonic radar observations [OSBORNE et al 1999, GOULSON & STOUT 2001, GATHMANN & TSCHARNTKE 2002]. Dispersal data could improve the understanding of how species cope with increasing fragmentation and isolation of habitats [STEFFAN-DEWENTER & TSCHARNTKE 2002]. One tool to answer such questions are mark-recapture experiments that are commonly used for butterflies [e.g SETTELE et al 1998, BAGUETTE et al 2000], but for bees only in the context of homing experiments [e.g GARY 1971, OSBORNE et al 1999, GATHMANN & TSCHARNTKE 2002].

Body weight of bees and wasps depends on both evolutionary selection pressures and environmental habitat conditions and is assumed to be a key factor for reproductive success, competitive capacity, and dispersal abilities [STROHM & LINSENMAIER 1997, KIM 1997, STROHM 2000]. Female weight at emergence depends on the quality and quantity of brood cell provisions [GATHMANN & TSCHARNTKE 2002, ROULSTON & CANE 2002]. Individual fecundity, success of nest usurpation behaviour and foraging distances are positively related to female body weight [KIM 1997, GATHMANN & TSCHARNTKE 2002]. Furthermore, body weight may influence dispersal behaviour. For example, heavier ♂♂ of the mason bee *Osmia rufa* have been shown to stay at their paternal nest-site whereas lighter, competitively inferior ♂♂ leave the maternal nest-sites [SEIDELMANN 1999].

O rufa is a solitary, above-ground nesting species which is common in central Europe. It has normally one generation which emerges in spring; female adults are flying for about eight weeks [WESTRICH 1989]. Local population size can be easily enhanced by trap nests made from bundles of common reed (*Phragmitis australis*) that are put into plastic tubes to protect them from rain [TSCHARNTKE et al 1998]. Bee nests built inside the reed internodes can be opened and bees inside the cocoons can be individually marked before emergence. Trap nests allow quantification of most aspects of nest construction and provisioning [STROHM et al 2002].

In this study marked red mason bees, *Osmia rufa* L, were recaptured after emergence by observing trap nests in order to answer the following questions:
a) Which proportion of emerging ♀♀ stays at the maternal nest-site?
b) Over which distance do ♀♀ disperse within habitat patches?
c) How large are local populations of *O rufa* in natural nesting conditions as compared to populations in trap nests?
d) Does female body weight affect nest-site fidelity?

2 Material and methods

2.1 Study sites

The study was conducted at five spatially separated orchard meadows (mean area 10842 m² ± 4900 SD, distance to nearest neighbouring study site > 1800m) in the vicinity of Göttingen (Germany) in 2002 (Tab 1). Three wooden posts each with four empty trap nests were placed on each meadow in 1998 [STEFFAN-DEWENTER 2003]. Each trap nest consisted of 153 ± 14.3 stems of common reed (20 cm length) with a mean diameter of 5.3 ± 1.5 mm (range 2–10 mm, n= 1531). From 1998–2001 local populations of *O rufa* had established in these artificial nesting sites which were used as basis for mark-recapture experiments. The mean distance between the three trap nest locations per study site was 52.4 ± 18.7m with a range between 26.3 and 114.1m.

Extensively used orchard meadows are a typical habitat of *O rufa* providing nesting places in dead wood and rich food resources during the flight period. The main flight period lasts from the end of April to the beginning of June. *O rufa* is a polylectic species using a wide variety of pollen sources. ♀♀ prefer as nesting substrate holes of 6–8 mm in diameter. They build linear nests with several brood cells separated and sealed by loam walls at the opening. Larvae feed on pollen provision, spin into a cocoon, pupate and hibernate as adults in their cocoons [WESTRICH 1989].

2.2 Mark-recapture experiments

Trap nests exposed over the season were collected in autumn 2001 from the five study sites and stored at +4°C during the winter. In the laboratory, all reed stems with *O rufa* nests were taken from the trap nests and opened with a scalpel to obtain the individual cocoons. Each cocoon was opened at the tip to check for the sex of the hibernating imagines. All cocoons which contained ♀♀ were weighed (Scaltec SBC 31, Heiligenstadt, Germany, d= ±0.1mg) and individually marked with numbered tags of five different colours that are normally used to mark honey bee queens (Opalith Zeichenplättchen, Imkereibedarf Seip, Butzbach–Ebersgöns, Germany) in March. The cocoons were only partially opened with a small scalpel to fix the tags with glue on the thorax. After marking, the cocoons were put back into the reed stems, these were closed again to make sure that emergence was comparable to undisturbed conditions and stored at +4 °C until spring. For each of the three wooden posts per study site, a different colour was used so that ♀♀ which changed posts within the orchard meadows could be easily detected during the field observations. Altogether, 974 ♀♀ were marked, but the number of individuals varied considerably between study sites depending on local abundance in the trap nests (**Tab 1**). On 25 April 2002 all marked ♀♀ and the unmarked ♂♂ were put into emergence boxes that were placed on the post from where the individuals came from.

About ten days after the calculated emergence of the ♀♀, standardised observations were started to record nest building *O rufa* ♀♀. Each post was observed for 30–60 min depending on the number of released, marked individuals during each of two observation periods (16–17 May and 21–22 May 2002). A total of 215–290 min observation time was spent at each study site. Additionally, for three sites with high numbers of marked ♀♀ a third observation (27 May) was performed to check for the completeness of earlier observations. The tag number and colour of marked individuals and the number of observations of unmarked nest-provisioning ♀♀ were recorded. Unmarked ♀♀ from other natural nest-sites were marked with colour pen (Edding 751 paint marker) to exclude double counting. The number of nest provisioning marked ♀♀ in relation to unmarked ♀♀ was used to estimate the local natural population size, according to the following formula (similar to the Lincoln-Petersen method to estimate population size, SETTELE et al 1998):

Number of emerged marked ♀♀ (M_e)/Number of observed marked ♀♀ (M_o) = Number of emerged ♀♀ from local population in natural nesting sites (N_e)/Number of observed unmarked ♀♀ (N_o) and thus $N_e= M_e*N_o/M_o$.

After the end of the experiment the number of dead female *O rufa* individuals inside the emergence boxes was counted to calculate rates of pre-emergence adult mortality.

2.3 Statistical analyses

The statistical analyses of the data were performed with Statgraphics Plus 5.1. Spearman rank correlations were used for not normally distributed data and simple regressions for data which achieved normality to test for correlations between habitat characteristics, population size and mark-recapture data. Two-way Anova with type-three sums of squares was used for categorical factors. Arithmetic means ± one standard deviation (SD) are given in the text.

Tab 1: Population parameters of *Osmia rufa* Linnaeus 1758 [Hymenoptera: Megachilidae] on five study sites.

Study site (number)	Gauss-Krüger coordinates (RW/HW)	Number of marked *O. rufa* ♀♀	Number of re-observed ♀♀	Re-observed marked ♀♀ (% of marked ♀♀)	Total mortality rates of *O. rufa* ♀♀	Estimated number of emerged marked ♀♀	Number of unmarked ♀♀	Unmarked ♀♀ (% of all observed ♀♀)	Estimated number of emerged ♀♀ from natural nesting sites
Deiderode (1)	3660330/5698644	21	3	14.3 %	12.8 %	18	16	84.2 %	96
Bodensee (2)	3580750/5719964	83	37	44.6 %	2.2 %	81	9	19.6 %	20
Gieboldehausen (3)	3582500/5720288	232	65	28.1 %	8.1 %	213	16	19.8 %	52
Atzenhausen (4)	3555877/5698758	234	9	3.9 %	26.4 %	172	12	57.1 %	229
Wöllmarshausen (5)	3575614/5706400	404	108	26.7 %	7.8 %	372	14	11.5 %	48
		Σ 974	Σ 222	22.8 %	12.1 %	Σ 856	Σ 67	23.2 %	Σ 445

3   Results

3.1   Dispersal rates and population size

Altogether 222 nest-provisioning ♀♀ out of the 974 marked ♀♀ were re-observed at the trap nests. The number of re-observed ♀♀ ranged from 3 to 108 individuals and the proportion varied between 3.9 % and 44.6 % for the five study sites (**Tab 1**). Orchard area (r_s= 0.5, p= 0.317), cover of oilseed rape in the surrounding landscape (r_s= 0.7, p= 0.16) and local population size (r_s= -0.2, p= 0.689) did not explain this variation, but the mortality rate was negatively correlated with the proportion of re-observed ♀♀ (Fig 1). The mean mortality rate of *O rufa* was 12.1 % and varied between 2.2 % and 26.4 % (**Tab 1**). Using these mortality rates we estimated the number of remaining emerged marked ♀♀ per study site which varied between 18 and 372 individuals (**Tab 1**). Thus, there was a considerable discrepancy between the estimated total number of emerged ♀♀ (856 individuals) and the number of re-observed marked ♀♀ (222 individuals) indicating that a significant proportion (strictly calculated 74.1 %) of the ♀♀ emerged but did not start nest building activities in the maternal nesting habitat. Alternatively, we did not re-observe nest-provisioning ♀♀ due to restricted observation time. However, for three sites with three observation periods, 59.8 % of all recaptured ♀♀ were observed during the first observation period, further 31.8 % after the second and only 8.4 % were first observed during the third observation period indicating that only a low proportion of marked nest building individuals were not observed.
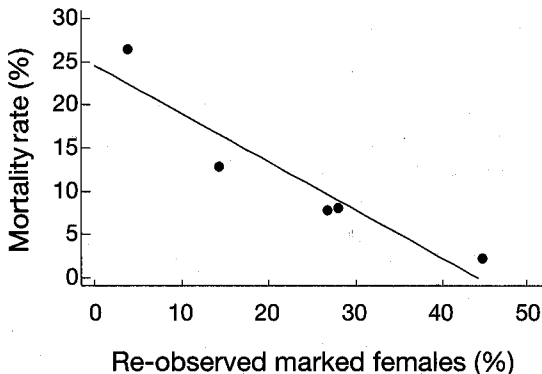

Fig 1: Relationship between the mortality rate (%) of *Osmia rufa* Linnaeus 1758 [Hymenoptera: Megachilidae] and the proportion of re-observed marked *O rufa* ♀♀ (%) at five study sites: F= 21.7; r= 0.937; p= 0.019, n= 5

A total of 67 unmarked nest-building ♀♀ (23.2 % of all recorded ♀♀) were observed at the trap nests on the five study sites. Using the estimator formula (see methods) this translates to a mean number of emerging ♀♀ from natural nesting sites of 89±83 individuals with a range between 48 and 258 individuals (**Tab 1**). Thus, on average only about one quarter of the trap nesting *O rufa* females came from populations in natural nesting sites.

3.2 Body weight

The mean body weight of the 974 marked ♀♀ was 108.7 ± 18.2 mg. In a two-factor Anova the mean body weight of re-observed ♀♀ was significantly higher than the body weight of marked but not re-observed ♀♀ (**Fig 2A**). Thus, small ♀♀ had a higher dispersal probability or a higher mortality rate than large ♀♀. However, mean body weight per study site was not correlated with mortality rate (r_s= -0.176, p= 0.777, n= 5) or the proportion of recaptured ♀♀ (r_s= 0.60, p= 0.23, n= 5) although mean body weight varied significantly between the five study sites (**Fig 2B**).
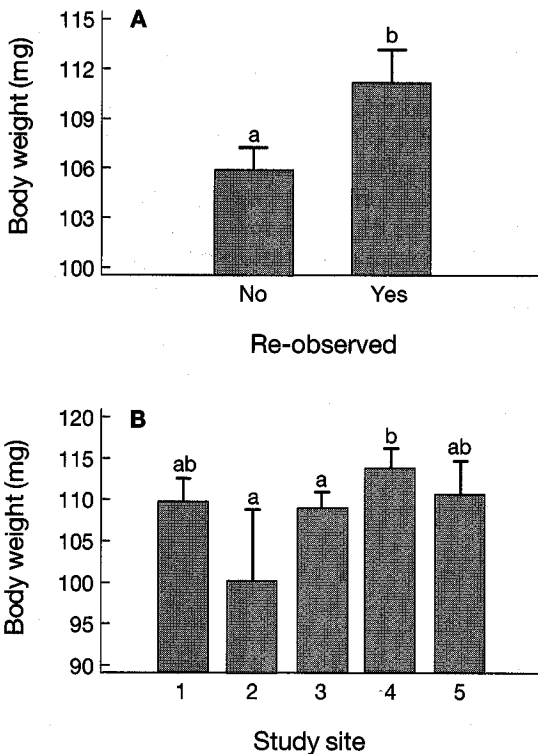

Fig 2: Results of two-way Anova for body weight of marked females of *Osmia rufa* Linnaeus 1758 [Hymenoptera: Megachilidae]. (a) Mean body weight for re-observed versus not re-observed ♀♀: F= 13.43, p= 0.0002, n= 974. (b) Mean body weight on the five study sites (numbers refer to Table 1, first column): F= 4.23, p= 0.0021, n= 974. Arithmethic means and 95 % Scheffe intervals are given. Significantly different groups are marked by different letters.

3.3 Nest-site fidelity

As a further estimate of nest-site fidelity of female *O rufa* individuals the post-emergence dispersal of re-observed individuals within each of the five habitats was analysed. The majority of all re-observed ♀♀ (80.2 %) built their nest at the maternal nest-site. Only 19.8 % colonised other trap nests within the same habitat at a maximum distance of 70.3 m. No clear distance-dependent decrease in colonisation probability could be detected (**Fig 3**).

Possible colonisations at larger distances outside the studied habitats could not be detected with the here used experimental design. The body weight of ♀♀ at maternal nest-sites (n= 178) and other nest-sites within the same study site (n= 44) was not significantly different (F= 0.22, p= 0.641).
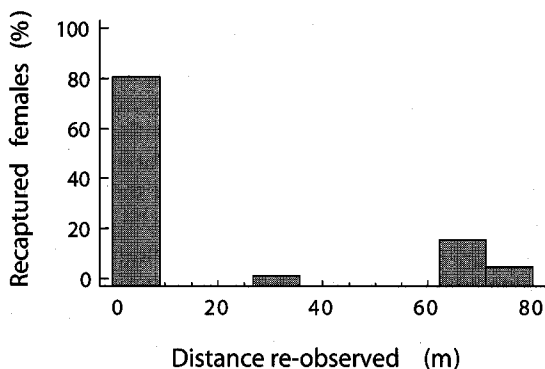

Fig 3: Frequency histogram of marked and re-observed ♀♀ of *Osmia rufa* Linnaeus 1758 [Hymenoptera: Megachilidae] on five study sites. The % of re-observations in nine distance classes are given.

4   Discussion

The results suggest a bimodal pattern of dispersal and nest-site fidelity for *O rufa*. On the one hand, about 75 % of all marked emerged ♀♀ were not re-observed on the study sites. This suggests that a large proportion of the emerged ♀♀ disperse to other habitats. However, it is possible that the proportion of dispersing ♀♀ has been overestimated because mortality due to predation or other factors can not be disentangled from long-distance dispersal. Earlier studies also suggest high dispersal abilities of *O rufa*, in that colonisation of trap nests by *O rufa* did not depend on isolation from natural habitats or landscape context [STEFFAN-DEWENTER 1998, 2002].

On the other hand, within the habitat patches, 80 % of all re-observed ♀♀ started nest provisioning activities at the maternal nest-site, and only 20 % colonised other trap nests at a maximum distance of 70 m, suggesting high local nest-site fidelity. High nest-site fidelity was found for other solitary bee species with aggregated nesting [POTTS & WILLMER 1997]. In general, *O rufa* showed an uneven distribution to the three trap nest locations within a study site indicating that either differences in microclimate or a tendency for individuals to nest near conspecifics affected nest-site selection [CANE 1991, WCISLO & CANE 1996, POTTS & WILLMER 1997].

For solitary bees, the knowledge of local population size is very restricted, although it is generally assumed that most species occur at low densities [WESTRICH 1989, MICHENER 2000]. The here presented experimental study allows to estimate the number of reproductive ♀♀ coming from natural nest-sites by using the relation between marked and unmarked nest-provisioning individuals at the trap nests. According to these calculations, local populations in natural nest-sites were small and ranged between 1.4–56 ♀♀ per 1000 m² (mean 15 ♀♀/1000 m²). These estimates are based on the assumption that trap nests and natural nest-sites had the same attractivity. A preference of unmarked ♀♀ for natural nest-sites

would result in an underestimation of local population size, whereas a preference for artificial trap nests would result in an overestimation. Furthermore, one can not distinguish, whether unmarked ♀♀ emerged within the local habitat or whether they immigrated from other habitat patches.

Interestingly, ♀♀ that were observed at the maternal nest-site were on average heavier than marked but not re-observed ♀♀. Thus, smaller ♀♀ have a higher probability to disperse (or experience higher mortality). This might be explained by two complementary reproductive strategies: first, large ♀♀ follow a conservative strategy and stay at the maternal nest-site. The fact that they have a high body weight indicates that the habitat was suitable in the last season, because habitat conditions significantly affect foraging effort, sex ratio and body weight of solitary bees [GATHMANN et al 1994, STONE 1994, GOODELL 2003]. Thus, large ♀♀ which stay in their maternal habitat should have a high probability that resources are abundant again. Second, small ♀♀ could be expected to follow a dispersal strategy, because their mothers were less successful in nest-provisioning, thereby indicating suboptimal habitat conditions. In this situation a more risky dispersal strategy might be more promising. Additionally, nest-sites are often limited for above-ground nesting solitary bees resulting in intra-specific competition and nest usurpation behaviour [WESTRICH 1989]. Larger ♀♀ have been shown to be competitively superior and regularly overtake already started nests of smaller individuals [KIM 1997, STROHM et al 2002]. Again, dispersal would be the better strategy for smaller ♀♀ to avoid disadvantageous interactions with competitively superior ♀♀. In conclusion, the here presented results give new insights into the possible local size of natural populations of a solitary bee species, its nest-site fidelity and the potential role of body weight for dispersal strategies.

5 Literature

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