Ann. Zool. Fennici 44: 405–414 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 19 December 2007

Pollen harvesting and reproductive rates in specialized solitary bees

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Received 23 Jan. 2007, revised version received 29 Oct. 2007, accepted 29 Oct. 2007

Franzén, M. & Larsson, M. 2007: Pollen harvesting and reproductive rates in specialized solitary bees. — *Ann. Zool. Fennici* 44: 405–414.

Andrena humilis is an endangered oligolectic solitary bee and has declined in recent decades throughout western Europe. The aim of this study was to explore the pollen harvesting pattern and to determine the reproductive rate in specialized andrenid bees. We measured the amount of pollen required to produce one brood-cell, the pollen harvesting rate and compared our results with data for other specialized andrenid bee species. Pollen-foraging trips were registered and the activity events (entering, leaving or digging) recorded at the nests. The mean number of pollen-foraging trips per day was 5.3 and an average bee nest was active (and open) 88 min day^{-1}. The bees were highly efficient in harvesting pollen and spent on average 10.7 min to complete one pollen-foraging trip. Most pollen-foraging trips (77%) were completed in less than 15 min. The duration of pollen-foraging trips increased over the day, presumably because pollen became more costly to harvest. Based on pollen counts (pollen loads on bees and pollen provisions) an average bee required 3.85 foraging trips to complete one brood cell and one bee managed to accomplish 1.37 brood cells in one day with suitable weather. In the literature we found data on an additional 19 specialized andrenid bee species. *Andrena humilis* seems to be extremely efficient compared with most other species, with an average trip for pollen lasting almost one hour (average for andrenid bees = 46 min). An extremely low reproductive rate seems to be a common trait among specialized bees in the family Andrenidae with an average 0.9 offspring produced per day and less than ten offspring produced during the whole lifetime. The high degree of specialisation and the low reproductive rate among andrenid bees can explain the severe decline in many species today.

Introduction

Most animals have to bridge some distances in space and time to provide all resources necessary for survival, and many species only survive in landscapes that provide access to multiple required resources (Michener & Rettenmeyer 1956, Matheson *et al*. 1996). The more limited a resource becomes, the higher degree of specialization is required to effectively utilize that

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This article has been scientifically edited by: Johan Kotze

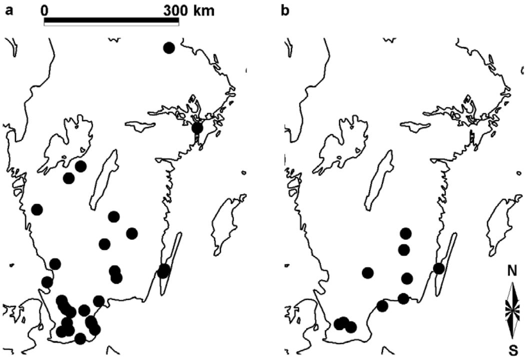

Fig. 1. The distribution of *Andrena humilis* in Sweden. (**a**) until 1989 and (**b**) 1990–2007.

resource (Gillman & Crawley 1990). It is also advantageous to utilize a resource of high quality and to minimise the cost of travel (Mayr 1963, Plowright & Laverty 1984). Thus, time and energy budgets are important to optimize while collecting food, and therefore influence population survival, growth and reproduction (Stephens & Krebs 1986). Consequently, to maximize the number of offspring, foraging should be most efficient at times when food is abundant.

Food resources in terms of nectar or pollen limit the population size of many insects (Minckley *et al.* 1994), and specialized solitary bees depend on abundant pollen resources (Larsson & Franzén 2007). Most non-parasitic solitary bees are obligate pollen consumers and often forage for pollen from a limited number of plant species. Each single adult female bee constructs a nest, gathers pollen from flowers and constructs separate brood cells for each egg. Pollen-foraging females of solitary bees have evolved morphological and behavioural adaptations to forage pollen efficiently (Wcislo *et al.* 1994, Herrera 1996). Specialized solitary bees generally harvest pollen more efficiently on their preferred pollen-plant than do generalist bees (Strickler 1979, 1982). Also, bees restricted to plant species where pollen is available only during a short period of time, have a particularly high pollen harvesting rate (Giovanetti & Lasso 2005).

Many andrenid bees are declining and knowledge about their foraging behaviour and reproductive rate are essential for the conservation of plant–pollinator systems. In this study we explored the foraging behaviour and reproductive rates in specialized andrenid bees. We studied the endangered and specialized solitary bee *Andrena humilis* Imhoff (Andrenidae). Our measurements included observations of daily bee activities, the rate of pollen harvested and the pollen required to produce one offspring. We expected the duration of pollen-foraging trips to be negatively related to the time of day (when pollen becomes more costly to harvest), and female bees to differ in pollen harvesting efficiency. Our results were subsequently compared with studies of other specialized andrenid bees.

Material and methods

Study area and study species

This study was performed in Råshult, Stenbrohult parish in southern Sweden (56°37´N, 14°11´E). Råshult consists of ca. four hectares of traditionally managed, dry meadows where the pollen plant *Leontodon hispidus* occurs (Nilsson & Nilsson 2004). We studied the endangered solitary bee *Andrena humilis,* which is a black, medium-sized bee (ca. 10 mm), specialized on foraging pollen from species in the group Lactuceae (Asteraceae) (Westrich 1990). In the study area this bee was observed to forage pollen mainly from *L. hispidus*. In Sweden *A. humilis* have been reported to forage pollen from *Pilosella officinarum*, *L. hispidus* and *Hypochoeris radicata* (M. Larsson unpubl. data). This bee species has probably matched its emergence to the phenology of its pollen plant, as described in similar systems (Minckley *et al*. 1994, Minckley *et al.* 1999). It nests gregariously in the ground where vegetation is sparse or absent. In Sweden, *A. humilis* has faced a dramatic decline during the last 50 years and is red-listed as endangered (Gärdenfors 2005). Currently, *A. humilis* is known from less than 10 areas in southern Sweden (Fig. 1).

Nest observations

A total of 450 nests were found in the study area in 2005. The nests were found in three separate aggregations on or close to sun-exposed pathways extending through the hay meadows. We observed the bees at their nests in one of these aggregations. The nest entrances were closed during the night but left opened during the day between the pollen-foraging trips. For each nest observed, the observations started when the bee opened the nest entrance in the morning and continued until the nest was closed for the day. Each nest was uniquely labelled and one person could observe up to 20 nests simultaneously. On 21 June 2005 a pilot study was performed and activities in 10 nests were observed. On 30 June 52 nests were labelled and observed by three persons and on 1 July 64 nests by four persons. The nests were observed the entire day, from 08:00 (before activity started) until activity ceased. For each nest we recorded the time for departures, arrivals and when digging occurred at the entrance. Thirty-six observations were excluded from the statistical analyses as it was uncertain at what time bees left or entered the nest. To be able to correct for possible temperature-related effects, the temperature was measured each hour between 9:00–13:00 on both days and the mean temperature for each day calculated.

Pollen samples

To quantify pollen provisions, nests of *A. humilis* were excavated. Fifteen cells that contained pollen provisions with eggs were collected and preserved in 70% ethanol. In the laboratory, the provision samples were sonicated (KS101, Kerry Ultrasonics Ltd.) for 35 min and quantified by counting a known volume proportion of the sample under a binocular microscope (the procedure was modified from Kearns & Williams 1993). In order to measure the pollen amount gathered per pollen-foraging trip we sampled 15 females at the nest site at ca. 12:00 on 30 June 2005 when they returned from a pollen-foraging trip. These sampled bees were stored in 70% ethanol and sonicated to release pollen from their bodies. The bees were then moved to a new jar filled with 70% ethanol and sonicated again. This process was repeated three times and the bees were then put under a binocular microscope for visual counting of any remaining pollen grains. The pollen content in the jars was quantified as described for the pollen provision samples.

Statistical analyses

The statistical analyses were based on data from two days when the nests were observed from opening until closed. A Generalised Linear Mixed Model was used to test the duration (min) of pollen-foraging trips in relation to the time (h) of day and the nestcode (nestcode as a random factor, h as covariate). The time of day of nest arrival (h) was categorized into periods of one hour. Tukey's post hoc test was performed to test for differences in hours of arrival. We were not able to re-identify and give the nests the same code as the day before, thus it was not possible to analyse day-effects correcting for the nestcode. ANCOVA was used to test the number of foraging trips (trips) of each female in one day in relation to the mean duration (min) of the pollen-foraging trips, the activity length measured from the time when the nest was open until closed per day (activity time) and the study day (study day used as a fixed factor, trips and activity time as covariates). Student's *t*-test was used to see if there was any difference in the duration (min) of pollen-foraging trips and the number of foraging trips (trips) during one day between the two study days. Linear regression was used to relate the effect of the number of pollen-foraging trips per day to the mean duration of pollen-foraging trips. The relationship between the number of pollen-foraging trips per day and the time when the nest were opened and closed was analysed using Pearson correlation. The opening and closing time of the nest could not be included in the ANCOVA because the variables were correlated to each other and related to the activity length during one day (activity time). All statistical analyses were performed in SPSS 14.0. Mean values are given with ±1 SE.

Results

Observations of *Andrena humilis*

In total, 529 pollen-foraging trips were registered

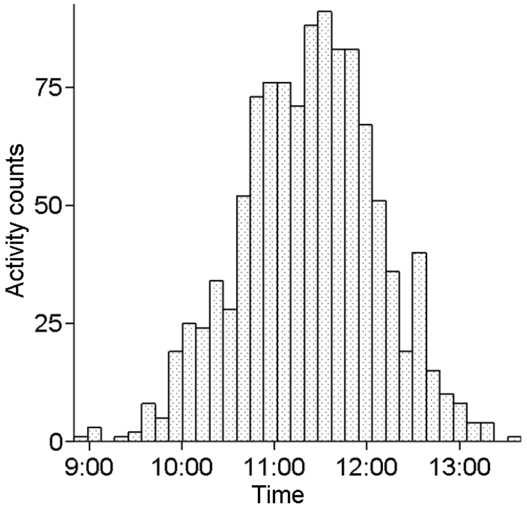

Fig. 2. Activity at the nest in a colony of *Andrena humilis* in southern Sweden 2004. Each count refers to either when a bee enters, leaves or digs at the nest.

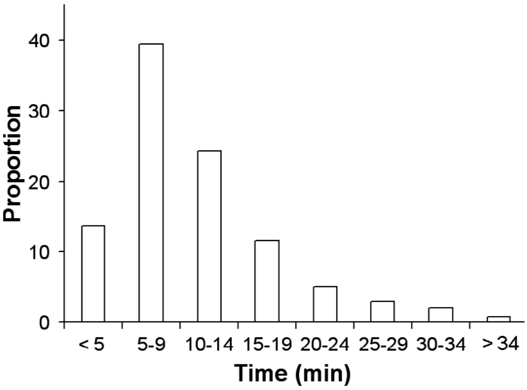

Fig. 3. The duration of one pollen-foraging trip in *Andrena humilis* (n = 101).

and 1120 activity events (entering, leaving or digging) recorded at 116 nests. Bees were active on average 88 ± 4.1 min between 8:50–13:30 with a distinct peak at 11:30 (Fig. 2).

Pollen harvesting

The bees were highly efficient in harvesting pollen and spent on average 10.7 ± 0.3 min to complete a pollen-foraging trip (range 2–35, median 9.00, n = 529). Most pollen-foraging trips (77%) were completed in less than 15 min (Fig. 3). The bees spent 7.1 ± 0.28 min inside the nests between the foraging trips (range 2–34, median 6.00, n = 269). The duration of pollen-foraging trips increased over the day (Table 1 and Fig. 4). Trip duration was shorter in the second study day (t-test: $t = 0.56$, $p = 0.01$, df = 528). The difference between the two study days can be explained by the temperature that was lower during the first day (mean pollen-foraging duration 11.27 ± 0.44 min, median 12.0 min, n = 252, mean temperature 18.8 °C) as compared with that during the second day (mean pollen-foraging duration 9.68 ± 0.39 min, median 10.0 min, n = 266, mean temperature 19.9 °C). There was no difference in the number of pollen-foraging trips between the days (mean day one 5.43 ± 0.44, mean day two 5.86 ± 0.51, t-test: $t = 0.645$, $p = 0.520$, df = 90).

The mean number of pollen-foraging trips per day and bee was 5.3 ± 0.33 (range 1–17, median 5.0, n = 101). The bee individuals that completed more pollen-foraging trips per day spent less

Table 1. The duration of pollen-foraging trips in relation to the hour of nest entrance and the nestcode (random factor). The number of pollen-foraging trips was related to the duration of pollen-foraging trips by one individual, the total activity-time of one bee and the study day (fixed factor).

Dependent variable	Source of variation	df	*F*	*P*
Duration of pollen-foraging trip	Nestcode	1, 357	1.47	0.015
	Hour	1, 357	52.7	< 0.001
	Nestcode × Hour	1, 357	1.46	0.02
Number of pollen-foraging trips per day	Study day	1, 88	7.65	0.007
	Mean duration of trips[a]	1, 88	33.0	< 0.001
	Activity time	1, 88	231	< 0.001

[a] Mean duration of pollen-foraging trips by one individual.

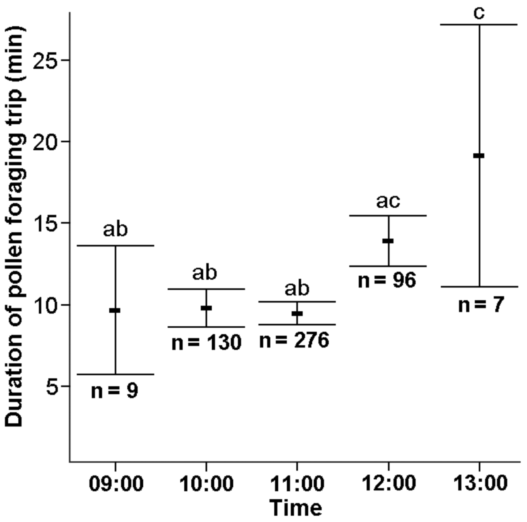

Fig. 4. The duration of pollen-foraging trips in *Andrena humilis* in relation to the time of the day. Error bars show 95% CI of the mean. Error bars not sharing same letters are significantly different ($p < 0.05$, *see* Table 1).

time per foraging trip than did individuals that completed fewer trips, and bees that were active for longer completed more foraging trips than bees that were active for a shorter period of time (Table 1 and Fig. 5). The number of pollen-foraging trips per day was not related to the time when the nest was first active during the day ($r = -0.16$, $p = 0.16$; Fig. 6a) but the number of pollen-foraging trips increased the later the nest was closed ($r = 0.52$, $p < 0.001$, Fig. 6b).

Pollen provisions and daily harvest

On average 876 159 ± 78 141 ($n = 15$) pollen grains were collected during a foraging trip. The complete pollen provisions per cell consisted of on average 3 378 585 ± 134 340 pollen grains ($n = 12$). No evidence was found for a sex biased pollen provision. Based on this, an average bee requires 3.85 foraging trips to complete one brood cell and manages to accomplish 1.37 brood cells per day.

Discussion

Highly specialized bee–flower systems are subject to strong selective forces that shape the behaviour and morphology in bees (Minckley *et al.* 1999, Goulson 1999). For example, the rate of pollen-harvesting is an important adaptive constraint in systems involving a limited pollen resource. The solitary bee *Andrena humilis* is specialized on utilizing its pollen plants and possesses a number of behavioural adaptations. In the present study an average pollen-foraging trip was only ca. 10 min and contained ca. 880 000 pollen grains. In other systems involving specialized andrenid bees, the pollen-foraging trips have been reported to be considerably longer (on average 46 min, *see* Table 2) and result in a smaller pollen load. It is notable that pollen-foraging

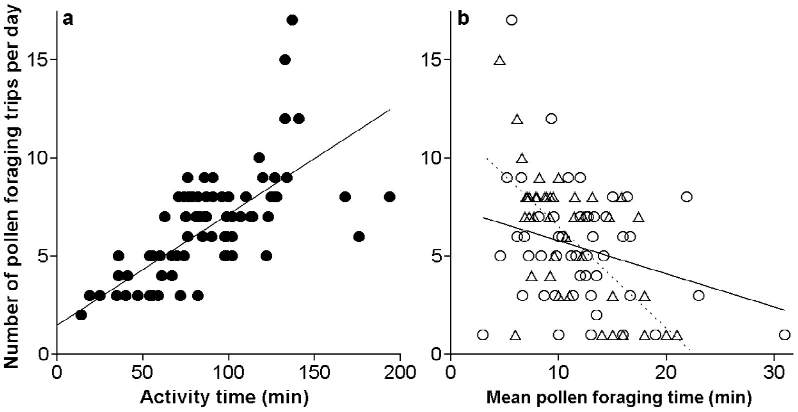

Fig. 5. — **a**: The number of pollen-foraging trips per day in relation to the total activity period during one day (from the time the nest was open until closed) ($n = 92$). Number of foraging trips = 1.46 + 0.06 × activity time (min) ($r^2 = 0.67$). — **b**: The number of pollen-foraging trips per day in relation to the mean pollen-foraging duration. ○: day 1 ($n = 49$); solid line: number of foraging trips = 7.45 – 0.17 × time (min) ($r^2 = 0.08$). △: day 2 ($n = 43$); dotted line: number of foraging trips = 11.69 – 0.52 × time (min) ($r^2 = 0.43$).

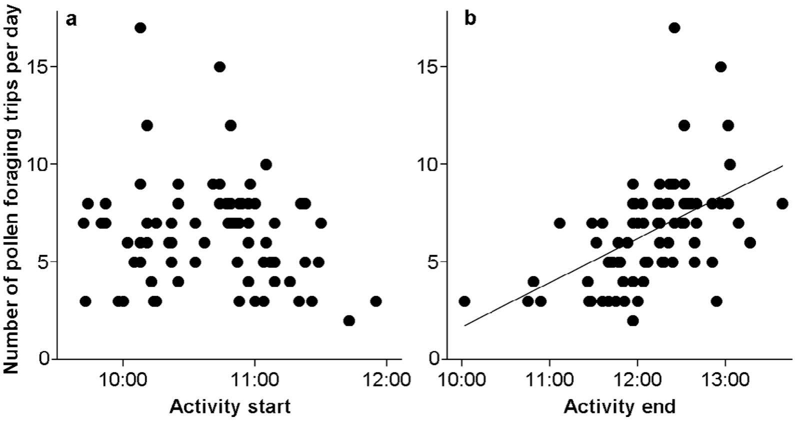

Fig. 6. — **a**: The relationship between the number of pollen-foraging trips accomplished in one day and the time when the nest were opened ($n = 77$). — **b**: The number of pollen-foraging trips in one day related to the time when the nests were closed ($n = 77$). Number of foraging trips = –20.93 + activity end ($r^2 = 0.27$).

patterns differ between solitary bee species. One of the most efficient bees is *Ptilothrix plumata* (Anthophoridae) that spend only ca. 2.4 min on a pollen-foraging trip (Schlindwein & Martins 2000). Other bees are reported to spend 2 h or more on a single pollen-foraging trip (e.g. Gebhardt & Röhr 1987). The high pollen harvesting rate of *A. humilis* is likely to be the result of an adaptation to the predictable, but time restricted, pollen resource provided by *L. hispidus*.

Plants presenting pollen over a long period of time normally attract pollen foragers throughout the day. For example, in the case of pollen foraging on Dipsacacaeae herbs (*Knautia arvensis* — e.g. *Dasypoda argentata* and *Andrena hattorfiana; Succisa pratensis* — e.g. *Andrena marginata*), specialized bees harvest pollen for most of the day and are characterized by long foraging trips (Table 2). Larsson and Franzén (2007) found that the foraging trips of *A. hattorfiana* lasted ca. 58 min and result in a load of ca. 29 000 pollen grains. In contrast, solitary bees such as *A. humilis*, but also *A. chalybaea* and *A. haynesi* (Thorp 1969, Osgood 1989) that are specialized on plants with short pollen presentation, are favoured by harvesting pollen rapidly and have only brief stays in the nest between trips.

An ability to switch from one pollen host-plant to another has been observed in several species of *Andrena* (Cruden 1972), but *A. humilis* was found to utilize a few pollen plants in the study area. Apparently, for efficient pollen harvesting, many plant taxa require a specific set of characters that specialized bees need to possess. For example the solitary bee *Megachile pilicrus* has evolved a special hindleg brush to be able to harvest pollen more efficiently from its exclusive pollen-plants (Müller & Bansac 2004). Similarly, a number of bee species have adapted to harvesting high pollen quantities from plants that present pollen during short periods of the day (Table 2). For *A. humilis*, the duration of pollen-foraging trips increased with time of day, but was distinctly higher at the very end of the day. Early in the day the humidity and the low temperatures influence the duration of pollen-foraging trips. Over the day pollen availability is believed to decrease as flower visitors of all kind collect or remove pollen. Pollen availability may become particularly low near the nesting site during the day and some flowers are closing already around 12:00. Therefore the bees are forced to visit more flowers to fill their scopae and to fly longer distances from the nest. These features may explain the observed increase in duration of foraging trips late in the day. Osgood (1989) found a similar result for *Andrena rudbeckiae* which required longer foraging trips towards the end of the day. This indicates that *A. humilis* require dense plant populations close to the nesting ground to prevent increased mortality due to prolonged foraging duration.

The total number of foraging trips accomplished in one day was negatively related to the

Table 2. Host-plant information and reproductive traits of specialized solitary bees in the Andrenidae family. [a–g] Values valid for an average female bee of respective species. [e–g] Estimated values from calculations based on time measurements from nest observations.

Species	Pollen-plant family	Main pollen-plant species	Foraging per day (min)[a]	Foraging trip (min)[b]	Nest stay (min)[c]	Trips per day[d]	Trips per cell[e]	Cells per day[f]	Lifetime offspring[g]	Reference
Andrena agilissima	Brassicaceae	Several	360	–	–	ca. 2.4	ca. 11	ca. 2	ca. 3.6	Giovanetti & Lasso 2005
Andrena clarkella	Salicaceae	*Salix* spp.	450	ca. 95	ca. 24	ca. 4	ca. 12	ca. 0.4	ca. 2.5	Gebhardt & Röhr 1987
Andrena erythronii	Liliaceae	*Erythronium mesochoreum*	570	ca. 60	ca. 30	ca. 4	–	–	ca. 6	Michener & Rettenmeyer 1956
Andrena erigeniae	Portulacaceae	*Claytonia virginica*	270	33.3 ± 2.3	7.54 ± 0.56	ca. 6	ca. 6	ca. 1	–	Davis & Laberge 1975
Andrena fuscipes	Ericaceae	*Calluna vulgaris*	585	ca. 52	ca. 18	ca. 4	ca. 6	ca. 0.7	ca 2.5	Gebhardt & Röhr 1987
Andrena rudbeckiae	Asteraceae	Several	243	33.5 ± 2.1	11.0 ± 0.7	ca. 7	ca. 11	ca. 0.6	–	Neff & Simpson 1997
Andrena vaga	Salicaceae	*Salix* spp.	350	ca. 65	–	–	4.63 ± 0.10	–	–	M. Larsson unpubl. data, Vleugel 1947
Andrena humilis	Asteraceae	*Leontodon hispidus*	82	10.7 ± 0.3	7.1 ± 0.28	5.3 ± 0.33	3.85	1.37	–	This paper
Andrena erythrogaster	Salicaceae	*Salix* spp.	540	59 ± 3.4	ca. 23	ca. 5	–	–	ca. 8.3	Miliczky 1988
Andrena polita	Asteraceae	Unknown		ca. 16	ca. 24	–	–	–	–	Popova 1983
Andrena ssp. (2)	Ranunculaceae	*Ranunculus californicus*	420	ca. 44	ca. 20	ca. 3	ca. 4	–	–	Linsley & MacSwain 1959
Andrena hattorfiana	Dipsacaceae	*Knautia arvensis*	464	57 ± 3.0	9.2 ± 0.7	ca. 7	10.4 ± 0.54	ca. 0.6	–	Larsson & Franzén 2007
Andrena marginata	Dipsacaceae	*Succisa pratensis*	605	74 ± 6.7	–	ca. 8	14 ± 2.5	ca. 0.6	ca. 11.2	M. Larsson unpubl. data
Andrena spp. (3)	Onagraceae	*Oenothera dentata*	45	ca. 3.0	ca 2.0	ca. 7	–	–	–	Linsley & MacSwain 1955
Andrena crataegi	Rosaceae	*Spiraea latifolia*	610	ca. 170	–	ca. 3	–	–	–	Osgood 1989
Andrena chalybaea	Onagraceae	*Camissonia ovata*	188	ca. 12	ca. 0.5	ca. 7	–	–	–	Thorp 1969
Andrena haynesi	Asteraceae	*Helianthus anomalus*	82	ca. 12	–	–	–	–	–	Parker & Griswold 1982
Andrena nycthemera	Salicaceae	*Salix* spp.	563	38 ± 2.2	55 ± 9.1	ca. 5	–	–	–	Schönitzer & Klinksik 1990
Panurgus banksianus	Asteraceae	*Hypochoeris radicata*	135	ca. 14	–	ca. 8	–	0.53 ± 0.03	ca. 6.7	Münster-Swendsen 1968, 1970
Panurginus crawfordi	Brassicaceae	*Brassica* spp.	180	ca. 30	ca. 4	–	–	–	–	Hirashima 1972
MEAN			338	46	17	5.5	8	0.9	5.8	

[a] Cumulative time (min) one bee is active searching for pollen outside her nest during one day.

[b] The time (min) from the time when leaving the nest, until returning to the nest with the pollen loads filled with pollen (i.e. the time required to accomplish one pollen foraging trip).

[c] The time (min) a bee stay in the nest between pollen foraging trips.

[d] The number of pollen foraging trips one bee perform in one day.

[e] The number of pollen foraging trips required to produce one brood cell (pollen provision).

[f] The number of brood cells (pollen provisions) produced in one day.

[g] The number of brood cells (pollen provisions) produced during the lifetime.

duration of the pollen-foraging trips of individuals and positively related to the activity length during one day. Possibly, some individuals concentrate on pollen-foraging during certain days, or perhaps some individuals are much more effective than others. Linsley and MacSwain (1959) suggested that the number of trips per day are related to the state of the nest and that bees accomplish more trips to complete unfinished brood cells. The total number of foraging trips accomplished in one day was related to the activity length but not the time of nest opening. The pollen resource is probably superabundant only for a short period of the day. During the peak of bee activity at 11:30 the pollen-foraging trips were the shortest. This suggests that the factor limiting *A. humilis* populations is the time of pollen presentation rather than the resource amount in terms of pollen. This short pollen presentation scheme of the pollen plant *L. hispidus* has potentially evolved to reduce pollen loss to flower visitors and thereby increase the plant's fitness. The timing and control of pollen release to flower visitors reflect selection for successful pollination (Wilson & Thomson 1999, Fenster *et al.* 2004). The pollination system of *L. hispidus* has not been studied, but the short pollen presentation might have evolved to avoid species such as *A. humilis,* that harvest large amounts of pollen (cf. Westerkamp 1996).

The number of pollen provisions made per day and the reproductive rate depend on the time spent and the amount of pollen transported during an average pollen-foraging trip. *Andrena humilis* made on average 1.4 pollen provisions per day. In the Andrenidae family one pollen provision per day seems to be the norm (average 0.9, Table 2). The amount of pollen carried during one pollen-foraging bout was also very high in *A. humilis*, thus the number of trips required to produce one offspring is low (3.8) as compared with that in other andrenid bee species (average 8, Table 2).

Implications for conservation

Solitary bees utilize multiple resources for building nests, and harvesting pollen and nectar (Eickwort & Ginsberg 1980), and it is beneficial to forage close to the nest (Naef-Daenzer 2000, Williams & Tepedino 2003). In fragmented landscapes an optimal forager must decide how long to stay in a patch and where to continue its search if it leaves the patch. Increased habitat destruction will especially affect species using multiple and spatiotemporally separated resources such as flower-visiting bees and wasps (Cane 2001, Ewers & Didham 2006). A low fecundity and thus a low reproductive rate seem to be a general pattern among several bees and influences population size and extinction risks (cf. Hanski & Singer 2001). Further studies are required to compare different traits in specialized *vs.* generalist bees.

From a conservation point of view it is important to highlight that some bees are active during extremely short periods and are, thus, hard to study and detect. Immediate conservation measures are required to rescue *A. humilis* and its cleptoparasite *Nomada integra* from extinction in several European countries, such as Sweden (Gärdenfors 2005) and Ireland (Fitzpatrick *et al.* 2006). *Andrena humilis* may particularly suffer from a decline of *L. hispidus* (Nilsson & Nilsson 2004). Bees are important pollinators and contribute important ecosystem services and should bee highlighted in conservation (Kearns *et al.* 1998). Many solitary bees may serve as umbrella species encompassing many other insects and probably indicate a long history and high habitat quality of floral resources and nesting ground. *A. humilis* is probably one example of such a species.

Acknowledgement

We thank Sofia Larsson and Charlotte Jonsson for help in the field. We thank L. Anders Nilsson, Sven G. Nilsson, Claire Holeton, Anna Persson, Henrik Smith and Erik Öckinger for fruitful discussions and comments on the manuscript. Financial support was provided by Lunds Djurskyddsfond, Societas Phytogeographica Suecica and FORMAS. Johan Kotze improved the English.

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