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Weather-Dependent Pollinator Activity in an Apple Orchard, with Special Reference to *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae and Apidae)

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ABSTRACT The foraging activity of pollinator insects in relation to weather factors (ambient temperature, solar radiation, relative humidity, and wind speed) was studied in an apple orchard with special reference to two managed bee species, *Osmia cornuta* (Latreille) and *Apis mellifera* L. Over the range of observed weather values, *A. mellifera* activity was significantly dependent on temperature, solar radiation, and wind speed; *O. cornuta* activity was dependent on solar radiation and wind speed. These results were confirmed through video recordings at one *O. cornuta* nesting shelter and one *A. mellifera* hive. For both species, daily activity started at lower temperatures than it ceased, whereas solar radiation did not differ between these two events. In general, *O. cornuta* was active from 10 to 12°C and 200 w/m^2, and *A. mellifera* from 12 to 14°C and 300 w/m^2. *O. cornuta* was the only bee species seen visiting apple flowers under strong wind or light rain. Because of its greater tolerance to inclement weather, *O. cornuta* pollinated apple flowers for longer periods (both daily and seasonally) than other flower visitors.

KEY WORDS *Osmia cornuta, Apis mellifera,* pollinator foraging activity, climatic factors, orchard pollination

CLIMATIC CONDITIONS STRONGLY affect the foraging activity of pollinating insects, even in those species that are able to increase their body temperatures endothermically (Kevan and Baker 1983, Corbet 1990). Thus, spells of unfavorable weather can significantly limit both the reproductive success of pollinating insects, and that of the plants depending on them for pollination (Eisikowitch and Galil 1971, Martínez del Río and Búrquez 1986, Bergman et al. 1996). Especially susceptible are many solitary bee species, which have short seasonal activity periods (Larsson and Tengö 1989, Vicens 1997; J.B., unpublished data). In temperate areas, pollination may be curtailed especially in those plant species that bloom early in the year, when inclement weather is frequent, and climatic factors have long been recognized as one of the main factors limiting production in fruit trees (Gould 1939).

To increase pollination, honey bee, *Apis mellifera* L., hives are frequently placed in orchards at bloom time (Free 1993). However, the foraging activity of this species is low at ambient temperatures below 12–14°C and solar radiation under 500 lux (Burrill and Dietz 1981, Kevan and Baker 1983, Winston 1987, Free 1993), conditions which frequently occur in late winter and spring.

In contrast, some early-flying bees (especially in the genera *Andrena, Bombus, Anthophora,* and *Osmia*) are known to forage on *Prunus, Malus,* and *Pyrus* flowers when weather conditions are unfavorable for *A. mellifera* (Free 1960, Chansigaud 1975, Boyle and Philogène 1985, Boyle 1987, Jacob-Remacle 1989, Batra 1994). *Osmia cornuta* (Latreille) is the earliest-flying megachilid in northeast Spain, where it nests from February to April, and is strongly associated with fruit trees (Vicens et al. 1993). Because of its nesting phenology in synchrony with fruit tree bloom (Taséi 1973, Asensio 1984), its preference for pollen of Rosaceae (Márquez et al. 1994), and its high pollinating efficacy on almond, pear, and apple (Bosch and Blas 1994, Monzón 1998, Vicens and Bosch 2000), *O. cornuta* has been studied as an alternative orchard pollinator (Bosch 1994a, 1994b, 1994c). Results on the closely related species *Osmia rufa* (Stone and Willmer 1989) suggest that *O. cornuta* may be strongly endothermic, and likely to have lower temperature thresholds for activity than *A. mellifera* (Maddocks and Paulus 1987, Bosch 1994c). Information on the influence of climatic factors on the foraging activity of *O. cornuta* would be useful to evaluate its potential performance in different climatic areas and on different crops. With this objective, the foraging activity of *O. cornuta* in relation to ambient temperature, relative humidity, solar radiation, and wind speed was measured and compared with that of other pollinators in an apple orchard.

Materials and Methods

The study was undertaken in 1993, 1994, and 1995 in a 0.5-ha apple orchard located in Canet de la Tallada

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(Girona, northeast Spain). Trees were ≈3 m tall and trellised, which facilitated pollinator counts. More than 20 strong honey bee hives managed for pollination (with abundant brood) were placed in neighboring orchards in all 3 yr; and in 1993 and 1995, two *O. cornuta* nesting shelters were installed at one end of the orchard. Details on the composition of the orchard and the structure of *O. cornuta* nesting shelters are given in Vicens and Bosch (2000). In 1995, ambient temperature, relative humidity, solar radiation, and wind speed were recorded every 10 min by a weather station (Campbell Scientific CR10, Logan, UT) located 2 m above the ground, 800 m away from the orchard on flat terrain.

Pollinator Activity at the Flowers. Insect counts were made on 11 trees of each of three rows of the main cultivar ('Royal Red Delicious'). Distance between sampled trees within a row was 20 m. All observations were made during peak bloom in April (7 d in 1993, 9 d in 1994, and 9 d in 1995). In 1994 and 1995, four counts were completed daily, at 0930–1030, 1200–1300, 1500–1600, and 1800–1900 hours. In 1993 the latter count was omitted. During each count, each tree was observed for 1 min, and all insects seen visiting flowers were recorded. To avoid altering visitation frequencies, recorded insects were not captured. For this reason, some insects, notably among the Diptera, could only be determined to family level. Insect frequencies recorded in the 1995 counts (9 d × 3 rows × 4 daily counts = 108 counts) were used to analyze the effect of weather factors (independent variables: ambient temperature, relative humidity, solar radiation, and wind speed) on the foraging activity of *O. cornuta* and *A. mellifera* (dependent variable: insect frequency). To characterize ambient conditions for each count, we used the average of weather variable values at the beginning and at the end of each count. Because counts for observed insect frequencies were low, the assumptions of normality and homogeneity in standard regression were not well met. Consequently, we fit a multiple regression model with Poisson errors using PROC GENMOD of SAS (SAS Institute 1998). We included quadratic terms to capture the observed curvature in the foraging responses of *O. cornuta* and *A. mellifera.* Regression tree analysis for each species were computed with S-Plus 2000 (MathSoft 1999) and suggested interactions between radiation and wind and between radiation and temperature. Thus, the full regression model for each bee species included all four independent variables, their squared values, and the two interaction terms. Terms with $P > 0.05$ were dropped from the full model to produce the final reduced model.

Bee Activity at the Nesting Sites. In 1995, two video cameras were used to register bee activity at one *O. cornuta* nesting shelter and one *A. mellifera* hive. The *O. cornuta* shelter contained 25–38 nesting females during the recording periods. The *A. mellifera* hive contained a strong colony (estimated 10,000 foragers [Rallo 1987]) and a wider than normal (10 cm) entrance to facilitate bee counts. Video recordings were made on 20, 21, 23, 25, and 26 April from 0900 hours until activity ceased, and were later used to count the number of bees exiting each nesting site for 1 min every 10 min, in synchrony with recordings taken at the weather station. Different individuals within a population start and cease activity at different times. Because we were interested in thresholds for complete or nearly complete activity, we first counted the number of bees exiting each nesting site during periods of favorable weather conditions. Under these conditions, a minimum of two *O. cornuta* females (5–8% of the nesting females) exited the shelter per minute, and ≥five *A. mellifera* workers (an estimated 0.05% of the foraging population) left the hive per minute. Thus, two females per minute and five workers per minute were used as full activity indices for *O. cornuta* and *A. mellifera,* respectively. The relationship between daily initiation and termination of full activity and the climatic factors was analyzed through multivariate analysis of variance (MANOVA); (SPSS 1993).

Results

Pollinator Composition. Weather conditions in 1993 were rather unfavorable for insect activity and, as a result, pollinators were registered in only 12 of the 21 counts made. In 1994 and 1995, weather was more benign and pollinators were registered on 28 and 35 of the 36 respective counts. A total of 2,672 insects was counted during the 3-yr study: 179 in 1993, 1,204 in 1994, and 1,289 in 1995. Visitation rates (total insects recorded per total sampling minutes per total trees sampled) were 0.26 insects per minute per tree in 1993, 1.01 in 1994, and 1.09 in 1995. Pollinators were grouped in the following six categories: (1) *A. mellifera,* (2) *O. cornuta,* (3) other Apoidea, (4) Syrphidae, (5) Muscoid flies, (6) other insects. The percentages of each of these categories combined across trees, days, and daily counts for each of the 3 yr are shown in Fig. 1.

Apis mellifera was the most abundant species in all 3 yr (37.4, 77.0, and 39.6%, respectively). Given the agricultural characteristics of the area, the presence of feral colonies was unlikely, so most *A. mellifera* were probably coming from cultivated hives. In 1993 and 1994, no distinction was made between nectar and pollen gatherers, but in 1995, 97% of the workers collected only nectar. Although only 60 *O. cornuta* nested in the nesting shelters in 1993 and 130 in 1995, they were the second most abundant pollinator species on apple flowers (20.1% and 17.8%, respectively). In 1994, when no *O. cornuta* were released, this species was not registered in the counts, suggesting the absence of wild populations in the surroundings.

Wild bees were uncommon in all 3 yr (5.0, 10.4 and 4.5%, respectively). *Andrena* [mostly *Andrena haemorrhoa* (F.)] was the only genus registered in all 3 yr (2.8, 6.1, and 4.3%, respectively). *Bombus terrestris* (L.) and, to a lesser extent, *Bombus pascuorum* (Scopoli) were only present in 1993 (2.2%) and 1994 (3.3%). Other wild bees, *Xylocopa violacea* (L.), *Osmia caerulescens* (L.), *Eucera* spp., *Anthophora* spp., and *Nomada* spp., were sporadic and only recorded in

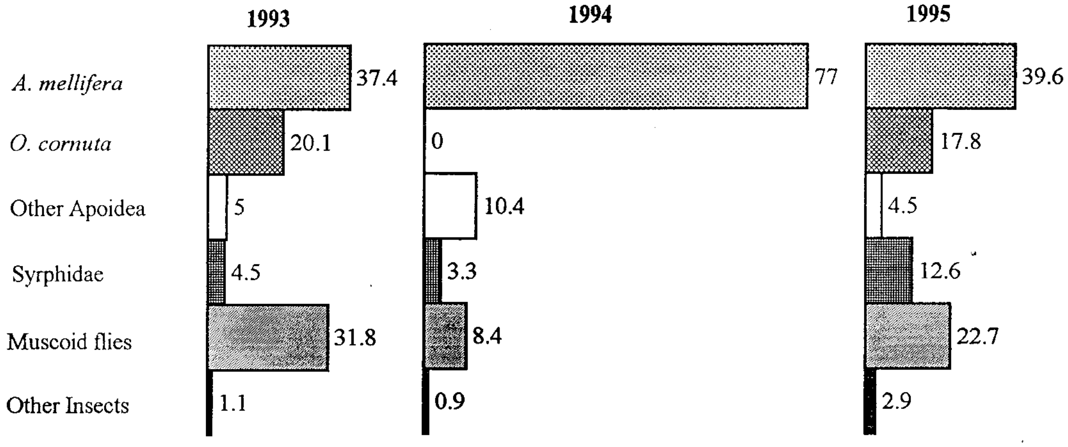

Fig. 1. Pollinator composition (in percent of insects recorded on apple flowers) in the Canet orchard in 1993 (n = 179), 1994 (n = 1,204), and 1995 (n = 1,289).

one of the 3 yr. Among Diptera, Syrphidae (mainly *Eristalis tenax* L., *Episyrphus balteatus* De Geer, and *Syrphus ribesii* L.) were relatively abundant in 1995 (12.6%). Other Diptera, almost exclusively belonging to the families Muscidae, Calliphoridae, Tachinidae, and Anthomyidae (Muscoid flies), made up a high proportion of total visitation in 1993 (31.8%) and 1995 (22.7%), but their mobility both within and between flowers was very low. Other anthophiles such as beetles, butterflies, and wasps in the families Vespidae and Eumenidae always were rare.

Activity at the Flowers. The distribution of each pollinator category throughout the four daily counts on the trees in 1995 (all days combined) is shown in Fig. 2. Most insects, including *A. mellifera* and the wild bees, have a clear peak of activity in the late morning and early afternoon, and are very scarce after 1800 hours. In contrast, visitation by *O. cornuta* is more evenly distributed throughout the day, being the only pollinator present at the flowers in relatively high numbers early and late in the day. Muscoid flies were most scarce during the central hours of the day, because they moved to the flowers in the evening and used them as night refuges until the following morning. During this time, they rested near the base of the stamens and occasionally reached the nectaries, but only rarely contacted the stigmas.

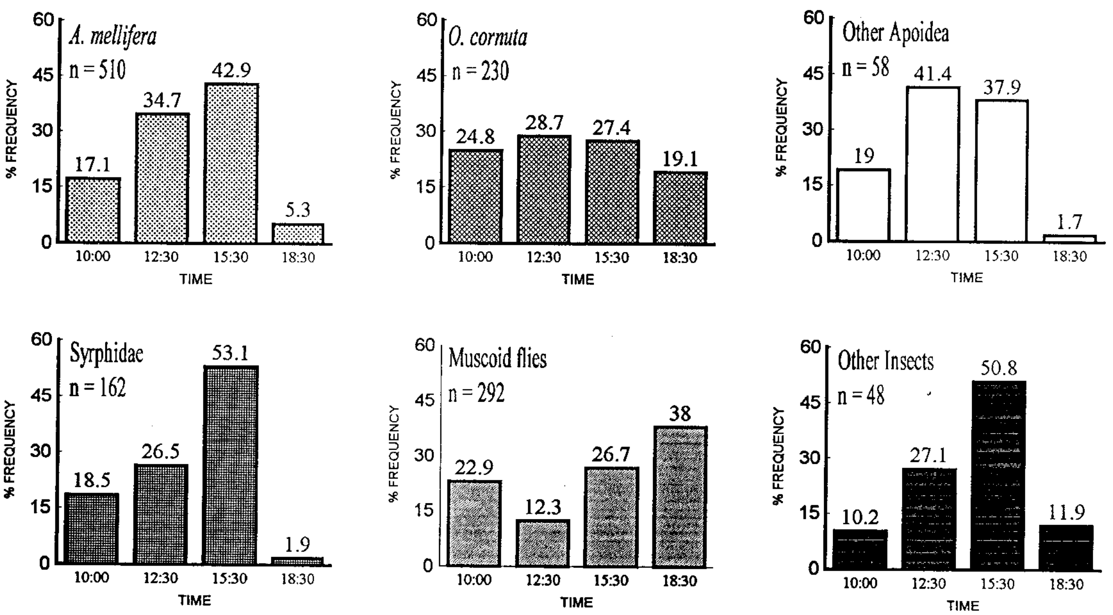

Fig. 2. Percent frequencies of different pollinator groups recorded on apple flowers at 1000, 1230, 1530, and 1830, hours (pooled data from 9 d) in the Canet orchard in 1995.

Table 1. Multiple regression model with Poisson errors between bee frequencies at the apple flowers and weather factors (solar radiation, wind speed, ambient temperature and relative humidity) in 1995

Bee species	Selected parameters	Parameter estimates	*F*	df	*P*
O. cornuta	Radiation	0.59	7.84	1,103	0.006
	Radiation^2	−0.06	5.47		0.021
	Wind	0.54	7.09		0.009
	Wind^2	−0.09	8.99		0.003
A. mellifera	Radiation	2.07	25.99	1,102	<0.0001
	Radiation^2	−0.10	10.74		0.001
	Wind	−0.23	12.33		0.0007
	Temperature	0.45	14.75		0.0002
	Radiation × Temperature	−0.09	4.74		0.032

During the 1995 insect counts, ambient temperatures ranged between 9 and 22°C, solar radiation between 34 and 779 w/m^2, relative humidity between 19.1 and 96.6%, and wind speed reached 7.2 m/s (moderate wind). *O. cornuta* and the muscoid flies were the only pollinators relatively abundant at radiations of 100–200 w/m^2. The remaining insects were more heliophilic, with >40% of their visits recorded above 700 w/m^2. *O. cornuta* was also the only species actively pollinating apple flowers at 10–13°C. Other insect groups (Muscoid flies, Syrphidae, and beetles) were also observed on the flowers at these temperatures, but they were mostly inactive. All pollinator groups showed some activity at relative humidities below 90%, but *O. cornuta* and the muscoid flies were also registered at higher humidities, and even under light rain (up to 0.9 mm/h). Finally, all insect groups were active at wind speeds of up to 6 m/s, with *O. cornuta, A. mellifera,* and the syrphids also active above this value. In 1993, *O. cornuta* was the only pollinator observed foraging under strong wind conditions reaching maximum values of 50 km/h.

The regression tree analysis between *A. mellifera* frequencies and climatic factors selected temperature as the main factor determining *A. mellifera* activity at radiations <474.5 w/m^2, and wind as the main factor at radiations above this value. Similar results were obtained with *O. cornuta,* although the radiation threshold for this species was 176.5 w/m^2. The results of the multiple regression analysis with Poisson errors for the two bee species are given in Table 1. Within the weather values registered, *A. mellifera* activity was significantly dependent on ambient temperature, solar radiation, and wind speed, with an interaction between solar radiation and ambient temperature. *O. cornuta* activity was significantly dependent on solar radiation and wind speed.

Activity of *O. cornuta* and *A. mellifera* at the Nesting Sites. On all 5 d on which video recordings were taken, *O. cornuta* was fully active for longer periods (range: 3 h 20 min - 9 h 50 min; sum: 33 h 40 min) than *A. mellifera* (range: 0 min - 5 h 30 min; sum: 15 h 10 min) (Fig. 3). Both activity initiation and termination occurred at lower temperature and solar radiation in *O. cornuta* (minimum values: 9.8°C and 69 w/m^2) than in *A. mellifera* (minimum values: 12.5°C and 229 w/m^2) (Table 2), and these differences were statistically significant (Table 3). On 25 April when *O. cornuta* showed its highest temperature threshold for activity initiation (13.1°C), *A. mellifera* was completely inactive (Fig. 3). For both species, temperature values were significantly lower at activity initiation than at termination, whereas solar radiation values did not differ between these two events (Table 3). Relative humidity and wind speed remained moderate during the recording periods, and did not seem to influence daily flight initiation or termination of either bee species.

Activity Thresholds of *O. cornuta* and *A. mellifera*. Fig. 4 combines the data of the bee counts on the trees and the activity counts at the *O. cornuta* and *A. mellifera* nesting sites in relation to ambient temperature and solar radiation. These data establish the approximate temperature-radiation thresholds for the two species. The lowest temperature at which *O. cornuta* activity was registered was 9.8°C, with a solar radiation of 225 w/m^2. At higher temperatures, this species was active at lower radiations (e.g., 69 w/m^2 at 10.5°C or 34 w/m^2 at 16.0°C). *A. mellifera* had a similar response but at higher thresholds (12.2°C - 329 w/m^2, 13.2°C - 233 w/m^2, 15.8°C - 151 w/m^2).

Discussion

The abundance of *A. mellifera* in the Canet apple orchard when no other pollinators were introduced (77%) agrees with results obtained in other orchards, where values higher than 80% are often reported (review in Free 1993). This appears to be largely caused by the presence of managed hives in orchards. Wild bees have been recorded in relatively high numbers (Chansigaud 1975, Boyle and Philogène 1983, Scott-Dupree and Winston 1987, Jacob-Remacle 1989), and several studies emphasize their pollinating activity on fruit trees, and their capacity to fly at low temperatures (Løken 1958; Free 1960, 1968; Emmett 1971; Kendall 1973; Chansigaud 1975; Mayer 1984). Some wild bee species (*Bombus, Anthophora*) are capable of sustained flight at low temperatures by physiologically raising their thoracic temperature high above ambient temperatures (Heinrich 1975, 1993; Stone and Willmer 1989; Stone 1994a). Other species (*Andrena*), with reduced ability to thermoregulate physiologically, are nevertheless able to fly at low ambient temperatures because they require relatively low thoracic temperatures for flight, which they attain mostly by behavioral means (basking) (Stone and Willmer 1989, Herrera 1995). Unfortunately, wild bees were scarce in our study area (from 0.01 individuals per minute per tree in 1993, to 0.13 in 1994). The absence of *O. cornuta* in the orchard in 1994, and its relative abundance in 1993 and 1995, despite the small size of the nesting populations, confirms the scarcity of wild bees in the surroundings of the orchard.

The abundance of Diptera does not reflect their pollinating efficacy. Our observations are consistent with the long-recognized low pollinating contribution

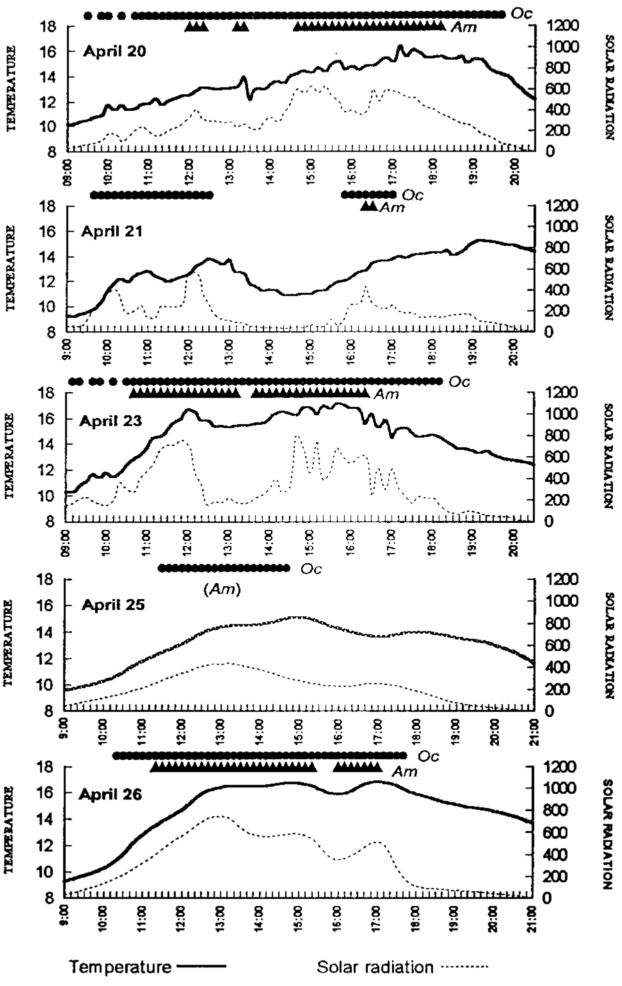

Fig. 3. Periods of full daily activity at *O. cornuta* (circles) and *A. mellifera* (triangles) nesting sites in the Canet orchard on 5 d in April 1995. *A. mellifera* remained inactive throughout 25 April. Ambient temperature (solid line) and solar radiation (broken line) records from 0900–2100 hours are also shown.

Table 2. Ambient temperature (T) in °C and solar radiation (R) in w/m^2 registered at the beginning and the end of *O. cornuta* and *A. mellifera* foraging activity recorded at the nesting sites on 5 d of April 1995

Date		Activity initiation		Activity termination	
		O. cornuta	*A. mellifera*	*O. cornuta*	*A. mellifera*
20 April	T	10.5	12.5	14.2	15.6
	R	69	332	79	364
21 April	T	9.8	12.9	13.8	13.5
	R	225	432	257	278
23 April	T	10.3	12.8	14.6	15.6
	R	170	273	158	613
25 April	T	13.1	—	15.1	—
	R	347	—	279	—
26 April	T	11.5	13.8	16.4	16.8
	R	229	229	312	513
Mean	T	11.0	13.3	14.8	17.0
	R	208	328	217	430

A. mellifera remained inactive throughout 25 April.

of these insects to apple pollination (Atwood 1933, Brittain 1933, Palmer-Jones and Clinch 1968). The apparent greater activity of Muscoid flies during the daylight hours with lowest temperature and solar radiation is the result of their habit of spending the night on the flowers. In *Crataegus monogyna*, another white-flowered Rosaceae, flowers in the sun had temperatures up to 3.7°C higher than ambient, a result of radiation reflection from the petals (Corbet et al. 1979). It is possible that flies spending the night at the apple flowers benefit from radiative heat gain with the morning sunlight.

Of the two managed bee species, the activity of *A. mellifera* was more dependent on climatic factors than that of *O. cornuta*. *O. cornuta* tended to be distributed uniformly on the flowers throughout the day, and were active on days when other pollinators were scarce or absent. The establishment of precise activity thresholds is difficult because responses depend on a combination of factors that include not only weather

Table 3. MANOVA table of ambient temperature and solar radiation registered at activity initiation and termination (event) in *O. cornuta* and *A. mellifera* (species)

Factors	Multivariable			Univariable					
				Temp			Solar radiation		
	F	df = 2, 13	P	F	df = 1, 14	P	F	df = 1, 14	P
Species	5.19		0.022	6.44		0.024	10.29		0.006
Event	20.04		<0.0005	3.38		<0.0005	1.67		0.217
Species × Event	2.94		0.088	1.65		0.220	1.26		0.281

variables, but also the physiological and behavioral state of the insect, as well as floral resource availability (Stone 1994b). Thus, activity thresholds vary, not only among individuals, but also throughout the day and the nesting season. In *Megachile* spp., daily activity starts at lower temperatures and higher solar radiation than it ends (Lerer et al. 1982, Abrol and Kapil 1986, Abrol 1988). This result implies that activity initiation is limited by temperature, and activity termination is determined either by a decline in light intensity or, possibly, by a decline in pollen-nectar availability (Lerer et al. 1982, Abrol and Kapil 1986, Abrol 1988). Both in *O. cornuta* and *A. mellifera*, as well as in *Megachile rotundata* (Szabo and Smith 1972), there is an inverse correlation between temperature and solar radiation during daily activity initiation, so that females start foraging at lower temperatures on days with clear skies. When conditions are particularly unfavorable, however, bees will wait until both weather factors rise above "normal" levels. For example, 25 April, with cool and overcast conditions, was the day on which *O. cornuta* started flying later and at highest temperature and solar radiation (Fig. 3; Table 2). Standing crops of pollen and nectar may also condition daily activity rhythms, and mask the effect of weather factors, especially in endothermic species (Corbet et al. 1979, Willmer 1983, Stone et al. 1998). Observations in Canet and in other orchards indicate that although pollen levels do not greatly fluctuate throughout the day because new anthers open over several hours, nectar levels tend to decrease from morning to evening (J.B., unpublished data). Therefore, nectar availability might have affected the termination of foraging activity in this study, notwithstanding the significant influence of weather factors found for both species.

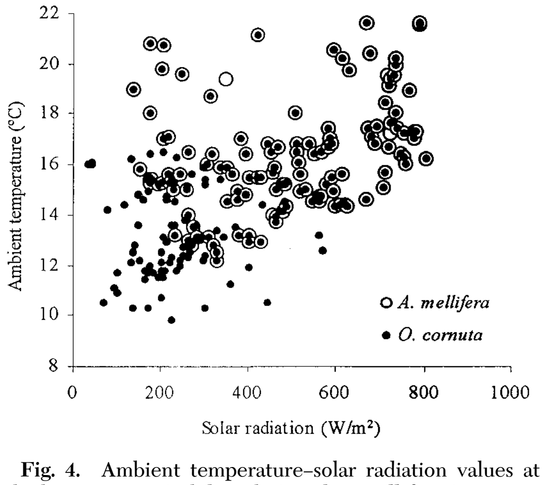

Fig. 4. Ambient temperature–solar radiation values at which *O. cornuta* (solid circles) and *A. mellifera* (open circles) were active in the Canet apple orchard in 1995. Both data from pollinator counts on the trees and from recordings at nesting sites are included.

As a rule, under moderate wind and relative ambient humidity <95%, *O. cornuta* is fully active from 10 to 12°C (see also Maddocks and Paulus 1987, Bosch 1994c) and 200 w/m^2. Some females even forage under light rain or strong wind. *O. cornuta* is a relatively large *Osmia* with abundant pilosity and dark coloration on the head and thorax (completely black in females), and these traits are commonly associated with bees able to fly at low temperatures (Heinrich 1993, Stone 1994a). To our knowledge, the thermoregulation of *O. cornuta* has not been studied, but *Osmia rufa* (L.) (another early-flying *Osmia* in the same subgenus) has a very high thoracic warm-up rate (10.5°C/min), and is able to raise its thoracic temperature 13.6°C above ambient temperature before take off (Stone and Willmer 1989, Stone 1994a). These same studies indicate that thermal biology in Apoidea has a strong phylogenetic component at the family, genus, and subgenus levels, suggesting similar thermoregulatory mechanisms in *O. cornuta.* In areas where both species coexist, the seasonal activity of *O. cornuta* always starts earlier (Taséi 1973, Westrich 1989, Vicens et al. 1993), and when both nest simultaneously, *O. cornuta* starts flying at lower temperatures (Maddocks and Paulus 1987; N.V., unpublished data). *O. cornuta* is a larger species (female body mass: 116–148 mg) than *O. rufa* (female body mass: 91 mg) (Maddocks and Paulus 1987, Vicens 1997). The well-documented correlation between endothermic ability, tolerance to low ambient temperatures, and body size (Stone and Willmer 1989; Stone 1993, 1994a, 1994b) suggests, again, high endothermic warm-up rates in *O. cornuta.*

Temperature and radiation thresholds for *A. mellifera* found in this study are similar to those reported elsewhere (Burrill and Dietz 1981, Kevan and Baker 1983, Winston 1987, Free 1993). *A. mellifera* is fully active at temperatures higher than 12–14°C and solar radiation higher than 300 w/m^2, being particularly sensitive to drops in solar radiation below this limit. Moderate wind, even at favorable temperatures and light intensity may also cause activity to cease. *A. mellifera* is an endothermic species, able to warm up through shivering of the flight muscles, and attain thoracic temperatures 15°C above ambient temperature (Heinrich 1979). However, because it requires a high thoracic temperature to fly, it cannot make uninterrupted flights at ambient temperatures lower than 12–15°C (Heinrich 1979, 1993).

Fruit trees have a short flowering period, interrupted by frequent periods of inclement conditions. Even on days with good weather, the foraging activity of most insects is low or nonexistent in the early morning and late afternoon, limiting further the time available for pollination. Because stigma receptivity and embryo sac viability decline rapidly over the flower life span, pollination shortly after anthesis is considered highly desirable (Free 1993). The use of *O. cornuta* as a pollinator in orchards reduces the dependence of pollen transfer on good weather, and therefore ensures a more uniform pollination throughout the day and over the years. The estimated numbers of nesting *O. cornuta* females necessary to pollinate 1 ha are 750 for almonds (Bosch 1994c) and 530 for apples (Vicens and Bosch 2000), in contrast to 2–7 colonies of *A. mellifera,* with thousands of foragers per colony (McGregor 1976, Free 1993). These differences between the two bee species in numbers of individuals required are the result of the higher pollinating efficacy of *O. cornuta* on fruit tree flowers (Bosch and Blas 1994, Monzón 1998, Vicens and Bosch 2000), its strong preference to visit fruit trees (Márquez et al. 1994), and its capacity to forage for longer periods, both daily and seasonally (this study). Because of its greater tolerance to cool, overcast weather, *O. cornuta*'s beneficial effects as an orchard pollinator will be comparatively greater on years with inclement conditions during flowering.

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