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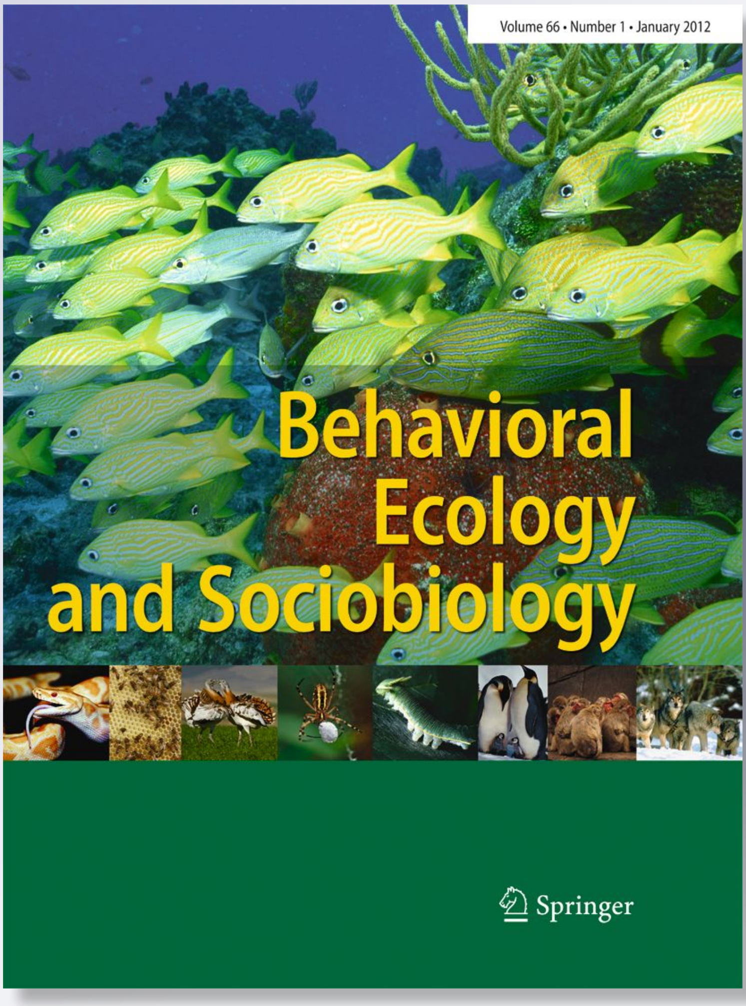

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ORIGINAL PAPER

Body size, demography and foraging in a socially plastic sweat bee: a common garden experiment

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Abstract Phenotypic plasticity may evolve when conditions vary temporally or spatially on a small enough scale. Plasticity is thought to play a central role in the early stages of evolutionary transitions, including major transitions such as those between non-sociality and sociality. The sweat bee *Halictus rubicundus* is of special interest in this respect, because it is socially plastic in the British Isles: Nests are social or non-social depending on the environment. However, sociality comprises a complex suite of interrelated traits. To further investigate social plasticity in *H. rubicundus*, we measured traits that are potentially integral to social phenotype at a northern site, where nests are non-social, and a southern site where nests can be social. We found that foundresses at non-social sites were smaller, produced offspring of a size more similar to themselves, initiated nesting later, and took longer to produce their first female offspring. They began provisioning earlier in the day, finished earlier, and collected more pollen loads. Common garden experiments suggested that these differences represent mainly plasticity, as expected for traits involved in the overall plastic social phenotype, with only limited evidence for fixed genetic differences in foraging. Conditions during overwintering did not have major effects on a foundress' subsequent behaviour.

Keywords Phenotypic plasticity · Sweat bees · *Halictus* · Social phenotype · Common garden

Introduction

Phenotypic plasticity, in which the same genotype expresses different phenotypes in different environments, may evolve when conditions vary temporally or spatially on a small enough scale (Whitman and Agrawal 2009). Plasticity is thought to play a central role in the early stages of evolutionary transitions, including major transitions such as those between non-sociality and sociality (West-Eberhard 2003; Chapuisat 2010; Field et al. 2010). The transition to eusociality has occurred multiple times within the ecologically highly successful Hymenoptera (Brady et al. 2006). During the past 40 years, there has been considerable research into functional questions concerning these transitions (reviewed by Strassmann and Queller 2007), but comparatively little into the underlying mechanisms (see, Smith et al. 2008).

Eusociality has been gained and lost repeatedly in sweat bees (Halictidae) (Danforth 2002). The sweat bee *Halictus rubicundus* Christ is of special interest in this respect because it is socially polymorphic (Eickwort et al. 1996; Soucy 2002; Soucy and Danforth 2002; Field et al. 2010). It has a Holarctic distribution, and the following life cycle summary is based on work in the UK, Ireland and North

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America (Yanega 1989, 1990, 1996; Eickwort et al. 1996; Soucy 2002; Soucy and Danforth 2002; Field et al. 2010). In spring, each overwintered, mated female, known as a foundress, digs a separate nest burrow where she alone rears a first brood (B1) of ≈6 offspring. Each offspring is provided with a ball of pollen and nectar placed in a separate, closed brood cell at the end of a short side-tunnel. Northern or high-altitude populations of *H. rubicundus* are non-social: There is a single brood of male and female offspring each year, and mated B1 females overwinter to become the following year's new foundresses. Southern, low-altitude populations, however, are social: Some B1 females become helpers, which forage to provision a second brood (B2) of offspring (Yanega 1989; Soucy 2002; Soro et al. 2010). These offspring are produced by the foundress if she is still alive, or by one of the B1 females if the foundress is dead (Yanega 1989; Field et al. 2010). After mating, all B2 females overwinter. Males die before winter and are not involved in nesting.

The first attempt to investigate the underlying basis of social phenotype in *H. rubicundus* focussed on US populations. Soucy and Danforth (2002) found significant mitochondrial differentiation between the two social forms and tentatively suggested that variation in social phenotype itself might therefore have a genetic basis. However, more recent work showed that, in British and Irish populations, social phenotype is plastic (Field et al. 2010). When foundresses were transplanted from a southern site, where nests are social, to a northern site where native nests are non-social, transplanted bees all had non-social nests. Similarly, the reverse transplant caused a proportion of bees from a northern, non-social site to have social nests (Field et al. 2010). While this work demonstrates that sociality is plastic in Britain, sociality comprises a complex suite of inter-related traits. Here, we test for plasticity in four such traits: body size, nest initiation date, offspring maturation date and adult (foundress) foraging. These traits may be intimately linked to social phenotype. For example, workers are often smaller than foundresses in social populations of sweat bees (Packer and Knerer 1985; Soucy 2002; Soucy and Danforth 2002). And because non-social populations have only one offspring brood per year, while sociality requires at least two broods (Soucy and Danforth 2002; Field et al. 2010), sociality may require earlier nest initiation and offspring production than non-sociality.

As in other ectotherms, adult activity and offspring development are strongly influenced by temperature in bees (Kamm 1974; Heinrich 1979; Willmer 1985; Weissel et al. 2006; Hirata and Higashi 2008). This consideration alone leads to the expectation that, at higher latitudes, reproduction will be initiated later in spring, foundress foraging rates will be reduced, larval development will be slower and there should be a shorter growing season for larval development, perhaps resulting in smaller offspring. However, other adaptive patterns might result from the social plasticity that *H. rubicundus* exhibits. Because sociality requires an extra annual brood, southern bees might be more time-stressed than northern bees, perhaps favouring faster development and foraging in the south rather than the north. Alternatively, since foraging is probably costly in terms of both mortality risks and physiological wear, southern foundresses that expect to eventually have helpers might forage less hard because they stand to lose more reproduction if they die before offspring emergence (Cant and Field 2001). In this paper, we measure body size, nest initiation, offspring maturation and foraging at a northern (non-social) and a southern (social) site. We also test whether these traits are plastic, by transplanting individuals from different locations to a common environment ('garden'). Laboratory common gardens can be used to test how specific variables affect the phenotype, but the natural common gardens that we utilize retain greater realism, including the effects of unidentified variables associated with different environments. Our results indicate that the considerable differences we find primarily reflect plasticity rather than genetically fixed differences, as expected for traits involved in the overall plastic 'social phenotype'.

Methods

Study sites

We used two common garden sites: a northern garden (Peebles, Scottish Borders) where native nests are all non-social and a southern garden (Sherborne, Dorset) where pilot observations showed that native nests often become social (Fig. 1; Field et al. 2010). In addition to observing bees native to the two common gardens, we transplanted them from three other sources (Fig. 1): Penrith and Belfast in the north, where all nests are non-social, and Wicklow in the south, where most or all nests are social (Fig. 1; Field et al. 2010). Penrith and Wicklow bees were transplanted to both common gardens, whereas Belfast bees were transplanted to only the southern garden. Further information about the sites is given in Table 1.

The northern common garden comprised 5 m of a low, near-vertical sandy bank approximately 2 m from the River Tweed where it passes through pasture land. There were approximately 500 native *H. rubicundus* nests in the bank. The bank faced south-west, and nests began to receive direct sunlight between 08:00 and 08:30 AM during our behavioural observations (see below). The southern common garden comprised a 1.5 × 0.75 m mound of light, sandy soil situated in a large walled garden. There were approximately 300 native *H. rubicundus* nests on the side of the mound facing north/north-west (a wall shaded the southern side). During behavioural observations, nest

Fig. 1 Map of Great Britain and Ireland showing locations of the common gardens (*squares*) and sources of transplanted bees (*circles*). *Filled symbols*: southern sites with social nests. *Open symbols*: northern sites with non-social nests

entrances received direct sunlight starting between 09:30 and 11:00 AM. Average daily temperature was 2–5°C lower at the northern garden than the southern garden in all but one month of the study (Fig. 2).

Transplanting bees

We observed bees at the northern common garden in 2006 and at the southern garden in 2007. In both years, observations began before nests were initiated in spring and ended on 31 July. *H. rubicundus* foundresses were captured outside their nests using an insect net and then transplanted to the appropriate garden in both the spring of the year when bees were subsequently observed and in the autumn of the previous year. In autumn, we transplanted recently emerged future foundresses, easily recognizable by their fresh colouration and intact hair. These foundresses were collected from source sites in late August/early September, as they returned to the nesting area in the afternoon, probably after feeding at flowers or mating. Spring transplants involved foundresses that had just emerged from winter hibernation at source sites and were flying around in the nesting area before nesting had begun. Thus, autumn transplants experienced winter in the common garden, whereas spring transplants were moved after they had overwintered at source sites. Dissection showed that nearly all autumn-transplanted foundresses had mated before transplantation (Field et al. 2010). Thus, B1 offspring produced at the common gardens will usually have carried genes entirely from the source site. Because all males die before winter, this must also have been true for spring-transplanted foundresses.

Transplanted bees were given marks specific to their source site and collection date, using spots of enamel paint applied to the thorax. They were then stored individually for 1–5 days in plastic vials kept at 4°C until weather was suitable for release at the appropriate common garden. When releasing foundresses, we introduced them individually into artificial and naturally occurring holes within the native nest aggregation. Natural holes appeared to be disused *H. rubicundus* nests. Artificial holes were made by inserting a metal rod into the soil to a depth of 15–20 cm. The diameter of the rod matched that of a natural *H. rubicundus* burrow. To test how autumn transplantation affected nest establishment the following spring, we marked and then released a sample of newly emerged foundresses native to the common gardens, on the same dates when we released bees transplanted from other sites. These newly emerged foundresses, again recognizable by their fresh colouration and intact hair, were captured using an insect net in the same

Table 1 Details of locations used in the study

Location	Latitude/longitude	Temperature (°C)	Altitude (masl)	Social phenotype (Native bees)
Northern common garden (Peebles)	N 55°38′/W 3°10′	7.93	159	Non-social
Southern common garden (Sherborne)	N 50°55′/W 2°29′	10.54	90	Social
Northern transplant source (Penrith)	N 54°34′/W 2°55′	8.80	238	Non-social
Northern transplant source (Belfast)	N 54°32′/W 5°58′	7.68	41	Non-social
Southern transplant source (Co. Wicklow)	N 52°58′/W 6°15′	10.14	115	Social

Temperature is given as the mean for January through July averaged across 8 years (2001–2008). Weather data are derived from the nearest Web-based meteorological station. Non-social sites are where all native nests are non-social. Social sites are where nests often become social after B1 females reach adulthood

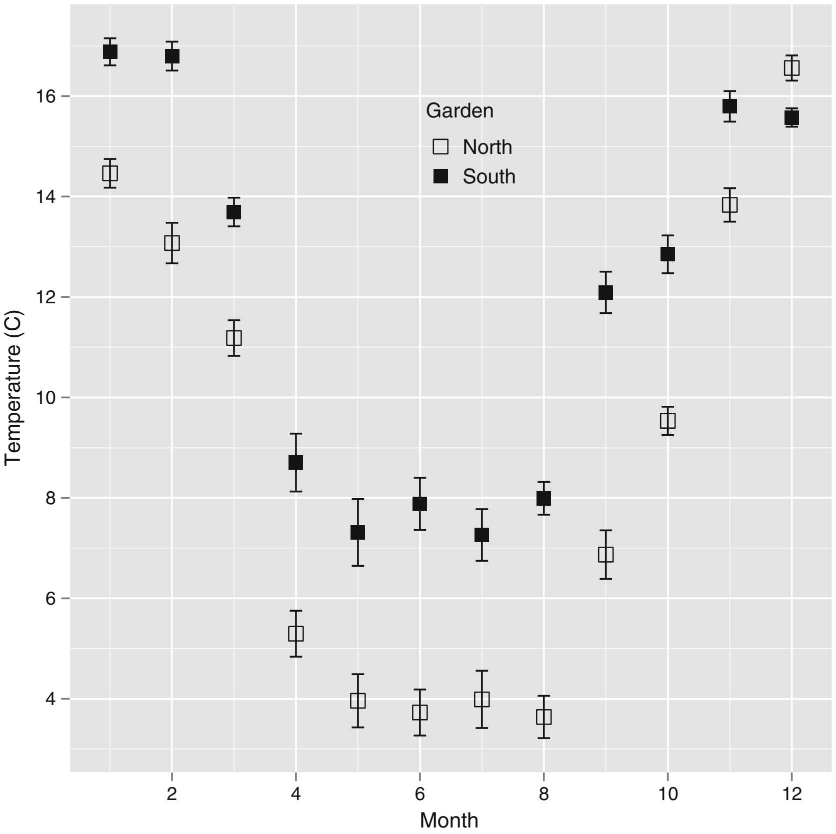


Fig. 2 Temperature (°C) during the experimental period at the Web-based meteorological stations nearest to the northern (2005–2006) and southern (2006–2007) common gardens. Data are monthly averages (±1SE) for mean daily temperature. Months are numbered from *1* (August) to *12* (the following July). Autumn-transplanted foundresses arrived at the common gardens in August–September (months 1–2), whereas spring-transplanted foundresses arrived in April (month 9)

way that transplanted foundresses were captured at their source sites (above). Failure to establish a nest the following spring could represent death or dispersal. Excavations during winter at our Belfast source site showed that at least some foundresses overwinter below ground within the nesting area.

Demography and offspring development

We recorded three aspects of demography: (1) Initiation of reproduction: the first date in spring when each foundress brought pollen to her nest; (2) B1 offspring maturation: the date when the first female offspring left each nest; (3) Time taken to produce the first female offspring, calculated as (2) −(1). B1 offspring were easily recognized because, unlike foundresses, they were unmarked and had unworn wings and unfaded brown thoracic hair. They remained associated with their natal nests for at least a few days, whether they subsequently entered hibernation or became workers. Note that (3) could be influenced by physical factors that affect rates of immature development, such as temperature, but also by the B1 offspring sex-ratio, which is more male-biased in non-social than eusocial populations in the USA (Yanega 1989; Eickwort et al. 1996; Soucy 2002), and by any deaths during development of the first-produced offspring in particular nests. We also recorded whether nests were taken over by conspecifics before B1 offspring reached adulthood. A takeover occurred when a previously marked foundress disappeared and was replaced by a foundress with a different mark or an unmarked foundress.

Foundress foraging behaviour and body size

We recorded foundress foraging behaviour in spring/early summer, before any offspring had reached adulthood. We focussed on three aspects of daily foraging: time of first return to the nest with pollen; time of last return with pollen; total number of pollen loads collected in the day. The first two of these could be recorded only if a bee collected at least one pollen load in the day. Nest entrances (marked with numbered nails) were watched continuously by two to three observers throughout the foraging period (08:00 to 18:00). Each time a bee entered a nest with pollen, we recorded time of day and nest number and checked the mark on the bee. Nests of transplanted and native bees were intermingled, and samples of marked native bees were observed at the same time as transplanted bees. Observation days (n=17 in 2006, 12 in 2007) ranged from days with only brief periods of sun to continuously hot, sunny days. No provisioning occurred on other, totally overcast days, and such days are excluded from analysis. Shade temperature was recorded hourly between 10:00 and 15:00 during foraging observations. Wherever possible, we briefly recaptured each foundress during one of the foraging observation days and used digital calipers to measure her forewing length from the outer edge of the tegulum to the wing tip. Approximately 50% of bees were successfully measured.

Data analysis

In order to investigate plasticity in each aspect of demography or behaviour, we carried out three tests. First, we tested whether there were differences between the bees native to the two common gardens: Unless natives behave differently at their respective sites, there may be no need for transplanted bees to exhibit plasticity. Second, we tested whether bees transplanted from the same source site behaved differently at the two common gardens (plasticity). For this analysis, we focussed on bees transplanted from Penrith (northern, non-social) and Wicklow (southern, social), since only they were transplanted to both of the gardens. An effect of 'common garden' would indicate plasticity, whereas an effect of 'source' would suggest genetic differences. We simultaneously tested for a source/garden interaction, which would indicate that bees from different sources were plastic to different degrees. Third, we used within-garden analyses to test how far transplanted bees adjusted their behaviour to match bees native to each garden. No difference between native and transplanted bees would be consistent with complete plasticity. For the within-garden analyses at the southern garden (Sherborne), we included bees transplanted from Belfast (northern, non-social) as well as from Penrith and Wicklow. We present results from analyses in which Belfast and Penrith bees are combined into a single category of 'northern transplants'. Categorizing Belfast bees separately did not alter results.

Demographic parameters, for which there was a single value per bee, were analysed using generalised linear models, assuming binomial or normal errors as appropriate. In addition to effects of common garden and source site (as above), covariates tested were bee wing length and whether the bee had overwintered at the common garden or at the source site. When analysing B1 maturation date or the time taken to produce a female offspring, the date of initiation of reproduction was an additional covariate.

For foraging parameters, we observed the same individual bees on multiple days, so that the data were naturally hierarchical. We therefore used generalised linear mixed models (GLMMs) with Poisson (number of pollen loads per day) or normal (time of first arrival with pollen, time of last arrival with pollen) errors. In addition to effects of common garden and source site, covariates tested were whether bees had overwintered at the common garden or the source site, bee wing length and maximum daily temperature. We compared models where each bee was fitted with a random intercept, or a random slope and intercept, or no random structure at all, for the relationship between the *y*-variable and temperature (Zuur et al. 2009). In all cases, the random structure, or lack of it, did not affect the results for fixed effects, and we focus on the fixed effects in the "Results" section. Data for each bee were included in the foraging analyses until the last day on which it was observed alive. When the *y*-variable was number of pollen loads, the data deviated slightly from a Poisson distribution because there was an excess of zeros, i.e. days when no pollen was collected by a bee. Such 'zero inflation' is common in ecological datasets (e.g. Martin et al. 2005). To take this into account, we repeated the analysis, this time fitting a mixture model suitable for a zero-inflated Poisson (ZIP) distribution. The mixture model contained an extra parameter, which determines the probability of an observation being derived from the underlying Poisson distribution or being an additional zero. We fitted the ZIP model using Bayesian MCMC with code for WinBUGS (Lunn et al. 2000) adapted from Martin et al. (2005). We used an uninformative, uniform prior with a burn-in of 3,000 iterations with a further 3,000 iterations used for inference. Results from ZIP models were similar to those from Poisson GLMMs, and we discuss only the latter below.

In all analyses, we used all available data, but sample sizes differed between analyses. For example, no offspring maturation data were available for nests that produced no offspring within our observation period. Wing length was not significant as a covariate in any analysis (see also Yanega 1996). We therefore report results from analyses using all bees available, irrespective of whether their wing lengths were known. All analyses apart from the ZIP models were conducted in the *R* environment (R Development Core Team 2011), using the nlme and lme4 packages for GLMMs with normal and Poisson errors, respectively. In each analysis, we first fitted potential explanatory variables, and then, starting with the interactions, we subtracted terms from the model until further removals led to significant ($p<0.05$) increases in deviance (Crawley 2007). We report significance levels for terms when removing them last from this minimal adequate model. For GLMMs, we followed the protocols recommended by Zuur et al. (2009), and report χ^2 (Poisson) or likelihood ratio (*L*) (normal) test statistics. Throughout the "Results," we generally mention explanatory variables only if they had significant effects ($p<0.05$). We obtained standardized effect sizes (*d*) using the calculator at http://www.campbellcollaboration.org/resources/effect_size_input.php (accessed 6 January 2012).

Results

Transplant success: overwintering survival/dispersal

At the northern common garden, 136 foundresses, 57 from the northern source site at Penrith (35% of those transplanted) and 79 from the southern source site at Co. Wicklow (33%), successfully established nests in spring. In addition, 42% of the 59 native foundresses we had marked in autumn successfully established. At the southern common garden, the numbers establishing were 38 (24%), 31 (24%) and 21 (45%) for northern transplants, southern transplants and natives, respectively. The figures for natives are at the high end of the range of philopatry estimates (14–42%) for *H. rubicundus* foundresses over a 5-year period in New York (Yanega 1990). Bees transplanted from different sources did not differ in their probability of nest establishment. However, bees that we transplanted in autumn were less likely to successfully initiate nests at the common garden the following spring (23% success) than bees transplanted in spring itself (56%). This difference was smaller at the northern garden (time of transplant/garden interaction, $\chi_1^2=14.5$, $p=0.0002$; autumn-transplanted, 31% establish; spring-transplanted, 54% establish) than at the southern garden, where autumn-transplanted bees were unlikely to establish (autumn, 9%; spring 47%). Transplanted bees in general were less likely to establish nests (30% established) than the samples of native bees we marked in autumn (44%), and this difference was again significantly larger at the southern garden (garden/source interaction, $\chi_2^2=12.7$, $p=0.002$).

Social phenotype

As reported previously, all nests were non-social at the northern common garden, irrespective of whether foundresses originated from social or non-social source sites (Field et al. 2010). At the southern garden, although spring weather in 2007 was normal, weather after B1 emergence was some of the worst ever recorded for the south of England, so that there was almost no opportunity to ascertain social phenotype. Nevertheless, we recorded B1 females provisioning 14 identified nests in the presence of the foundress, including nests initiated by foundresses from all source sites. These included four nests produced by foundresses from Penrith, a northern source site at which we have never observed B1 females provisioning despite extensive monitoring (Field et al. 2010). This parallels results from another year, in which approximately half of the foundresses transplanted from the non-social Belfast site produced social nests at a southern destination site (Field et al. 2010).

Bee size

Foundresses native to the northern garden were smaller than natives at the southern garden (Fig. 3a, $F_{1,27}=26.3$, $p<0.0001$, $n=13$ from north, $n=15$ from south). Similarly, foundresses that initiated nests after transplantation from the northern source site (Penrith) were smaller than those transplanted from the southern source (Co. Wicklow) across both years (Fig. 3a, $F_{1,64}=6.2$, $p=0.015$, $n=32$ from north, $n=34$ from south) and in each year separately (2006, $p=0.007$; 2007, $p=0.04$).

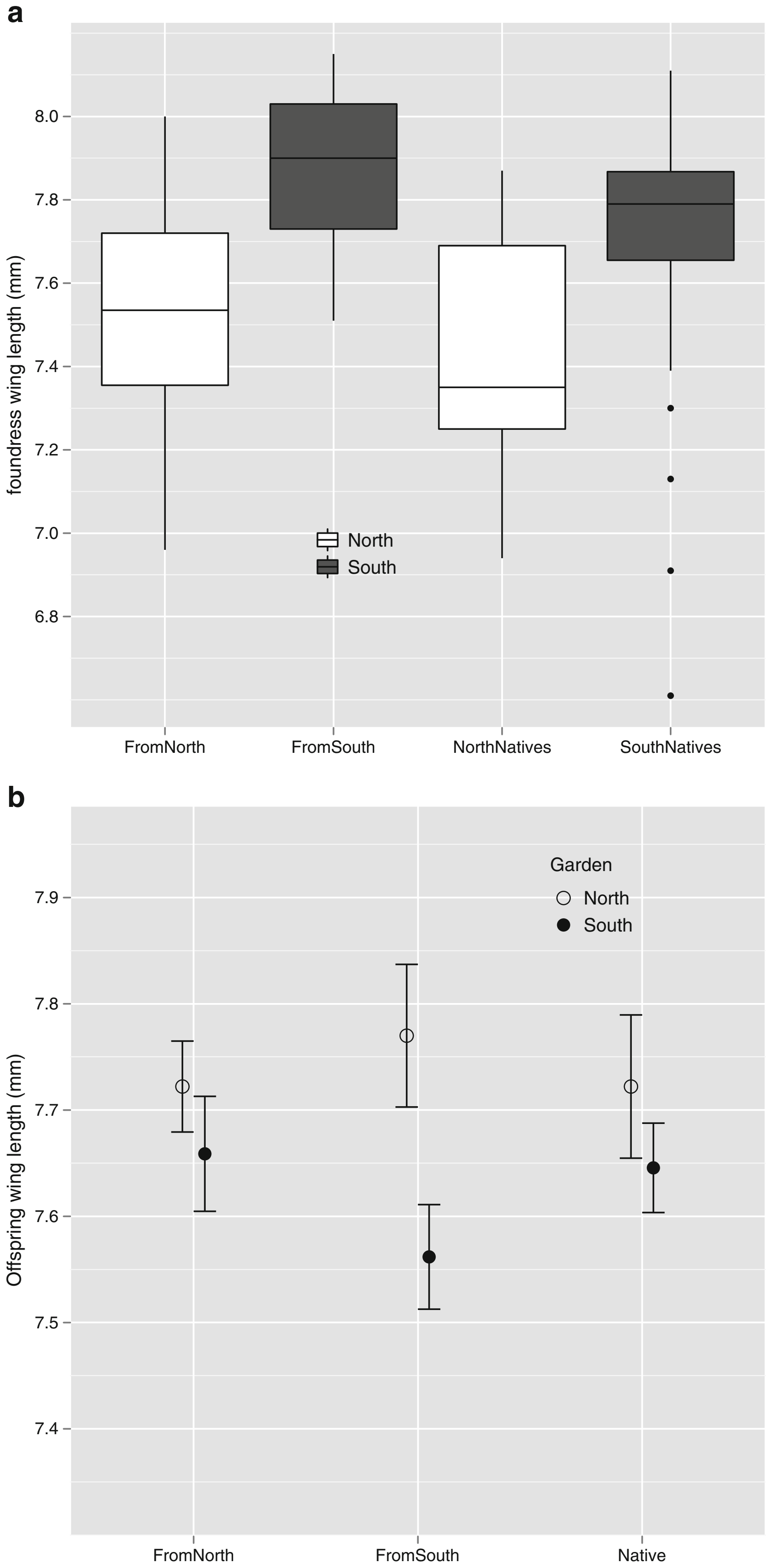
Despite these source-related differences in the size of foundresses, northern transplanted foundresses produced B1 female offspring ($n=31$) at the common gardens that did not differ in size from those produced by southern transplanted foundresses ($n=31$) or natives ($n=45$). The only pattern among offspring was that those produced by transplanted bees at the southern garden were slightly smaller than those produced at the northern garden (Fig. 3b, $F_{1,61}=4.8$, $p=0.033$). Offspring of native bees did not differ in size between the two gardens. Although the sample size for natives from the northern garden was small ($n=13$ from north; $n=32$ from south), the standardized effect size (d) was also small (0.14, 95% CI −0.51–0.78). For 22 nests at the northern garden where sizes of both foundress and B1 offspring were known, foundresses and offspring did not differ in size ($t_{21}=-0.52$, $p=0.61$). At the southern garden, however, offspring were smaller than foundresses ($n=15$ nests, $t_{14}=2.58$, $p=0.02$). At both gardens, source site had no effect on the size difference: Sample sizes were small, but so were effect sizes (northern garden, $n=11$, 11, $d=0.03$, 95% CI −0.81–0.87; southern garden, $n=6$, 9, $d=0.32$, 95% CI −0.72–1.36).

Initiation of foundress provisioning in spring and offspring maturation

Initiation of provisioning and the time of offspring maturation were plastic, with no evidence of genetic differences between bees from different sources. Native bees at the northern common garden began offspring provisioning nearly 1 month later than did natives at the southern garden (Fig. 4, $F_{1,85}=83.7$, $p<10^{-13}$, $n=33$ from north, $n=54$ from south; Wilcoxon test, $W=19052$, $p<10^{-15}$) and produced their first adult female offspring later ($F_{1,38}=58.0$, $p<10^{-8}$). Within each garden, however, date of initiation of provisioning and date of first female offspring maturation did not differ between nests of foundresses from different sources. Thus, regardless of their source, bees began provisioning earlier and produced their first B1 offspring earlier, at the southern garden (Fig. 4).

There were no differences between foundresses transplanted from different sources in the time they took to produce their first female offspring. This time was shorter at the southern common garden ($F_{1,55}=121$, $p<10^{-14}$) and if the foundress began provisioning later in spring ($F_{1,55}=488$, $p<10^{-15}$, Fig. 4). The latter pattern meant that, within each garden, there was no correlation between when foundresses initiated provisioning in spring and when their first female offspring matured: The shorter time that late-starting

Fig. 3 **a** *Boxplots* showing wing lengths (millimetres) of foundresses native to the northern and southern common gardens and those transplanted from the northern and southern source populations. *Boxes* for bees from the south are *shaded*; those for bees from the north are *unshaded*. **b** Mean (±1SE) wing lengths (millimetres) of first brood female offspring produced by foundresses from different sources at the northern and southern common gardens



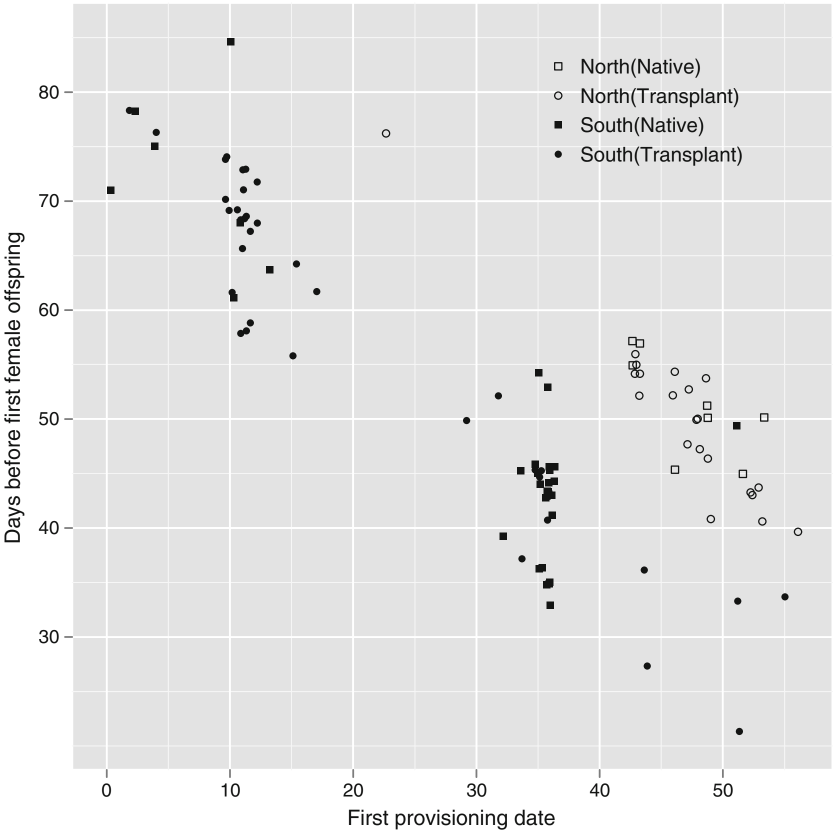


Fig. 4 Relationship between the date when a foundress first began provisioning her nest in spring and the number of days before her first female offspring reached adulthood. Data are shown for native and transplanted foundresses at the northern and southern gardens. Dates are days after 18 April. Gaps in the distribution of first provisioning dates reflect periods of weather unsuitable for activity. For example, at the northern garden, a few foundresses began provisioning nests on 10–11 May (days 22–23), of which only one nest eventually produced offspring. After 11 May, there was no weather suitable for activity until a spell of warm weather beginning 31 May (day 43), during which provisioning was initiated at further nests

foundresses took to produce their first offspring made up for their later start. Foundresses from different sources were equally likely to have their nests taken over by other bees (18% takeover rate).

Foraging behaviour

At the northern common garden, we recorded foraging behaviour on 17 different dates before B1 offspring reached adulthood, ranging from 10 May to 16 July. At the southern garden, there were 12 dates, ranging from 20 May to 19 June. Analysis of these data revealed considerable plasticity in foundress foraging behaviour. There was also evidence of limited differences between foundresses from different sources when placed in a common garden.

First and last daily provisioning events were recorded for 158 foundresses at the northern garden and 91 at the southern garden, with on average 3.7 and 2.7 different dates per foundress, respectively. In all analyses, the first provisioning event occurred significantly earlier on days when temperature was higher ($p<0.00001$). Transplanted bees were plastic and behaved like the bees native to each common garden. They started provisioning approximately 1.8 h earlier at the northern garden than at the southern garden (Fig. 5a; $L_1=174.7$, $p<0.0001$). Within the northern garden, time of first provisioning did not differ between bees from different sources. In the southern garden, native bees and bees transplanted from the south first provisioned half an hour earlier in the day than did bees transplanted from the north, but the difference was not quite significant (Fig. 5a: $L_2=5.4$, $p=0.07$).

In contrast with time of first provisioning, the time when foundresses last provisioned in a day was independent of temperature in all analyses. Native foundresses at the southern garden last provisioned later in the day than natives at the northern garden (Fig. 5b; $L_1=111.3$, $p=0.0008$). Transplanted bees exhibited considerable plasticity in this respect, so that they finished provisioning on average 1.8 h later in the day at the southern garden than at the northern garden (Fig. 5b; $L_1=75.5$, $p<0.00001$). However, there was also a significant effect of ‘source’: Bees transplanted from the north stopped provisioning half an hour later than bees transplanted from the south across both common gardens (Fig. 5b, $L_1=4.5$, $p=0.033$). This effect also occurred within each garden, involving bees transplanted in two different years. At the northern garden, bees transplanted from the south stopped provisioning earlier than both bees transplanted from the north and northern natives ($L_2=7.9$, $p=0.02$). At the southern garden, bees transplanted from the north stopped provisioning later than both bees transplanted from the south and southern natives ($L_2=7.3$, $p=0.026$).

We recorded the number of pollen loads collected in the day for 180 foundresses at the northern garden and 114 at the southern garden, with on average 5.5 and 4.7 different

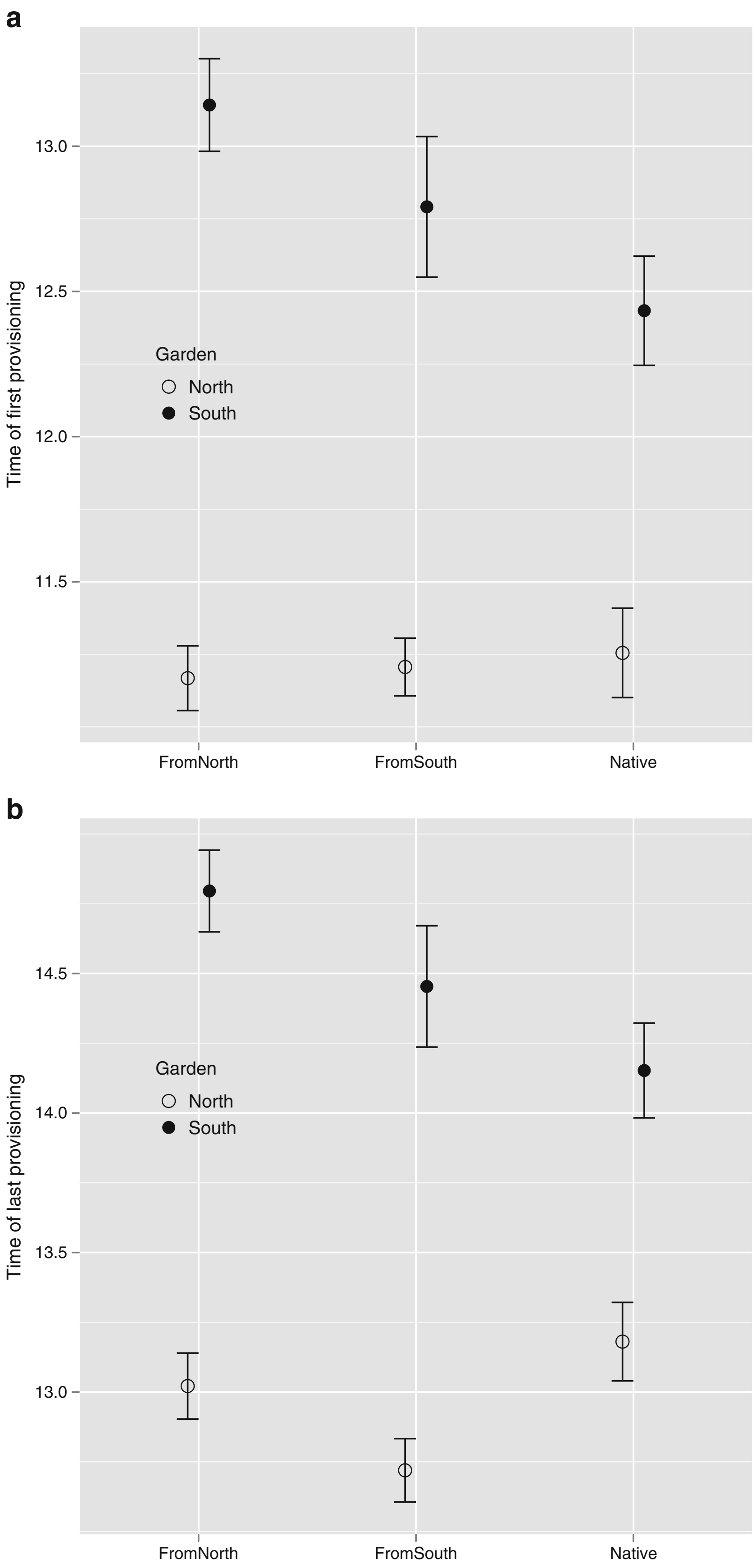


Fig. 5 Mean (±1SE) time of day (24-h clock, BST) when foundresses from different sources **a** first provisioned their nests and **b** last provisioned their nests at the northern and southern common gardens

dates per bee, respectively. In all analyses, foundresses collected more pollen loads on days with higher maximum temperatures ($p<0.00001$; e.g. Fig. 6b). In addition, native bees at the northern garden collected more pollen loads than natives at the southern garden (Fig. 6a; $\chi_1^2=50.4$, $p<10^{-11}$). Transplanted bees from both the north and the south exhibited plasticity: They collected 1.6 times as many pollen loads per day when transplanted to the northern garden (Fig. 6a; $\chi_1^2=42.5$, $p<0.00001$). However, there was also a significant source/temperature interaction across the two gardens: At higher temperatures, bees transplanted from the north collected more pollen loads than bees transplanted from the south ($\chi_1^2=5.2$, $p=0.022$). Analyses within gardens revealed that this was primarily because of differences at the northern garden, where there was the same source/temperature interaction ($\chi_1^2=12.4$, $p=0.0004$; Fig. 6b). Within the southern garden, although bees transplanted from the north again collected more pollen loads than both bees transplanted from the south and southern natives (Fig. 6a), the difference was not significant. However, at the southern garden, foundresses that overwintered before transplantation collected 1.4 times more pollen loads than natives and bees that overwintered after transplantation ($\chi_1^2=7.6$, $p=0.006$).

Discussion

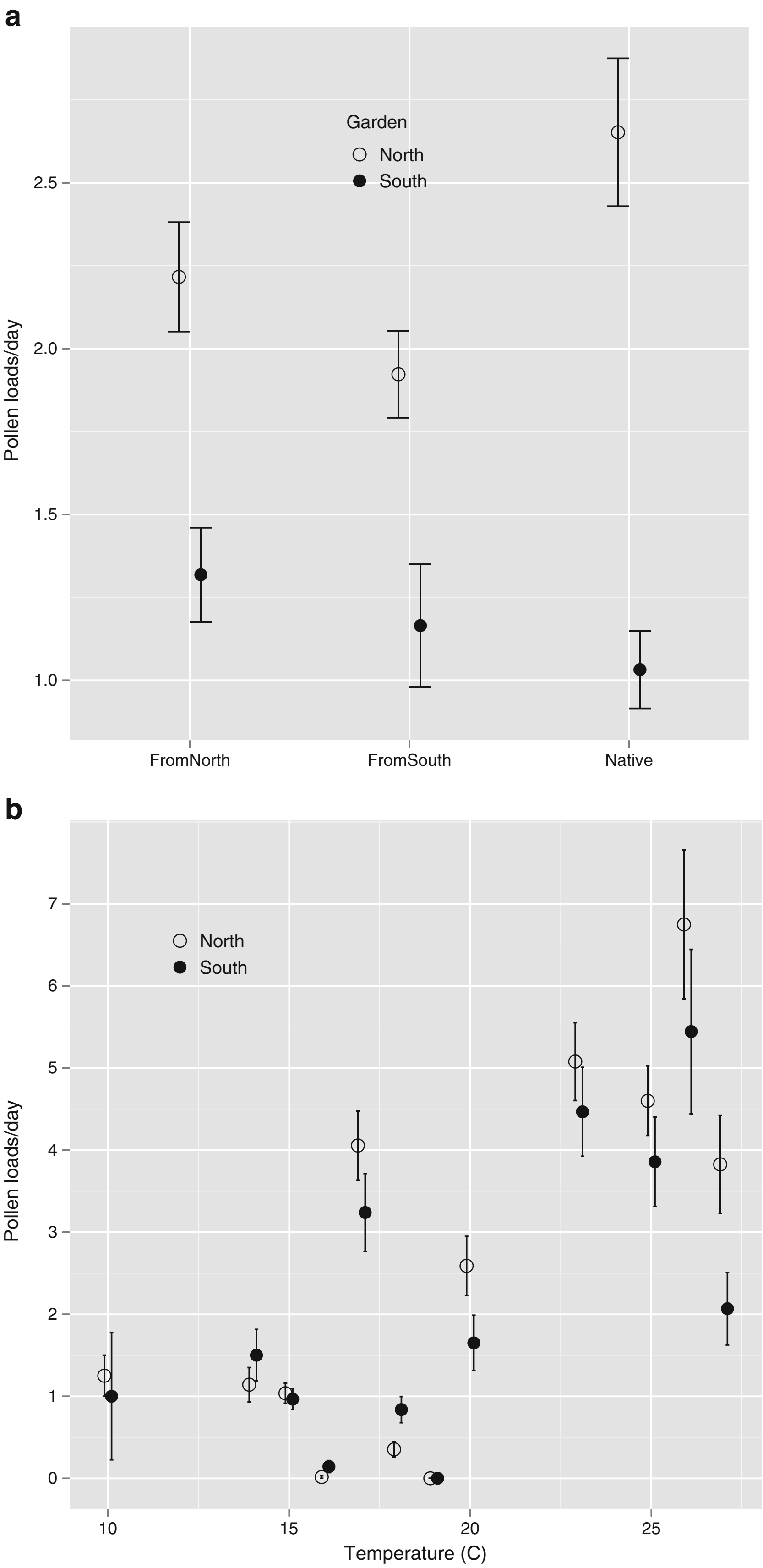
Transplants of mobile taxa in natural environments are rare, presumably because individuals may emigrate after transplantation (but see Cronin 2001; Baglione et al. 2002). This study and our previous work on *H. rubicundus* (Field et al. 2010) represent the most comprehensive field-based test for plasticity in an insect that exhibits eusociality and non-sociality in separate populations (see also Plateaux-Quenu et al. 2000 for a lab test in sweat bees, Baglione et al. 2002 in carrion crows). Our major finding from this study was that *H. rubicundus* foundresses were plastic, in terms of the date when they began producing offspring in spring, the size and maturation time of those offspring, the time of day when they started and finished provisioning, and the number of pollen loads that they collected in a day. This is consistent with these traits being intimately linked to social phenotype, which itself exhibits plasticity in the British Isles (Field et al. 2010). Although bees that were native to our two common gardens differed significantly, and often markedly, in the traits that we measured, most of our results are consistent with complete plasticity in that transplanted bees did not differ detectably from natives. The only exceptions were relatively small effects of source population on foraging. In addition, at the southern garden, bees that had experienced the winter at their source sites before transplantation collected more pollen loads than other bees. This was the only detectable difference between spring- and autumn-transplanted bees, suggesting that conditions experienced by spring transplanted bees during the additional 6 months that they spent at source sites did not have major effects on their behaviour after transplantation. We now discuss our findings in the contexts of both sociality and plasticity in general.

Body size and demography

At the time of nest initiation in spring, foundresses native to our northern garden were smaller than those from our southern garden (Fig. 3a). Similarly, in both years, foundresses transplanted from our northern sources were smaller than those from our southern sources (Fig. 3a). This pattern matches that found in US populations of *H. rubicundus*, in which foundresses from non-social populations living in cooler environments were smaller than both workers and foundresses from social populations living in warmer environments (Soucy 2002). In two other sweat bees, individuals in milder conditions are also larger (Richards and Packer 1996). This suggests that sweat bees may exhibit so-called ‘reverse-Bergmann’ latitudinal size clines, which are common in ectotherms (Blanckenhorn and Demont 2004). Our results suggest that, in British Isles *H. rubicundus*, these body size differences represent plasticity, because foundresses from different sources produced offspring of the same size within each common garden (Fig. 4; see also Richards and Packer 1996 for evidence of temporal plasticity within a population of *H. ligatus*). A general explanation for reverse-Bergmann clines is that because the growing season is shorter further north, immatures have less time to feed so that resulting adults are smaller (Blanckenhorn and Demont 2004). In sweat bees, however, the amount of food that a larva receives is controlled by the adults that provision its cell. A cline might result if mothers at higher latitudes provide each offspring with less food, as a response to having less time suitable for foraging, fewer resources available or because their larvae will have less time in which to feed. Although we detected no effect of body size on the foraging parameters that we measured, smaller size probably leads to reduced potential fecundity, as in other insects (Honek 1993; Nylin and Gotthard 1998; see Strohm and Liebig 2008 for a discussion in bees). However, smaller *H. rubicundus* foundresses at higher latitudes may in any case have fewer opportunities to oviposit, because the cooler conditions allow them less time to forage for larval provisions and because foundresses in non-social populations will never have helpers (workers) to boost productivity later in the season.

The general scenario where bees in northern populations are assumed to be more time-stressed than bees in southern populations (Blanckenhorn and Demont 2004) is complicated by the social polymorphism exhibited by *H. rubicundus*.

Fig. 6 **a** Mean (±1SE) number of pollen loads per day collected by foundresses from different sources at the northern and southern common gardens. **b** Relationship between maximum daily shade temperature (°C) and the number of pollen loads (±1SE) collected by foundresses from northern and southern populations at the northern common garden. Northern bees represent natives and transplants from the north combined. Points are slightly jiggled along the *x*-axis for clarity



Social nests, which occur only in the south, rear two successive broods, the first including workers that help to rear a second brood of entirely reproductives. A second brood is more likely to be reared if first brood offspring reach adulthood earlier in the season, suggesting that southern populations may in fact be time-stressed (Field et al. 2010). Thus, length of growing season may not always limit offspring development time more strongly in the north, where only one brood is reared, than in the south where there can be two broods, potentially leading to a saw-tooth size cline similar to those induced by latitudinal changes in voltinism in non-social insects (Roff 1980). Single-brooded bees just north of the latitude where voltinism changes should then be larger than double-brooded bees just south of that latitude. Denser sampling with respect to latitude will be required to determine whether such effects occur in *H. rubicundus* (Roff 1980; Nylin and Gotthard 1998). Further sampling could be particularly interesting within the range of latitudes where nests rear two successive broods and are social. Larger body size may be critical to enable future foundresses to overwinter, e.g. Beekman et al. (1998) and Heinze et al. (2003); but see Richards and Packer (1996) and Weissel et al. (2012). Thus, at higher latitudes, as the total growing season gradually shortens, a foundress' strategy might be to produce smaller first brood workers, leaving more time for the development of second brood foundresses large enough to survive the winter. Queen-worker size dimorphism would then gradually increase at higher latitudes, with potential consequences for the outcome of queen–worker conflict (Reeve and Ratnieks 1993; Richards and Packer 1996).

One way in which northern populations can compensate for a shorter growing season is to grow or develop faster (Nylin et al. 1989; Conover and Schultz 1995; Nylin and Gotthard 1998; Gotthard et al. 2000). We found no evidence for such patterns in *H. rubicundus*. Foundresses began provisioning earlier in spring and produced their first female offspring earlier, at the southern common garden, and this was independent of foundress source. At both gardens, the time taken to produce the first female offspring declined linearly as reproduction was initiated later (Fig. 4), presumably because, later in the season, developing larvae experience higher temperatures (Fig. 2). Indeed, this decline nullified any effect that date of initiation might have been expected to have on date of first offspring maturation: At each garden, the first female offspring did not mature earlier in nests where foundresses had initiated foraging earlier in spring. However, a different pattern can occur under other conditions. When foundresses from our Belfast source population were transplanted to a site in southeast England, not only did earlier-starting foundresses produce their first female offspring earlier, but their nests were more likely to become social (Field et al. 2010). The latter pattern probably occurs because B1 females are more productive if they can start helping when there is more time left in the season (Field et al. 2010).

Although foundresses from different sources produced offspring of the same sizes in each common garden, those offspring were significantly smaller than their mothers at the southern but not the northern garden. Some of the B1 offspring at the southern garden were destined to be workers, and workers are commonly smaller than queens in social insects, including many sweat bees (Packer and Knerer 1985; Soucy 2002; but see Field et al. 2010). The pattern we found suggests that foundresses from all sources are capable of varying offspring size according to anticipated social phenotype.

Foraging

Native foundresses at our southern common garden brought back consistently fewer pollen loads per day than natives at our northern garden (Fig. 6a). Transplanted bees behaved much like natives, bringing back fewer pollen loads at the southern garden than at the northern garden (Fig. 6a). However, there were also small differences according to whether bees originated from the north or south. In both gardens, northern bees continued foraging for approximately half an hour longer than southern bees (Fig. 5b). And especially in the northern garden, natives and bees transplanted from the northern source brought back more pollen loads at high temperatures than did bees transplanted from a southern source (Fig. 6b). These differences could represent genetic variation, or maternal/environmental effects if transplanted bees receive cues before transplantation, either from their mother or their natal environment. However, the difference in the number of pollen loads remained when only bees transplanted the previous autumn were included in the analysis, so that any maternal effect would have to involve cues received during larval development or early in adult life before transplantation.

The differences in foraging between our two common gardens could partly reflect adaptations associated with latitude or social phenotype. One possibility is that because the warmer climate at the southern site (Fig. 2) is, overall, more favourable for foraging, bees do not need to forage as intensively there. Given plenty of days suitable for foraging, bees might prolong their lives and so increase their lifetime reproductive success by not paying short-term costs potentially incurred through foraging maximally on any given day (e.g. Strohm and Marliani 2002). At the northern site, in contrast, bees with an expectation of fewer days suitable for foraging might do best to work maximally on the few days available. A second adaptive explanation would reinforce this pattern. Reduced foraging effort might be associated with the possibility of nests becoming social later in the season at our southern garden, but never at our northern garden (Field et al. 2010). Foundresses at the southern site could have more to lose by working hard (Cant and Field 2001) and might maximise their lifetime reproductive success by ensuring that they survive until offspring emergence, when they could dramatically increase their reproductive rate with the help of offspring workers.

Differences in foraging could also partly reflect idiosyncrasies of our particular study sites not associated with latitude or social phenotype. For example, if pollen availability was lower at the southern site, bees would obtain fewer pollen loads passively, despite foraging just as intensively as at the northern site. We cannot discount this possibility, but the southern site was in a large garden with a dedicated gardener and was well stocked with flowers throughout the nesting season. In contrast, there were few flowers near to the nest site at the northern garden. Site-specific idiosyncrasies probably were the main reason why bees at the southern common garden began foraging approximately 1.8 h later than bees at the northern garden (Fig. 6a): nest entrances at the southern garden first received sunlight 1–3 h later than at the northern garden. It is interesting that, although they started foraging 1.8 h later, bees also finished 1.8 h later in the southern garden (Fig. 5b). This suggests that *H. rubicundus* might have a fixed total daily foraging time, at least on average.

Conclusion

Our results indicate that body size, demography and foraging are plastic in UK *H. rubicundus*, with little indication of fixed genetic differences between social and non-social populations. This is consistent with these traits being part of *H. rubicundus*' overall plastic social phenotype. Further progress towards understanding social plasticity in *H. rubicundus* will require investigating these and other components of the social phenotype in more detail and understanding the proximate cues that influence how bees behave.

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