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## The scramble competition mating system of the sphecid wasp *Palmodes praestans* (Kohl)

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### Abstract

Males of the wasp *Palmodes praestans* engage in non-territorial patrolling behaviour within a scramble competition mating system, showing great fidelity to their wide-ranging patrolling routes without attempting to monopolize the areas covered. Scramble competition appears adaptive given that mating opportunities are not spatially aggregated in this species, whose females build isolated, single-celled nests. Because of the female distribution pattern, a male's reproductive success in *P. praestans* probably depends upon the ability to find highly scattered, unmated females. The females of some close relatives of this sphecid wasp form fairly dense nesting aggregations. As mating system theory predicts, the males of some (but not all) of these species focus their searching at these concentrated nesting/emergence sites where potential mates are clustered spatially.

**Keywords:** *Mating tactics*, *Palmodes praestans*, *Sphécidae*, *Sphex*

### Introduction

Little is known of the biology of the sphecid wasp *Palmodes praestans* (Kohl). The only report to date on the species is a note on the wasp's prey, *Capnobotes fuliginosus*, a long-winged, shield-backed katydid in the Tettigoniidae (Caudell 1919). Here we summarize our observations of male and female behaviour of this species as a contribution to the natural history of the Sphécidae. Our focus is on the mating tactics of males. We contrast the mating system of this species with the mate-locating behaviour exhibited by some members of the genus *Sphex*, a slightly better-studied group of katydid-hunting sphecids.

### Materials and methods

This study was conducted within the period from 16 April to 14 May in the Utery Mountains, Maricopa County, near Mesa, Arizona. This mountain range has a maximum elevation of about 900 m. The habitat is characterized by gravelly soil and sparse vegetation

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typical of the Upland Sonoran Desert, including foothills paloverdes (*Parkinsonia microphyllum*), saguaro cacti (*Carnegie gigantea*) and other smaller cacti as well as jojoba (*Simmondsia chinensis*), creosote bush (*Larrea divaricata*) and other smaller desert shrubs. Additional descriptions of the area are provided in Alcock (1979) and Alcock and Schaefer (1983).

During the study period, we captured and marked samples of patrolling male *P. praestans* at three locations on sloping hillsides, all within a kilometre of one another. No focal area was larger than  $15 \times 40$  m. The wasps were given distinctive dots of paint on the thorax and wing edges, using Liquid Paper Typewriting Correction Fluid or a fine-tipped paint pen (Edding 780 silver marker and DecoColor Opaque Paint Pens). After release, the areas were monitored, usually for an hour or so during the morning on days scattered through the study period. An effort was made to identify all males seen flying through or perching in the areas under observation. On occasion, identification was achieved by netting the wasps and then releasing them; on other occasions, it was possible to identify the males by visual inspection with binoculars.

In addition to our mark-recapture and resighting programme for males, we recorded any sightings of females in the area, including all information on male-female interactions.

Means are presented throughout  $\pm$  SE.

## Results

When active, males of *P. praestans* generally fly slowly, close to the ground, although occasionally they rise up over the surface of shrubs before dropping down again. During the cooler early morning, they sometimes perch briefly on the ground before resuming flight. Males usually cannot be followed in flight for more than 30 s before they travel out of view, flying more or less in one direction down, up or across the hillside.

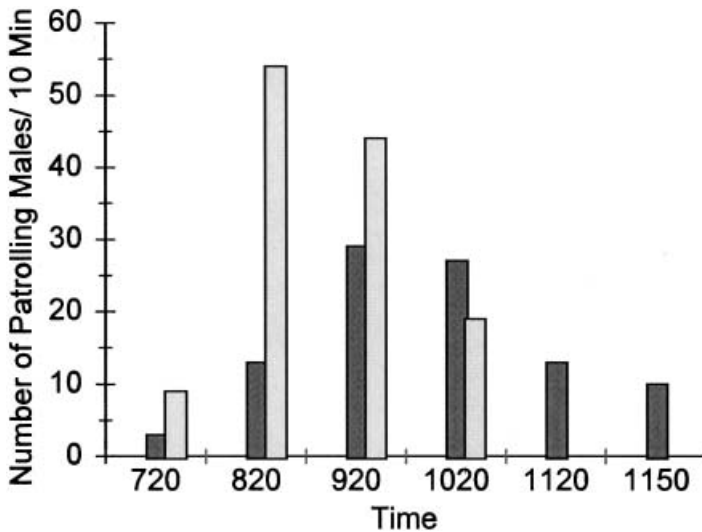


Figure 1. The total number of records of males of *Palmodes praestans* seen patrolling in an area roughly  $15 \times 40$  m in the Utery Mountains, Arizona on two mornings in April 2004. Each sample was made over a 10-min period beginning at the time shown on the x-axis.

The number of males seen in one focal area peaked at mid-morning, based on two samples taken on 21 and 25 April (Figure 1). At times of highest activity, males regularly encountered one another, with one individual pursuing the other and often making mid-air contact, even pouncing upon a fellow male before separating. Two males sometimes tumbled to the ground in these cases. Male–male interactions were extremely brief with a mean duration of only  $1.87 \pm 0.14$  s ( $N=86$  records made on 3 days from 17 to 26 April 2004).

Several lines of evidence suggest that at least some males had repetitive patrolling routes. First, the same individual was often resighted or recaptured in the same general area more than once within the same morning. Thus, on 21 April 2004, for example, seven of eight marked males seen in location A were spotted anywhere from 2 to 10 times during five observation blocks totalling 2.5 h, with a mean of  $5.1 \pm 1.3$  resightings for this group. The maximum interval between resightings on this day was over 4 h, with a mean of  $2.3 \pm 0.5$  h ( $N=7$ ).

Second, marked males regularly returned over many different days to the same area in which they were marked. Site fidelity was high with 36 of 46 males (78%) marked at the three locations returning on at least one day after the day of capture (see also Figure 2). Moreover, the mean intervals between first and last sightings was substantial at each location:  $8.7 \pm 2.1$  days at location A,  $8.9 \pm 1.2$  days at location B, and  $9.2 \pm 2.0$  days at location C. These are surely underestimates of the actual site-fidelity of patrolling males, given that some of the wasps captured on the first day of the study exhibited substantial wing wear, suggesting that the flight season was already well under way. The maximum interval between first and last sighting of a marked male in his patrolling area was 28 days, with eight males known to remain in the same location for at least two weeks, despite our intermittent and generally brief (ca 1 h per day) observation periods.

Some males were much more frequently sighted than others (Figure 2), suggesting that males varied in the degree to which their patrol routes overlapped and fell within the focal observation areas.

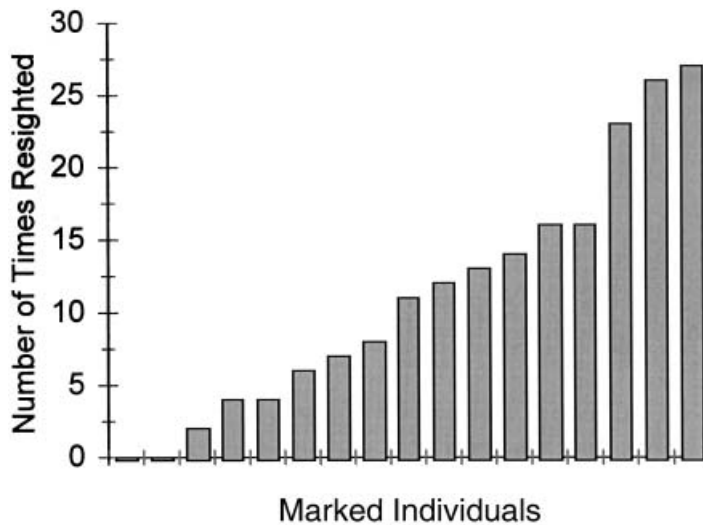


Figure 2. The number of times each of 17 different males was seen again within the observation site where he was captured initially and marked.

Male–female interactions occurred rarely. On seven occasions, males pounced upon flying or nest-digging females but released them instantly. However, on two occasions much longer interactions were observed, each involving a male mounted upon a female that he grasped firmly with his mandibles (Figure 3). In one instance starting at 09:22 h on 22 April, a male–female pair was first seen on the ground where they were approached and contacted briefly by a patrolling male. Soon thereafter, after being disturbed by a whiptail lizard (*Aspidoscelis tigris*), the pair flew to a nearby paloverde where the male remained mounted for 13 min, while attempting to copulate at intervals. The female blocked all these attempts, by twisting her abdomen away from her partner or by keeping her wings between her abdomen tip and that of the male. The pair was still together when we left the area.

On 19 April, a pair also consisting of a male mounted on a female was spotted moving about on the ground at 10:09 h. This pair remained together for 44 min before we abandoned the site. During this period, the male made repeated efforts to copulate with what appeared to be an uncooperative female. She almost always moved or twisted her abdomen away whenever the male probed with his abdomen tip in an apparent effort to reach her genital opening. However, the male did succeed in copulating briefly in the middle of the 44-min block. We do not know if copulation also occurred before or after this period but for most of the time when we saw them together, the male was mounted on the female but not *in copula*.

Nesting females were observed near or within all three male patrolling zones but at very low density ( $N=1, 1, \text{ and } 2$  nests). In two cases, the nest was located when the female was seen dragging a penultimate instar of the katydid *Capnobotes fuliginosus* to the burrow.

## Discussion

The mating system of *P. praestans* involves non-territorial patrolling of a home range by site-faithful males that evidently engage in scramble competition to find rare and dispersed



Figure 3. A male (marked with a white dot on the thorax) mounted on a female of *Palmodes praestans* during a period when the pair was not copulating.

receptive females. These females can be assumed to be recently emerged virgins, given the apparent lack of receptivity of nesting females. Recently emerged virgins must be widely scattered in space because the wasps' nests are not clumped, judging from our discovery of only a few active burrows. Moreover, these nests remained active for only a couple of days, indicating that females fill in their burrows after provisioning for only one offspring, the standard pattern for the genus (see Krombein et al. 1979, p 1584). Not only are virgin females widely separated spatially, they are also surely temporally dispersed, based on the relatively lengthy male flight season of at least one month.

Among the Sphecidae (and many other animal groups) when receptive females are scarce and widely dispersed, males often engage in scramble competition for mates (Thornhill and Alcock 1983). In contrast, when females emerge in clusters or when resources that attract females are concentrated in small areas, the fitness benefits of territoriality often outweigh its costs, and the result is female defence or resource defence polygyny (Emlen and Oring 1977; Alcock et al. 1978; Thornhill and Alcock 1983). Unfortunately, we cannot examine the relation between female distribution patterns and male mating tactics among species of *Palmodes* because only *P. praestans* has been studied in this regard.

We can, however, compare the mating system of *P. praestans* with that of a few species in the closely related genus *Sphex*, another sphecid whose females also specialize in the capture of katydids that are subsequently placed in underground nests. In *Sphex cognatus*, for example, females nest in moderately dense aggregations and they retain their sexual receptivity while nesting; males of this species fly out from perches within the nesting area to capture and mate with prey-laden females that are returning to their nests (Ribi WA and Ribi L 1979; Evans et al. 1982). The fact that males have specific perches and are larger than females (a feature associated with physical competition among males) strongly suggests an element of territoriality and a female-defence mating system related to the spatial clustering of potential mates.

Likewise, Gillaspay (1962) observed a prey-laden female of *S. tepanecus* mating twice in short succession at her nest entrance, which occurred within an area containing a number of other burrows of this species. Therefore, at least two species of *Sphex* with aggregated nests feature males that locate mates at the nesting site.

A third species, *S. ichneumoneus*, is also known to form substantial nesting aggregations. Moreover, females provision multi-celled nests. One would therefore predict that males would focus their search at nesting sites (if nesting females retain their sexual receptivity) or at these sites during the emergence period (if virgin females mate just once). However, females apparently are not receptive immediately upon emergence nor do they retain their receptivity when nesting. Brockmann and Dawkins (1979) specifically note that mating does *not* occur within emergence/nesting aggregations in *S. ichneumoneus*. Thus, not every sphecid wasp mating system matches the expectation that males will search widely for mates, if females are scattered widely, but will focus on nesting/emergence areas, when nesting females aggregate. Clearly, we have more to learn about the evolution of mating system diversity in insects.

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