

THE SOCIAL ORGANIZATION OF MALE POPULATIONS OF *CENTRIS PALLIDA* (HYMENOPTERA, ANTHOPHORIDAE)*

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This report is one in a series of papers on the reproductive behavior of the solitary bee *Centris pallida* Fox. Elsewhere we have shown that males of this species exhibit a behavioral dimorphism in mate-location strategies, with some males flying low over the ground searching for virgin females about to emerge and other males hovering around the borders of emergence sites as well as by flowering trees (Alcock et al., 1976; in press). The patrollers excavate virgin females from their emergence tunnels and then copulate with them; hoverers secure mates by pursuing air-borne virgins which they capture in flight.

Our earlier studies left unanswered several questions about the spatial organization of male populations of this bee, including

- 1) Do patrolling males exhibit loyalty to a particular portion of an emergence site and if so, for how many days?
- 2) How much area do patrollers examine?
- 3) Do males that hover remain at a particular aerial station for any length of time?

Almost nothing is known of the behavior of male solitary Hymenoptera with respect to the size of the territory or home range of individuals and the duration of time males spend on a territory or home range (Alcock et al., in prep.). After following a large sample of marked bees from the start of the emergence season to its conclusion, I am able to provide information on the social structure of male populations of *C. pallida*, especially with reference to the degree of site tenacity and degree of territoriality shown by hovering and patrolling males.

*Manuscript received by the editor October 4, 1976

MATERIALS AND METHODS

This study was conducted from April 30-May 31, 1976 at two locations separated by about 0.7 km in the floodplain of the Salt River about 4 km south of Saguaro Lake, north of Mesa, Arizona. Both emergence sites were open areas with well-packed soil ranging from sand to clay in composition. These areas had a sparse covering of grasses with scattered shrubs (*Ambrosia deltoidea*) and were bordered by mesquite (*Prosopis* sp.) and palo verde (*Cercidium* spp.) trees.

In order to follow the history of individual males, bees were captured with an insect net and given an identifying color combination of enamel paint marks on the dorsum of their thorax. Marking did not appear to disrupt the behavior of the bees seriously as most individuals quickly resumed their activities prior to capture. Six samples of patrolling males ($N = 153$) were collected and marked at Site 1 between April 30-May 15. Three samples totalling 76 males were taken at Site 2 from May 19-May 23. In addition, 47 hovering males were marked at Site 1 from May 1-17 as well as 20 copulating males; at Site 2, 41 copulating males were captured and marked (all copulating males were believed to have been patrolling prior to copulation).

Data on marked bees was gathered by censusing the study site on a daily basis from 30 April to 31 May with four exceptions (on two of the four days there was little or no male activity because it had rained heavily the night before). During the period from 0800-1030 my assistants and I tried to recapture as many marked males as possible; sometimes when a male was seen on the ground digging it was not necessary to capture the bee in order to identify it. A map was made of Site 1 and the points where several bees were captured and recaptured were recorded on the map. In other cases, the distance between successive sightings of a male were paced off to collect information on the approximate length of movements by known individuals.

RESULTS

Home ranges of patrolling males

In large emergence sites dozens to hundreds of males may be present in the period from 0800-1030 cruising rapidly within a few cm of the ground. The patrolling males are not distributed

Table 1

Recapture data on samples of marked males of *Centris pallida*.

	Number Marked	Number Recaptured on Another Day
Patrolling Males		
Study Site 1	153	83 (54%)
Study Site 2	76	58 (76%)
Copulating Males		
Study Site 1	20	13 (65%)
Study Site 2	41	26 (63%)
Hovering Males		
Study Site 1	47	18 (38%)

evenly; it is not uncommon for a location 10 m² to have several dozen males swirling over it while an adjacent area of equivalent size has fewer than ten individuals. The samples of males were taken for marking from limited areas (rarely covering more than 20 m² and usually less) where males were relatively abundant. Follow-up searches on subsequent days were concentrated in these areas and they quickly revealed that many marked individuals returned day after day to the same limited portion of the total emergence site. A large majority of the marked patrolling males were seen again on at least one other day (Table 1) and for the population as a whole, the average interval between the day of capture and the day of last sighting was 3.44 days (Fig. 1). Because patrolling males tend to return to the same area but do not defend it they can be said to possess home ranges (patrolling males ignore other flying males but will fight intensely for a specific digging site containing a pre-emergent female).

If we analyze the recapture frequencies of patrolling and copulating males in Site 1 vs. Site 2 (lumping copulating males with patrollers because copulating males had been patrolling prior to their capture *in copula*) we find that patrollers were significantly more likely to have been recaptured after marking in Site 2 than Site 1 ($X^2 = 6.61$, d.f. = 1, $P < .01$). This difference probably reflects higher mortality experienced by males in the first study area. There were two heavy rains accompanied by unusually cold weather

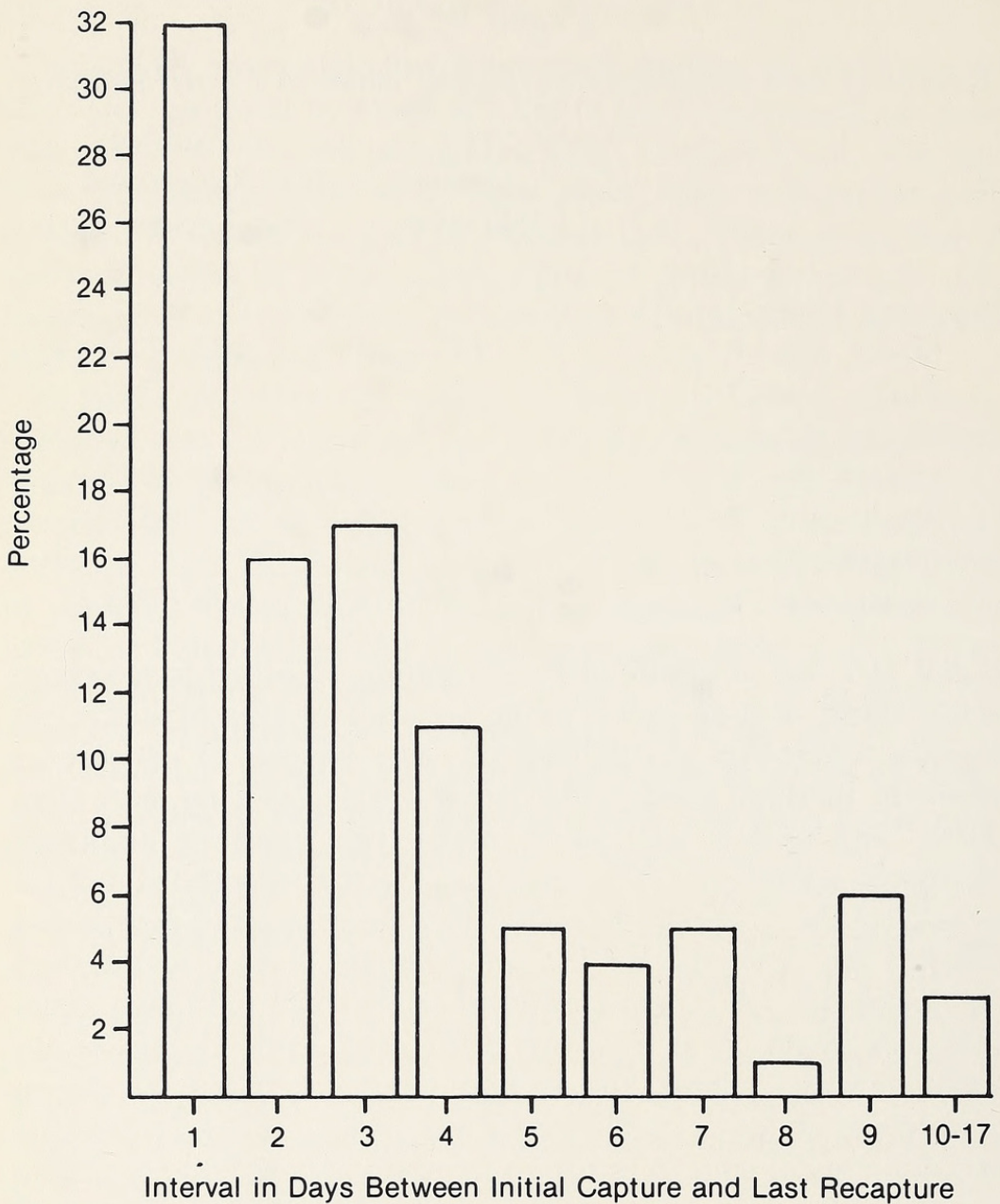


Fig. 1. Data on the duration of occupation of a home range by males initially captured while patrolling an emergence site and then marked and released.

in early May. Because males spend the night in shallow burrows and under rocks they run the risk of becoming drenched during rains. Judging from the matted thoracic hairs of survivors observed after the rains, many males did become soaked and this may have caused mortality in some cases.

Efforts to determine the size of home ranges of individual males were hindered by the great rapidity with which the bees flew over

the ground when searching for digging sites. It was impossible to determine the color combination of flying males and it was difficult to capture them as well. Often a marked male was seen close up (while digging) or was captured only once or twice during the morning flight period over emergence areas. Nevertheless, a considerable number of males were seen frequently in the same general area over a period of days. The positions of twelve of these males were plotted on maps of the study sites for periods of 2-9 days of observation; these individuals covered areas roughly 8-46 m² (\bar{X} = 18 m²; s.d. = 12.5 m²). This seemed to be the typical pattern although we have records of eight males that were seen at two separate centers of emergence about 25-35 m apart. Three additional males moved back and forth several times between locations that were separated by at least 80 m. Finally, at least some males moved permanently from one emergence area to another distant one, with five males found patrolling sites 60-100 m from the point of their capture and two others patrolling about 200 m from where they were taken initially.

To repeat, the very large majority of males that were recaptured were never found outside an area of about 50 m² around the point of original capture. Those males known to patrol two searching areas and those known to have moved large distances make up a very small minority of the total recaptured males. Thus although the activity in a large emergence area appears chaotic and random, in reality the region is divided into a large number of broadly overlapping home ranges with individual males systematically patrolling small portions of the total available searching area.

The behavior of hoverers

At Site 1 males were found hovering a few cm above the ground centered in depressions or openings surrounded by short desert shrubs under a meter in height, as well as close to the ground around the edges of mesquite trees, and at all altitudes in flowering palo verde trees. Those males hovering at low aerial stations in and around emergence sites were present primarily during the peak hours for emerging females (0830-1100). Males hovering at or near flowering trees were present throughout the day although there may be a slight decline after the period of female emergence (Fig. 2).

Hovering males continually leave their aerial station to pursue passing insects, usually for a few seconds only, before returning

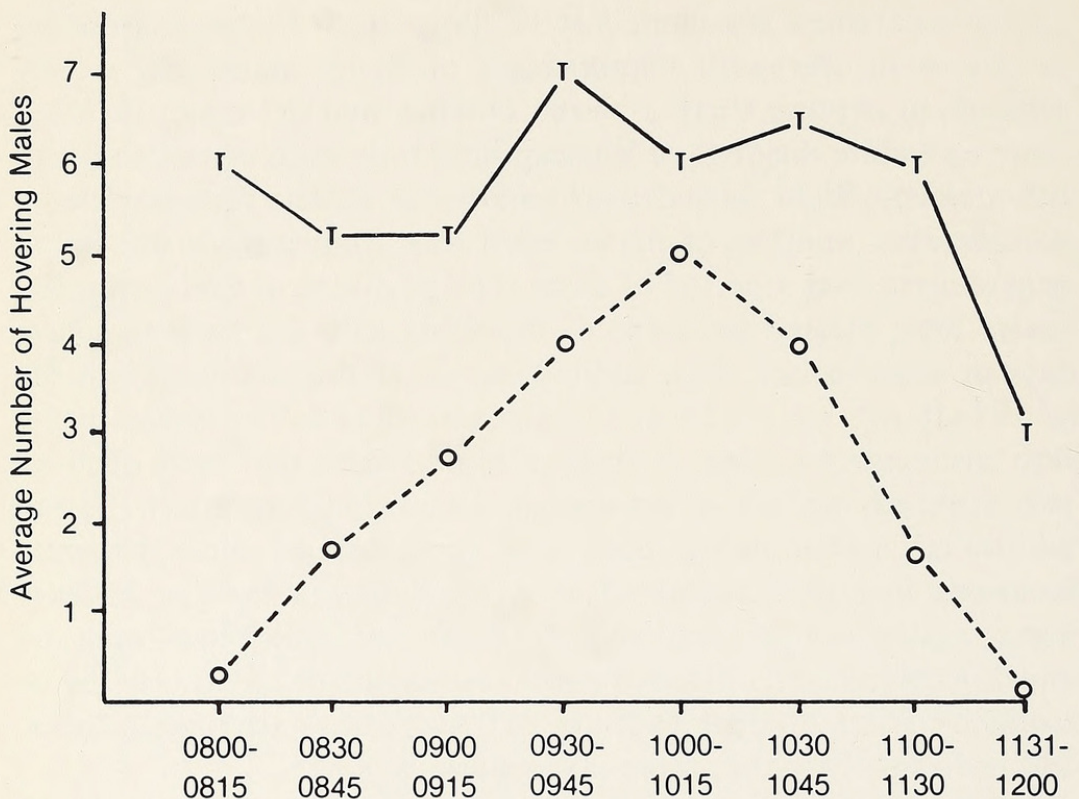


Fig. 2. The average number of males seen at different times in the morning hovering in and around a flowering palo verde tree (solid line) and close to the ground near small bushes and by the edge of a mesquite tree along a census strip through an emergence site (dotted line). Each point represents 2-4 counts (mean = 3.2) with the censuses made between 30 April - 3 May, 1976.

to their hovering point. Conspecific males that come within a meter or two of a hoverer are usually pursued and I saw a few aggressive interactions with butting and very brief midair grappling bouts. These males might be considered territorial because of these rare aggressive events and the fact that hoverers are spaced a meter or more apart. Nevertheless, as noted in an earlier paper (Alcock et al., in press), the spatial distribution of hovering males may result from a generally passive dispersal of individuals into available hovering areas rather than from the active, vigorous defense of chosen aerial stations. Many of the male-male pursuits probably involved attempts by the pursuer to determine if the passer-by were a receptive female.

Hovering males were significantly less likely to be recaptured than males that had been patrolling prior to initial capture and marking (Table 1; $X^2 = 5.02$; d.f. = 1; $P = 0.025$). In addition,

the interval between marking and last sighting for those males captured while hovering was only 2.62 days. Included in these results are four males that were hovering when first captured but which later switched to become patrollers. (A small minority of all marked males, $N=20$, exhibited the capacity to patrol and to hover, frequently doing both on the same day, patrolling in the early morning and later hovering.) Thus unless hovering males experienced a much higher rate of mortality than patrollers (which seems unlikely), one must conclude that these males were more likely to move long distances from day to day. This is not to say hoverers completely failed to exhibit site tenacity. Hovering males were continuously present at their aerial stations for several hours, while patrolling males often appeared only at irregular intervals in their searching ranges. Moreover some hoverers did return to a general area, and often a specific site, over a period of days. One male appeared at a specific location among the branches of a palo verde for four days running; another maintained a low aerial station by a creosote bush for five consecutive mornings. These males were, however, definitely the exception to the rule.

DISCUSSION

Males of the bee *C. pallida* are unusual in exhibiting two very different techniques of mate-location (patrolling and hovering), although one or the other of the two patterns is associated with a great many species of Hymenoptera (e.g. Evans, 1966; Frison, 1917; Linsley, 1965; Rozen, 1958; Shinn, 1967) including various other species of *Centris* (Frankie & Baker, 1974; Raw, 1975). The coexistence of these two divergent strategies in a single species appears related to the great variation in size of males of *C. pallida*. Size influences the ability of males to claim digging sites in competition with other males (Alcock et al., in press). Thus large males patrol and dig, small males hover. As I have shown in this paper, these two activities are linked with different tendencies to defend space against conspecific intruders and to return to a particular location. These differences are discussed below.

The pattern of short-term (several hours) residence at an aerial station or perch associated with apparent defense of the area (or at least non-overlapping distributions of males) is not unique to *C. pallida*. These traits occur in such unrelated solitary Hymen-

optera as the oaxaeid bee *Protoxaea gloriosa* (Cazier & Linsley, 1963; Linsley & Cazier, 1972; Alcock, pers. obs.) and a number of philanthine wasps (Alcock, 1975). The question arises for all these species, why should a male remain in an area for a period of hours, holding the site exclusively, only to abandon it completely, taking up residence at distant sites on subsequent days? The key to this problem may lie in the very low frequency of mating by the hovering/perched males mentioned above. Judging from the extreme rarity of observed copulations, a waiting male in these species has almost no chance of encountering a receptive female, no matter where he chooses to hover or to perch. Thus the value of a vast array of potential waiting sites must be nearly equivalent (i.e. close to zero). Given the equivalence of many sites it is not surprising that males often shift their hovering/perching sites from day to day (probably selecting an unoccupied suitable location that happens to be near the male at the moment). Shifting would also be promoted by a "musical chairs effect". If there are many males present, it is likely that a bee would find his old waiting site taken when he arrived to reclaim it on the following day. It may not pay to fight over an occupied site if there are many other equally good unoccupied places nearby. The result would be continual shifting of males as they avoided one another, taking whatever hovering/waiting site that happened to be open to them. When conspecifics are rare, hoverers might be expected to show more site tenacity because they would be less likely to find their previous day's hovering station occupied when they reached it on the next day. At Study Site 2, there were very few hoverers present and these appeared in the same aerial stations several days running. A male that has claimed a site might defend it to avoid the time costs of shifting to a new one and because it costs so little to defend it. A new arrival, finding the site taken, would have very little motivation to contest ownership because of the abundance of equally good waiting locations nearby.

In contrast to the weak territoriality and low site tenacity shown by hovering *C. pallida*, males of this species and others that patrol emergence areas ignore one another when searching the emergence site, yet show a stronger site attachment than hoverers. The persistence of home ranges in patrolling *C. pallida* almost certainly stems from the clumped nature of the resource, emerging virgin

females. Within a large emergence area there are patches from which a relatively large number of females emerge over a period of days. For example in Study Site 2, one area of about 10 m² produced a large proportion of the total copulations we observed at this location. The tendency of patrolling males to return to these areas of higher-than-average productivity is clearly adaptive, although the underlying basis for the ability to locate such sites is not known (perhaps males are attracted to sites that would attract nesting females, or perhaps males can judge from the abundance of digging males or numerous contacts with females that a particular location is superior and deserving of continuing inspection). The failure of males to defend searching areas is almost certainly a function of the high density of fellow searchers which would make defense of any but the smallest area extremely costly in terms of time and energy. Indeed, males become aggressive only when digging at a spot potentially containing a buried virgin female, repelling competitors from an area a few cm² around their body (Alcock et al., 1976; in press).

SUMMARY

Males of the bee *Centris pallida* that patrolled emergence sites in search of emerging females possessed highly overlapping home ranges of 10–25 m². Marked patrollers were found in the same general area for an average of 3.4 days. Males that hovered at spots while waiting for receptive females to fly near them possessed weakly defended non-overlapping territories a few m² in size. Marked hoverers rarely returned to a specific hovering site and averaged only 2.6 days from the date of capture to time of last sighting. Relatively long-term occupation of a home range may be adaptive for patrollers because of the clumped distribution of emerging females. In addition the high density of male competitors would make defense of a large area difficult and energetically expensive. Relatively short-term occupation of a hovering territory may be adaptive for hoverers because there are many potential hovering sites, all of which have the same low value to a male. This reduces competition for any one site making its defense feasible; at the same time, the low probability of mating

at a hovering site means that a male gains no particular advantage by returning to a specific location day after day.

ACKNOWLEDGMENTS

I would like to thank my assistants, Fred Lindstrom, Kathy Opfenring, Terry Ponder, David Post, and Patricia Ryan, for their hard work and good company in the field. This study was supported by NSF Grant DEB76-04503.

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