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Authors
Thomas, JF
Nonacs, P

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The characters that appeared to best show variations in the soldier caste of *M. strunckii* were the total length of the body and the minimum width of the postmentum.

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Size Dimorphism and Male Aggregation Behavior in the Sand Wasp, *Steniolia nigripes* (Sphecidae: Bembecinae)

by

Jeffrey F. Thomas[1] & Peter Nonacs[1]

ABSTRACT

We observed aggregations of the sand wasp, *Steniolia nigripes*, in the Granite Mountains of Southern California. Males gathered in open areas between bushes in a sun-dancing behavior very close to the ground. They did not hold exclusive territories. Aggregations were highly visible, but occurred at low densities in the area. Males often chased each other and females, who would approach the aggregation, then leave with males following closely or attached to her. Females often burrowed around the edges of the aggregation. We captured and measured male and female head width, dry weight and thorax length. Males were significantly larger than females in all of these measurements. Intrasexual selection resulting from scramble competition for access to mates may drive this dimorphism. As these aggregations did not occur at obvious landmarks, it is possible that the aggregations themselves serve as a landmarks for females.

INTRODUCTION

Male mating aggregations have been frequently described in various taxa. In insects, both ground (or substrate) based aggregations and aerial (or swarm) aggregations are found (Gullefors & Petersson 1993, Choe & Crespi 1997). Work on solitary wasps has begun to show a large range in male mating and aggregation behaviors (reviewed in O'Neill 2001), with males of some species gathering in clusters, others defending female nests or emergence sites and others gathering in non-aggressive groups.

Males and females of *Steniolia obliqua* (Sphecidae: Bembecinae) gather at clusters in the evening. Evans (1966) found close to 300 individuals clustered on a branch tip in Wyoming. Males and females were seen to leave the cluster together to mate. These clusters may have multiple functions: to act as a thermoregulatory roost in the evening and to provide mating opportunities (Evans & Gillaspy 1964, Evans 1966). Some species of *Bembix* (Sphecidae) also gather in aggregations

[1]Department of Organismic Biology, Ecology and Evolution, University of California, Los Angeles, CA 90095-1606 Email: Jfthomas@ucla.edu & Email: pnonacs@biology.ucla.edu

for sun dances (reviewed in O'Neill 2001) near female emergence sites. These males patrol areas in nearly continuous flight, remaining near the ground. Males overlap and intercept each other, but show no real aggression or territoriality.

While there is some work describing the mating and clustering behaviors of *Steniolia obliqua*, little other information exists on any of the other *Steniolia* species. *S. nigripes* is a poorly studied species of sand wasp that shows patterns of behavior similar to that described for the *Bembix* spp. This species has crowded male aggregations that are visited by females for mating.

The purpose of this paper is to describe the aggregating and some mating behaviors of male *S. nigripes*, a bembicine sand wasp found in the deserts of Southern California. Specifically, we will address wasp density in the aggregation; aggregation density in the area; the behaviors of individuals in the aggregation; and the size ranges of individuals at the aggregation sites.

METHODS

We observed the wasps at the University of California, Sweeney Granite Mountains Nature Reserve, Riverside County California, between May 26th and June 5th 1998. Male *S. nigripes* never appeared on the aggregation before 0800 during the study period and most individuals had departed the aggregations by 1300. We conducted all timed observations between 0930 and 1200. The reserve is a mid-elevation desert (1300m) with both Mojave and Sonoran desert characteristics. The habitat consisted of dry desert vegetation, mostly made of creosote (*Larrea tridentata*) and burrobush (*Ambrosia dumosa*). The research locations were all spaced on a flat bajada, with widely spaced vegetation.

We surveyed 108,000m^2 of habitat using 10 x 100m transects and 4 x 80m transects in search of mating aggregations to estimate overall density of these aggregations at this site. Each transect line was spaced 20-25m apart. Observers walked each transect and surveyed 12.5m on each side of the transect line looking for aggregations. At one of the mating aggregations, we caught and marked 23 wasps by sweep netting individuals at the site. We placed novel color combinations on the thorax of captured wasps, then released them within 50m of the capture site. Some individuals were seen on the mating grounds within 30 minutes of release. We made observations of activity patterns at each mating site by performing 20-minute activity censuses. We counted every instance of a behavior during each time block. Behaviors under observation were chases, connections and digs. We defined chase as any event in which patrolling males left the aggregation by chasing

another individual. Two categories of chases were seen: either of other patrolling males or of females moving through the site. We identified a behavior as a connection if (at least) one male mounted and maintained its position on a female or on another male. We classified events as digs when females entered a mating site low to the ground and began digging small burrows at the site. We often saw females returning later with other insects to stash in the burrow. Only the initial digging was categorized as a burrow. Males never burrowed, helped females to burrow, or pursued females down a burrow. We did not monitor female behaviors outside the aggregation.

On June 5th 1998, 59 wasps were captured and placed in alcohol. We measured thorax length, head width, forewing length, forewing width at its widest point and dry weight of each wasp. We sexed individuals by the number of antennal flagellomeres (Bohart & Gillaspy 1985).

RESULTS

In our survey of 180,000m^2 we found only four mating sites being used (including the three under study) with more than 10 individuals. At each location, multiple females had burrows and a number of patrolling males were present. We never found an aggregation consisting of only one sex, though males were the only ones present in the first hours of the morning. Mating site locations are relatively small, the largest of the three sites being only 16.5m^2. Up to 50 individuals could be counted at a single mating site during an observation and were not located at any apparent landmark. For males, the baseline activity consisted of flights at approximately 2 cm above the ground. These flights patrolled a small subset of the total aggregation area, so that a single individual never used the entire aggregation. The areas patrolled by a male overlapped the patrolled areas of from one to many other males. Males did occasionally land on the ground within the patrolled area, but would return to low, circular flight quickly. These alternations of patrolling flight and rest were only interrupted by chasing or connecting with other individuals during the observation period. Unlike some other species, *S. nigripes* aggregations were not located on plants, but in areas between them. Individual wasps might patrol areas bordered by plant material, but not every area within an aggregation contacted any plant material.

None of the three locations were elevated above neighboring areas, nor was there anything unusual about the vegetation surrounding the sites. The vegetation at each site was primarily creosote and burrobush. We never saw wasps feeding at flowers on any of the shrubs surrounding the aggregation, though feeding wasps could be found on flowers of the same species at locations outside of the aggregation. The soil in which females burrowed was hard packed dirt and gravel and not noticeably different from the surrounding areas.

Activity at an aggregation generally consisted of patrolling activities by males. Males began arriving to the aggregations at approximately 0830 on most mornings, or when the air temperature at ground level was approximately 17°C. A single male arriving first would patrol large portions of the aggregation area. As more males arrived, many chases and fights were seen between males and the areas used by individuals would become smaller, though still not exclusive. The most common activity of males was patrolling. Males would occasionally stop flying and sit on the ground and groom for a short period of time before returning to its patrol. Next to the basic patrolling behavior of males, chases were the most common behavior seen. Any wasp that landed on the ground, such as a burrowing female or resting male was highly likely to be approached and grabbed by a patrolling male. Chases were not always initiated towards females. Sometimes other males or other flying insects were briefly chased. We witnessed attempted copulations (males grabbing onto a female or other male) frequently, eight or more in a 20-minute block of time. At the initiation of observations, the number of males on the aggregation was near its peak and most males patrolled areas overlapped by several other males. By 1230, most males had left the mating sites and could sometimes be seen foraging elsewhere. Females would often remain near the mating site and continue to begin new nests and provision previously dug nest sites. Neither sex was observed resting overnight on or near the aggregation sites.

All wasp measurement characters differ significantly between males and females (table 1: t-test, $P<0.001$), with males being larger, on average, in each case. In thorax length and dry weight, males show more variance in the traits than females. Females have slightly more variance in head width than do males.

DISCUSSION

It is unclear why *S. nigripes* aggregates where it does. Neither males nor females are obtaining significant resources at the site, nor are there any apparent visual or floristic cues drawing individuals into a particular site. While females are using the area surrounding the aggregation for their nest burrows, there is no apparent reason why female nest sites are aggregated within the relatively uniform bajada. Nevertheless, these aggregations form at the same location over consecutive days and males can occupy the same site within an aggregation over multiple days. Males did not feed while in the aggregation and appear to be gathering

Table 1. Physical measurements (in mm) from *Steniolia nigripes*.

		Both (n=59)	Male (n=20)	Female (n=39)
Thorax:	Mean	5.52mm	5.91mm**	5.31mm**
	S.D.	0.403	0.363	0.227
	Range	4.8 -> 6.4mm	5.1 -> 6.4mm	4.8 -> 5.7mm
Head Width:	Mean	4.76mm	4.89mm**	4.70mm**
	S.D.	0.192	0.156	0.170
	Range	4.4 -> 5.1mm	4.5 -> 5.1mm	4.4 -> 5.1mm
Dry Weight:	Mean	0.039g	0.044g**	0.036g**
	S.D.	0.006	0.004	0.005
	Range	0.028->0.058g	0.034->0.058g	0.028->0.046g
Wing length:	Mean	10.7mm	12.262mm**	10.040mm**
	S.D.	1.2	0.838	0.541
	Range	8.7->13.4mm	9.8->13.4mm	8.7->10.9mm
Wing depth:	Mean	2.7mm	3.069mm**	2.566mm**
	S.D.	0.3	0.353	0.157
	Range	2.1->3.6mm	2.3->3.6mm	2.1->2.8mm

**= significant at $p<0.001$

in these locations solely to mate with adult females. Males were never seen burrowing or following females while they burrowed. Females, the limiting sex, may be drawn in to the male aggregations (Parker 1978).

There was a high level of male intrasexual chasing. Whether this behavior is aggression or recognition error is unclear in this species. Although male aggregation may be explained by female aggregation, why females nest in groups and are receptive to mating is not clear. There seems to be a minimal cost for the females in terms of female-female competition. We never observed aggression between females or raiding of other females' burrows. If there are no observable costs to such close nesting, neither are there any observable benefits. No parasites or predators were observed attacking the nests during the aggregations, so the possible benefits of a common defense could not be ascertained. After the wasp activity had subsided for the day, the burrows were on occasion discovered and destroyed by ants (*Myrmecocystus* spp.). Nesting aggregations would seem to increase this risk rather than decrease it.

It is possible that the male aggregations themselves could serve as landmarks for the females. Large aggregations are discernible both visually and audibly at a distance of at least 10m (to humans). *Polistes dominulus* (Beani & Calloni 1991) and several *Xylocopa* spp. are known to use chemical cues that may serve to attract females or to mark territories from other males (Vinson & Frankie 1990). Larger aggregations of males may be able to produce a stronger chemical signal to attract more females (Emlen & Oring 1977) and males of other species of the sphecid wasp are attracted to female pheromones (O'Neill 2001).

Copulations appear to be the result of multiple males chasing a female from the aggregation. After an initial fight, one male is left attached to the female and copulates. Size or flying ability may provide an advantage to a male for remaining attached to the female and receiving a copulation. It is unknown, however, if females are able to evaluate males and if there is a mating advantage to males of certain sizes.

Males in this species, sampled at the aggregation, are larger than females, the opposite situation from other sphecids (O'Neill 1985). Larger male body size may not be indicative of the actual population size ratios. In *Bembecinus quinquespinosus* males who patrol emergence areas are, on average, larger than females and have better success in holding onto a female during a mating flight and fending off other males. Males outside these aggregations are much smaller and rely on finding solo females for their mating opportunities (O'Neill *et al* 1989). Without a more in-depth sampling of wasps off the aggregations, it is difficult to tell whether there is only one, or more than one mating strategy for the males.

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