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Author(s): Colin M. Wainwright

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HYMENOPTERAN TERRITORIALITY AND ITS INFLUENCES ON THE POLLINATION ECOLOGY OF *LUPINUS ARIZONICUS*

COLIN M. WAINWRIGHT¹

Department of Plant Sciences, University of California, Riverside, 92521

ABSTRACT. Males of *Anthidium palmarum* Cockerell, and of *Anthophora* sp. display territorial behavior, presumably to gain advantage in reproduction through the dispersal of sexually mature males. The territories maintained by these insects are based on the food plants of their females. *Lupinus arizonicus* (Wats.) Wats. can be a food plant for females of both species. Consequently an individual lupine plant may occasionally occur in the overlapping territories of male *Anthidium* and male *Anthophora* bees. The peak activities of these two species are separate. *Anthophora* bees are active in the early morning and late afternoon, and *Anthidium* bees are active in the mid-morning and mid-afternoon. Territories are maintained through regular patrols and periodic confrontations. Confrontations were of three types: first, territorial defense against other territorial males; second, territorial protection against other insects; and, third, sexual encounters with their own females. The territorial and sexual behavior of *Anthidium* and *Anthophora* males influences the pollination ecology of *L. arizonicus* by altering the behavior of *Anthidium* and *Anthophora* females (which in this case are the primary pollinators of *L. arizonicus*) as well as honey bees, leafcutting bees, and several lepidopterans.

Territoriality among Hymenoptera has been reported for a few species, including a cicada killer bee (Lin 1963), several andrenid bees (Linsley and Michener 1962; Cazier and Linsley 1963; Shinn 1967), carpenter bees (Watanabe 1958; Linsley 1963; Cruden 1966), a crepuscular bee (Roberts 1971), two neotropical parasocial bees (Zucchi et al. 1969), a halictine (sweat) bee (Barrows 1976), leafcutting bees (Vleugel 1952; Hass 1960), bumble bees (Hass 1949), several species of *Centris* (Raw 1975), and several species of *Anthidium* (Green 1921; Ward 1928; Sitowski 1947; Hass 1960; Taylor 1962; Pechuman 1967; Jaycox 1967; Kurtak 1973).

Anthidium male bees exhibit extremely aggressive behavior while

¹ Current mailing address: Horticulture Dept., Grant High School, 13000 Oxnard St., Van Nuys, CA. 91401.

maintaining a territory (Green 1921; Ward 1928). These males physically ram and sometimes injure intruding insects other than female *Anthidium*. Confrontations between *Anthidium* males have been described by Jaycox (1967). However, territorial disputes between *Anthidium* males and other territorial hymenopteran males are apparently undescribed. Observations on the pollination ecology of *Lupinus arizonicus* (Wats.) Wats. (Arizona lupine) revealed such territorial disputes between a male *Anthidium palmarum* Ckll. and a male *Anthophora* sp.

The purpose of this paper is to describe the territorial behavior and interactions between a male *Anthidium* and a male *Anthophora*, and to relate this behavior to the pollination ecology of *L. arizonicus*. Data are given for a 24 h period and are representative of data gathered on other days and for other populations. Where there were much larger populations of *L. arizonicus*, the major pollinator was *Apis mellifera*.

MATERIALS AND METHODS. Field observations were made on the east-facing alluvial fan of Henderson Canyon (elevation 488 m), in Anza-Borrego Desert State Park, San Diego Co., California. A 25 m² portion of a small population of scattered *L. arizonicus* (density of 0.08/m²) was selected for studying pollination activity during 19-31 Mar 1976. Two individual lupine plants occurred at the site selected for observation of pollination behavior. Plant #1 had three inflorescences and plant #2 had 18 inflorescences. The two plants had a combined total of approximately 126 flowers at the proper stage for insect visitation (Wainwright 1977).

Observations were made continuously from 1 h before dawn to 1 h past dusk, with one 45 min break during the day. Observational records of the time, duration, and type of insect activity including pollination behavior and territorial behavior, insect confrontations, and the air temperature were tape recorded on a Norelco 0085 pocket recorder. The number of times that an insect appeared in the observation area (frequency) was calculated for every half hour. Similarly frequency of confrontations was based on a half-hour period.

Insects were collected on 31 May in duplicate from this study site and from a second location approximately 250 m away. All individuals were examined for pollen deposition. Pollen loads were analyzed for composition (Wainwright 1977) and the contributing pollen was identified. Voucher insect specimens are deposited with the Los Angeles County Museum of Natural History.

OBSERVATIONS AND DISCUSSION. *Territory establishment*.—On 30 Mar sunrise was at 0540 (Pacific Standard Time). An *Anthophora* male appeared at the observation site 1 h after sunrise and a male *Anthidium* 2 h later. They each proceeded to set up territories (Fig. 1) by regular patrolling and acts of aggression. The

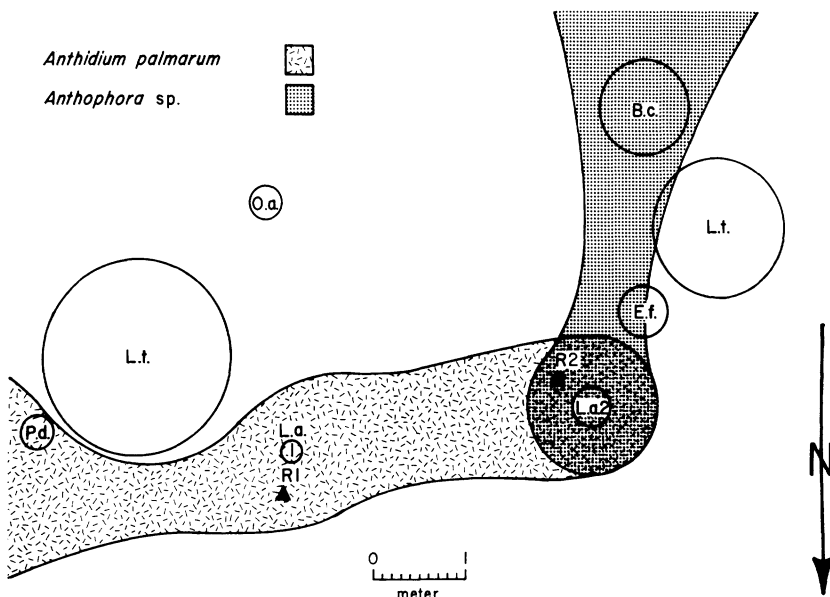
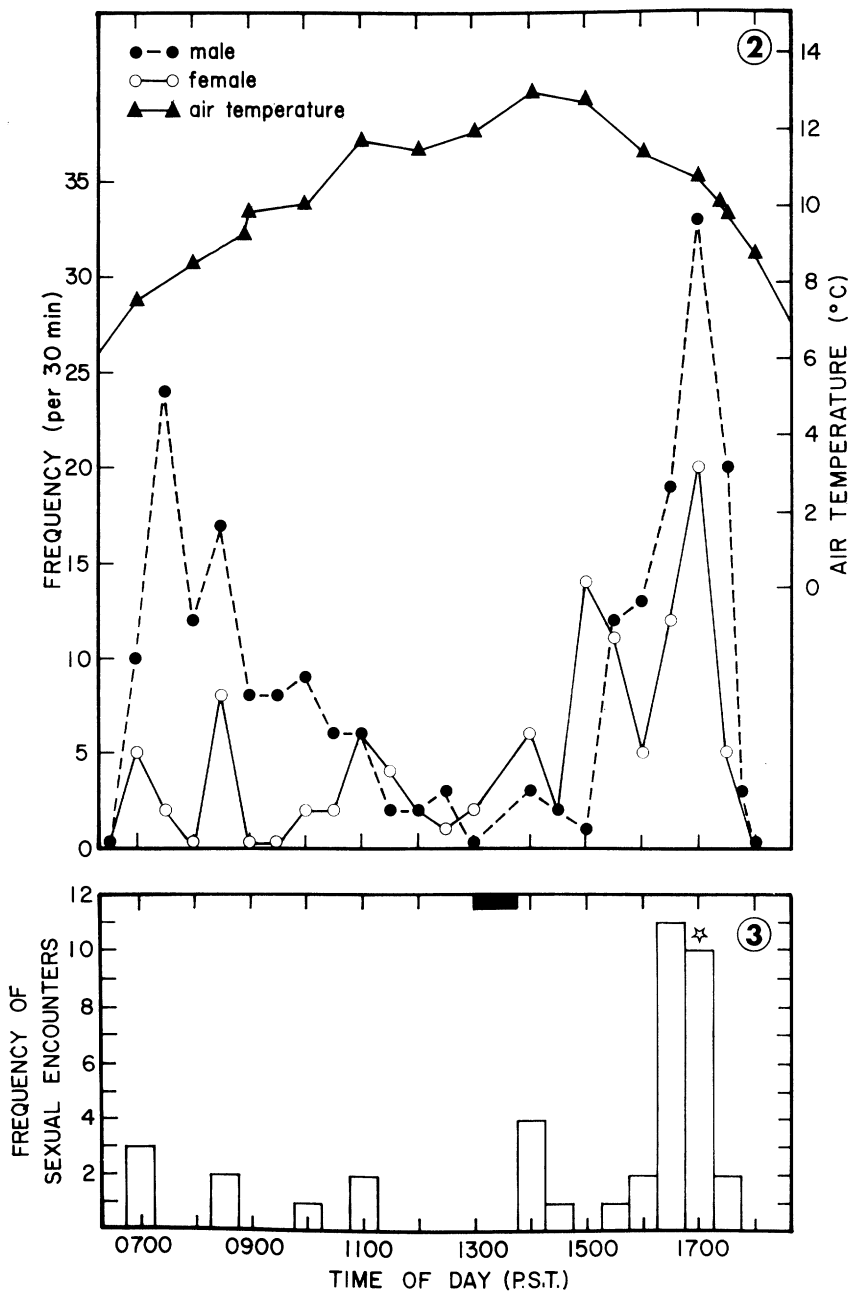


Fig. 1. Schematic diagram of the main study site in Henderson Canyon with approximate outlines of the territorial boundaries of a male *Anthidium palmarum* and a male *Anthophora* sp. B.c. (*Beloperone californica*), E.f. (*Encelia farinosa*), L.a. 1 (*Lupinus arizonicus*, plant #1), L.a. 2 (*Lupinus arizonicus*, plant #2), L.t. (*Larrea tridentata*), O.a. (*Opuntia acanthocarpa*), P.d. (*Phacelia distans*), R 1 (rock #1), R 2 (rock #2).

patrols of the *Anthophora* male included hovering in the vicinity of the flowers of *Lupinus arizonicus* and a large *Beloperone californica* (Benth.) and occasional stops on a twig of *Larrea tridentata* Cov. or a leaf of *Encelia farinosa* Gray. The male *Anthidium* patrolled by hovering in the vicinity of lupine flowers on two plants and stopping occasionally on one of two rocks. The patrolled areas overlapped in an area which included one lupine plant and a rock. Both species never engaged in pollen collection in the study site but frequently approached the lupine flowers, inspecting each of the open flowers that had not undergone the spot color change which occurs about 4 h postpollination (Wainwright 1977). The times of maximum activity of these males of the two species were different (Figs. 2 and 4). *Anthophora* males had a peak activity during the early morning (0700-1000 h) and late afternoon (1500-1800 h), whereas *Anthidium* males were most active during late morning (0900-1100 h) and early afternoon (1400-1600 h). Both had intermittent activity through the rest of the day.

Anthophora sp.



Behavior of female bees—The activity of the females (Figs. 2 and 4) more or less followed the pattern of the males throughout the day, although they appeared less often than the males. The *Anthophora* females first appeared in the study site at 0706 h, some 20 min after the male *Anthophora*. By 0848 h (when the first male *Anthidium* appeared), the female *Anthophora* bees had made 14 trips into the study area and thoroughly visited all 21 inflorescences of both the lupine plants at least twice. The first female *Anthidium* bee visited a *Lupinus arizonicus* at 0815, shortly before the arrival of the male *Anthidium*. The *Anthophora* females occurred more frequently than the *Anthidium* females, and also had a marked increase in frequency in the afternoon (1430-1730 h), whereas the *Anthidium* females had scattered occurrences throughout the activity period.

The pollen foraging behavior of the two species differs (Wainwright 1977). The female *Anthophora* hovers in the air above each flower with the head facing the yellow-white banner spot of the unfertilized flower. The wing and keel petals are depressed by the legs and the pollen is gathered by the hind legs. The pollen is placed on corbicular sacks while in flight from flower to flower. On the other hand, the *Anthidium* female alights on the flower with its head against the banner spot. Head leverage is utilized to depress the wing petals with the middle and front legs, while the hind legs stroke the sides of the keel, forcing the pollen out of the keel-beak. Pollen is then packed on the ventral side of the abdomen. Both species are polylectic in their foraging behavior (Table 1). The pollen load from an *Anthophora* female consisted mostly of pollen from *Beloperone californica*, with smaller amounts from *Lupinus arizonicus* and *Camissonia boothii* (Dougl.) and trace amounts from *Chaenactis fremontii* (Gray), *Salvia columbariae* Benth., and one unknown plant. The pollen from an *Anthidium* female was mostly from *Phacelia distans* Benth. and smaller amounts from *Lupinus arizonicus* and *Malacothrix glabrata* Gray. The percentage of lupine pollen for each species was approximately the same.

Confrontations—Three types of confrontations were observed.

Fig. 2-3. 2. Frequency of male and female *Anthophora* bees within the study site on 30 May 1976 with hourly air temperature readings. 3. Frequency of sexual encounters between a territorial male *Anthophora* and *Anthophora* females. Solid bar indicates rest period. * indicates copulation.

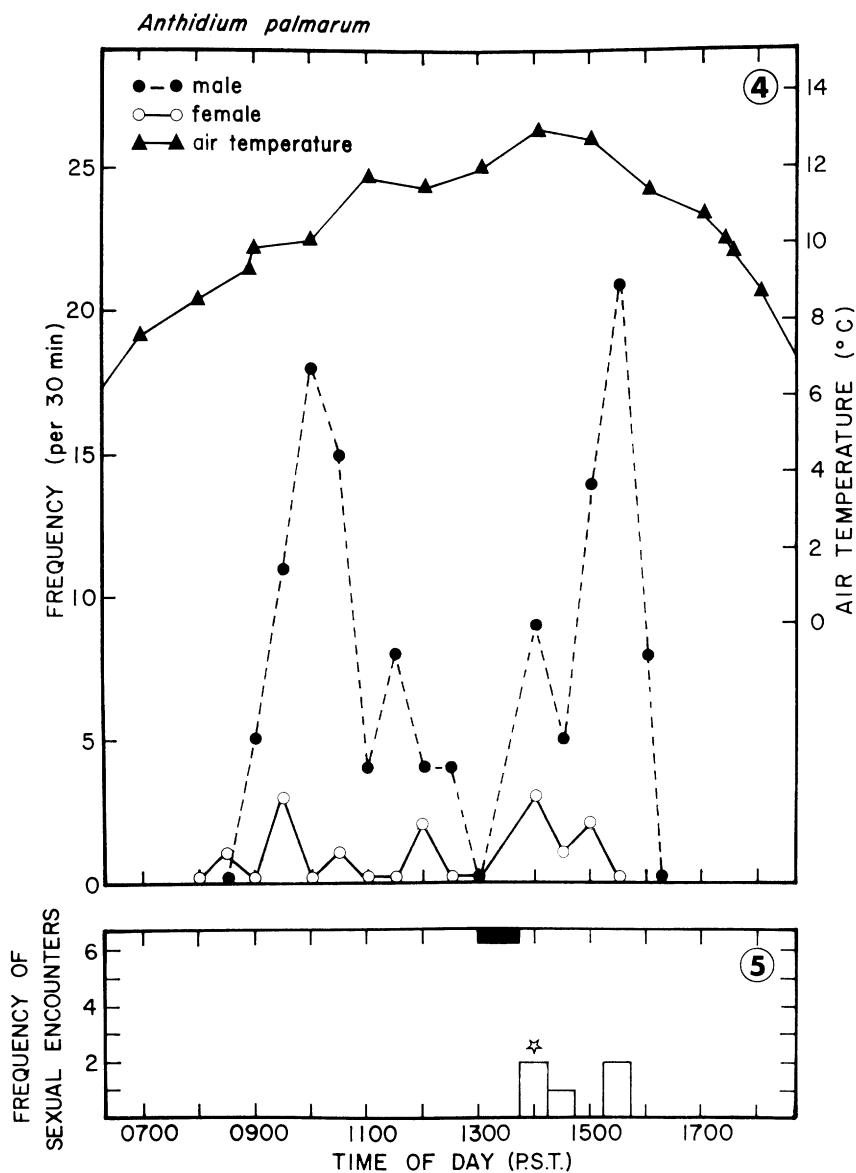


Fig. 4-5. 4. Frequency of male and female *Anthidium* bees within the study site on 30 May 1976 with hourly air temperature readings. 5. Frequency of sexual encounters between a territorial male *Anthidium* and *Anthidium* females. Solid bar indicates rest period. * indicates copulation.

TABLE 1

Analysis of pollen deposition of females of Anthidium and Anthophora bees. Values based on duplicate counts from two individuals. Each count totaled 750 to 1000 pollen grains.

Pollen species	Percent pollen composition	
	<i>Anthidium</i>	<i>Anthophora</i>
<i>Beloperone californica</i>		80.9
<i>Phacelia distans</i>	84.7	
<i>Lupinus arizonicus</i>	13.4	14.7
<i>Camissonia boothii</i>		4.1
<i>Malacothrix glabrata</i>	1.9	
<i>Chaenactis fremontii</i>		0.1
<i>Salvia columbariae</i>		0.1
unknown species		0.1

Firstly, there was defense of the territory against territorial males of the same or another species. Acts of territorial defense between the *Anthophora* and *Anthidium* males occurred within 6 min after the male *Anthidium* began establishing its territory, which overlapped that of the male *Anthophora* (Fig. 1). The defensive acts involved the flying of the aggressor directly at the intruder but without physical contact, whereupon the intruder withdrew. The first actual confrontation was initiated by the male *Anthophora* as a defense of its territory against the intruding male *Anthidium*. All subsequent male-male confrontations appeared to be initiated by the male *Anthidium* (Fig. 6). The male *Anthophora*, however, maintained its territorial patrols despite the assaults of the male *Anthidium*. This type of confrontation was at a maximum from 0900-1030 h and from 1530-1600 h, when the maximum activity of both males overlaps. Confrontations between the territorial male *Anthidium* and other male *Anthidium* bees were of a different type, involving direct physical assault by the territorial male.

Another type of territorial confrontation had to do with the protection of the flowering material within the territory against other insects, including both prospective foragers and non-foragers (Fig. 7). Acts of territorial protection by the male *Anthidium* did not begin immediately, even though other insects were within the territorial limits. The peak protective confrontations occurred during the peak *Anthidium* activity, with the greatest number of confrontations being directed towards the female *Anthophora* bees in

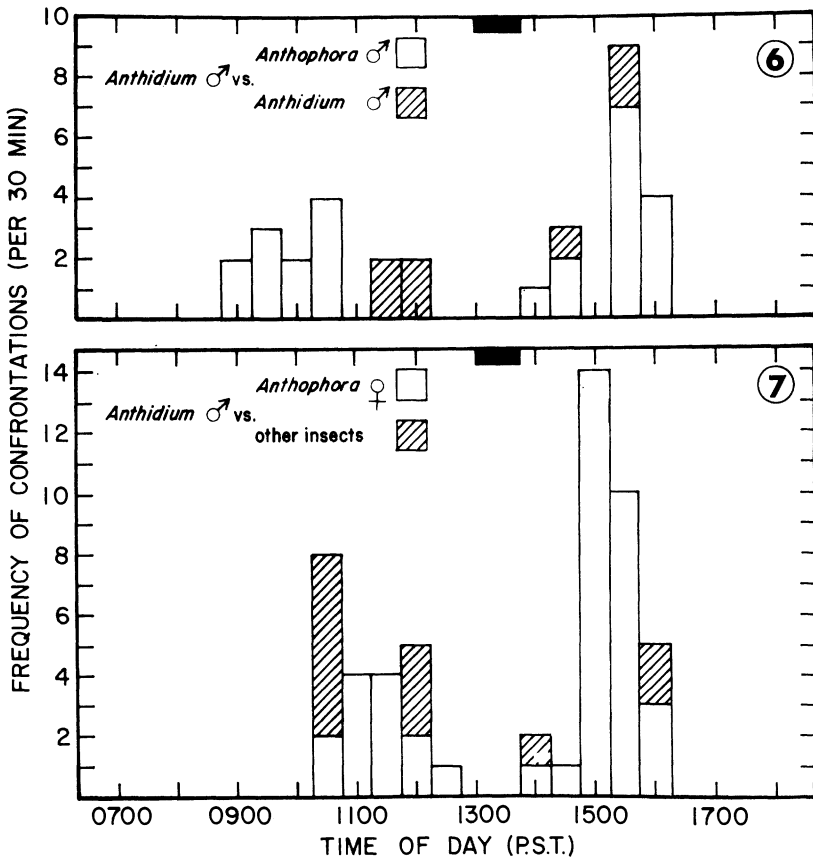


Fig. 6-7. Frequency of confrontations. 6. Territorial defense by a territorial male *Anthidium* versus a territorial male *Anthophora* and versus other territorial *Anthidium* males. 7. Territorial protection by a territorial male *Anthidium* versus *Anthophora* females and versus other insects. Solid bar indicates rest period.

the afternoon period. Acts of territorial protection during the morning period, however, were directed against other hymenoptera and some lepidoptera. All acts of territorial protection involved direct physical assaults against such intruders.

The third type of confrontation involved sexual encounters during which a territorial male attempted to copulate with females of that species while the female foraged for pollen among the flowers within the territory of that male (Figs. 3 and 5). *Anthophora* male-female encounters (Fig. 3) were scattered throughout the day, with the highest frequency occurring in the late afternoon activity peak (Fig.

4). *Anthidium* male-female encounters (Fig. 5) also occurred primarily during the mid-afternoon activity peak. Most attempts at copulation were unsuccessful due to the ready flight of the female. In the area under observation, encounters resulting in successful copulation appeared to occur once in the day for each species.

The influence of insect behavior on pollination of Lupinus arizonicus—As described previously (Wainwright 1977), *Lupinus arizonicus* flowers develop spirally along the inflorescence at a rate of 5-6 flowers per spiral per day. Anther dehiscence occurs prior to anthesis. However, the stigma, positioned at the apex of the keel, is receptive only 24 h postanthesis and, if not pollinated, remains receptive for 5-6 days before the flower aborts. Thus approximately each day there is a newly opened whorl of flowers which have pollen but no stigma receptivity. At the end of the first day post-anthesis, about 96 percent of the pollen has been removed from that whorl of flowers by insect vectors. During the second day post-anthesis, pollination operates on a false reward system.

The behavior of the territorial male *Anthidium* and *Anthophora* influences flower visitation. Territorial protection against females of the other species, as well as against other hymenoptera and lepidoptera, interrupt pollen foraging and other insect pollination mechanisms. In addition, attempts at copulation with their own species also appear to hinder pollination. The greatest intensity of pollen foraging by *Anthophora* females occurred in the early morning when the males were primarily involved in acts of territorial defense rather than in sexual encounters. In the afternoon, although the frequency of *Anthophora* females was high, foraging was minimal. This could be due to 1) the increase in acts of territorial protection by the male *Anthidium* between 1430 and 1630 (Fig. 7) and 2) the increase in sexual encounters with the territorial male *Anthophora* between 1600 and 1745 (Fig. 3). The pollen foraging by *Anthidium* females was similarly hindered in the afternoon, presumably by the increase in sexual encounters by the territorial *Anthidium*.

Since all the flowers are thoroughly visited in the morning, when there is virtually uninterrupted foraging, it is unlikely that the afternoon hinderance of pollen foraging has an adverse effect on pollination. On the contrary this scheduling of maximal territorial and sexual confrontations in the afternoon is probably of advantage to both the insects and *L. arizonicus* pollination.

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