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Morning floral heat as a reward to the pollinators of the *Oncocyclus* irises

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Abstract Relationships between flowering plants and their pollinators are usually affected by the amount of reward, mainly pollen or nectar, offered to pollinators by flowers, with these amounts usually positively correlated with floral display. The large *Oncocyclus* iris flowers, despite being the largest flowers in the East Mediterranean flora, are nectarless and have hidden pollen. No pollinators visit the flowers during daytime, and these flowers are pollinated only by night-sheltering solitary male bees. These iris flowers are partially or fully dark-colored, suggesting that they gather heat by absorbing solar radiation. Here we test the hypothesis that the dark-colored flowers of the *Oncocyclus* irises offer heat reward to their male solitary bee pollinators. Floral temperature was higher by 2.5°C than ambient air after sunrise. Solitary male bees emerged earlier after sheltering in *Oncocyclus* flowers than from other experimental shelter types. Pollination tunnels facing east towards the rising sun hosted more male bees than other aspects. We suggest that floral heat reward can explain the evolution of dark floral colors in *Oncocyclus* irises, mediated by the pollinators' behavior.

Keywords Bee behavior · Iridaceae · Nectar-less flowers · Night shelter · Solitary male bees · Thermal reward

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Introduction

Natural selection on floral traits is mediated by pollinator preference and visitation rate, which respond to the amount and availability of floral reward (Friedman and Shmida 1995). Floral reward can be of various types, the most common of which are pollen, nectar, oils, resins, or brood places (Simpson and Neff 1983). Heat has also been suggested as a reward for pollinators in the tropical (Seymour et al. 2003) and arctic regions (Kevan 1975), as well as in Mediterranean early-spring blooming herbs (Dafni et al. 1981; Herrera 1995). Whatever the reward offered, pollinators should be able to recognize it by visual or odor cues. Indeed, display size is usually positively correlated with the amount of nectar reward and pollinators quickly learn the association between size and reward (Blarer et al. 2002; Cohen and Shmida 1993).

Flowers classified as employing the bee-pollination syndrome (Kevan and Baker 1983; Proctor et al. 1996) are pollinated during the daytime. During night, however, bees are usually inactive and exhibit a sleep-like behavior (Kaiser 1995). Solitary male bees spend the night grasping stems with their mandibles and/or legs, often in aggregations (Alcock 1999; Kaiser 1995; Thoenes 1994), or shelter within flowers (Dafni et al. 1981; Danforth and Neff 1992; Gaglianone 2000; Horovitz 1976; Linsley 1962; Linsley and Cazier 1972). There may be two reasons for solitary male bees to night-shelter within flowers; hiding from nocturnal predators, with aggregations decreasing predation probability by a 'dilution effect' (Alcock 1999), or, as proposed here, early morning heat reward.

Bees depend on a threshold thoracic temperature to initiate flight at low-air temperatures (Heinrich and Raven 1972; Stone 1990). Insects may warm up passively by basking in the sun but large bees can also warm up actively through shivering thermogenesis, contracting the flight muscles to produce metabolic heat (Heinrich 1979). Insects may also profit from flowers whose temperature is

higher than that of the ambient air (Herrera 1995; Lack 1976; Patino et al. 2002; Totland 1996). Above-ambient floral temperature may result from heliotropic movement of concave flowers (Galen and Stanton 2003; Kevan 1975; Orueta 2002; Patino et al. 2002; Totland 1996) or floral metabolic thermogenesis (Dieringer et al. 1999; Jewell et al. 1994; Patino et al. 2000; Seymour et al. 2003). We suggest that dark flower pigmentation may also increase the temperature within the flower by absorbing solar radiation in the morning. Solitary male bees that shelter overnight in dark-colored flowers can thus start their activity earlier than bees that shelter elsewhere (Linsley and Cazier 1972).

Iris species of the section *Oncocyclus* (Siems.) Baker (Iridaceae) are among the largest flowers in the middle-eastern flora, with a diameter of up to 11 cm (Sapir et al. 2002). Despite the large advertisement, all species in the section are nectarless (Avishai 1977) and have their pollen well hidden within the flower. Consequently no nectar or pollen collecting pollinators can be seen visiting the flowers during daytime and these flowers are pollinated by solitary male bees, mainly of the genus *Eucera*, which shelter overnight in the pollination tunnels (Ivri and Eisikowitch 1988; Sapir et al. 2005). Since no nectar reward exists in the flowers and male bees collect no pollen, it is unclear what reward attracts these bees to the flowers.

Here we test the hypothesis that the dark color of the *Oncocyclus* iris flowers acts as sun collectors increasing early morning floral temperatures above ambient air temperature, which is the reward to night-sheltering solitary male bees. We also hypothesize that solitary male bees sheltering at night inside the *Oncocyclus* iris flowers have an advantage of utilizing the heat provided by the flower for early morning activity relative to male bees that shelter elsewhere.

Methods

Study sites and species

This study was conducted in Israel during the flowering season (February–March) 2003. The main study was carried out in populations of *I. atrofusca* Baker in the Goral Hills (Northern Negev, 31.2°N 34.5°E), *I. atropurpurea* Baker at Nes Ziona (Coastal plains, 31.5°N 34.5°E), and in *I. hermona* Dinsmore at Keshet (Golan Heights, 32.6°N 35.5°E). The flowers of *I. atrofusca* and *I. atropurpurea* are uniformly dark-purple to brown, while the flowers of *I. hermona* are bicolor, with heavy dark-spotted outer horizontal petals (falls), and bluish-white inner vertical ones (standards) (Avishai and Zohary 1980; Sapir and Shmida 2002). According to the current taxonomy (Fragman et al. 1999) these populations are considered as separate species, but recent studies suggest that the whole group may be treated as one taxon (Arafeh et al. 2002; Avishai and Zohary 1980; Sapir and Shmida 2002).

Temperature measurements and behavior of the bees

We used thermocouples with accuracy of $\pm 0.5^\circ\text{C}$ and data loggers (TC4000—ERTCO, W. Paterson, NJ, USA, and TES 1303, E&E Process Instrumentations, Concord, ON, Canada). Thermocouples were inserted into the base of the pollination tunnel to the place where male bees spend the night. To measure ambient air temperature thermocouples were mounted in the shade of the flower, at a similar level (ca. 20 cm) above ground, since the other night shelters of solitary male bees also shade them from the morning sun. Temperatures were measured from ca. 10 min before exposure to direct morning sunlight to 90 min after it, and from ca. 60 min before sunset to 30 min after it. Two randomly chosen flowers were used for each measurement session. Temperatures were also measured in intact flowers and flowers from which the standards were removed in dark colored *I. atropurpurea* on two mornings and light colored *I. hermona* on three mornings, one flower of each every morning. We measured temperatures in 22 individuals of five *Oncocyclus* iris species grown in the Botanical Garden at the Hebrew University, Mt. Scopus, Jerusalem. There, floral temperatures were measured within two flowers that differed in their standard colors between the 4th and 17th of April 2003. Every 24 h, sensors were moved to a different flower of each color type.

Bees were collected from *Oncocyclus* flowers 1/2 h before sunrise and placed in four shelter types at Goral and Keshet sites, and three shelter types at Har Gilo, where no *Oncocyclus* irises grow: (1) within iris flower (only at Goral and Keshet); (2) within a black plastic flower model; (3) within white plastic flower model; (4) on the ground surface in the grass. Flower models were made from foam plastic cones 4 cm in diameter placed on wooden sticks 25 cm high, similar to the *Iris* flowers' height. Observations started at sunrise and lasted until 1 h after the first male had emerged. In each experiment, the emergence time of the first male was set as time zero, the emergence times of all other males were recorded as the number of minutes elapsed since time zero.

In order to check the effect of the pollination tunnel aspect on the number of night-sheltering male bees, bees were recorded in *I. hermona* tunnels for three nights (10, 11, and 13 April 2003) in all three radiating tunnels of each flower. The number of sheltering male bees was counted and the aspect of each tunnel was recorded. All statistical analyses were performed with SPSS version 10.0.5, SPSS Inc., 1999.

Results

Floral relative temperature

Temperatures recorded within flowers did not differ from ambient air temperatures during the night but after sunrise floral temperature increased faster than the

ambient temperature. At noon, floral temperature stabilized, probably as the result of the wind, while the ambient temperature continued to increase. In the evening, floral and ambient temperatures decreased in concert to a minimum temperature at night.

Floral temperature was higher than ambient air temperature for the 100 min after sunrise (Fig. 1a). Since the temperature difference did not increase linearly over this entire period we separately regressed temperature difference between flowers and ambient air for the first hour after sunrise, roughly corresponding to the emergence time of male bees from flowers, and for the subsequent 40 min. The temperature difference increased significantly during the first hour after sunrise ($Y=0.03X+0.84$, $r^2=0.955$; $F_{1,6}=127.74$; $P<0.001$) but subsequently stabilized ($Y=3.35-0.01X$, $r^2=0.78$; $F_{1,2}=7.09$; $P=0.12$; Fig. 1a).

Floral temperature was higher than that of the ambient air before sunset. This difference did not change significantly from 100 to 60 min before sunset ($Y=0.003X+1.7$, $r^2=0.285$; $F_{1,3}=1.198$; $P=0.35$) but decreased significantly ($Y=0.63-0.012X$, $r^2=0.852$; $F_{1,3}=17.28$; $P=0.025$) in the last 50 min before sunset (Fig. 1b).

Floral temperature increased more rapidly after sunrise than that of ambient air (effect of time on the difference in temperature: $F_{1,6}=41.574$; $P<0.001$), both for flowers with their standards removed and intact flowers (effect of standard removal treatment: $F_{1,1}=1.505$; $P=0.231$). Dark colored *I. atropurpurea* flowers showed a smaller temperature difference over ambient air than the light colored *I. hermona* (species effect: $F_{1,1}=62.057$; $P<0.001$) but the temperature difference increased more rapidly with time after sunrise for *I. atropurpurea* (interaction effect between species and time: $F_{1,1}=37.509$; $P<0.001$; Fig. 2). The rate of increase in the temperature difference neither differed between the treatments (interaction effect between treatment and time: $F_{1,1}=0.575$; $P=0.455$) nor there was a significant interaction between treatment and species ($F_{1,1}=4.100$; $P<0.054$).

Floral temperatures were measured every 20 min for the 150 min after sunrise in differently colored flowers in the botanical garden in Jerusalem. The floral temperatures in dark- and light-colored flowers (both with dark-colored pollination tunnels) were similar for most measurements taken from the sunrise, the differences were smaller than 1°C and not significant (Table 1).

Fig. 1 a The mean (\pm SE) differences between floral and ambient air temperatures ($^{\circ}\text{C}$), in 10-min intervals after sunrise. **b** The mean (\pm SE) differences between floral and ambient air temperatures ($^{\circ}\text{C}$), in 10-min intervals before sunset. Datum point at -30 min was exceptionally higher and removed as an outlier

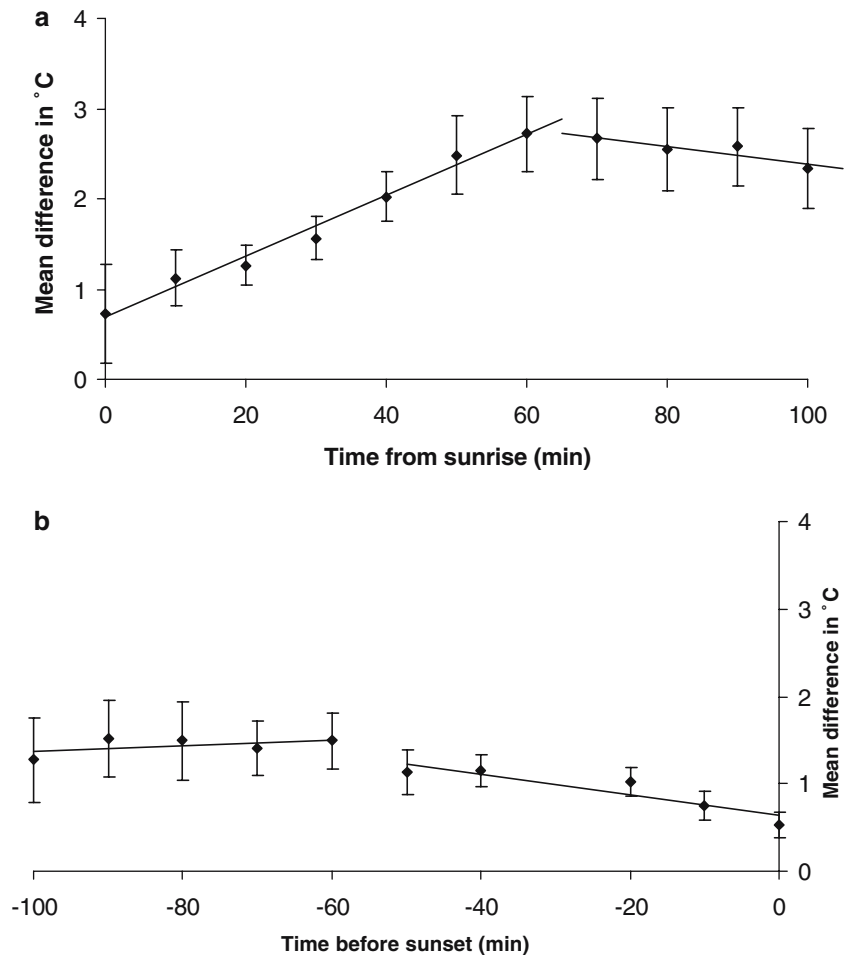
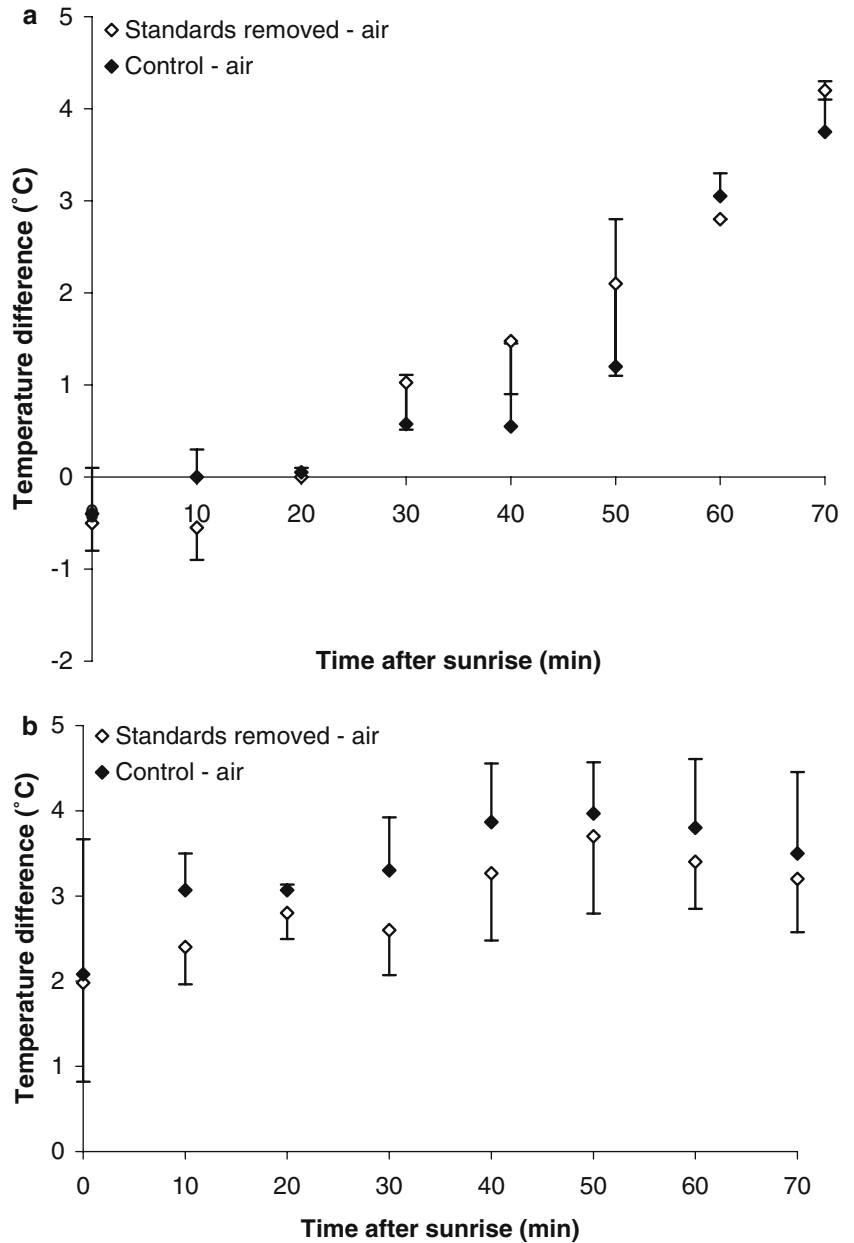


Table 1 Simultaneously measured temperatures (mean \pm SD) within light-colored, dark-colored and their mean differences in 20-min intervals from sunrise. None of the differences, tested by one-tailed paired t test, was significant ($P > 0.05$)

Time	n	Floral temperature in light-colored iris ($^{\circ}\text{C}$)	Floral temperature in dark-colored iris ($^{\circ}\text{C}$)
Sunrise	11	9.4 ± 4.2	9.5 ± 4.0
Sunrise + 20 min	11	10.0 ± 3.9	10.4 ± 3.4
Sunrise + 40 min	11	10.8 ± 4.0	11.5 ± 3.5
Sunrise + 60 min	11	11.8 ± 4.1	12.3 ± 3.9
Sunrise + 80 min	11	12.7 ± 4.4	12.9 ± 3.8
Sunrise + 100 min	11	13.2 ± 4.4	13.4 ± 3.8

Fig. 2 The mean (\pm SE) difference in floral temperatures ($^{\circ}\text{C}$) between flowers with removed standards and control intact flowers, and the ambient air, in 10-min intervals after sunrise. **a** Dark-colored flowers (*I. atropurpurea*). **b** Light-colored flowers (*I. hermona*)

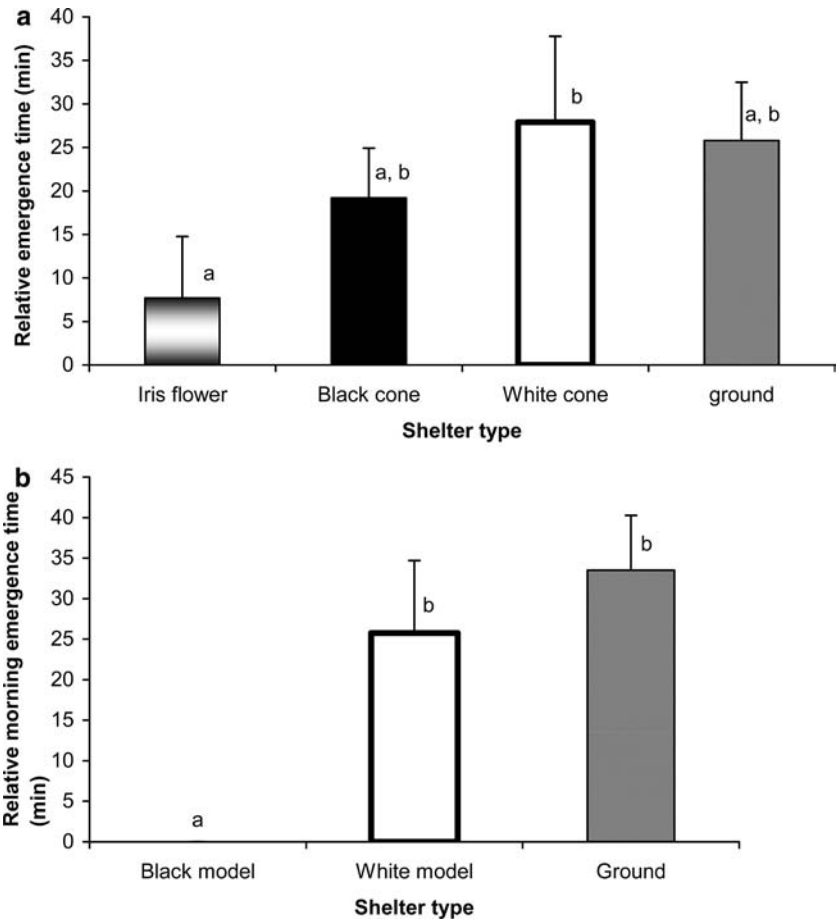


Morning emergence

Most of the solitary male bees that were experimentally deposited into the four night-shelter types emerged by

direct flight from the inner space of the shelter, with no basking or shivering. Out of 64 males used in the experiment, 44 were the first to emerge from each shelter type in each of the 11 repetitions and were included in

Fig. 3 a Mean relative morning emergence time (minutes + SE) of male bees experimentally relocated into different night-shelter types. Time zero (in minutes) was set when the first male emerged. The *Iris* flower includes *I. atropurpurea* ($n=2$), *I. atrofusca* ($n=4$), and *I. hermona* ($n=5$). Bars with identical letters are not significantly different ($P>0.05$). **b** Mean relative morning emergence time (minutes + SE) of male bees experimentally relocated into three different night-shelter types in Har Gilo, where no *Oncocyclus* irises grow ($n=4$)



the analysis. Night-shelter type significantly influenced emergence time of male bees (ANOVA: $F_{3,43} = 3.574$, $P = 0.022$; Fig. 3a). Bees that had sheltered in *Iris* flowers emerged earliest, on an average 25.2 min earlier than those that had sheltered in white floral models, 22.6 min earlier than those sheltering on the ground and 18.2 min earlier than those that had sheltered in black floral models.

At Har Gilo, where no *Oncocyclus* irises grew, males emerged significantly earlier from the black cones than from either white models (mean difference 25.7 min) or the ground (mean difference 33.5 min; ANOVA: $F_{2,11} = 7.32$, $P = 0.013$, Fig. 3b). In 202 *I. hermona* flowers, we recorded a total of 323 night sheltering male bees during three observation evenings. A two-way ANOVA revealed a significant effect of aspect ($F_{3,301} = 10.2$, $P < 0.001$) and date ($F_{2,301} = 5.8$, $P = 0.003$; treated as repeated measurement) with no interaction ($F_{6,301} = 0.89$, $P = 0.45$). On all nights, east-facing tunnels hosted more male bees than any other aspect (Fig. 4), suggesting that male bees prefer to shelter in tunnels facing the rising sun.

Discussion

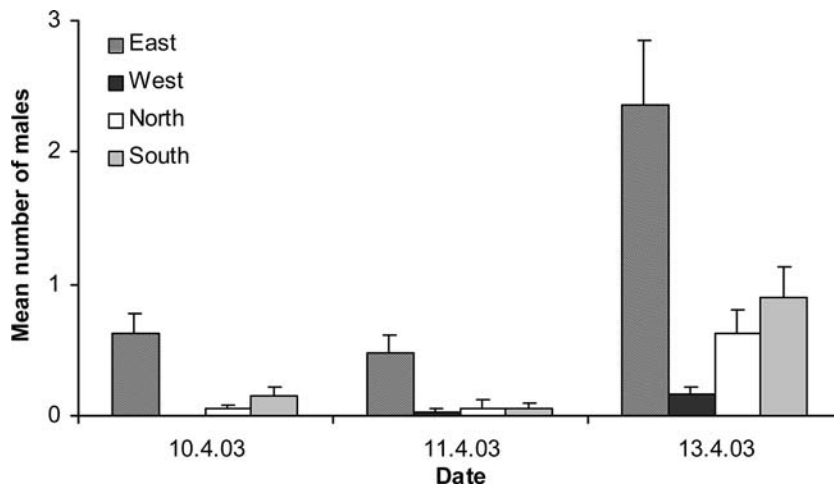
Temperatures within flowers of *Oncocyclus* irises could reach 2.5°C higher than ambient air and increased rap-

idly after sunrise. This allowed earlier emergence of the sheltering male solitary bees that pollinate these flowers.

Thermal energy was earlier described as an energetic reward for the pollinators (Dieringer et al. 1999; Herrera 1995; Kevan 1975; Totland 1996). However, except for the orchid *Serapias vomeracea* (Dafni et al. 1981) no plant has been shown to have heat as its only reward. Dafni et al. (1981) found that temperature within the orchid flowers was 3°C higher than ambient air during the day, and this was proposed as a reward to the night-sheltering male bees, but they also proposed that the *Serapias* orchid is pollinated by a deceptive system (Dafni et al. 1981). Ivri and Eisikowitch (1988), claimed sexual deception also in the pollination system of the *Oncocyclus* irises, where the dark pollination tunnel of the flower mimics a female bee-nesting hole. However, our results clearly demonstrate that the flowers of *Oncocyclus* irises offer a real reward to the night-sheltering male bees. The fact that the attraction of the male bees to the *Oncocyclus* flowers is not specific (Sapir and Shmida 2002) and that the same bees also use other flowers as overnight shelters (Sapir et al. 2005) further support our findings that this is not a deceptive system.

The earlier and faster warming of the iris flowers immediately after sunrise enable the night-sheltering solitary male bees to emerge earlier than other male bees sheltering elsewhere, as we have demonstrated (Fig. 3).

Fig. 4 Mean number (+ SE) of male bees hosted in tunnels of *I. hermona*, facing the four aspects on three evenings of observations



More male bees were found sheltering in east-facing pollination tunnels (Fig. 4) that face away from the sun during sunset but warm up first after sunrise. We did not observe the behavior of an individual bee in its first nights of sheltering, but there we hypothesize that a learning process is involved in the preference for the shelter that will potentially be the warmest in the morning.

Removal of the standards had no effect on floral temperature after sunrise relative to intact flowers (Fig. 4). Increase in floral temperature faster than the ambient air seems to be the result of the dark color of other floral parts, even in the light colored *Oncocyclus* irises. Given that heat is the major reward to the night-sheltering solitary male bees, we propose that the standards are not an adaptation for increasing the temperature within the flowers in the morning, and are not a target for pollinator-mediated selection. Some differences were found in the pattern of temperature increase between light- and dark-colored standards (compare a to b in Fig. 2), but the small sample size does not allow further inference. Note that such a difference was not found in comparisons of intact flowers in the botanical garden (Table 1). This could be due to the difference in temperature/wind regimes in the coastal (*I. atropurpurea*) and inland (*I. hermona*) regions in the morning (Jaffe 1988), whereas in the botanical garden conditions were identical for each pair of flowers in any given day.

Our results clearly demonstrate that the complete or partially dark-colored flowers of the *Oncocyclus* irises absorb morning sun rays and offer heat reward to their pollinators. Morning heat reward may also explain other cases of pollination by night-sheltering solitary male bees as in other flowering species observed hosting night-sheltering male bees (Dafni et al. 1981; Sapir et al. 2005). All these species are dark-colored and can provide thermal reward for the male bees. The *Oncocyclus* irises, unlike the other examples, are totally dependant on night-sheltering male bees as their obligatorily pollinators. Thus, it is likely that the solitary male bees' behavior and preferences of flowers serving as the best

night-shelters created strong selection on the *Oncocyclus* irises floral traits.

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