Ecology, 76(1), 1995, pp. 218–228

FLORAL BIOLOGY, MICROCLIMATE, AND POLLINATION BY ECTOTHERMIC BEES IN AN EARLY-BLOOMING HERB[1]

CARLOS M. HERRERA
Estación Biológica de Doñana, CSIC, Apartado 1056, E-41080 Sevilla, Spain

Abstract. Abiotic factors may constrain the functioning of species interactions such as plant–pollinator mutualisms. I investigated how thermal environment affects the interaction between the early-blooming daffodil, *Narcissus longispathus* (Amaryllidaceae) and its major bee pollinator (*Andrena bicolor*; Andrenidae), focusing simultaneously on plant and pollinator sides of the interaction. I studied fruit and seed set, flower duration, and the intrafloral thermal environment of *N. longispathus,* and the thermal biology, foraging behavior, and thermoregulatory ability of *A. bicolor,* over a 6-yr period in southeastern Spain.

N. longispathus flowers from February to April, when unsuitable weather often limits pollinator activity, yet most flowers are successfully pollinated in all years and sites. Fruit set was weakly pollen limited, but among flowers setting fruit the proportion of ovules developing into seeds was not. Individual flowers lasted for 17 d on average, remaining functional during this period. On sunny days, the air inside *N. longispathus* flowers was significantly warmer than outside. Mean temperature excess inside flowers was as high as 8°C, and was positively related to solar irradiance. Within flowers, air temperature was highest around the anthers; this intrafloral gradient was consistent with variation among perianth parts in radiation transmittance.

Andrena bicolor foraged in *N. longispathus* flowering patches only on sunny days with air temperature >12°–13°C, and foraging behavior and flower visitation rate were temperature dependent. Bees were able to fly at relatively low thoracic temperatures (T_{th}; range 22°–31°C) and this was essential for successfully foraging at *N. longispathus.* Under the range of irradiance and air temperature found at foraging sites, *A. bicolor* individuals inside flowers were able to reach T_{th} suitable for flight by passive means alone. Under laboratory conditions, *A. bicolor* was unable to raise or otherwise regulate T_{th} by physiological means, but free-flying individuals thermoregulated behaviorally. Basking was used to raise T_{th}, and intrafloral microclimate, by influencing the proportion of foraging time devoted to basking, played an important role in thermoregulation. Flower visitation rate was positively related to the average temperature inside visited flowers, and the probability of basking immediately after one floral visit declined with increasing flower temperature. I conclude that the favorable microclimate within *N. longispathus* flowers, their long duration, and the thermal biology of *A. bicolor,* were critical elements in this early-season pollination system.

Key words: Amaryllidaceae; Andrenidae; behavioral thermoregulation; ectothermy; floral microclimate; flower duration; foraging behavior; phenology; pollen limitation; pollination; southern Spain; thermal biology; thoracic temperature.

INTRODUCTION

Interactions between plants and animal pollinators are influenced by both biotic factors (e.g., floral structure, timing of anthesis, quantity and quality of floral rewards, presence of other species) and abiotic ones (e.g., temperature, wind, solar radiation). Considerable effort has been devoted to studying the former, but the abiotic interface between flowers and pollinators remains relatively neglected (see Corbet 1990 for review). Physical factors constrain the activity of pollinators (Lundberg 1980, Bailey et al. 1982, Willmer 1983, Stone et al. 1988, Herrera 1990), influence their behavior at flowers (Hocking 1968, Kevan 1975, Corbet 1978, Willmer 1986, Stanton and Galen 1989), and modify the quality, quantity, and presentation of floral rewards (Corbet et al. 1979, Corbet and Willmer 1981, Corbet and Delfosse 1984). Through such indirect and direct effects, abiotic factors may thereby become critical determinants of plant reproductive success via their effects on pollinators (Eisikowitch and Galil 1971, Cruden 1972, Cruden et al. 1976, Martínez del Río and Búrquez 1986). The importance of abiotic factors in plant–pollinator systems will presumably be greatest when flowering occurs primarily during climatically unfavorable periods. Under these circumstances, physical environmental constraints may seriously limit pollinator activity and pollination success, and both plant and pollinator traits acting to reduce these limitations will be at a premium (Schemske et al. 1978, Motten 1986).

Previous investigations on the influence of abiotic factors on plant–pollinator systems, however, have generally emphasized either the plant's or the pollinator's

[1] Manuscript received 17 January 1994; revised 21 April 1994; accepted 22 April 1994.

side. The temperature excess in the interior of flowers from arctic and alpine habitats, for example, has been interpreted as a trait enhancing flower visitation by ectothermic insects, but empirical data on reproductive biology of the plants are scarce (Hocking 1968, Kevan 1975, Smith 1975, Knutson 1981). Conversely, investigations of abiotic environmental effects on the reproductive biology of early-blooming herbs have mainly focused on phenology and floral biology, while the thermal biology and foraging behavior of pollinators have received relatively little attention (Schemske et al. 1978, Motten 1986). This paper attempts to synthesize these two approaches by elucidating the role of thermal environment in the interaction between the early-blooming daffodil, *Narcissus longispathus,* and its main insect pollinator, placing similar emphasis on the plant's (floral biology, reproductive success) and pollinator's (thermal biology, foraging behavior) sides of the interaction. *N. longispathus* grows in mountain habitats, flowers during a prevailingly cool and rainy period in late winter–early spring, and its major pollinator is a small-bodied andrenid bee (*Andrena bicolor*), yet fruits are produced in abundance in all years and populations. The specific questions addressed are as follows: (1) To what extent does fruit production depend on pollination? (2) Does *N. longispathus* exhibit floral traits that promote pollinator visitation during its climatically unfavorable flowering season? (3) Does *A. bicolor* possess behavioral or physiological attributes enabling it to forage under prevailing weather conditions during *N. longispathus* flowering?

Study Organisms

Narcissus longispathus Pugsley (Amaryllidaceae) is a perennial herb endemic to a few southeastern Spanish mountains (Gómez-Campo 1987, Moreno Saiz and Sainz Ollero 1992). It is closely related to the more widely distributed *Narcissus pseudonarcissus* L. (Caldwell and Wallace 1955; C. M. Herrera, *unpublished data*). In the Sierra de Cazorla area, where the study was conducted, *N. longispathus* occurs as scattered populations confined to stream margins and poorly drained meadows at elevations of 1000–1500 m.

Leaves and floral scapes start to emerge from underground bulbs in February. Each bulb produces one scape (30–50 cm in height) bearing a single hermaphroditic flower with a pale yellow, tubular perianth. The corolla tube is 40.1 ± 3.6 mm long and 23.0 ± 3.0 mm wide at its opening (N = 15; mean ± 1 SD; this notation is used henceforth unless otherwise stated). Flowering occurs from late February to mid April. This period is characterized by cool, rainy weather. Monthly means for minimum and maximum air temperature at the Vadillo-Castril weather station (1000 m elevation) are −1.4°–11.2°C (February), 0.5°–13.5°C (March), and 2.0°–14.9°C (April). Snowstorms are frequent during February–April, and *N. longispathus* flowers sometimes remain covered by snow for several days without apparent damage.

During 6 yr of observation (1988–1993), pollinator activity was recorded exclusively on the few sunny, clear days that occurred during the flowering period. The most common pollinator was *Andrena bicolor* Fabr. (Andrenidae), which accounted for 70–90% of all visits. Females of this small solitary bee (mass = 29.1 ± 7.8 mg, N = 17) visited *N. longispathus* flowers mainly for pollen. Due to their small size, *A. bicolor* individuals remained hidden within the perianth while collecting pollen from anthers (located midway along the perianth tube). During foraging, they frequently basked at the perianth entrance or outer surface. Other pollinators of *N. longispathus* included the bees *Anthophora acervorum* L., *Anthophora dispar* Lep. (Anthophoridae), *Bombus terrestris* L. (Apidae), *Osmia cornuta* Latr., *Osmia rufa* L., and *Osmia tricornis* Latr. (Megachilidae), but these were much less abundant than *A. bicolor* and were recorded only in some years and populations. *Andrena bicolor* was never seen visiting flowers of other species that occurred in the same habitats and flowered at the same time as *N. longispathus* (e.g., *Primula vulgaris, Helleborus foetidus, Daphne laureola*).

Study Area

The study was conducted during 1988–1993 in the Reserva de Navahondona-Guadahornillos, Parque Natural de Cazorla-Segura-Las Villas (Jaén province, southeastern Spain; see Valle et al. [1989] for descriptions of flora and vegetation). Most work was performed at populations located in Tornillos de Gualay (1480 m elevation), Valdecuevas (1420 m), Valdetrillos (1400 m), Barranco del Guadalentín (1280 m), Cuevas Bermejas (1200 m), and Fuente del Perro (1160 m). The two most distant sites were 12.5 km apart.

Methods

Narcissus longispathus

Reproductive biology.—I studied dependence of *N. longispathus* on pollinators at Fuente del Perro by assessing fruit set within pollinator exclosures. Flower duration was studied by marking and periodically monitoring individual flowers exposed to natural pollination. Flowers are very long lived, and two experiments were conducted to determine whether flower fertility declined with age. One experiment tested the effect of stigma age on fruit set with pollen age held constant. I emasculated flowers emerging within pollinator exclosures shortly before perianth dehiscence, and then hand-pollinated when they were 1–2, 7, or 14 d old using fresh pollen from flowers outside exclosures. The other experiment tested simultaneously the combined effects of stigma and pollen age on fruit set. Unemasculated flowers within exclosures were hand-pollinated at ages of 1–2, 7, or 14 d using their own pollen.

I studied pollen limitation of fruit set (proportion of flowers setting fruit) during 1988–1991 in five different populations. Flowers exposed to natural pollination were marked in each site, and a subsample subjected to additional pollination by rubbing a newly dehisced anther from a different flower against the stigma. In some sites and years, vertebrate and invertebrate herbivores consumed most marked flowers and developing fruits. This precluded some comparisons of fruit set between experimental (natural pollination + extra pollen) and control (natural pollination alone) flowers. Seed set (proportion of ovules developing into seeds) of control and experimental flowers was studied in the Fuente del Perro population in 1989 and 1990. All fruits produced by marked flowers were collected shortly before dehiscence and examined under a dissecting microscope, and numbers of mature seeds, and of ovules that had failed to develop, were counted.

Floral microclimate.—I tested the hypothesis that flowers of *N. longispathus* provided a favorable thermal environment by measuring air temperature inside and outside the flowers. Measurements were conducted on 31 flowers from five populations in two different years, and were taken under different conditions of ambient temperature (range = 8°–21°C), time of day (0900–1500 h Greenwich Mean Time), and solar irradiance (24–1080 W/m^2). Two fine copper-constantan thermocouples (diameter 0.22 mm; Models IT-23 or IT-1E, Physitemp Instruments, Clifton, New Jersey) were attached to each sampled flower using small pieces of tape. One was placed inside the flower (1 cm from the bottom of the perianth tube without touching the corolla), and the other was held outside the flower and 1 cm away from the perianth (unshaded 0.22-mm thermocouples were used in this study for all measurements of air temperature, as the heating effect of direct solar radiation on their tiny junctions was found to be negligible). Paired temperature measurements were recorded automatically at 1-min intervals during 1 h using a datalogger. Mean temperature excess was obtained for each sampled flower by computing the difference between mean temperatures inside and outside the perianth. I also measured mean solar irradiance on flowers during the temperature recording period using a LI-COR LI-200SZ Pyranometer Sensor (calibrated spectral range 400–1100 nM) connected to a LI-1000 datalogger (LI-COR, Lincoln, Nebraska). All irradiance measurements were taken holding the sensor surface horizontal and thus refer to incident radiation on a horizontal plane.

I examined intrafloral variation in air temperature by simultaneous recording at different positions along inside the corolla of fully insolated flowers. Four 0.22-mm diameter thermocouples were affixed onto a 1-mm diameter, straight wooden stick which provided rigid support. Thermocouple junctions were spaced at 15-mm intervals along the distal portion of the support, and held 2 mm from it. The whole assembly was introduced into the perianth of an experimental flower and left in place for 5 min to equilibrate. Air temperatures were then simultaneously recorded every 5 s for 1 min. I took measurements on four different flowers. To allow for possible effects on measurements of the angle of the perianth axis with respect to the solar beam, four different orientations (main compass directions) were used for each flower. Data from all flowers and positions were pooled for analyses.

To assess if intrafloral variation in air temperature was related to differences among flower parts in transmitted radiation, I measured irradiance through perianth pieces cut from different locations. For each of 12 different flowers, pieces were cut from the perianth base, the "petals" and the corona. Transmitted irradiance was measured by holding the piece of perianth on top of the pyranometer sensor using a transparent plastic film. Incident irradiance was then measured immediately after removal of the perianth piece. For each sampled flower, all measurements were completed within 5 min of collection. The pyranometer is calibrated for the daylight spectrum, and measurements may not be accurate for light filtered through flower parts. To account at least for possible systematic departures between measurements of incident and filtered radiation due to this effect, comparisons between flower parts will be based on slopes of regressions of transmitted vs. incident radiation, obtained for the whole range of irradiance occurring in the field.

Andrena bicolor

Laboratory studies.—I investigated the ability to warm up by endothermy and the warming and cooling rates of bees in 1992 and 1993. Specimens were netted in the field, 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 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}) was ≈8°C, 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 recorded every 10 s, and monitored continuously with a computer. The bee was first allowed to warm up spontaneously until T_{th} stabilized. During this period, I repeatedly pinched its abdomen gently with forceps to test for flight ability. After T_{th} stabilization, the bee was heated using an irradiance of 750 W/m^2 from a narrow-beam halogen lamp until T_{th} rose to ≈38°C. Then the bee was allowed to cool until T_{th} stabilized. Finally, the bee was killed, briefly cooled in a refrigerator, and the same protocol was repeated on the dead bee. I measured six different bees in this fashion. In the series with live animals, I noted the T_{th} at which bees were first able to fly and at which they

actively avoided the heat source (by making obvious efforts to move out of the lighted area). These T_{th} values correspond, respectively, to the "minimum flight temperature" and "maximum voluntary tolerance" defined by May (1976).

The ability of bees to thermoregulate physiologically can be tested by examining if their warming and cooling rates depart significantly from those theoretically predicted for an inert object equilibrating with air temperature according to Newton's law of cooling (Casey 1988):

$$dT/dt = K(T - T_a), \quad (1)$$

where T is the temperature of the object, t is time, T_a is ambient air temperature, and K is the cooling constant. I regressed $\Delta T_{th}/\Delta t$ against $(T_{th} - T_a)$ for the series of data points in the spontaneous warming and spontaneous cooling sequences. In the computations, Δt was taken at 10-s intervals (the interval between consecutive temperature readings).

Field studies.—I studied the foraging behavior of *A. bicolor* in 1993 in four *N. longispathus* populations. Individual bees were followed as long as possible while foraging in flower patches. I tape-recorded the sequence and duration of each major activity: flying between consecutive floral visits ("flying"), basking on flowers ("basking"), and visiting flowers ("within flowers"). During each observation sequence, I measured air temperature inside and immediately outside visited flowers as often as possible. Foraging sequences were obtained for 63 different bees, totaling 204 min of observation. Average flower visitation rate, mean duration of floral visits, and percent time spent basking, in flight and within flowers, were computed for each sequence. The accuracy of these estimates was expected to vary among sequences, as these differed widely in duration (range = 0.25–19.3 min; median = 1.7 min). To correct for this effect, the total observation time for each sequence was used as a weighting factor in regression and correlation analyses.

I measured thoracic temperature (T_{th}) of *A. bicolor* individuals, and air temperature at the foraging site, on five different dates during March–April 1992. Bees were captured while gathering pollen within *N. longispathus* flowers or while flying between flowers. For each bee, T_{th} was measured within 5 s of netting to the nearest 0.1°C using a fast-response (time constant 0.025 s), 0.33 m-diameter needle microprobe (Type MT-29/1; Physitemp Instruments). Readings were obtained by inserting the probe 1 mm into the bee's thorax while it was restrained in the net. For bees captured within flowers, air temperature was measured in the perianth's interior (T_{fl}) and in the open air 5 cm away from the perianth opening (T_a). For bees captured in flight, T_a was measured at the same spot where the bee had been caught. T_a and T_{fl} were always measured within 1 min of the bee's capture.

I assessed the bees' perception of the thermal environment by measuring operative temperatures (T_e). T_e is essentially equal to the steady-state temperature that an organism would reach under stable conditions in the absence of metabolic input, and it represents the sum of air temperature and a temperature increment or decrement subsuming radiative and convective factors (Bakken 1989, 1992, Walsberg 1993). A thermocouple (Model MT-29/1) was inserted into the thorax of a freshly killed bee, and the insect was placed in the interior of a flower, lying flat on the external surface of the perianth ("basking"), or suspended in the air 5 cm away from the flower. In each case, thoracic temperature (T_{th}) was recorded continuously until variation became negligible (<0.5°C in 30 s), and this value was used as an estimate of T_e. I also recorded air temperature 5 cm away from the experimental bee. Measurements were made around noon on one cool and one warm day using nine different bees.

Data analysis

Unless otherwise indicated, all analyses were performed with the SAS statistical package (SAS 1990). Analyses of variance and covariance were done with procedure GLM (Type III sum of squares), and linear models based on logistic regression with procedure CATMOD (maximum likelihood estimation).

Results

Reproductive biology of N. longispathus

Floral biology.—*N. longispathus* flowers are fully self-compatible (C. M. Herrera, *unpublished data*), but spontaneous selfing occurs infrequently; only 3.8% of flowers ($N = 26$) within pollinator exclosures set fruit. Mean duration of individual flowers exposed to natural pollination was 16.5 ± 3.5 d (range = 11–26 d; $N = 128$). Flower duration was significantly shortened by pollination. The proportion of flowers remaining open at age 16 d declined from those unpollinated within exclosures (100%, $N = 26$) through those exposed to natural pollination alone (86.7%, $N = 26$) to those receiving extra hand-pollination (32.3%, $N = 31$) ($P \ll 0.0001$; Fisher exact probability test).

Results of the two pollination experiments on flowers of different age were analyzed simultaneously using a linear model based on logistic regression (flower age treated as an ordinal variable). Variation with flower age in the probability of fruit set was similar for the experiments involving cross- (testing the effect of stigma age alone) and self- (testing both stigma and pollen age) pollinations, as revealed by the nonsignificance of the interaction term in the model ($\chi^2 = 1.07$, df = 1, $P = 0.30$). Likewise, probability of fruit set did not differ for self- and cross-pollinated flowers ($\chi^2 = 1.24$, df = 1, $P = 0.27$). Flower age had a marginally significant effect on fruit set ($\chi^2 = 3.43$, df = 1, $P = 0.064$). Fruit set declined steadily with flower age (75.0%, $N = 24$ for 1–2-d-old flowers; 67.9%, $N = 28$

TABLE 1. Proportion of *Narcissus longispathus* flowers setting fruit under natural and experimental (extra pollen added) pollination regimes. Ellipses indicate no data available.

		Fruit set			
		Natural pollination		Additional pollen	
Population	Year	%	*N*	%	*N*
Cuevas Bermejas	1990	88.8	178	100.0	27
Fuente del Perro	1988	60.0	65	84.1	145
	1989	74.5	137	83.0	53
	1990	86.9	168	91.4	105
Guadalentín	1989	87.9	33	88.5	26
Valdecuevas	1989	84.6	65	78.9	19
	1990	67.0	321	...	...
Valdetrillos	1989	65.5	87	...	...
	1990	88.9	81	92.3	13
	1991	95.5	269	...	...
Mean ± 1 SD		80.0 ± 12.2		88.3 ± 7.0	

for 7-d-old flowers; 50.0%, $N = 24$ for 14-d-old flowers), but flowers up to 14 d old retained considerable male and female fertility.

Fruit production.—Fruit set of *N. longispathus* flowers exposed to natural pollination was generally high at all populations and years (range = 60.0–95.5%; Table 1). Adding extra pollen to stigmas, however, increased fruit set relative to natural pollination alone (Table 1). The effects of pollen addition, site, and year on probability of fruit set were tested simultaneously using logistic regression-based linear models. The most parsimonious model included only site and pollination treatment as independent variables. These two variables had significant effects on the probability of individual flowers setting fruit ($\chi^2 = 11.3$, df = 1, $P = 0.0008$; $\chi^2 = 56.5$, df = 4, $P < 0.0001$; for pollination treatment and site effects, respectively). The model fit was significant, as revealed by nonsignificance of the model's residual likelihood ratio ($\chi^2 = 3.9$, df = 4, $P = 0.41$). Fruit set, despite its generally high levels, was thus consistently pollen limited in the populations studied.

At the Fuente del Perro population, marked *N. longispathus* flowers that set fruit ($N = 197$) had 56.2 ± 13.4 ovules, yet individual fruits contained only 28.7 ± 15.5 mature seeds. The proportion of ovules developing into seeds in individual flowers (%SET) ranged between 4 and 98% (mean = 50.3 ± 22.7%). The effects of year (1989 and 1990) and pollination treatment (natural vs. natural + extra) on %SET were examined using a two-way ANOVA with interaction (%SET arcsine-transformed for the analysis). Neither pollination treatment ($F_{1,193} = 0.16$, $P = 0.69$), year ($F_{1,193} = 0.74$, $P = 0.39$) nor their interaction ($F_{1,193} = 2.12$, $P = 0.15$) had significant effects on %SET.

The floral microclimate

Temperature excess within flowers.—When *N. longispathus* flowers were exposed to solar radiation (irradiance ≥ 100 W/m²), the air was always significantly warmer inside than immediately outside (paired *t* tests on data for individual flowers; $P < 0.001$ in all cases). There was a direct relationship between mean temperature excess inside flowers (MTE) and mean solar irradiance during the recording period ($F_{1,29} = 54.2$, $P \ll 0.0001$) (Fig. 1). MTE was around zero for shaded flowers (irradiance < 100 W/m²), and increased steadily with increasing irradiance. Maximum MTE values (up to 8°C) occurred at irradiance of 900–1100 W/m², typical of noon on clear days.

Intrafloral variation in air temperature.—There was significant heterogeneity in air temperature along the interior of the perianth tube ($F_{3,1036} = 7.9$, $P < 0.0001$). Temperature was highest close to the anthers, and lowest near the perianth bottom and opening (Fig. 2). The decline in temperature around the perianth opening must be related to the temperature gradient between flower interior and exterior. Variation among the three other sampling points is consistent with differences among flower parts in irradiance transmittance. Regressions of transmitted against incident irradiance computed separately for the three perianth parts (Fig. 3), had significantly heterogeneous slopes ($F_{2,30} = 10.1$, $P = 0.0005$). On average, the base of the perianth let a smaller proportion of solar irradiance (46.1%) pass into the flower than either the corona (58.2%) or the "petals" (65.7%). Corona and "petals" did not differ significantly in transmittance ($F_{1,20} = 3.05$, $P = 0.10$; test for homogeneity of regression slopes).

Thermal biology of Andrena bicolor

Laboratory data.—Average values for minimum flight temperature and maximum voluntary tolerance

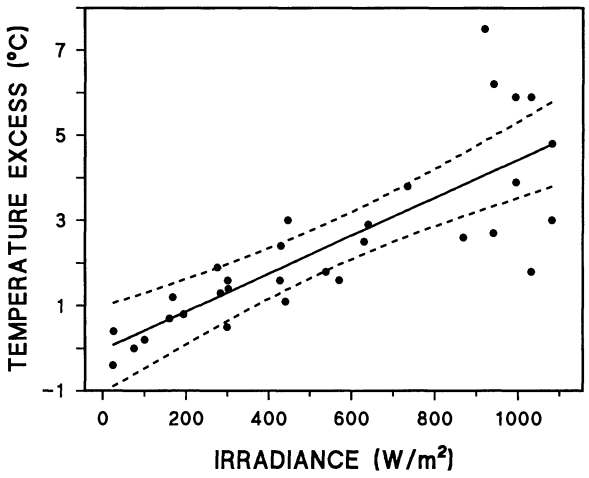

FIG. 1. Relationship between mean temperature excess inside *Narcissus longispathus* flowers (relative to the surrounding air) and solar irradiance. Individual data points represent average values for single flowers over 1-h periods. Shown are also the least squares fitted regression line (———; $R^2 = 0.651$) and the 95% confidence interval of regression-predicted values (— —).

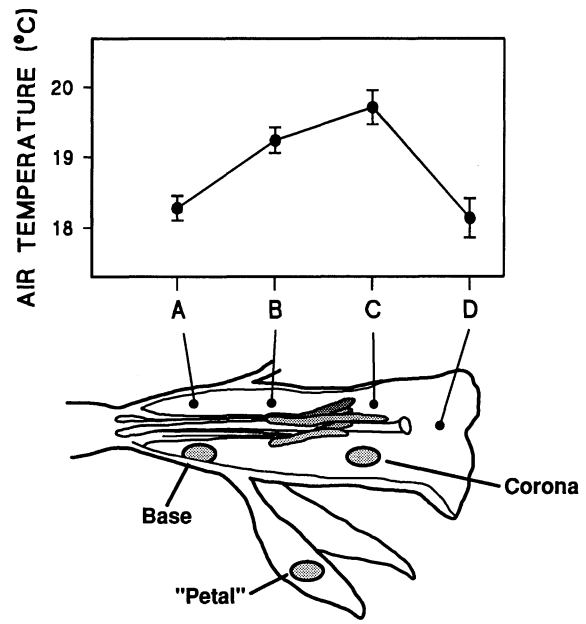

FIG. 2. Variation in air temperature inside *N. longispathus* flowers. The upper graph represents mean temperature (±2 SE) at the four measuring points (A–D) located along the longitudinal axis of the flower. The lower graph depicts schematically a longitudinal section of a *N. longispathus* flower. The perianth zones labelled Base, "Petal," and Corona denote the locations where pieces were cut for measurements of radiation transmittance.

recorded for live bees were 21.9° ± 1.9°C (N = 4) and 31.3° ± 1.0°C (N = 13), respectively.

Curves describing changes in the thoracic temperature (T_{th}) of experimental bees were similar in all trials, and a single representative example is shown in Fig. 4. No evidence of endothermic warming was found, as none of the studied bees exhibited measurable T_{th} excess over the surrouding air at the end of the spontaneous warming phase. When either warming or cooling, changes in T_{th} of live bees were indistinguishable from that of an inert object equilibrating with ambient temperature. All the linear regressions of $\Delta T_{th}/\Delta t$ against ($T_{th} - T_a$) were statistically significant ($P \ll 0.0001$). Furthermore, regression R^2 values ranged between 0.744 and 0.981 (mean = 0.898 ± 0.067, N = 12), denoting a close fit of T_{th} sequences to theoretical predictions derived from Eq. 1. Results for dead bees were similar.

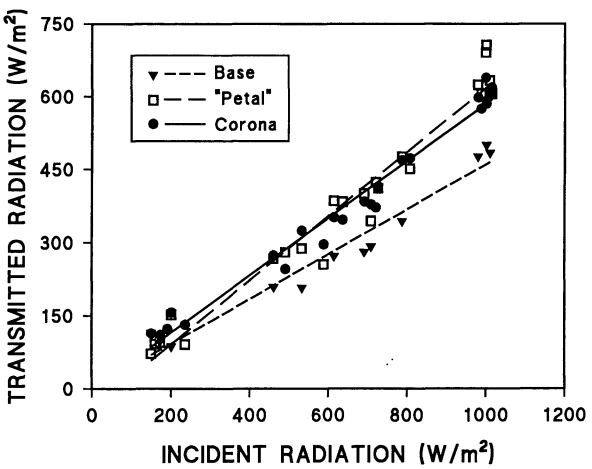

FIG. 3. Transmitted radiation through different parts of the perianth of *N. longispathus* flowers as a function of incident radiation (see Fig. 2 for locations of perianth parts). Each symbol corresponds to a single measurement. Lines are least squares fitted regressions.

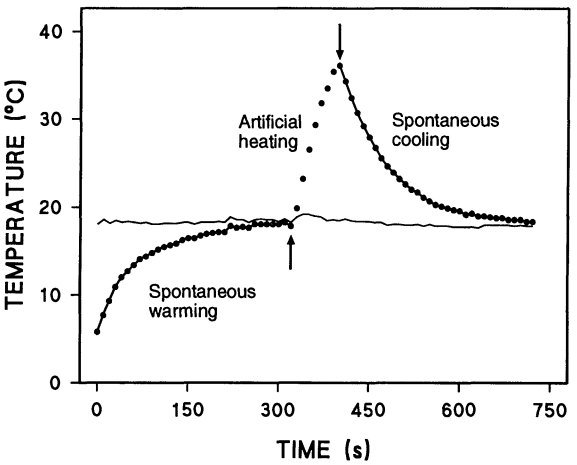

FIG. 4. Variation in thoracic temperature (dots) of *A. bicolor* during one experimental run (Bee no. 5, Dead). The experimental protocol consisted of a succession of spontaneous warming, artificial heating (starting time indicated by top-pointing arrow), and spontaneous cooling (end of artificial heating indicated by bottom-pointing arrow). The roughly horizontal, thin continuous line represents air temperature 10 cm away from the experimental bee.

The slopes of regressions of $\Delta T_{th}/\Delta t$ against ($T_{th} - T_a$) (estimates of K, the cooling constant, in Eq. 1) for experimental bees are summarized in Table 2. No significant differences in regression slopes were found

TABLE 2. Cooling constants (estimates of K in Eq. 1, expressed as degrees Celsius per 10 s per degree Celsius) obtained for experimental *Andrena bicolor* individuals. Spontaneous warming and cooling sequences were induced on live experimental bees, and the same protocol was immediately repeated on the dead individuals (see Fig. 4 for one representative thermal trajectory).

Bee no.	Warming		Cooling	
	Alive	Dead	Alive	Dead
1	−0.252	−0.241	−0.163	−0.216
2	−0.235	−0.195	−0.260	−0.168
3	−0.193	−0.183	−0.168	−0.178
4	−0.200	−0.244	−0.198	−0.196
5	−0.150	−0.156	−0.136	−0.121
6	−0.153	−0.169	−0.129	−0.185
Mean	−0.197	−0.198	−0.190	−0.179

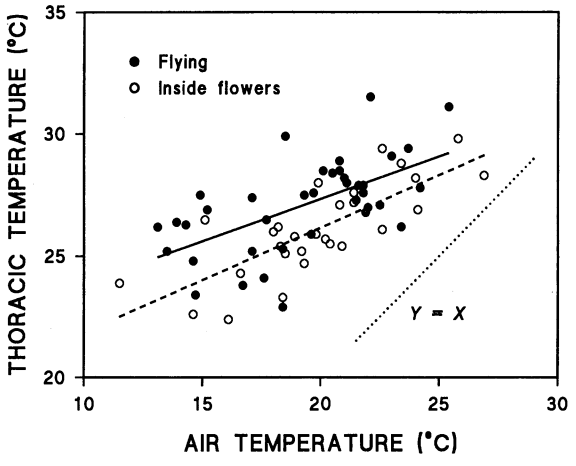

FIG. 5. Relationship between thoracic temperature of *A. bicolor* foragers and air temperature (outside flowers) at the point of capture. Separate regression lines are shown for bees captured in flight (———) and inside *N. longispathus* flowers (— —). The line $Y = X$ is also shown for reference.

between dead and live individuals under either cooling ($P = 0.95$) or warming ($P = 0.99$) conditions (two-tailed paired comparisons using a randomization method with 1000 repetitions; Manly 1991).

Field data.—Air temperatures (T_a) at the spots in *N. longispathus* flowering patches where *A. bicolor* individuals were trapped ranged between 11.5° and 26.9°C (mean = 19.6° ± 3.3°C, $N = 66$). On the same dates, no *A. bicolor* individual was observed foraging at lower T_a.

T_{th} of sampled *A. bicolor* individuals ranged between 22.4° and 31.5°C (mean = 26.7° ± 1.9°C, $N = 66$). The lower and upper extremes are virtually identical, respectively, to average minimum flight temperature (21.9°C) and maximum voluntary tolerance (31.3°C) values (see *Laboratory data* above).

T_{th} was positively related to T_a ($F_{1,64} = 41.2$, $P < 0.0001$). When separate regressions were run for bees captured in flight ($N = 38$) and within flowers ($N = 28$) (Fig. 5), the relationship between T_{th} and T_a remained significant in both cases ($F_{1,36} = 20.0$ and $F_{1,26} = 38.4$, respectively; $P < 0.001$), and regression slopes did not differ significantly ($F_{1,62} = 0.59$, $P = 0.45$). The two regression slopes were significantly <1 (0.347 ± 0.078 [SE] and 0.430 ± 0.069 [SE] for bees in flight and within flowers, respectively). Mean T_{th} of bees in flight and within flowers, after adjusting for T_a, differed significantly ($F_{1,63} = 11.5$, $P = 0.001$; analysis of covariance), but the difference was small (27.2° ± 0.23°C and 26.0° ± 0.27°C for bees in flight and within flowers, respectively; least squares estimates of marginal means [±1 SE] obtained using the LSMEANS statement in procedure GLM).

While they were within flowers, T_{th} of bees depended most closely on air temperature inside the flower (T_{fl}). When T_{th} of bees netted within flowers was regressed simultaneously on T_{fl} and T_a, the partial regression coefficient for T_a was not significant ($t = 0.17$, df = 1, $P = 0.86$), and T_{fl} alone explained as much as 71.9% of variation in T_{th} (R^2 of regression).

Operative temperatures.—On both the cool and warm sampling days, the operative temperature (T_e) of bees increased from those suspended in the air through those inside flowers to those basking on flowers (Table 3), and differences were statistically significant ($F_{2,82} = 16.3$ and $F_{2,73} = 32.3$; $P \ll 0.0001$ for the two comparisons). In addition to revealing the heterogeneity of the thermal environment faced by *A. bicolor* while foraging at *N. longispathus,* measurements of T_e also indicate that, at the irradiance levels occurring around noon (900–1100 W/m²), bees were able to reach thoracic temperature excesses ($T_{exc} = T_{th} - T_a$) of 6°–10°C by purely passive means (Table 3). On the warmer sampling day, the passively generated T_{exc} was sufficient for T_{th} to exceed the minimum required for flight (see *Laboratory data* above).

Foraging behavior of A. bicolor

Mean T_a and T_{fl} during foraging sequences ranged between 13.7°–23.6°C and 14.8°–29.7°C, respectively. On the same dates, >5 h were spent watching for *A. bicolor* bees at *N. longispathus* flowering patches at $T_a < 13$°C, but none was observed. While in flowering patches, bees spent 66.2% of the time within flowers, 17.0% basking, and 16.8% in flights between flowers (all foraging sequences pooled). Time budgets were distinctly temperature dependent; percent time within flowers increased, and percent time basking decreased significantly with increasing T_a (Fig. 6; $F_{1,60} = 40.7$, $P < 0.0001$, and $F_{1,60} = 59.7$, $P \ll 0.001$, respectively). Percent time in flight was unrelated to T_a ($F_{1,60} = 1.9$, $P = 0.17$), hence the major effect on time allocation

TABLE 3. Mean operative temperature (T_e, °C) for *Andrena bicolor* individuals at different sites in a flowering patch of *Narcissus longispathus.* Measurements were conducted around noon at the same *N. longispathus* population on two clear days differing in ambient temperature.

Date (1992)	Air temperature			Operative temperature								
				Suspended in air			Inside flower			Basking on flower		
	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD
17 April	166	11.4	2.0	22	17.1	2.3	38	18.4	3.3	25	21.5	2.1
18 April	121	18.6	1.7	17	23.1	2.0	32	25.5	2.9	27	29.5	2.9

of variation in air temperature was a steady shift between basking-dominated and within-flower-dominated foraging sequences (Fig. 6). Around the lower extreme of T_a bees basked for up to 88% of foraging time. Near the upper extreme, they spent >90% of foraging time gathering pollen within flowers and did not bask at all.

The relationship between floral microclimate (T_{fl}) and flower visitation rate (FVR; flowers visited per min) was tested by computing the correlation between these two variables partialled on T_a and mean duration of floral visits (DFV; seconds per flower). FVR was positively correlated with T_{fl} when differences in DFV and T_a were statistically accounted for (partial r = 0.420, P = 0.013). This indicates that, for a given air temperature and duration of visit, bees visiting flowers with a warmer interior visited more per unit time. This increase in efficiency with increasing T_{fl} was a proximate consequence of a reduction in the frequency of postvisitation basking. The probability of bees basking just before leaving a flower was negatively related to the temperature in its interior (χ^2 = 10.18, df = 1, P = 0.0014; logistic regression).

Discussion

Thermal biology of A. bicolor

In contrast to many other bee species (e.g., Heinrich 1979*b*, 1993, Stone 1993), *A. bicolor* apparently lacks the ability to regulate thoracic temperature by physiological means, as revealed by the failure to generate T_{th} excess spontaneously and the statistical analyses of thermal trajectories obtained in the laboratory. The failure to detect physiological regulation of thoracic temperature in captive bees is not attributable to methods. When the same protocol was applied to species with well-known ability to thermoregulate physiologically (e.g., bumble bees, anthophorid bees, hawk moths; Heinrich 1993), I always obtained unequivocal evidence of regulation (including spontaneous T_{th} excesses and thermal trajectories significantly departing from those predicted by Eq. 1; C. M. Herrera, *unpublished data*). Free-flying *A. bicolor* individuals did regulate thoracic temperature while foraging at *N. longispathus* flowering patches, as revealed by the regression of thoracic vs. air temperature, whose slope was significantly <1. As in other ectothermic insects (May 1979, Casey 1988), regulation was achieved by behavioral means, and the proportion of time spent basking by bees was inversely related to air temperature inside and outside flowers.

Data from both free-flying and experimental *A. bicolor* individuals indicate that the minimum thoracic temperature (T_{th}) for flight was around 22°C, and that bees became heat stressed at T_{th} around 31°C. Average T_{th} for free-flying bees was 27°C. These figures are ≈10°C lower than those reported in previous studies on endothermic bees from a broad range of habitat types and taxonomic affiliations (Inouye 1975, Heinrich 1979*a*, *b*, Chappell 1982, May and Casey 1983, Baird 1986, Heinrich and Buchmann 1986, Stone and Willmer 1989*a*, Heinrich 1993, Heinrich and Vogt 1993, Stone 1993). It has been suggested that the "grab and stab" technique for measuring body temperature in insects can lead to biased estimates (Stone and Willmer 1989*a*). The nearly perfect coincidence in this study between extreme values of field-measured T_{th}'s and minimum flight temperature and maximum voluntary tolerance temperature of bees under laboratory conditions suggest, however, that any such biases were minor.

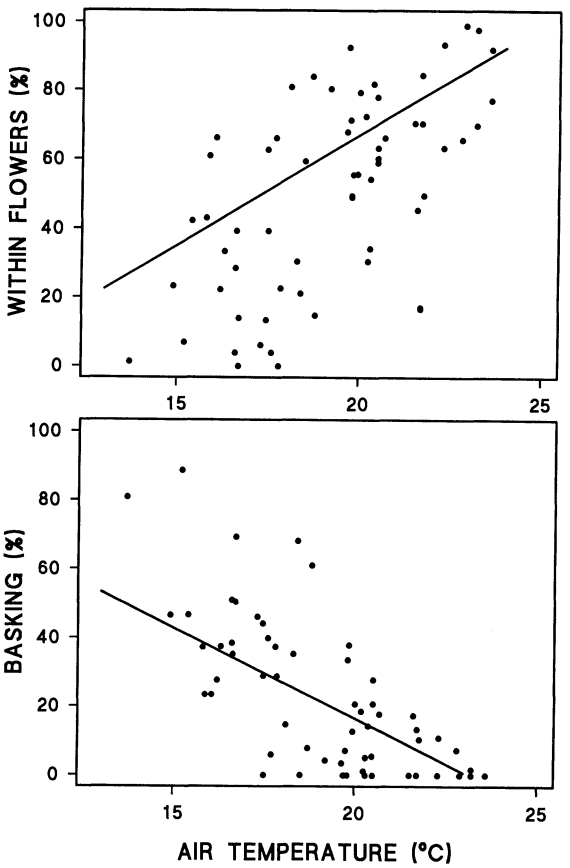

FIG. 6. Variation of the proportion of foraging time spent within flowers (upper panel) and basking (lower panel) by *A. bicolor* individuals foraging on *N. longispathus* flowers. Symbols correspond to foraging sequences by different bees. Air temperature (outside flowers) values are mean values computed over the duration of the sequence. Lines are least squares fitted regressions obtained using the total duration of the foraging sequence as a weighting factor.

The low thoracic temperature requirements of *A. bicolor* were essential for successfully foraging at *N. longispathus*. Measurements of operative temperatures (T_e) indicate that, under the range of irradiance and air temperature found at foraging sites on clear days, *A. bicolor* individuals inside flowers and, particularly, basking on them, were able to reach thoracic temperatures suitable for flight by passive means alone. This

would have been impossible had bees' thoracic temperature requirements been only a few degrees higher. On a cool day, when mean air temperature was below the activity threshold for *A. bicolor,* mean T_e was below the minimum thoracic temperature required for flight at all sites sampled. On a moderately warm day, in contrast, mean thoracic temperature of bees netted while foraging (26.7°C) was intermediate between mean T_e inside (25.5°C) and on flowers (29.5°C). The similarity between T_e and thoracic temperatures of free-flying bees further supports the ectothermy of *A. bicolor* under field conditions.

Microclimate and pollinator foraging

In sunny weather, the interior of *N. longispathus* flowers represents an improved thermal environment for pollinators. Under the irradiance levels occurring around noon, mean temperature excess (MTE) inside flowers reached values of up to 8°C. In fact, MTE figures in this study are average values for individual flowers computed over 1-h periods, and instantaneous excesses of 11°C were not infrequent. Temperature excess is expected to be especially important for small pollinators that enter deep within the corolla, rather than introducing only their mouthparts (Corbet and Willmer 1981). This was the case with *A. bicolor,* which is considerably smaller than *N. longispathus* flowers, and thus can take advantage even of the small-scale peak in temperature that occurs around the anthers, where the bees spent most of their time within flowers.

Elevation of temperature has been reported previously within parabolic and tubular flowers. In the former case, heating is produced by reflection of incident solar radiation by the petals and may be significant for both pollinator visitation and pollen, ovule and seed development (Hocking 1968, Kevan 1975, Smith 1975, Knutson 1981, Stanton and Galen 1989, Corbett et al. 1992). Temperature elevation inside flowers with tubular corollas has been reported less frequently (Corbet and Willmer 1981, Corbet 1990), and has been explained as a "microgreenhouse" effect caused by radiation transmitted through the corolla (Corbet 1990). The results of the present study are consistent with this interpretation. MTE of *N. longispathus* flowers was positively related to solar irradiance, and the temperature gradient within flowers was consistent with variation among flower parts in radiation transmittance.

A direct demonstration that floral microclimate influenced pollinator visitation and fruit set was beyond the scope of this study. However, an indirect demonstration comes from the influence of thermal environment on foraging of the main pollinator. *Andrena bicolor* foraged in *N. longispathus* flowering patches only on sunny days with air temperature >12°–13°C. These figures are identical to the temperature thresholds for activity reported for other solitary bees (including species of *Andrena*; Michener and Rettenmeyer 1956, Schemske 1978, Schemske et al. 1978, Motten 1986). Even when the minimal temperature threshold for activity was met, however, the foraging behavior of *A. bicolor* was also sensitive to variations in air temperature. On cooler days (air temperature 12°–16°C), bees spent most foraging time basking, and their flights between flowers were sometimes interrupted by sudden falls to the ground. Fallen bees crawled into some nearby flower and basked before resuming normal foraging. The proportion of foraging time spent basking (vs. visiting flowers) steadily decreased with increasing air temperature, and the probability of basking immediately after one floral visit declined significantly with increasing flower temperature. The temperature excess within *N. longispathus* flowers was thus significant for both the bees (that were able to visit more flowers per foraging time unit) and the local plant population (that received more pollinator visits per time unit).

Pollination and seed production

Long-term, detailed meteorological records are not available for the study area. Nevertheless, it may be estimated that, in most years, weather conditions during nearly half of the *N. longispathus* flowering season were unsuitable for the activity of its main pollinator. At one locality of the study area, only 40% of days in the period 20 February–20 April 1993 had at least one 1-h period with air temperature >12°C (C. M. Herrera, *personal observation*). One unexpected finding of this study was that, despite weather limitations on pollinator activity, most *N. longispathus* flowers were successfully pollinated in all years and sites. Mean fruit set of flowers exposed to natural pollination (80.0%) even exceeded the average value reported by Sutherland and Delph (1984) for a large sample of hermaphroditic self-compatible species (72.5%). High levels of fruit set have been reported for other early-blooming herbs that also flowered when weather limitations of pollinator activity occurred (Motten 1986, Campbell 1987).

Fruit or seed production are pollen limited in some, but not all early-blooming species studied so far (Schemske 1977, Schemske et al. 1978, Motten et al. 1981, Motten 1986). In *N. longispathus,* fruit production was only weakly pollen limited and, among flowers setting fruit, the proportion of ovules developing into seeds was not pollen limited. This suggests that failures to set fruit were mainly due to absence of pollinator visits, rather than to insufficient number of pollen grains delivered when a visit occurred. Since flower duration was significantly shortened by pollination, the extended average longevity of flowers exposed to natural pollination further suggests a prevailing scarcity of pollinator visits.

For species that produce few flowers and face unreliable pollinator services, long duration of flowers will increase the probability of being visited at least once (Primack 1985). Long floral durations and posi-

tive correlations (across species) between floral longevity and fruit set have been reported for some early-flowering plants (Schemske et al. 1978, Motten 1986). *N. longispathus* fits this pattern well. Compared with reported flower longevities (e.g., Primack 1985, Motten 1986, Stratton 1989), *N. longispathus* flowers are extraordinarily long lived, and this trait most likely contributed decisively to observed reproductive success. Although the viability of flowers declined slightly with age, it was remarkable that they still retained considerable fertility 14 d after opening.

Implications of this study

Pollination by andrenid bees, extended flower longevity, and high fruit set exhibited by *N. longispathus* seem to be typical features of many other early-blooming herbs from boreal and temperate habitats (e.g., Schemske 1978, Schemske et al. 1978, Motten et al. 1981, Ginsberg 1983, Motten 1986, Armbruster and Guinn 1989). This suggests that some of the results of this study might apply to other early-blooming species. Previous investigations on early-flowering herbs, however, have mainly focused on plant features (e.g., phenology, floral biology, pollen limitation), rather than on the pollinators, including their thermal biology. It is not possible at present to assess whether the distinctive elements of the thermal biology of *A. bicolor* are typical for the genus *Andrena,* since previous studies on the thermal biology of bees have focused almost entirely on endothermic species of Apidae and Anthophoridae. Stone and Willmer (1989*b*) have shown, however, that thermal biology in bees has a strong phylogenetic component at the familial and generic levels, hence some aspects of the thermal biology of *A. bicolor* most likely apply to other congeneric species as well. *Andrena* is the most species-rich genus of bees (Stephen et al. 1969), and members of this genus are seasonally dominant components of the bee fauna in many parts of the world (Sakagami and Matsumura 1967, Motten et al. 1981, Ginsberg 1983, Motten 1983). An improved knowledge of the thermal biology of *Andrena* is therefore expected to shed light on the role of abiotic factors in the pollination systems of other early-blooming plant species.

Acknowledgments

For generous help with field and laboratory work, useful ideas for experimental designs, and continuous encouragement, I am most grateful to my wife, Dori, and son, Carlos. Enrique Asensio identified the bees, and Manolo Carrión and Rocío Requerey provided technical assistance. The comments and suggestions of Sarah Corbet, Javier Herrera, Pedro Jordano, Nick Waser, Regino Zamora, and two anonymous referees improved the manuscript. The Agencia de Medio Ambiente, Junta de Andalucía, authorized my work in the Sierra de Cazorla and provided helpful facilities. This study was supported by DGICYT grants PB87-0452 and PB91-0114.

Literature Cited

Armbruster, W. S., and D. A. Guinn. 1989. The solitary bee fauna (Hymenoptera: Apoidea) of interior and arctic Alaska: flower associations, habitat use, and phenology. Journal of the Kansas Entomological Society **62**:468–483.

Bailey, W. G., H. Lerer, and P. F. Mills. 1982. Humidity and the pollination activity of *Megachile rotundata.* Environmental Entomology **11**:1063–1066.

Baird, J. M. 1986. A field study of thermoregulation in the carpenter bee *Xylocopa virginica virginica* (Hymenoptera: Anthophoridae). Physiological Zoology **59**:157–168.

Bakken, G. S. 1989. Arboreal perch properties and the operative temperature experienced by small animals. Ecology **70**:922–930.

———. 1992. Measurement and application of operative and standard operative temperatures in ecology. American Zoologist **32**:194–216.

Caldwell, J., and T. J. Wallace. 1955. Biological flora of the British Isles. *Narcissus pseudonarcissus* L. Journal of Ecology **43**:331–341.

Campbell, D. R. 1987. Interpopulational variation in fruit production: the role of pollination-limitation in the Olympic Mountains. American Journal of Botany **74**:269–273.

Casey, T. M. 1988. Thermoregulation and heat exchange. Advances in Insect Physiology **20**:119–146.

Chappell, M. A. 1982. Temperature regulation of carpenter bees (*Xylocopa californica*) foraging in the Colorado Desert of southern California. Physiological Zoology **55**:267–280.

Corbet, S. A. 1978. Bee visits and the nectar of *Echium vulgare* L. and *Sinapis alba* L. Ecological Entomology **3**: 25–37.

———. 1990. Pollination and the weather. Israel Journal of Botany **39**:13–30.

Corbet, S. A., and E. S. Delfosse. 1984. Honeybees and the nectar of *Echium plantagineum* L. in southeastern Australia. Australian Journal of Ecology **9**:125–139.

Corbet, S. A., and P. G. Willmer. 1981. The nectar of *Justicia* and *Columnea*: composition and concentration in a humid tropical climate. Oecologia (Berlin) **51**:412–418.

Corbet, S. A., P. G. Willmer, J. W. L. Beament, D. M. Unwin, and O. E. Prys-Jones. 1979. Post-secretory determinants of sugar concentration in nectar. Plant Cell and Environment **2**:293–308.

Corbett, A. L., P. G. Krannitz, and L. W. Aarssen. 1992. The influence of petals on reproductive success in the arctic poppy (*Papaver radicatum*). Canadian Journal of Botany **70**:200–204.

Cruden, R. W. 1972. Pollinators in high-elevation ecosystems: relative effectiveness of birds and bees. Science **176**: 1439–1440.

Cruden, R. W., S. Kinsman, R. E. Stockhouse, and Y. B. Linhart. 1976. Pollination, fecundity, and the distribution of moth-flowered plants. Biotropica **8**:204–210.

Eisikowitch, D., and J. Galil. 1971. Effect of wind on the pollination of *Pancratium maritimum* L. (Amaryllidaceae) by hawkmoths (Lepidoptera: Sphingidae). Journal of Animal Ecology **40**:673–678.

Ginsberg, H. S. 1983. Foraging ecology of bees in an old field. Ecology **64**:165–175.

Gómez Campo, C., editor. 1987. Libro rojo de especies vegetales amenazadas de España Peninsular e Islas Baleares. Instituto para la Conservación de la Naturaleza, Madrid, Spain.

Heinrich, B. 1979*a*. Thermoregulation of African and European honeybees during foraging, attack, and hive exits and returns. Journal of Experimental Biology **80**:217–229.

———. 1979*b*. Bumblebee economics. Harvard University Press, Cambridge, Massachusetts, USA.

———. 1993. Hot-blooded insects. Strategies and mechanisms of thermoregulation. Springer-Verlag, Berlin, Germany.

Heinrich, B., and S. L. Buchmann. 1986. Thermoregulatory

physiology of the carpenter bee, *Xylocopa varipuncta*. Journal of Comparative Physiology **B 156**:557–562.

Heinrich, B., and F. D. Vogt. 1993. Abdominal temperature regulation by arctic bumblebees. Physiological Zoology **66**: 257–269.

Herrera, C. M. 1990. Daily patterns of pollinator activity, differential pollinating effectiveness, and floral resource availability, in a summer-flowering Mediterranean shrub. Oikos **58**:277–288.

Hocking, B. 1968. Insect-flower associations in the high Arctic with special reference to nectar. Oikos **19**:359–388.

Inouye, D. W. 1975. Flight temperatures of male euglossine bees (Hymenoptera: Apidae: Euglossini). Journal of the Kansas Entomological Society **48**:366–370.

Kevan, P. G. 1975. Sun-tracking solar furnaces in high arctic flowers: significance for pollination and insects. Science **189**:723–726.

Knutson, R. M. 1981. Flowers that make heat while the sun shines. Natural History **90**:75–80.

Lundberg, H. 1980. Effects of weather on foraging-flights of bumblebees (Hymenoptera, Apidae) in a subalpine/alpine area. Holarctic Ecology **3**:104–110.

Manly, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, London, England.

Martínez del Río, C., and A. Búrquez. 1986. Nectar production and temperature dependent pollination in *Mirabilis jalapa* L. Biotropica **18**:28–31.

May, M. L. 1976. Thermoregulation and adaptation to temperature in dragonflies (Odonata: Anisoptera). Ecological Monographs **46**:1–32.

———. 1979. Insect thermoregulation. Annual Review of Entomology **24**:313–349.

May, M. L., and T. M. Casey. 1983. Thermoregulation and heat exchange in euglossine bees. Physiological Zoology **56**:541–551.

Michener, C. D., and C. W. Rettenmeyer. 1956. The ethology of *Andrena erythronii* with comparative data on other species (Hymenoptera, Andrenidae). University of Kansas Science Bulletin **37**:645–684.

Moreno Saiz, J. C., and H. Sainz Ollero. 1992. Atlas corológico de las monocotiledóneas endémicas de la Península Ibérica y Baleares. Instituto para la Conservación de la Naturaleza, Madrid, Spain.

Motten, A. F. 1983. Reproduction of *Erythronium umbilicatum* (Liliaceae): pollination success and pollinator effectiveness. Oecologia (Berlin) **59**:351–359.

———. 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. Ecological Monographs **56**:21–42.

Motten, A. F., D. R. Campbell, D. E. Alexander, and H. L. Miller. 1981. Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. Ecology **62**:1278–1287.

Primack, R. B. 1985. Longevity of individual flowers. Annual Review of Ecology and Systematics **16**:15–37.

Sakagami, S. F., and T. Matsumura. 1967. Relative abundance, phenology and flower preference of andrenid bees in Sapporo, North Japan (Hymenoptera, Apoidea). Japanese Journal of Ecology **17**:237–250.

SAS. 1990. SAS/STAT user's guide. Version 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.

Schemske, D. W. 1977. Flowering phenology and seed set in *Claytonia virginica* (Portulacaceae). Bulletin of the Torrey Botanical Club **104**:254–263.

———. 1978. Sexual reproduction in an Illinois population of *Sanguinaria canadensis* L. American Midland Naturalist **100**:261–268.

Schemske, D. W., M. F. Willson, M. N. Melampy, L. J. Miller, L. Verner, K. M. Schemske, and L. B. Best. 1978. Flowering ecology of some spring woodland herbs. Ecology **59**: 351–366.

Smith, A. P. 1975. Insect pollination and heliotropism in *Oritrophium limnophilum* (Compositae) of the Andean Páramo. Biotropica **7**:284–286.

Stanton, M. L., and C. Galen. 1989. Consequences of flower heliotropism for reproduction in an alpine buttercup (*Ranunculus adoneus*). Oecologia (Berlin) **78**:477–485.

Stephen, W. P., G. E. Bohart, and P. F. Torchio. 1969. The biology and external morphology of bees. Agricultural Experiment Station, Oregon State University, Corvallis, Oregon, USA.

Stone, G. N. 1993. Endothermy in the solitary bee, *Anthophora plumipes*: independent measures of thermoregulatory ability, costs of warm-up and the role of body size. Journal of Experimental Biology **174**:299–320.

Stone, G. N., J. N. Amos, T. F. Stone, R. L. Knight, H. Gay, and F. Parrott. 1988. Thermal effects on activity patterns and behavioural switching in a concourse of foragers on *Stachytarpheta mutabilis* (Verbenaceae) in Papua New Guinea. Oecologia (Berlin) **77**:56–63.

Stone, G. N., and P. G. Willmer. 1989*a*. Endothermy and temperature regulation in bees: a critique of 'grab and stab' measurement of body temperature. Journal of Experimental Biology **143**:211–223.

Stone, G. N., and P. G. Willmer. 1989*b*. Warm-up rates and body temperatures in bees: the importance of body size, thermal regime and phylogeny. Journal of Experimental Biology **147**:303–328.

Stratton, D. A. 1989. Longevity of individual flowers in a Costa Rican cloud forest: ecological correlates and phylogenetic constraints. Biotropica **21**:308–318.

Sutherland, S., and L. F. Delph. 1984. On the importance of male fitness in plants: patterns of fruit-set. Ecology **65**: 1093–1104.

Valle, F., F. Gómez-Mercado, J. F. Mota Poveda, and C. Díaz de la Guardia. 1989. Parque Natural de Cazorla, Segura y Las Villas. Guía botánico-ecológica. Editorial Rueda, Madrid, Spain.

Walsberg, G. E. 1993. Thermal consequences of diurnal microhabitat selection in a small bird. Ornis Scandinavica **24**: 174–182.

Willmer, P. G. 1983. Thermal constraints on activity patterns in nectar-feeding insects. Ecological Entomology **8**:455–469.

———. 1986. Foraging patterns and water balance: problems of optimization for a xerophilic bee, *Chalicodoma sicula*. Journal of Animal Ecology **55**:941–962.