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ARTICLE

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Seasonality of pollinators in montane habitats: Cool-blooded bees for early-blooming plants

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Abstract

Understanding the factors that drive community-wide assembly of plant-pollinator systems along environmental gradients has considerable evolutionary, ecological, and applied significance. Variation in thermal environments combined with intrinsic differences among pollinators in thermal biology have been proposed as drivers of community-wide pollinator gradients, but this suggestion remains largely speculative. We test the hypothesis that seasonality in bee pollinator composition in Mediterranean montane habitats of southeastern Spain, which largely reflects the prevalence during the early flowering season of mining bees (*Andrena*), is a consequence of the latter's thermal biology. Quantitative information on seasonality of *Andrena* bees in the whole plant community (275 plant species) and their thermal microenvironment was combined with field and laboratory data on key aspects of the thermal biology of 30 species of *Andrena* (endothermic ability, warming constant, relationships of body temperature with ambient and operative temperatures). *Andrena* bees were a conspicuous, albeit strongly seasonal component of the pollinator assemblage of the regional plant community, visiting flowers of 153 different plant species (57% of total). The proportion of *Andrena* relative to all bees reached a maximum among plant species which flowered in late winter and early spring, and declined precipitously from May onward. *Andrena* were recorded only during the cooler segment of the annual range of air temperatures experienced at flowers by the whole bee assemblage. These patterns can be explained by features of *Andrena*'s thermal biology: null to weak endothermy; ability to forage at much lower body temperature than strongly endothermic bees (difference ~ 10°C); low upper tolerable limit of body temperature, beyond which thermal stress presumably precluded foraging at the warmest period of year; weak thermoregulatory capacity; and high warming constant enhancing ectothermic warming. Our results demonstrate the importance of lineage-specific pollinator traits as drivers of seasonality in community-wide pollinator composition; show that exploitation of cooler

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microclimates by bees does not require strong endothermy; and suggest that intense endothermy and precise thermoregulation probably apply to a minority of bees. Medium- and large-sized bees with low upper thermal limits and weak thermoregulatory ability can actually be more adversely affected by climate warming than large, hot-blooded, extremely endothermic species.

KEYWORDS
Andrena bees, Andrenidae, bee endothermy, climate warming, cooling/warming constant, Mediterranean montane habitats, plant-pollinator community assembly, pollinator seasonality, thermal biology, thermoregulation

INTRODUCTION

Composition of pollinator assemblages at the plant community level often varies predictably along major ecological gradients such as plant cover, habitat type, elevation or time of year, such variation generally involving a turnover in the relative importance of different pollinators along the environmental axis considered (CaraDonna et al., 2021; Cruden, 1972; Dellinger et al., 2021; Herrera, 2020; Kalin Arroyo et al., 1982; McCabe et al., 2019; Shmida & Dukas, 1990). Some well-known examples of elevational or seasonal gradients in pollinator composition at the plant community level include the predominance of dipterans at high elevations or latitudes (Elberling & Olesen, 1999; Hingston & McQuillan, 2000; Kearns, 1992; Koch et al., 2020; McCabe & Cobb, 2021; Warren et al., 1988); the shift from bee to vertebrate pollinators with increasing elevation in tropical mountains (Cruden, 1972; Dellinger et al., 2021; Perillo et al., 2017); and the seasonal turnover of major orders and families of insect pollinators in Mediterranean plant communities (Bosch et al., 1997; Petanidou & Vokou, 1993; Shmida & Dukas, 1990). Since distinct groups of pollinators generally differ in crucial aspects of pollinating service which influence plant fitness and reproductive success (Herrera, 1987; Schemske & Horvitz, 1984; Valverde et al., 2019), understanding the causal mechanisms that drive the assembly of plant-pollinator systems along ecologically meaningful gradients has considerable evolutionary and ecological importance (Albor et al., 2022; Cruden, 1972; Dellinger et al., 2021; LaManna et al., 2021; Motten, 1986).

Differences between pollinator groups in thermal optima, thermal tolerance limits, and/or thermoregulatory biology, acting in concert with spatial or temporal variation in abiotic factors (e.g., solar radiation, air temperature), have been traditionally the favored mechanistic explanation for elevational or seasonal gradients in pollinator composition (e.g., Dellinger et al., 2021; Shmida & Dukas, 1990; Warren et al., 1988). Rather strikingly, however, no study has hitherto gone one step further beyond plausible explanations and actually undertaken comprehensive empirical work on the thermal biology of taxa involved in seasonal or elevational turnovers in pollinator composition. In addition to serving for a better understanding of the factors that drive the assembly of plant-pollinator systems, investigations on pollinator thermal biology have recently acquired special relevance because of the increasing concerns on the impact of climate change on pollinator populations, since the latter's responses to accelerating changes in the thermal environment could possibly be contingent on their thermal biology (Ghisbain et al., 2021; Herrera, 1997, 2019; Marshall et al., 2018; Ploquin et al., 2013; Scaven & Rafferty, 2013; Shrestha et al., 2018; see also Burdine & McCluney, 2019; Hamblin et al., 2017, for work on the potential role of bee physiology as a driver of community composition along urbanization gradients). The central goal of this paper is to present an explicit test of the oft-mentioned but empirically untested hypothesis that the intrinsic thermal biology of pollinators can be a major driver of pollinator composition at the plant community level. We will focus on a community-wide seasonal pattern in bee pollinator composition that is apparently universal at mid and high latitudes in the Holarctic realm, namely the prevalence of mining bees (*Andrena*) during the early stages of the flowering season, as detailed in the following section.

Seasonality of *Andrena* bees in the Holarctic realm

Mining bees (Andrenidae) are a major family with >3000 described species, ~1600 of which are in the predominantly Holarctic genus *Andrena*, the second largest genus of bees (Bossert et al., 2022; Pisanty et al., 2022). *Andrena* bees are pollinators of many wild plants in a broad variety of boreal and temperate habitats of Eurasia and North America, particularly of species flowering in winter and early spring (Anderson & Beare, 1983; Kato, 2000; Motten, 1986; Motten et al., 1981; Ostaff et al., 2015; Schemske et al., 1978; Turley et al., 2022; Wood et al., 2022). The association between early blooming and *Andrena* pollination

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stems from the prevailing phenology of these bees, which are among the earliest-flying ones in temperate and boreal habitats, can nest when it is often cold and rainy, and are able to withstand thermally unfavorable climates, as illustrated by their abundance and diversity in arctic and subarctic habitats (Armbruster & Guinn, 1989; Batra, 1990; Hicks & Sheffield, 2021; Kato, 2000; Sakagami & Matsumura, 1967; see Larkin et al., 2008 for examples of summer- and autumn-flying species of the North American subgenus *Callandrena* which represent remarkable exceptions to this pattern).

Studies on the pollination ecology of early-blooming plants have mainly focused on the reproductive features of the plants (phenology, floral biology, pollen limitation; Motten et al., 1981; Schemske et al., 1978), yet the thermal characteristics of their associated *Andrena* pollinators have been addressed on few occasions. One of these studies showed that pollination of the early-flowering daffodil *Narcissus longispathus* was facilitated by the thermal biology of *Andrena bicolor*, its main pollinator, which flies at low body temperature and has a low upper thermal tolerance limit in comparison to other bees (Herrera, 1995). It remains unknown, however, whether these distinctive thermal features apply to the genus *Andrena* as a whole, as knowledge on bee thermal biology largely refers to a few lineages of extremely endothermic bees in the family Apidae (Chappell, 1982; Heinrich, 1993; Inouye, 1975; May & Casey, 1983; Oyen et al., 2016; Roberts et al., 1998; Stone, 1993; Stone & Willmer, 1989). The thermal biology of *Andrena* bees remains essentially unexplored (Danforth et al., 2019; but see Bishop & Armbruster, 1999; Herrera, 1995; Schmaranzer et al., 1997), which represents a remarkable gap in our knowledge given their extraordinary biological diversity, broad geographical distribution, high seasonal abundance, and importance as pollinators of many cultivated and wild plants. In particular, it is unknown whether the characteristically early flying period of *Andrena* bees that enhances their role as pollinators of early-blooming plants can be explained by their thermal biology.

We present in this paper a quantitative analysis of the seasonal occurrence and thermal environment of *Andrena* pollinators in a montane area of southeastern Spain, along with observational and experimental evidence on the thermal biology of *Andrena* bees obtained in the field and the laboratory. The following specific questions were addressed: (1) How does the proportional abundance of *Andrena* pollinators relative to other bees vary seasonally?; (2) Does the thermal environment experienced by foraging *Andrena* bees differ from that of other bees?; (3) To what degree does body temperature of *Andrena* bees in the field depend on ambient temperature and operative body temperature (sensu Bakken, 1992, see definition later), and what are the shapes of the relationships?; and (4) To what extent are *Andrena* individuals able to warm by themselves through endothermy? Questions (1) and (2) were addressed for the whole regional community of insect-pollinated plants and their bee pollinators, while questions (3) and (4) were answered for a taxonomically diverse sample of *Andrena* species comprising a substantial fraction of those occurring in the region studied. Responses to these specific questions will allow us to evaluate the hypothesis that *Andrena* seasonality is a consequence of its thermal biology. More generally, our results will bear on the role of pollinators' thermal biology as a driver of seasonal community-wide variations in pollinator composition and on the expected impact of climate warming on bee pollinator assemblages.

MATERIALS AND METHODS

Study area and sampling periods

Data on bee pollinator composition and air temperature at the foraging sites of different bee species were collected during January–December 1997–2022 in a relatively small area of the Sierra de Cazorla, Jaén Province, southeastern Spain (see Figure 2 in Herrera, 2021, for a detailed map of sampling sites). This region is characterized by well-preserved montane habitats and outstanding biological diversity (Gómez Mercado, 2011; Médail & Diadema, 2009). All *Andrena* bees used in laboratory experiments, and most of those whose thoracic temperatures were measured in the field, were also caught there during February–May 1994–2022. This seasonal sampling schedule closely matched the main activity period of *Andrena* species in the region (see the *Results* section). To increase sample size for some species that are infrequent in Sierra de Cazorla, or to augment the number of subgenera and hence the taxonomic breadth represented in the sample, additional field measurements of *Andrena* thoracic temperature were gathered in February–April 2022 at two locations in Sierra Morena (Córdoba province) and the lowlands of the Guadalquivir River valley (Sevilla province), 160 and 300 km away, respectively, from the Cazorla main study area. Data for all bee specimens considered in this study, including sampling dates and locations, are available in Herrera et al. (2023).

Bee pollinators and their thermal microenvironment

Pollinator composition was quantitatively assessed for 275 plant species in 179 genera from 47 families (Herrera

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et al., 2023). This sample is a superset of the 221 species studied by Herrera (2021), and includes virtually all entomophilous plants occurring in the area of the Sierra de Cazorla sampled for bees. Mean pollinator sampling date for each plant species roughly matched its peak flowering date; hence, the seasonal distribution of sampling times closely matched the pattern of flowering times in the region (see Herrera, 2019, 2020, for further details). About 75% of plant species in the sample ($N = 208$) were sampled for pollinators only 1 year, and the rest were sampled on ≥2 years. Pollinator sampling was conducted on a single site in the vast majority of the species considered here ($N = 258$), while 17 species were sampled on two or more sites. Pollinators of some plant species considered here vary among sites or years, but such intraspecific variation is quantitatively minor in comparison to the broad interspecific variation (i.e., across plant species) occurring in the large species sample considered here, as previously shown by Herrera (2020: Table 2, Figure 2) by means of formal variance partitions. Pollinator data for the same plant species obtained in more than one site or year were thus combined into a single sample for the analyses. The quality of pollinator composition data, as assessed with Good-Turing's "sample coverage" parameter (= estimate of the proportion of the total population of pollinators that is represented by the species occurring in the sample; Hsieh et al., 2016), was very high (>85%) in the vast majority of plant species (Herrera, 2021).

The proportions of *Andrena* and non-*Andrena* bees were obtained for each plant species using quantitative data on pollinator composition obtained using the field methods described in detail by Herrera (2019, 2020). The elemental sampling unit was the "pollinator census", consisting of a 3 min watch of a flowering patch whose total number of open flowers was also counted. On each date, censuses were evenly distributed from 0.5 to 2.5 h past sunrise (depending on season; censuses started earlier in summer) through 1 h past noon. All pollinators visiting some flower in the focal patch during the 3 min period were identified. For all plant species combined, a total of 33,446 censuses were conducted on 696 different dates, yielding a total of 1431 *Andrena* and 11,386 non-*Andrena* bee individuals (Herrera et al., 2023).

Air temperature at bee foraging sites was measured over January–August for a total of 1326 bees from 59 species (19 *Andrena* and 40 non-*Andrena*, collectively representing ~20% of the documented regional bee fauna) and 19 genera while they were visiting flowers of 18 different plant species in fine weather (see Appendix S1: Table S1 for full list of bee species and sample sizes). Measurements were taken in localities where pollinator censuses were also carried out, and were representative of all major habitat types occurring in the region (sclerophyllous evergreen forest and scrub, mixed pine-oak forest, open pine woodland and dwarf mountain scrub; see Appendix S1 in Herrera, 2019 for photographs of some sampling sites). Foraging bees were hand netted, identified to species (or collected to be identified later), and air temperature (T_a hereafter) 2–5 cm away from the flower where the bee had been caught was measured shortly after the bee's capture using a digital thermometer and a fast-response 0.22 mm-diameter thermocouple. These data were used here to compare the thermal profiles of the foraging sites of *Andrena* and non-*Andrena* bees on an annual basis ($N = 328$ and 999 measurements, respectively).

Thermal biology of *Andrena*

Data were obtained in the laboratory and/or the field on the thermal biology of 30 species of *Andrena* belonging to 16 different subgenera (Table 1). They represent about one third of the ~90 species of *Andrena* recorded to date in our study area (C. M. Herrera, A. Núñez, and C. Alonso, personal observations), and encompass the whole range of body sizes occurring there excepting those in the subgenus *Micrandrena*, whose minute body sizes precluded the application of the methods used in this investigation.

Laboratory experiments

The ability of live *Andrena* bees to warm-up endothermically, and the intrinsic warming constants of the same individuals, were assessed experimentally. Bee specimens for experiments were netted in the field while they were foraging at flowers, placed into sealed microcentrifuge tubes kept in the dark in an ice bath, and quickly brought to the laboratory. All measurements were made within 4 h of capture. The junction of a 0.22 mm Type T thermocouple was implanted in the thorax to a depth of 1 mm, and held in place using a small amount of a wax-resin mixture. The bee was briefly cooled in a refrigerator until its thoracic temperature (T_{th} hereafter) was about 8°C, which was deemed a realistically low temperature under field conditions, and then placed on a piece of styrofoam in a small room with still air and without any source of radiation (room temperature 18–21°C). T_{th} and air temperature 10 cm away from the bee were continously recorded every 10 s using a data logger. The bee was allowed to warm up until T_{th} stabilized. During this period its abdomen was gently pinched with forceps to test for its ability for postural control and sustained wing beating. After T_{th} stabilized

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TABLE 1 The 30 species of *Andrena* considered in this study, listed in alphabetical order of subgenera.

Species	Subgenus	Sample sizes	
		Field measurements	Laboratory experiments
Andrena fulva (Müller, 1766)	Andrena	24	6
Andrena lagopus (Latreille, 1809)	Biareolina	40	
Andrena humilis (Imhoff, 1832)	Chlorandrena		2
Andrena livens (Pérez, 1895)	Chlorandrena	27	4
Andrena rhenana (Stöckhert, 1930)	Chlorandrena	15	
Andrena rhyssonota (Pérez, 1895)	Chlorandrena	42	1
Andrena bicolor (Fabricius, 1775)	Euandrena	71	11
Andrena vulpecula (Kriechbaumer, 1873)	Euandrena		2
Andrena labialis (Kirby, 1802)	Holandrena	32	9
Andrena trimmerana (Kirby, 1802)	Hoplandrena	39	17
Andrena baetica (Wood, 2020)	Lepidandrena	39	
Andrena sardoa (Lepeletier, 1841)	Lepidandrena	29	3
Andrena albopunctata (Rossi, 1792)	Melandrena		1
Andrena assimilis (Radoszkowski, 1876)	Melandrena	23	7
Andrena hispania (Warncke, 1967)	Melandrena		2
Andrena nigroaenea (Kirby, 1802)	Melandrena	25	15
Andrena thoracica (Fabricius, 1775)	Melandrena		8
Andrena schencki (Morawitz, 1866)	Opandrena		1
Andrena pilipes (Fabricius, 1781)	Plastandrena		5
Andrena tibialis (Kirby, 1802)	Plastandrena		1
Andrena impressa (Warncke, 1967)	Ptilandrena		8
Andrena antigana (Pérez, 1895)	Simandrena	22	
Andrena combinata (Christ, 1791)	Simandrena		1
Andrena congruens (Schmiedeknecht, 1884)	Simandrena		1
Andrena lepida (Schenck, 1861)	Simandrena		3
Andrena ovatula (Kirby, 1802)	Taeniandrena		1
Andrena haemorrhoa (Fabricius, 1781)	Trachandrena		7
Andrena ferrugineicrus (Dours, 1872)	Truncandrena		1
Andrena villipes (Pérez, 1895)	Truncandrena	28	
Andrena flavipes (Panzer, 1799)	Zonandrena	41	8

Note: Sample sizes indicate the number of individual bees measured in the field or tested in the laboratory.

for at least 30 s, the bee was killed, weighed to the nearest 0.1 mg and briefly cooled in a refrigerator. The dead bee was then quickly placed again on the same styrofoam piece and allowed to warm up until T_{th} stabilization. As with the live bee, T_{th} and air temperature 10 cm away from the bee were recorded every 10 s with a data logger. This experimental protocol was applied to 125 individuals from 25 *Andrena* species, and the data were used to obtain quantitative estimates of their warming ability and warming constants (see *Data analyses* below). Representative examples of experimental warming curves for live and dead experimental specimens of eight species differing in warming ability are shown in Figure 1.

Field measurements

Free-ranging individuals of *Andrena* species were hand netted in fine weather while foraging at flowers of different species. Efforts were made to sample bees over as broad ranges as possible of habitat type and ambient temperature. For each bee, T_{th} was measured within 10 s of

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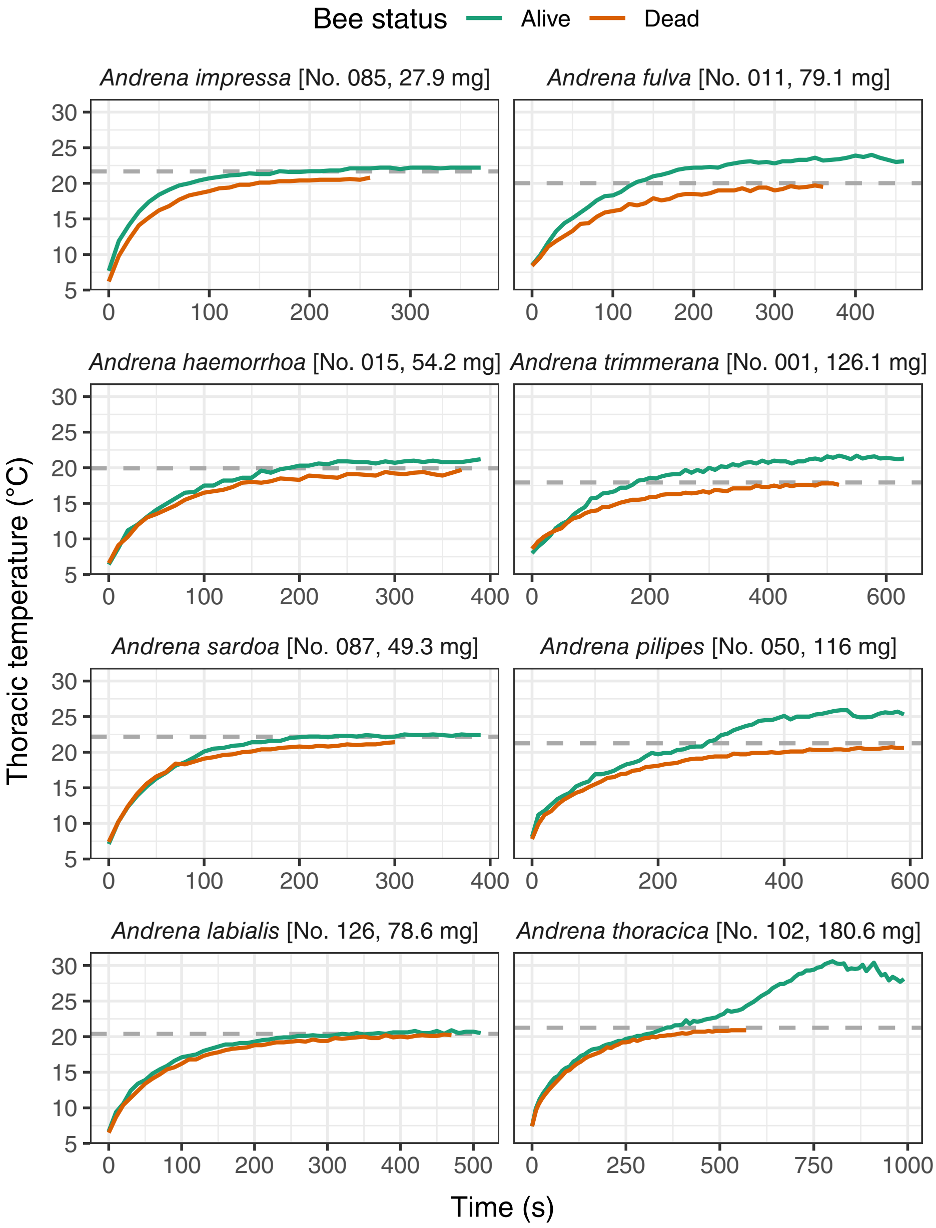

FIGURE 1 Experimental warming curves for eight individuals of different *Andrena* species, chosen to illustrate the range of variation in autonomous endothermy represented in the sample. Individuals in the left and right columns exhibited null and weak endothermic ability, respectively. Horizontal scales vary among graphs. Horizontal dashed lines denote the mean ambient temperature during each experimental run. In brackets beside species names are the specimen's identifier and fresh body mass.

netting to the nearest 0.1°C using a fast-response (time constant 0.025 s), 0.33 mm-diameter needle microprobe with sharpened tip (Type MT-29/1; Physitemp Instruments, Clifton, New Jersey, USA). Readings were obtained by inserting the probe 1 mm into the bee's thorax dorsally while it was restrained in the net. Air temperature (T_a) 2–5 cm away from the flower where the bee had been caught was measured within 2 min of the bee's capture using a digital thermometer and a fast-response 0.22 mm-diameter thermocouple. A total of 497 paired T_{th} and T_a measurements on foraging individuals of 15 *Andrena* species were obtained in the field on 43 different sampling dates.

A subset of the individuals with paired T_{th} and T_a field data ($N = 186$ individuals from seven species) were killed immediately after thoracic temperature measurement using ethyl acetate, and their "perception" of the natural thermal environment was assessed by measuring their operative temperatures (T_e). T_e represents the equilibrium temperature that an organism would reach under stable conditions in the absence of metabolic input, and it simultaneously reflects air temperature and

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a temperature increment or decrement subsuming radiative and convective factors (Bakken, 1989, 1992; Bishop & Armbruster, 1999). The needle thermocouple was inserted into the thorax of the freshly-killed bee, which was then placed lying flat on the surface of the same flower on which it had been previously captured. T_{th} was subsequently recorded with a digital thermometer until variation became negligible (<0.5°C in 30 s), and this final value was used as an estimate of T_{e} (see also, e.g., Bishop & Armbruster, 1999, for a similar T_{e} estimation method). All individuals used for T_{e} estimation were weighed to the nearest 0.1 mg within 0.5–2 h of measurements.

Data analyses

All statistical analyses reported in this paper were carried out using the R environment (R Core Team, 2020). The proportional importance of *Andrena* bees relative to all bees combined (Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae) was estimated for each plant species by dividing the total number of *Andrena* individuals recorded in censuses by the total number of individuals for all bees combined. Nine plant species without any bee pollinator were excluded from all analyses. The shape of the seasonal trend in the relative importance of *Andrena* as pollinators in the study region was assessed by regressing the proportion of *Andrena* for every plant species ($N = 266$) against the mean census date for the species (expressed as days from 1 January), using the generalized additive model smoother implemented in function gam of the mgcv package for R (Wood, 2017).

Since many *Andrena* species are oligolectic on one or a few phylogenetically related plant species (Larkin et al., 2008; Wood & Roberts, 2018) and the flowering period of plant species is known to have a strong phylogenetic signal (Davies et al., 2013; Kochmer & Handel, 1986), then *Andrena* seasonality could actually depend more on a close association with certain groups of plants which happen to flower during a particular time of year rather than on time of year itself. To analytically address this possibility, statistical significance of the seasonal trend in frequency of *Andrena* bees was evaluated by fitting two separate generalized linear mixed models with *Andrena* proportion for each plant species as the response variable, mean census date for the species as the single fixed effect, and either plant family or plant genus as random effects to account for phylogenetic signal. This approach allowed us to dissect the effects of time of year and plant taxonomical composition on *Andrena* frequency. Computations were performed with the glmer function of the lme4 package (Bates et al., 2015), the response variable was modeled as a binomial process, and dates (expressed as days from 1 January) were scaled to mean zero and standard deviation unit, so that fixed-effect parameter estimates represented standardized effects. Confidence intervals for model parameter and variance estimates were obtained using function confint.merMod.

Laboratory runs on *Andrena* bees yielded estimates of two thermal parameters for each tested individual: the maximum thermal excess relative to ambient temperature reached autonomously (i.e., endothermically) by the living bee and maintained during at least 30 s ($T_{\mathrm{exc}} = T_{\mathrm{th}} - T_{\mathrm{a}}$); and the constant K describing heat transfer rate obtained by fitting the passive warming curve of the dead bee to the equation $dT/dt = K\ (T - T_{\mathrm{a}})$ (Newton's law of cooling; Casey, 1988; Willmer & Unwin, 1981), in which T is the temperature of the object, t is time, T_{a} is ambient temperature, and K is the cooling/warming constant ("warming constant" will be used hereafter). The nonlinear least-squares method implemented in the function nls of the stats package was used to estimate K from empirical experimental data. T_{exc} and K values were used to describe the warming ability and intrinsic heat transfer rates of the species tested, respectively.

The functional relationships linking either thoracic (T_{th}) or operative (T_{e}) temperatures with ambient temperature (T_{a}) under natural field conditions were assessed by regressing T_{th} or T_{e} against T_{a} separately for each species. As we were interested in the shape of the functional relationships between temperatures and their possible departures from linearity, nonparametric regressions based on the generalized additive model smoother in function gam of the mgcv package were used (Wood, 2017). This method, in contrast to ordinary parametric linear or quadratic regressions, does not make a priori assumptions on the shape on the statistical relationship linking predictor and response variables.

Results obtained here for two key thermal features of *Andrena* bees (warming constant K estimated in the laboratory, and thoracic temperatures of foraging individuals measured in the field) were compared with those obtained previously in the study region as part of other studies for a taxonomically diverse sample of 20 bee species from five families and 11 genera, using identical field and laboratory procedures (Herrera, 1997; Herrera et al., 2023, C. M. Herrera unpublished observations). The statistical relationships across species between mean K and mean body mass (both log-transformed), and between mean thoracic temperature and mean air temperature, for *Andrena* and non-*Andrena* species were compared by fitting two simple linear models to the data which included bee group (*Andrena* vs. non-*Andrena*), either mean body mass or mean air temperature, plus the

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corresponding interaction term, as predictors. Fits and parameter estimates were obtained with the function lm of the stats package.

RESULTS

Distribution of *Andrena* bees over the seasonal and air temperature gradients

Andrena bees were important pollinators in the regional assemblage of entomophilous plants. They were recorded visiting flowers of 153 different plant species, or 57.5% of species with flowers visited by bees. Their proportional importance relative to all bees varied widely among plant species, and exhibited a distinct seasonal trend. The proportion of *Andrena* individuals in pollinator censuses tended to be highest among plant species flowering during February–May (Figure 2). Individuals of *Andrena* contributed >50% of all bees in 29 of the 137 species flowering during that period (Figure 2), and were the exclusive bee pollinators of some very early-blooming herbs such as six species of Brassicaceae in the genera *Alyssum*, *Erophila*, *Iberis*, *Jonopsidium* and *Lepidium*. The proportion of *Andrena* in the bee pollinator assemblages of individual plant species tended to decline precipitously from May onward, remaining unrecorded or having negligible importance for plant species which flowered from late June through October (Figure 2; adjusted R^2 of the fitted generalized additive model smoother = 0.189, deviance explained = 22.6%). The effect of time of year on the frequency of *Andrena* in the pollinator assemblages of individual plant species remained statistically significant after controlling for the variance among plant genera and families in flowering phenology (Table 2), thus indicating that *Andrena* seasonality was not the spurious consequence of associations with particularly early-flowering plant taxa.

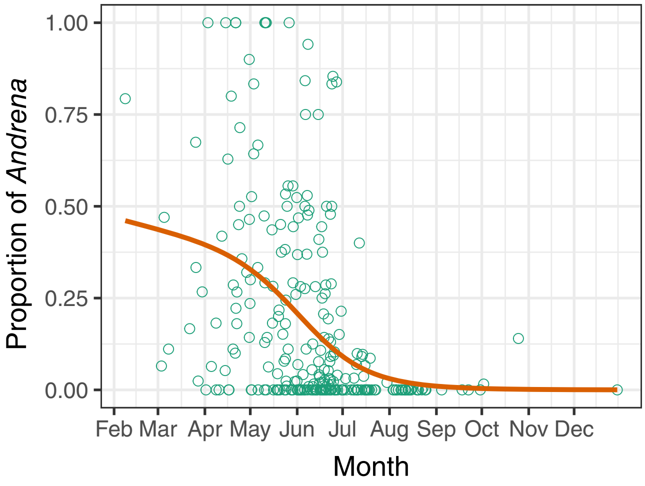

FIGURE 2 Seasonal variation in the proportion of *Andrena* relative to total bees in the pollinator assemblages of 266 species of bee-pollinated plants from montane habitats in the Sierra de Cazorla study area. Each symbol represents a different plant species. The horizontal axis is the mean census date for each species, and the vertical axis the proportion of bee individuals contributed by species of *Andrena* in pollinator censuses. The red line is a nonparametric regression fitted to the data using a binomial smoothing spline.

On an annual basis, *Andrena* and non-*Andrena* bees tended to be associated with contrasting thermal microenvironments while foraging, as revealed by the divergent frequency distributions of air temperatures at capture points (Figure 3). Both the central trend and the spread of the distribution were lower for *Andrena* (interquartile range = 16–22°C) than non-*Andrena* bees (interquartile range = 20–31°C). In addition, the upper limit of air temperatures at foraging sites was considerably lower for *Andrena*, as denoted by the observation that only 13% of all *Andrena* were found foraging at sites with air temperatures above the median of the combined distribution for all bees (23.3°C), while the corresponding figure for non-*Andrena* bees was 62% (Figure 3). These differences in thermal environment between *Andrena* and non-*Andrena* bees are the consequence of the earlier, cooler flying period of the former, as differences vanish after excluding the data from non-*Andrena* bees for dates posterior to the *Andrena* flight period (Appendix S1: Figure S1).

TABLE 2 Summary of results of generalized linear mixed models testing for the effect of flowering date on the frequency of *Andrena* relative to all bees while controlling for differences in blooming time among plant genera and families ($N = 266$ plant species).

	Fixed effect: flowering date (days from 1 January)*				Random effect's variance (plant family or plant genus)	
Random effect:	**Standardized parameter estimate**	**99% CI**	**Chi-squared**	***p*-value**	**Estimate**	**99% CI**
Plant family	−0.884	−0.995 – −0.776	435.5	<2e-16	1.710	0.855–3.817
Plant genus	−0.709	−0.935 – −0.498	69.9	<2e-16	5.072	3.358–7.903

*Standardized parameter estimates and confidence intervals are expressed in the scale of the link function (logit).

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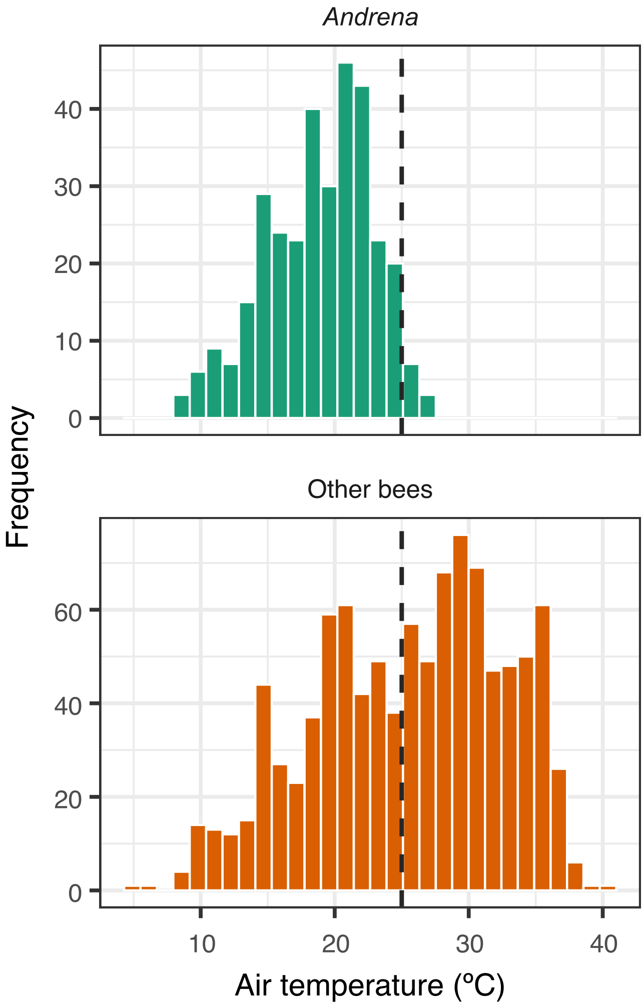

FIGURE 3 Frequency distributions of air temperature at foraging sites of *Andrena* and non-*Andrena* bees sampled throughout the year in the Sierra de Cazorla study area. The median value for the combined distribution of the two groups (23.3°C) is shown for reference (vertical dashed line).

Endothermic ability and warming constant

Laboratory experiments revealed from null to weak endothermic ability in the sample of 25 *Andrena* species tested (Table 3). The increase in thoracic temperature above the ambient ranged between <1°C (e.g., *A. impressa*, *A. sardoa*, *A. livens*) and ~ 3°C (e.g., *A. nigroaenea*, *A. pilipes*, *A. thoracica*). There was a close positive linear relationship across species between mean T_{exc} and mean body mass ($r = 0.791$, $N = 25$, $p = 2.5\text{e-}06$; Figure 4A). The endothermic ability of all small species (<50 mg body mass) was consistently null or negligible (mean T_{exc} 0–0.5°C), and in the case of the largest-sized species mean T_{exc} values were ~ 3°C at most (Table 3; see also Figure 1 for some individual examples). The warming constant K ranged between 0.0071 and 0.0141 s^{-1} in the set of species studied (Table 3), and this parameter was closely, inversely correlated with body mass across species ($r = -0.845$, $N = 25$, $p = 1.1\text{e-}07$; Figure 4B).

Thoracic temperature in relation to ambient temperature

Mean T_{th} for the 15 *Andrena* species sampled in the field are summarized in Figure 5. There was little interspecific variation in mean T_{th} values, which ranged between 25.6°C (*A. livens*) and 31.3°C (*A. labialis*). Interspecific variation in mean T_{th} was not significantly correlated with variation in mean body mass ($r = 0.112$, df $= 13$, $p = 0.69$).

All individual *Andrena* bees sampled in the field while foraging at flowers were substantially warmer than the air at the capture site, and T_{th} was significantly, positively related to T_{a} in all species (Figure 6). The shape of the relationship between T_{th} and T_{a} was essentially linear in most species despite the fitting method used (generalized additive model smoother) not imposing linearity a priori on the data. Only in a few instances (*A. lagopus*, *A. livens*, *A. sardoa*) there was some evidence of weakly nonlinear, convex relationships (Figure 6). In general, regressions tended to run parallel to the $y = x$ isothermal line, thus denoting that variation in T_{th} closely followed variation in ambient temperature.

Thoracic temperature in relation to operative temperature

Thoracic and operative temperatures (T_{th} and T_{e}, respectively) were measured concurrently on 186 individuals of seven species (*A. assimilis*, *A. flavipes*, *A. fulva*, *A. labialis*, *A. nigroaenea*, *A. sardoa*, *A. trimmerana*) that roughly encompassed the whole range of body mass and endothermic ability represented in the species sample considered in this study (Table 3). Despite differences in body size and endothermic ability, the shape of nonparametric fits of T_{th} against T_{e} were conspicuously similar in all species. Thoracic temperature was positively, nonlinearly related to operative temperature (Figure 7). The fitted curves for all species consistently intersected the $y = x$ isothermal line at $T_{\text{e}} = 28$–31°C (estimated mean = 29.6°C), which revealed the existence of distinct thresholds, or "breakpoints", in the functional relationship between T_{th} and T_{e}. To the left of each breakpoint, the thoracic temperature of the living bees (T_{th}) was roughly equal to, and varied in unison with, the temperature of the dead bee placed at the same spot and experiencing identical thermal environment (T_{e}). To the right of breakpoints, in contrast, thoracic temperature was

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TABLE 3 Mean body mass and thermal parameters for 25 species of *Andrena* tested experimentally in the laboratory (see Table 1 for sample sizes).

Species	Live mass (mean ± SE) mg	T_{ex} (mean ± SE) °C	K (mean ± SE) s^{-1}
Andrena impressa	35 ± 1	0.4 ± 0.1	0.0134 ± 0.0008
Andrena bicolor	38 ± 3	0.6 ± 0.2	0.0130 ± 0.0006
Andrena rhyssonota	38	1.2	0.0107
Andrena tibialis	39	0.8	0.0126
Andrena vulpecula	41 ± 7	0.5 ± 0.5	0.0122 ± 0.0014
Andrena congruens	41	0.5	0.0120
Andrena humilis	41 ± 2	0.5 ± 0.3	0.0129 ± 0.0017
Andrena sardoa	45 ± 2	0.4 ± 0.04	0.0127 ± 0.0005
Andrena livens	47 ± 2	0.5 ± 0.3	0.0115 ± 0.0004
Andrena ovatula	47	0.0	0.0107
Andrena lepida	51 ± 3	1.6 ± 0.4	0.0107 ± 0.0003
Andrena haemorrhoa	61 ± 3	1.5 ± 0.3	0.0107 ± 0.0004
Andrena combinata	59	2.0	0.0111
Andrena ferrugineicrus	66	0.7	0.0107
Andrena flavipes	68 ± 4	1.1 ± 0.3	0.0103 ± 0.0010
Andrena schencki	68	0.8	0.0141
Andrena hispania	81 ± 12	0.7 ± 0.4	0.0116 ± 0.0006
Andrena fulva	86 ± 6	2.5 ± 0.4	0.0093 ± 0.0004
Andrena labialis	93 ± 4	0.7 ± 0.2	0.0107 ± 0.0003
Andrena trimmerana	100 ± 4	2.4 ± 0.4	0.0084 ± 0.0002
Andrena nigroaenea	103 ± 4	3.0 ± 0.7	0.0088 ± 0.0004
Andrena albopunctata	104	2.0	0.0076
Andrena pilipes	135 ± 10	3.8 ± 0.8	0.0078 ± 0.0004
Andrena assimilis	143 ± 6	1.9 ± 0.3	0.0071 ± 0.0004
Andrena thoracica	146 ± 6	3.7 ± 1.0	0.0076 ± 0.0003

Note: Species are listed in increasing order of body mass. T_{ex} = maximum difference between thoracic and ambient temperature reached by live bees by spontaneous endothermy and maintained for at least 30 s; K = warming constant for dead bees, estimated by fitting to the equation for Newton's law of cooling the observed temperature sequences of bees as they equilibrated thermally with the ambient.

lower than, and tended to increasingly diverge from, operative temperature (Figure 7). Breakpoints must thus be interpreted as transition thresholds from passive warming to active cooling.

Comparisons with other bees

Mean warming constants (K) for the species of *Andrena* studied here were significantly higher ($F_{1,29} = 15.01$, $p = 0.0006$), and tended to decline more slowly with mean body mass ($F_{1,29} = 4.68$, $p = 0.038$; interaction term in the linear model), than those of eight bee species from seven other genera sampled in the study region (Figure 8A). As a consequence of the different slopes of the declining relationships of mean K with mean body mass, the divergence between *Andrena* and non-*Andrena* bee species in average warming constant tended to broaden as mean body mass increased (Figure 8A).

Mean thoracic temperature of foraging bees measured in the field (T_{th}) was significantly lower for all species of *Andrena* than for the sample of 18 species of bees from eight genera measured in the same region ($F_{1,29} = 187.7$, $p = 3.4\text{e-}14$) (Figure 8B). The relationship across species between mean T_{th} and mean air temperature (T_a) was roughly parallel for *Andrena* and non-*Andrena* species, as denoted by the statistical nonsignificance of the interaction term in the linear model ($F_{1,29} = 0.19$, $p = 0.66$). Mean T_{th} of *Andrena* species was on average (± SE) 10.8 ± 3.8°C lower than mean T_{th} of non-*Andrena* ones over the entire T_a range represented in the sample (Figure 8B).

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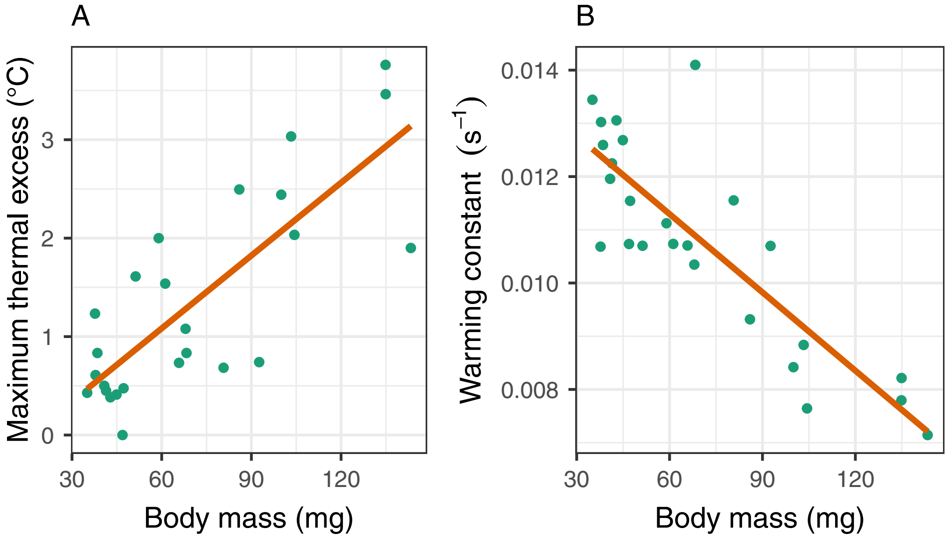

FIGURE 4 Relationships across *Andrena* species ($N = 25$) of endothermic ability (A) and warming constant (B) with mean body mass, as determined experimentally in the laboratory. Lines are nonparametric regressions fitted to the data using a generalized additive model and cubic splines, which implies that linearity of relationships was not a condition imposed a priori on the data by the fitting method.

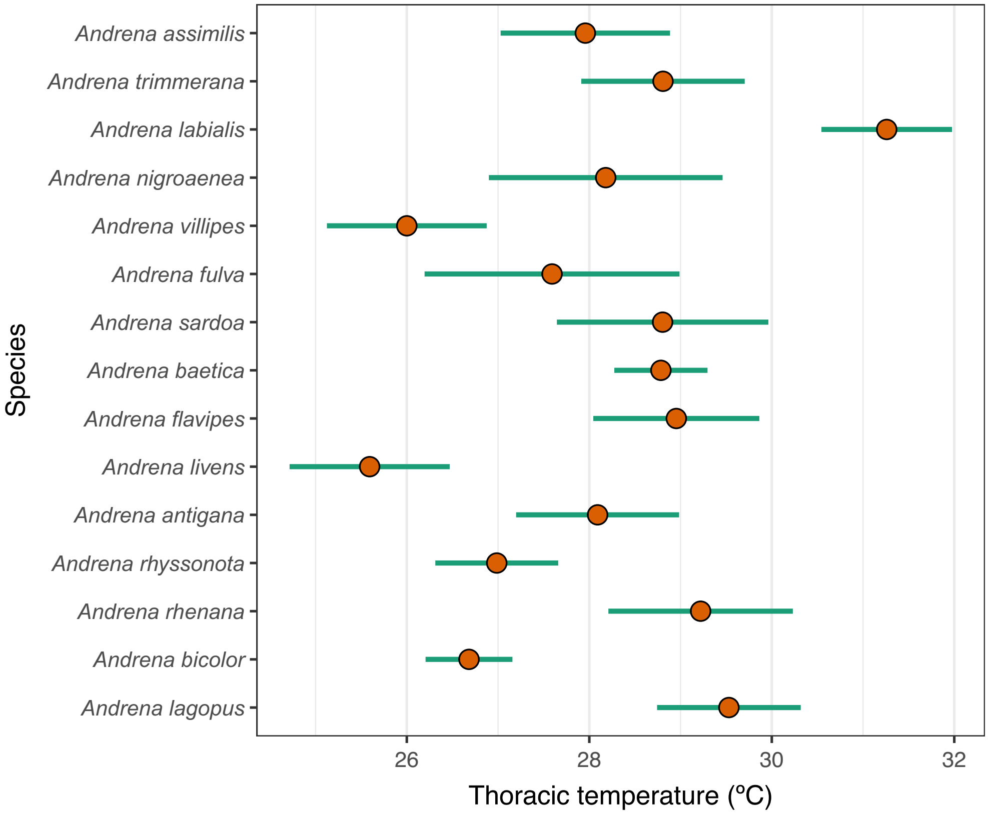

FIGURE 5 Mean thoracic temperature of foraging individuals of 15 species of *Andrena* measured in the field. Dots are means and segments extend over ± 2 standard errors. Species are ranked by increasing mean body mass from bottom to top (see Table 3 for actual values).

DISCUSSION

At the plant community level, the numerical importance of *Andrena* bees as pollinators was strongly seasonal, reaching a maximum among those plant species which flowered in late winter and early spring. This pattern was largely independent of seasonal shifts in the family- and genus-level composition of plant

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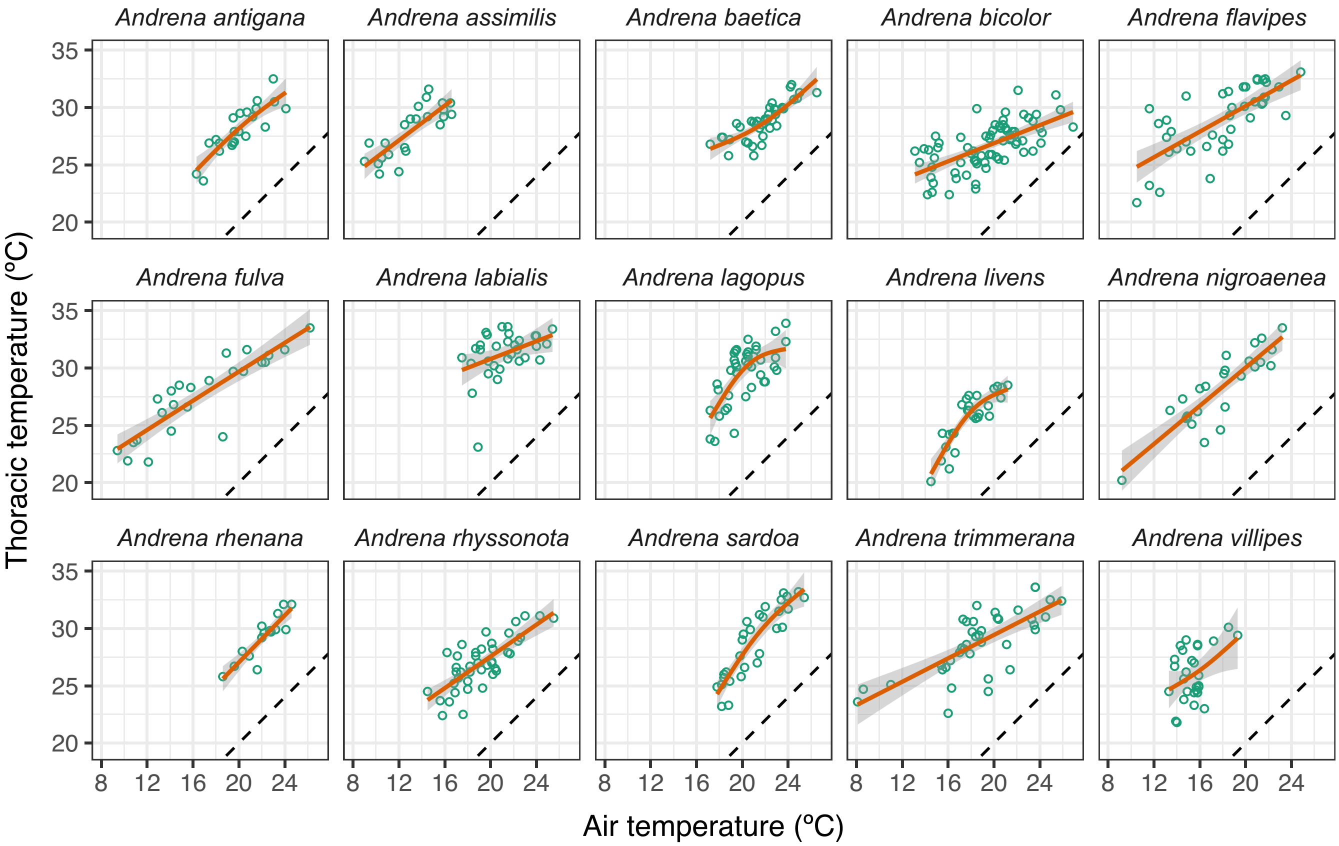

FIGURE 6 Relationship between bee thoracic temperature and air temperature at capture spot for 15 *Andrena* species sampled in the field. Each symbol corresponds to an individual bee, red solid lines are nonparametric regressions fitted using smoothing splines, and the shaded bands are 95% confidence envelopes around the fit. The dashed line depicts the $y = x$ isothermal line.

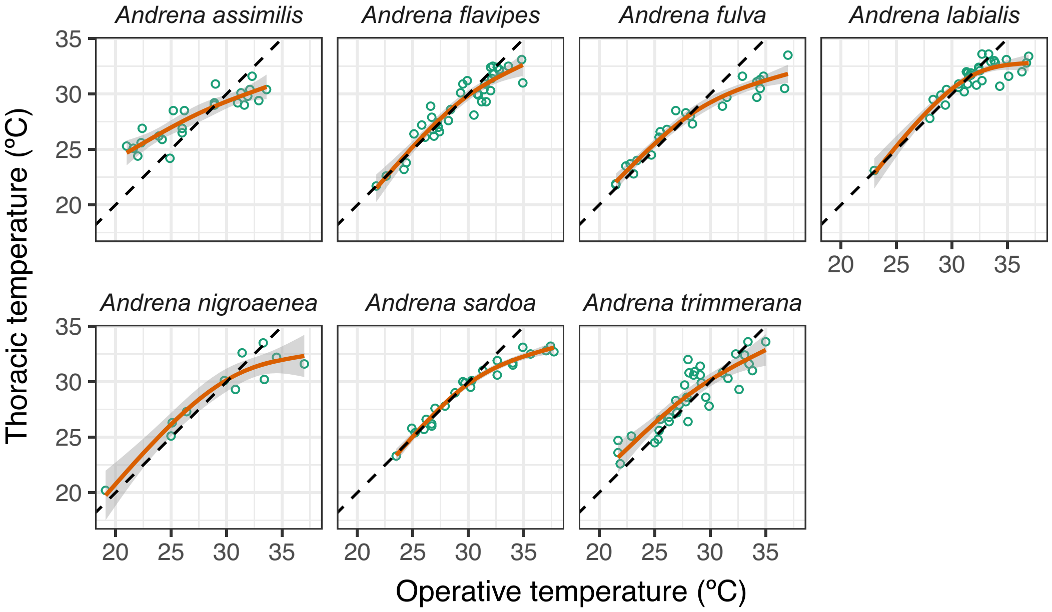

FIGURE 7 Relationships between thoracic and operative temperatures measured in the field for seven *Andrena* species. Each symbol corresponds to an individual bee, red solid lines are nonparametric regressions fitted using smoothing splines and the shaded bands are 95% confidence envelopes around the fit. The dashed line depicts the $y = x$ isothermal line.

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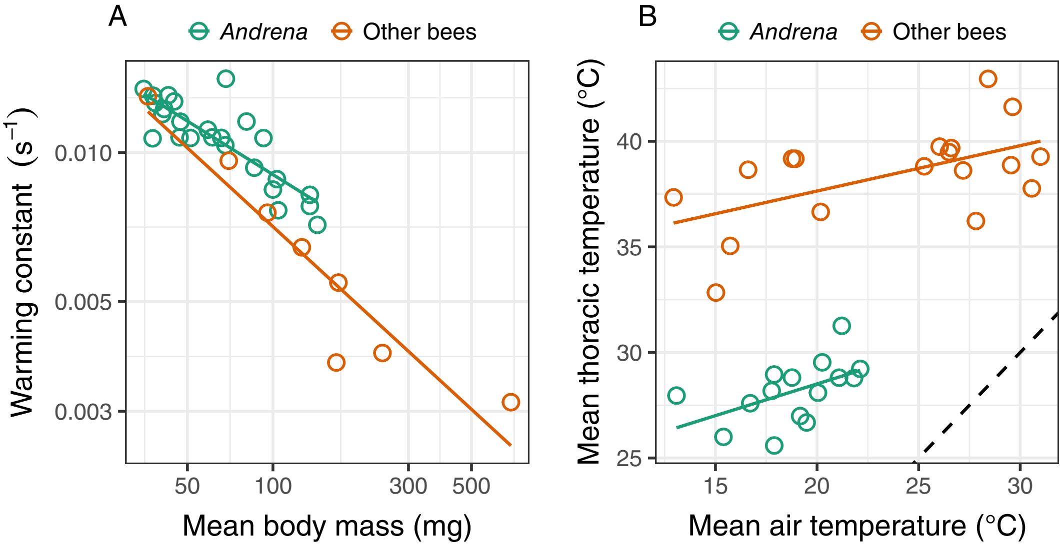

FIGURE 8 A comparison of species means for warming constant (A; note logarithmic scale on both axes) and thoracic temperature (B) of the *Andrena* species considered in this study with the corresponding means for species in other bee genera (*Amegilla*, *Anthidium*, *Anthophora*, *Apis*, *Bombus*, *Colletes*, *Dasypoda*, *Megachile*, *Osmia*, *Panurgus*, *Xylocopa*) which were sampled in the same study area and measured using identical laboratory and field methods. Solid lines are fitted linear regressions. The dashed line in B depicts the $y = x$ isothermal line.

species in bloom. *Andrena* pollinators were recorded only during the cooler half, and were absent during the warmer half, of the annual range of air temperatures experienced at flowers by the entire bee assemblage. These ecological restrictions of *Andrena* bees, and the ensuing community-level pattern in plant-pollinator assembly, can be related to distinctive features of their thermal biology: higher warming constants than bees of other genera for the same body mass; null or weak endothermy; ability to forage at lower body temperatures than bees with stronger endothermic ability; low upper tolerable limit of body temperature beyond which thermal stress probably precluded foraging at the warmest season of the year; and weak thermoregulatory capacity, as shown by the steep linear relationship between thoracic and air temperature and the nearly coincident variation of body and operative temperature over most of the thermal range. These thermal features and their functional relationships, as well as some of their ecological implications in relation to the assembly of plant-pollinator communities and climate change are discussed below.

Seasonality: Cool-blooded bees for early-blooming plants

Results of the present study corroborate for a whole plant community the earlier findings obtained with smaller species samples in other habitats of Eurasia and North America, which likewise revealed an association between early blooming plants and pollination by *Andrena* (see references in *Introduction*). When the whole regional community of entomophilous plants from our Sierra de Cazorla area was considered, *Andrena* bees emerged as numerically important bee pollinators for the subset of species which flowered during the earliest period of the community-wide flowering season. Early-flowering, *Andrena*-pollinated plants were mostly herbs in the families Amaryllidaceae, Brassicaceae, Geraniaceae, Ranunculaceae, and Rosaceae from open, sunny habitats whose flowers had open, non-restrictive corollas with pollen and nectar easily accessible by short-tongued insects. The association between *Andrena* bees and these plants for pollination, however, is unlikely to reflect mutual adaptations evolved in the particular ecological context of our study. On one side, plant flowering times and bee activity periods are both phylogenetically conserved traits at the family, genus and, at least in the case of *Andrena*, subgenus levels (Davies et al., 2013; Kochmer & Handel, 1986; Larkin et al., 2008; Turley et al., 2022). And on the other, the early season peak in proportional importance of *Andrena* as pollinators persisted after statistically accounting for effects of plant phylogeny (using families and genera as proxies) on the frequency of *Andrena* as pollinators. It must be stressed here that the generalized linear mixed models fitted to *Andrena* frequency in bee pollinator assemblages of individual plant species did reveal substantial variance associated with plant families and genera. This points to the existence of a phylogenetic signal of

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Andrena pollination in the plant community studied which would deserve further study.

In accordance with an activity period predominantly restricted to late winter and spring, the thermal range experienced by *Andrena* bees while foraging at flowers ($T_a = {\sim}10\text{–}25^\circ\text{C}$) was substantially narrower, and had a much lower upper limit, than the thermal range experienced by all bees over the whole flowering season ($T_a = {\sim}10\text{–}37^\circ\text{C}$). Since it has been sometimes emphasized that substantial endothermy is a crucial adaptive response of bees to northern or cool climates (Bishop & Armbruster, 1999; Gérard et al., 2018; Heinrich, 1993; Stone & Willmer, 1989), it would have been expected that the association between *Andrena* bees and cool microclimates in the montane habitats studied should be linked to widespread, substantial endothermy. Our results falsify this expectation and illustrate that successful exploitation of cooler microclimates by bees does not require significant endothermy, provided that the bees possess an ability to forage at the low body temperatures attainable primarily by passive, ectothermic warming. In *Andrena*, however, this latter feature apparently comes with a restriction of foraging activity at higher ambient temperatures, which parsimoniously explains their absence from the warmer parts of the seasonal thermal spectrum as discussed in the next section. A comparative study on the thermal biology of species in the anomalously summer- and autumn-flying *Callandrena* from North America (Larkin et al., 2008) could possibly allow a test of this interpretation.

Thermal biology

We characterized the thermal biology of many species of *Andrena* from different subgenera, yet field and laboratory results were remarkably homogeneous across species. In the field, the range and average values of thoracic temperatures for individual species fell within rather narrow limits, and the shape of the relationships between T_{th} and T_a were similar for all species, as were also the critical breakpoints above which T_{th} shifted from roughly equal to lower than operative temperature (active cooling). In the laboratory experiments, differences between species in endothermic ability and warming constant (K) were accounted for by variation in body size, two relationships that have been long known for insects (Bishop & Armbruster, 1999; May, 1976; Stone & Willmer, 1989; Willmer & Unwin, 1981). Since at least several of the subgenera included in our species sample most likely represent monophyletic lineages (e.g., *Chlorandrena*, *Lepidandrena*, *Melandrena*, *Simandrena*; Bossert et al., 2022), the prevailing homogeneity of thermal features across our species sample suggests that they represent evolutionarily conserved characteristics within the genus *Andrena* which probably apply to congeneric species from other continents and ecological scenarios as well. This is supported by the low minimum temperatures for flight reported by Stone and Willmer (1989) for three British species, including two of those studied here (*A. clarkella*, *A. fulva*, *A. nigroaenea*); the low takeoff thoracic temperatures and insignificant temperature elevation index found by Bishop and Armbruster (1999) for two species from Alaska (*A. thaspii*, *A. frigida*); and the reported inability of central European *Andrena taraxaci* to raise thoracic temperature under experimental conditions (Schmaranzer et al., 1997). The thermal features of *Andrena* reported here will thus most likely explain their seasonality in other plant-pollinator systems from the Holarctic realm as well (see references in the *Introduction* section).

Mean thoracic temperatures (T_{th}) were lower, and mean warming constants (K) were higher, for *Andrena* than for other bees from 11 different genera in five families sampled in the same area after controlling for variation in body size and air temperature, respectively. The vast majority of non-*Andrena* species used for comparisons belonged to the families Apidae and Megachilidae, which are expected to be from moderately to extremely endothermic (Bishop & Armbruster, 1999; Stone & Willmer, 1989). Therefore, the broad disparity between *Andrena* and non-*Andrena* bees in mean T_{th} is just what would be expected from a comparison between ectothermic and predominantly endothermic bees (Bishop & Armbruster, 1999; Stone & Willmer, 1989). The contrast between these two groups in intrinsic heat transfer properties, however, whereby *Andrena* had higher K values than species of other genera, was not anticipated and, as far as we know, has been not reported previously. K provides an estimate of the rate of heat gain of an object placed in a warmer environment or, alternatively, of the rate of heat loss when placed in a cooler environment. The higher K values of *Andrena* thus suggest an intrinsic ability to passively warm or cool significantly faster than other bees of the same body mass, which should have the obvious benefit of reducing thermal inertia and allowing faster adjustment of body temperature when moving across within-habitat mosaics of ambient temperatures. The structural or mechanistic basis of the higher K values shown by *Andrena*, as well as its generality, remains to be investigated, but it seems plausible to suggest that enhanced heat transfer in this genus should be related to some combination of coat color, body geometry, reflectance, and hairiness (May, 1976; Pereboom & Biesmeijer, 2003; Willmer & Unwin, 1981).

Other key thermal features of *Andrena* include the inability of most species to significantly warm up endothermically, and the low mean and low upper limits of thoracic temperatures in the field. For the same air

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temperature, mean thoracic temperature was ~10°C lower for *Andrena* than for other bees (Figure 8). The ranges of mean thoracic temperatures for *Andrena* (26–31°C) and the other bees sampled (33–43°C) did not overlap, and the upper limit for *Andrena* matched the critical thermal threshold beyond which T_{th} shifted to active cooling (~30–31°C). The T_{th} vs. T_a regression for *Andrena* species (Figure 8) leads to the projection that, on average, the critical T_{th} thermal ceiling of ~30–31°C would be reached at an ambient temperature ~ 25°C, remarkably close to the temperature above which *Andrena* pollinators virtually vanished from flowers in our study area (Figure 3). Taken together, these observations strongly support the interpretation that the absence of *Andrena* bees from the latter half of the community-wide flowering season was imposed by their intrinsic inability to withstand thoracic temperatures above ~31°C for long periods without overheating. We tentatively suggest that muscular power output, foraging activity and/or foraging efficiency would be severely depressed above this upper threshold (Coelho, 1991; Sinclair et al., 2016), and that the need for lowering thoracic temperature below operative temperature for long periods using behavioral means would severely reduce efficient foraging and constrain microhabitat selection (Corbet & Huang, 2016; Herrera, 1995).

Levels of endothermy in bees: Ecological implications

Studies on bee thermal biology have historically focused on a few, phylogenetically closely-related lineages of large bees in the family Apidae possessing outstanding endothermic and thermoregulatory ability (e.g., genera *Anthophora*, *Apis*, *Bombus*, *Xylocopa*; see references in the *Introduction* section). General statements on the thermal biology of bees have sometimes highlighted their endothermy and/or the importance of endothermy and thermoregulation for the occupation of cool environments or broadening their habitat ranges (see Appendix S2: Table S1 for references). These notions were mostly based on early ground-breaking work on a small group of extremely endothermic bees, particularly bumble bees, honeybees and *Anthophora* (Appendix S2: Table S1). Two concurrent lines of evidence, however, suggest that such inferences were premature. On one hand, thermal biology seems to have a strong phylogenetic component in bees, with different evolutionary lineages differing in body temperature, tolerable temperature limits, and minimum temperature required for flight (Bishop & Armbruster, 1999; Stone, 1994; Stone & Willmer, 1989). Generalizations based on phylogenetically biased species samples are thus prone to biases or distortions. And on the other hand, the few investigations which have so far examined the thermal biology of a modest number of bee species from three major families other than Apidae (Colletidae, Andrenidae, Halictidae; Bishop & Armbruster, 1999; Herrera, 1995; Potts, 1995; Shelly et al., 1993; Stone & Willmer, 1989, and the present study) have consistently failed to support significant endothermy. The combined number of species in these three families (Colletidae, ~2600 species; Andrenidae, ~3000; Halictidae, ~4500; Danforth et al., 2019) amount to a half of the ~20,000 bee species worldwide (Ascher & Pickering, 2020) and nearly doubles that of the most-frequently investigated family (Apidae, ~6000 species). It seems safe to predict, therefore, that future studies on bee thermal biology encompassing a broader, less phylogenetically biased spectrum of species will disclose that strong endothermy is far less frequent among bees than it has been sometimes implied or hypothesized; that predominantly or exclusively ectothermic bees comprise a sizeable fraction of bee pollinator communities worldwide; and that further studies on bee thermal biology in a broad phylogenetic context might reveal that endothermy is only weakly related to broader thermal niches (Glass & Harrison, 2022; Vicens & Bosch, 2000).

Energetic constraints have been long acknowledged to drive interactions between plants and bees for pollination (Heinrich, 1975, 1981; McCallum et al., 2013). Flower choice and foraging behavior of bees are constrained by the need of balancing foraging costs and the energy returns gained from pollen and nectar (Higginson et al., 2006; Kadmon & Shmida, 1992; Willmer, 2011). In comparison to weakly endothermic species, strongly endothermic ones incur additional energetic costs derived from raising body temperature by metabolic means (Heinrich, 1974, 1993; Waddington, 1990), which will most likely set the two groups apart with regard to their relationships with plants for pollination (Heinrich, 1975, 1981; Herrera, 1995, 1997; McCallum et al., 2013). For example, marked differences in thoracic temperatures between extremely endothermic and predominantly ectothermic bees will most likely lead to differences in muscular power output, foraging speed, and flower visitation rates (Coelho, 1991; Herrera, 1989, 1997). Contrasting thermal biologies (ectothermic cool-blooded vs. endothermic hot-blooded) could perhaps exemplify two distinct adaptive pathways allowing bees to exploit distinct segments of the seasonal thermal gradient and associated floral resources. Evaluation of this hypothesis will require, in the first place, collecting sufficient empirical information as to fill the current knowledge gap on thermal biology of quantitatively important worldwide but hitherto little-explored bee lineages, as exemplified by the present study on *Andrena* (see also Bishop & Armbruster, 1999; Herrera, 1995; Potts, 1995; Stone, 1994; Stone & Willmer, 1989). It could then be

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tested whether thermal excess of bees relative to ambient temperature is bimodally distributed across the phylogeny of bees, as provisionally suggested by Figure 8B.

Bee thermal biology and climate warming

In addition to helping to understand the mechanisms driving the assembly of plant-pollinator systems along environmental gradients, further research on the thermal biology of understudied but very species-rich families and genera of bees bound to contribute new insights on the heterogeneity of bee responses to climate warming. Recent reviews and empirical research on the impact of climate change on insect pollinators have often acknowledged the importance of thermal biology as a determinant of bee responses to climate warming, but most inferences have been based on studies of large-sized, strongly endothermic species, particularly bumble bees in the genus *Bombus* (Ghisbain et al., 2021; Marshall et al., 2018; Oyen et al., 2016; Ploquin et al., 2013; Rasmont et al., 2015; Scaven & Rafferty, 2013). In the same vein, concerns on wild bee declines have been almost invariably based on data from just two, extremely endothermic genera (*Apis*, *Bombus*) which collectively account for a tiny fraction of all species of bees (~1.5%) and whose biological and ecological attributes are far from representative of wild bees in most respects (Ghisbain, 2021; Wood et al., 2020). Results of this study suggest that medium- and large-sized weakly endothermic bees with low upper thermal limits and weak thermoregulatory ability (~50–100 mg body mass) can be more adversely affected by increasing ambient temperatures than the large, strongly endothermic species with high thermoregulatory ability most frequently investigated (>100 mg). For example, an increase in the annual number of days with maximum daily temperature >25°C as a consequence of the fast climatic warming which is underway in our study area (Herrera et al., 2022, and references therein) will reduce the total annual time available for foraging by *Andrena* bees. In contrast, accelerated climate warming in our study region is apparently favoring the increase of small ectothermic (or weakly endothermic) bees in pollinator communities through broadening of their daily and seasonal activity windows (e.g., species of *Heriades*, *Halictus* subgen. *Seladonia*, *Lasioglossum* subgen. *Evylaeus*, *Panurgus*; Herrera, 2019: fig. 10). Attaining a more balanced, nuanced and realistic apprehension of the impact of climate warming on bees and their pollinating services will require a taxonomically broader and biologically deeper understanding of their thermal biology, particularly of the most species-rich, but nearly uninvestigated ectothermic lineages.

AUTHOR CONTRIBUTIONS

Carlos M. Herrera conceptualized the study, performed field and laboratory work, analyzed the data, and led the writing. Alejandro Núñez and Luis O. Aguado identified all bee specimens considered in the study and contributed to the interpretation of results. Conchita Alonso provided financial support and project management during the latest stages of the study, and contributed to the analysis of data and interpretation of results. All authors participated in data assembly and curation, edited and revised manuscript drafts and approved the final version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and metadata (Herrera et al., 2023) are available in Digital.CSIC at https://doi.org/10.20350/digitalCSIC/15109.

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