Nest Site Orientation and Relocation of Populations of the Orchard Pollinator *Osmia cornuta* (Hymenoptera: Megachilidae)

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ABSTRACT   Moving actively nesting populations of the orchard pollinator *Osmia cornuta* (Latreille) from a pollinated crop to one beginning to bloom could increase both the number of flowers pollinated and the number of bee progeny produced. This study investigates the possibility of moving actively nesting *O. cornuta* populations, and evaluates the effects of moving distance and nest site artificial visual landmarks on orientation and establishment of moved females. Nesting shelters with known numbers of nesting females were nocturnally relocated for distances ranging from 0 to 240 km, and the numbers of nesting females were counted after each move. Nearly all females continued to nest at shelters that were moved short (0–3 m) distances. Moves of intermediate distances (135–235 m) resulted in considerable (30–76%) bee loss (dispersal), and many females flew back to the original nesting site. At long distances (3–240 km), dispersal was higher (63–78%) and no bees were seen hovering at the original site. Moving distance was correlated positively with dispersal and with orientation (zigzagging) flights made by females when they first exited their nests after the moves. The addition or removal of supplementary visual landmarks (2 by 1.5-m banner with colored patterns) at the nesting shelter did not affect dispersal rates. Bees appeared to respond to supplementary landmarks but used other signals as primary orientation cues. An additional experiment showed that *O. cornuta* populations can be removed and stored at low temperature for up to 4 d (e.g., to avoid pesticide treatments) and then reinstalled at their nesting site, without affecting female orientation or nesting.

KEY WORDS   *Osmia cornuta,* orchard pollination, orientation, nest location, homing ability

THE SOLITARY BEE *Osmia cornuta* (Latreille) has been developed recently as a pollinator for almonds, apples, and pears (Bosch 1994a, Vicens 1997, Monzón 1998). Although populations of *O. cornuta* nest for over a month (Bosch 1994a, 1994b; Vicens 1997), the flowering period of commercial orchards usually lasts <3 wk (McGregor 1976, Socias i Company and Felipe 1979), and therefore some females are still nesting after petal fall. At this time, floral resources in the orchard are usually scarce, and bees are exposed to frequent insecticide sprays. The possibility of moving *O. cornuta* populations from pollinated orchards to later-blooming orchards, could allow for increases in both the number of crop flowers pollinated and the bee progeny obtained. Moving active *O. cornuta* populations would also be desirable when orchards must be treated with insecticides during flowering. In such a situation, nesting materials could be temporarily removed from the orchard and then brought back once the insecticide had degraded.

However, nesting bees usually become disoriented when moved. *Apis mellifera* L. colonies lose more workers when hives are relocated within the colony's foraging area than when they are moved longer dis-

tances (Free 1958a, Gould and Gould 1988). Although several factors (e.g., removing all hives from the old site) are known to reduce worker losses (Free 1958b), some worker loss and drift among colonies always occurs, even in distant moves. Thus, Nelson and Jay (1989) reported 45% loss and 21% drift in colonies moved 14 km, in comparison to 22% loss and 10% drift in control (unmoved) hives.

Less information is available on the possibility of relocating nesting solitary bees. Nesting populations of the alfalfa pollinator *Megachile rotundata* (F.) are routinely moved in large trailers (Bohart 1972). Bee losses range from 8 to 43% when bees are moved between fields with few landmarks, compared with 51–95% when they are moved between sites with very different landmark composition (Osgood 1974). Torchio (1991) moved *Osmia lignaria* Say in their nesting materials in small shelters (front surface up to 81 by 43 cm) for distances between 30 cm and 193 km, and found that in all cases 100% of the nesting females were lost from the nesting site within 3 d. However, when nesting materials were attached to a large plywood sheet (2.4 by 2.4 m), most females (86%) continued to nest in the new location. Torchio (1991) concluded that visual landmarks that are sufficiently large and adjacent to the nesting shelter help females reorient to their nest and reduce dispersal.

In this study we set up 4 field experiments to investigate the possibility of moving actively nesting *O.*

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cornuta populations. We addressed the following 4 questions: (1) Does moving distance affect female reorientation and reestablishment? (2) Does the presence of visual landmarks adjacent to the nesting site help females reorient? (3) Is it possible to remove bees for some days and place them back at the same site without disrupting their nesting activity? (4) What is the maximum distance at which females are able to relocate their nest (homing ability)?

Materials and Methods

Experiments 1–3 were conducted in almond orchards in the neighboring towns of Santa Maria del Camí, Bunyola, and Lloseta (Mallorca, Spain) in 1995. Nesting shelters used in all 3 experiments consisted of a wooden box (53 by 35 by 40 cm) attached on its side to 4, 120-cm metal fence posts. *O. cornuta* females build linear series of cells in tunnels in wood, so that each shelter was provided with 12 solid wood blocks into which 25 holes (each 16 cm deep) had been drilled. Each of these holes contained a paper straw (15 cm long, 8 mm diameter), so that active nests could be pulled out and inspected. All shelters were installed between 2 almond rows, 2–4 m away from the nearest trees and facing SE. Distance between shelters was 500 m or more.

A group of 70 female and 140 male cocoons obtained from previous orchard pollination operations was used in each of 18 treatments, using 1,260 females and 2,520 males. Female cocoons were inserted individually in paper straws, and male cocoons were placed in an open cardboard box inside each nesting shelter. All cocoons were set out in the evening, when flowering was beginning (7–10 February 1995, depending on the orchard). Seven days after nesting activities began (females carrying pollen or mud) at each site, all of the straws in each shelter were inspected at night using a flashlight. The numbers of females found in the nesting materials were noted, and straws containing partially provisioned *O. cornuta* nests were marked on the outside at the level of the last partial or complete cell. Subsequently, the shelter was moved to a new orchard (experiments 1 and 2) or refrigerated (experiment 3). All relocations were to almond orchards in full bloom, except treatment 7 of experiment 1, in which the nesting shelter was moved to an area with ruderal vegetation. For most treatments, bees coming out of their nests the morning after the move were observed, and their flight sketched until they left the surroundings of the shelter. The same observation was repeated with females coming back to the shelter for the first time after the move. Both exiting and returning flights were scored as either *indirect*, when bees zigzagged or made wide loops in front of the shelters, or *direct,* when bees entered or exited their nest without zigzagging. Additional night counts of nesting females were conducted during the 2nd, 3rd, and 7th nights after relocation.

Within each experiment, differences among treatments on frequency of indirect exit flights were analyzed with the *G*-test. The simple correlation coefficient (*r*) was used to describe the relationships between moving distance (log transformed), percent indirect exit flights (arcsine transformed), and percent dispersing females (arcsine transformed).

Experiment 1. This experiment related moving distance to reorientation and establishment. The treatments were as follows: (1) Shelter not moved (control). (2) Shelter moved 3 m from original location. (3) Shelter moved 3 m from original location, additional identical shelter added to original location. (4) Shelter moved 135 m from original location. (5) Shelter moved 3 km from original location. (6) Shelter moved 8 km from original location. (7) Shelter moved 240 km from original location.

Experiment 2. This experiment assessed whether a visual landmark associated with the nesting shelter could help females reorient to a new site. A white plastic banner (2 m wide by 1.5 m high) with blue and yellow patterns (circles and diagonal bands) was tied between 2 trees, immediately behind the nesting shelters. This supplementary landmark was added, moved or removed according to the following treatments.

(A) Shelters without Initial Supplementary Landmark. (1) Shelter not moved, landmark added (control). (2) Shelter moved 3 m from original location, landmark added to new location. (3) Shelter moved 235 m from original location, landmark added to new location.

(B) Shelters with Initial Supplementary Landmark. (4) Shelter + landmark not moved (control). (5) Shelter + landmark moved 3 m from original location. (6) Shelter + landmark moved 200 m from original location. (7) Shelter not moved, landmark moved 5 m from original location. (8) Shelter not moved, landmark removed.

Experiment 3. To test whether a period of confinement affected the capacity of the bees to reorient, nesting materials were removed and maintained in a refrigerator (8°C) for 4 d. The 3 treatments were as follows: (1) Shelter relocated at original location after 4 d of confinement (control). (2) Shelter removed and relocated 3 m from original location after 4 d of confinement. (3) Shelter removed and relocated 900 m from original location after 4 d of confinement.

Experiment 4. The purpose of this experiment was to quantify the homing ability (distance at which females are able to relocate their nests) of *O. cornuta.* The experiment was conducted in 1996 in Sant Daniel (Girona, Spain) in a grassland surrounded by forage crops. A nesting shelter similar to the ones used in experiments 1–3 was placed in the grassland, and a total of 120 females and 200 males was released as described above on 21–25 March. Before release, each female was removed from her cocoon and individually marked with a numbered tag glued to her thorax. On 1–7 April, 50 females that had been nesting in the shelter for >7 d were imprisoned in their nesting straw with a cotton wad. These straws were immediately taken by car to one of several predetermined sites located at 0.8, 1.4, 1.6, 1.8, 2.0, 2.2, 2.4, and 2.6 km west of the nesting site, respectively. Once at the new site, the cotton plug was removed and the straw observed

Table 1. Number of *O. cornuta* females established at the nesting shelters of experiment 1 before and after treatment, and number and percent indirect exiting and entering flights the morning after treatment

Treatment	Before treatment n	Females established and % dispersal								% indirect flights			
		After treatment								Exiting		Entering	
		Night 1		Night 2		Night 3		Night 7					
		n	%	n	%	n	%	n	%	n	%	n	%
1 control	37	37	0	—	—	36	3	28	24	—	—	—	—
2 3 m	32	32	0	—	—	31	3	27	16	32	31	30	10
3 3 m + shelter	39	19	51	—	—	21	46	22	44	28	53	3	100
		20		—	—	17		17		—	—	—	—
4 135 m	30	21	30	—	—	23	23	25	17	30	53	3	100
5 3 km	41	9	78	11	73	7	83	8	80	32	91	4	100
6 8 km	35	13	63	14	60	13	63	15	57	35	68	3	100
7 240 km	46	13	72	13	72	—	—	13	72	—	—	—	—

In treatment 3 a new shelter was added at the original site and nesting females split between the 2 shelters.

until the bee came out and started flying. The straw was then taken back to the nesting site and inserted in its hole at the shelter, which was monitored for the arrival of the bee.

Results

Osmia cornuta flight activity began at 0740–1020 hours at 9–12°C and ended at 1800–1830 hours, often after sunset. Females in experiments 1, 2, and 3 emerged on the release day, and started nesting 2–3 d later. Prenesting females would hastily visit several holes in sequence, until they commenced a wide zig-zagging flight in front of the shelter, which signaled the selection of the last visited hole as a nesting cavity. Of bees that had established (at least 1 cell partially provisioned), 24% of the 1st morning exiting flights ($n = 110$) and 10% of the 1st morning returning flights ($n = 100$) were indirect. As nesting progressed, indirect flights tended to diminish.

Experiment 1. Females continued to nest in all marked straws from shelters 1 (0 m) and 2 (3 m) a day after treatment. The decline in the number of nesting females on subsequent days in both treatments (Table 1) is attributable to the natural aging of the population. Orientation flights for treatment 1 were not observed, but the behavior of treatment 2 females was similar to that described above for undisturbed females. Indirect flights were recorded for only 31% exiting bees and 10% entering bees (Table 1), and no females were seen flying around the original nesting site.

More than half of the females of treatment 3 (3 m + new shelter) made indirect exiting flights (Table 1), and some flew immediately to the new shelter (original site), but without entering any holes. Throughout the 1st hour, most females spent some time flying around the new shelter (100% indirect flights; $n = 30$), and briefly entering some holes, but none visited the old shelter. One hour later, several females were provisioning holes at the new shelter, whereas others were zigzagging in front of the old one, but without nesting. By evening, the population of females was divided between the 2 shelters (Table 1). Eighteen new nests were noted at the new shelter, and 21 abandoned nests at the old one. Throughout the fol-

lowing days, nesting progressed normally at both sites, but some of the 20 females at the new shelter returned to the old one, where some nests initially abandoned were provisioned again.

The percentage of indirect exiting flights at shelter 4 (135 m) was 53% (Table 1). In the next 2 h, only 3 females visited the shelter, entering and exiting several holes with indirect flights, whereas many females were seen flying at the exact original location of the shelter. At night, 70% of the females had reoriented and returned to the nesting shelter, and this percentage increased over the following days (Table 1). In this and other treatments, some of the females returning to the shelter after the 1st night following the move resumed their nesting activities in a partially provisioned nest (presumably their own), while others started a new nest.

Most exiting flights after treatments 5 (3 km) and 6 (8 km) were indirect (Table 1). Two hours later, only 2–5% of the females was seen visiting the shelters (indirect flights), repeatedly but without provisioning, and no females were seen returning to the original nesting site. No observations of initial exiting flights were made after setting out treatment 7 (240 km). The majority of females dispersed in treatments 5, 6, and 7 (63–78%), and, unlike treatment 4, the number of females staying at the shelters did not tend to increase over time (Table 1).

Differences among treatments in the frequency of indirect exiting flights were statistically significant ($G_4 = 28.122$, $P < 0.00001$).

Experiment 2. (*A*) *Shelters without Initial Supplementary Landmark.* No observations were made of the 1st flights after setting out treatment 1 (0 m + landmark), but in the following 2 h, only 5% of the females were seen approaching the banner. The number of nesting females was not affected by the addition of the landmark (Table 2). The percentage of indirect flights was high after treatment 2 (3 m + landmark) (Table 2), and 10% of the females were observed to approach the banner either when leaving the shelter or returning to it. However, all females continued to nest in the shelter (Table 2). We did not observe the 1st flights after treatment 3 (235 m + landmark), but 2 h after flight activity began, only 2 females were seen repeat-

Table 2. Number of *O. cornuta* females established at the nesting shelters of experiment 2 before and after treatment, and number and percent indirect exiting and entering flights the morning after treatment

Treatment	Before treatment n	Night 1		Night 2		Night 3		Night 7		Exiting		Entering	
		n	%	n	%	n	%	n	%	n	%	n	%
1 0 m + landmark	30	—	—	30	0	35	0	35	0	—	—	—	—
2 3 m + landmark	25	—	—	25	0	25	0	21	16	25	60	24	29
3 235 m + landmark	28	—	—	11	61	17	39	18	36	—	—	—	—
4 0 m with landmark	42	36	14	38	10	38	10	18	57	—	—	—	—
5 3 m with landmark	52	48	8	49	6	51	2	32	38	52	11	50	4
6 200 m with landmark	59	—	—	14	76	24	59	23	61	37	70	6	100
7 0 m, landmark moved	65	63	3	63	3	62	5	48	26	60	12	50	8
8 0 m, landmark removed	44	42	5	41	7	41	7	27	39	35	3	30	3

edly entering and exiting holes at the shelter. At the same time, many females were flying around the original nesting site. Night counts revealed a high initial dispersal (61%) that was reduced to 36% in consecutive nights (Table 2).

(B) Shelters with Initial Supplementary Landmark. The morning after treatments 4 (0 m with landmark) and 5 (3 m with landmark) bees did not fly near the banner. Although flights of treatment 4 were not scored, few exits and entries of treatment 5 were indirect (Table 2). The number of females that dispersed was low in both treatments (14 and 8%, respectively) (Table 1), and possibly attributable to weather factors (low temperatures and strong wind) rather than disorientation. In treatment 6 (200 m with landmark), 70% of the exiting females zigzagged widely in front of the banner (Table 2). A few of them flew along its edges. Only 6 females were found inspecting several holes and describing indirect flights at the nesting shelter 2 h later. Only 24% of the females spent the 1st night at the shelter, but an additional 15% returned to it over the following 2 d (Table 2). In treatments 7 (0 m, landmark moved 5 m) and 8 (0 m, landmark removed), few females exited or entered the nests with indirect flights (Table 2). Very few females were seen approaching the banner in treatment 7. Dispersal was very low (3 and 5%, respectively) in both cases (Table 2).

Differences among treatments of experiment 2B in the frequency of indirect exiting flights were statistically significant ($G_3 = 58.144$, $P < 0.00005$).

Experiment 3. All bees of experiment 3 survived after 4 d at 8°C. About half of the females in treatments 1 (0 m) and 2 (3 m) performed indirect exiting flights (Table 3), but dispersal was near zero in both cases (Table 3). In treatment 3 (900 m), 56% of the females flew indirect flights when leaving the shelter for the 1st time after the move. Only 2 returned to the shelter after 2 h, whereas many of them were hovering at the exact original nesting location. Dispersal was almost complete, and no females returned over the following days (Table 3).

Frequencies of indirect exiting flights for the 3 treatments were not statistically significant ($G_2 = 0.206$, $P = 0.902$).

Considering all treatments of all 3 experiments (except treatment 3 of experiment 1, in which a new shelter was added), moving distance (log transformed) was significantly correlated with percent dispersal (arcsine transformed) ($n = 17$, $r = 0.85$, $P < 0.0001$), and with percent indirect exit flights (arcsine transformed) ($n = 12$, $r = 0.73$, $P < 0.0075$).

Experiment 4. Nesting activity at the shelter of experiment 4 started on 24 March, and 66 females were counted in the nesting materials the night before the treatments. As many as 82% of the moved females flew in circles around the paper straw before flying away. The number of females that returned to the nesting shelter for each moving distance is indicated in Table 4. All females moved between 0.8 and 1.4 km and most (87%) of those moved between 1.6 and 1.8 km relocated their nest. Very few females returned after moves of greater distances (2–2.6 km). Return time logically increased with moving distance (Table 4), but 12 of the 25 females that returned had the scopa full of pollen, indicating that they had been foraging during the flight. All returning females entered their

Table 3. Number of *O. cornuta* females established at the nesting shelters of experiment 3 before and after treatment, and number and percent indirect exiting and entering flights the morning after treatment

Treatment	Before treatment n	Night 1		Night 2		Night 3		Night 7		Exiting		Entering	
		n	%	n	%	n	%	n	%	n	%	n	%
1 4 d 8°C + 0 m	47	46	2	42	11	37	21	29	38	45	51	23	13
2 4 d 8°C + 3 m	50	49	2	42	16	38	24	20	60	50	54	30	30
3 4 d 8°C + 900 m	45	1	98	1	98	1	98	1	98	32	56	2	100

Table 4. Number of *O. cornuta* females returning to their nesting shelter after being moved several distances

Moving distance, m	Females moved	Females returning	Return time, min	
			Mean	Range
800	5	5	51	23–72
1,400	5	5	81	26–155
1,600	5	4	148	31–>180
1,800	10	9	111	35–>180
2,000	5	1	63	—
2,200	5	1	127	—
2,400	5	0	—	—
2,600	10	0	—	—

nest in a direct flight, and, after spending a longer than usual time inside, resumed nesting normally.

Discussion

Homing Ability. The results of experiment 4, supported by observations from experiments 1 and 2, establish the maximum homing ability of *O. cornuta* at ≈1.8 km. This figure is greater than homing distances recorded for *Osmia cornifrons* (Radoszkowski) and *Osmia pedicornis* Cockerell (400–700 m) (Kitamura and Maeta 1969), but lower than those found for larger solitary bees (Rau 1929, Kapil and Dhaliwal 1969, Janzen 1971). Because *O. cornifrons* and *O. pedicornis* are smaller than *O. cornuta*, this result is in agreement with the generally perceived positive association between body size and homing ability (Michener 1974, Abrol and Kapil 1994, van Nieuwstadt and Ruano Iraheta 1996). Studies on honey bees and stingless bees indicate that the homing ability of a species is an approximate indicator of its maximum foraging range (Roubik 1989, van Nieuwstadt and Ruano Iraheta 1996), although most workers forage at much shorter distances (Visscher and Seeley 1982). Most *O. cornuta* females released in orchards forage within 100–200 m of their nesting shelter, depending on the availability of floral resources (Vicens 1997), but this distance probably increases in natural habitats, where floral resources are more scattered. Besides enabling females to forage for longer distances, distant homing abilities may allow them to relocate their nest after being blown away by strong winds.

Nest Location and Recognition. Mid- or long-distance nesting site moves are undoubtedly rare events in nature, and dispersal appears to be a common response to such moves in several bee species (Free 1958a, Kapil and Dhaliwal 1969, Osgood 1974, Torchio 1991). In this study, both dispersal and zigzagging flights, interpreted as orientation flights in which the insect memorizes a series of landmarks as references to locate its nesting site (Tinbergen 1958), increased in frequency with moving distance. This relationship may result from increasing differences in terrestrial or skylight orientation cues as moving distance increases, or simply from the vibrations associated with the transport of the nesting materials for longer periods. We favor the 1st explanation because, in experiment 3, nesting materials of all treatments were transported

for long periods to and from the refrigerator, but dispersal was negligible after shelters were relocated at 0 and 3 m from the original site.

Several observations indicate that artificial landmarks used in this study (banner, shelter) were detected by *O. cornuta* females: (1) some individuals inspected the edges of added banners the morning after the moves; (2) females whose shelter was moved 3 m hovered around the original nesting site only when a new shelter was installed; (3) in 3-m moves, zigzagging flights remained infrequent (11–31%) when the surroundings of the shelter were not modified with the move, but increased (53–60%) when supplementary landmarks were added or removed. However, these landmarks do not help to abate dispersal rates in moved populations, probably because they only act as secondary cues in nest location. Thus, zigzagging flights remained rare (3–12%) at unmoved shelters with added or removed landmarks, and females moved within their homing range were able to pinpoint their original nesting site even when the shelter had been removed.

At close range, nest location by female *Osmia* depends, at least partially, on visual landmarks, and nest recognition on olfactory cues (Steinmann 1976, Steinmann and Menzel 1990, Raw 1992). Females mark their nest entrance with secretions, probably from the mandibular glands (Rosner 1994), and individuals with severed antennae are unable to recognize their nesting cavity (Steinmann 1976). Nest recognition is well developed in *O. cornuta.* A. Lacasa (CIDA, Murcia, Spain; personal communication) rotated a nesting shelter 90°, and although females initially searched the side of the shelter where the cavity entrances originally were, they all had relocated their cavity and continued to nest normally after 2 h. This behavior contrasts with that of female *O. lignaria*, which were unable to find their nest on a wooden block when this was moved from one side of a tree trunk to the other (Torchio 1991). Another important difference between *O. cornuta* and *O. lignaria* is the capacity to resume nesting after the initial disorientation caused by shelter moves. In *O. cornuta*, even after the longest moves, some females continued to nest at the relocated shelter and, at medium distances, some initially dispersing females returned to the nesting shelter after 2 or 3 d. In contrast, *O. lignaria* females that initially stay at the relocated shelter soon abandon it and disappear from the site (Torchio 1991).

Relocation of Nesting Populations. The results of experiment 3 demonstrate that it is possible to remove active *O. cornuta* populations and reinstall them 4 d later without affecting the nesting activity or survival of nesting females. This treatment is similar to a natural situation in which bees are forced to remain in their nests during a long spell of bad weather (Vicens et al. 1994), and it can be used to avoid bee poisoning if quickly degrading insecticides need to be used during bloom. Metabolic expense may be reduced by keeping the bees under their thermal activity threshold (9–12°C; Vicens 1997).

However, the strong conditioning of *O. cornuta* females to their nesting site, and the secondary role of supplementary visual landmarks adjacent to the shelter in nest location, causes considerable female dispersal (30–76%) even in medium-distance moves. Although some females eventually return to the moved nesting shelter, these losses result in a significant decrease in pollination and reproductive capacity of the population. Because the foraging range of *O. cornuta* females extends for at least 200 m and their homing ability is ≈1,800 m, the benefit of moving populations a few hundred meters is little. At longer distances (kilometers), dispersal is still greater (63–78%), but such moves may be advisable depending on the benefit obtained by the increased pollination and reproductive success of the females that do not disperse. In *O. lignaria*, 86% nesting females returned to a nesting shelter moved 600 m when a large artificial landmark (2.4 by 2.4 m) was added (Torchio 1991), and commercial *M. rotundata* populations are moved routinely between alfalfa fields in large trailers, although there is little information on actual bee losses (Bohart 1972). When available, prominent landmarks (trees, buildings, nesting shelters) appear to be used by *M. rotundata* females as cues for nest location (Osgood 1974). In *A. mellifera*, prominent landmarks (roads, forest edges) may substitute for celestial cues (direct sunlight and polarized skylight) in orienting workers to familiar locations, especially on overcast days (von Frisch and Lindauer 1954, Dyer and Gould 1981). *A. mellifera* is also known to adapt rapidly to new "landmarks" (patterns that the bees fly past) but to learn "targets" (patterns seen ahead) more slowly and to ignore changes to them (Horridge 1996). Therefore, the possibility of providing landmarks different from the ones used in this study should be investigated as a potential means to reduce *O. cornuta* female dispersal in long distance moves. This would increase the pollinating and reproductive capacities of *O. cornuta* populations used for pollination of short-flowering crops.

Acknowledgments

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