

**AN ENORMOUS NEST OF *VESPULA SQUAMOSA* FROM  
FLORIDA, THE LARGEST SOCIAL WASP NEST REPORTED  
FROM NORTH AMERICA, WITH NOTES ON COLONY CYCLE  
AND REPRODUCTION**

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*Abstract.*—A nest of *Vespula squamosa* (Drury) is described including colony size, biomass, and ecological impact. This is the largest vespid nest described from North America to date.

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INTRODUCTION

Most species of social wasps in North America form small, seasonal colonies. The cosmopolitan genus *Polistes* (Vespidae; Polistinae) comprises most of the species diversity, with 28 species occurring in the United States (Carpenter, 1996). Their colonies rarely produce more than 100 contemporaneous adults, although *P. annularis* colonies can achieve more than 1,400 cells (Pierce, 1909; J.W.W., pers. obs.) Other polistines, including the swarming *Brachygastra mellifica*, are present in the United States (Richards, 1978), and their colonies can number into thousands of adults.

Three genera of Vespinae occur in North America (*Vespula*, *Dolichovespula* and the introduced *Vespa*), and all species live in colonies that can grow to many hundreds of individuals. These wasps are considered more highly eusocial, having obvious queen castes that differ from workers both behaviorally and morphologically. Duncan (1939: 159) reported a *Vespula pensylvanica* nest from California with 10,456 cells and an estimated 20,000 individuals produced over the life of the colony. This nest was deemed “typical” by Duncan, as it contained almost 5,000 contemporaneous workers and a lone queen at the time of collection. Duncan also reports a *V. vulgaris* nest measuring “forty-six inches from left to right, forty inches from front to back, and thirty inches in some twenty-one comb levels,” but considered this nest “non-typical” as it was the result of more than one season of construction, many of the combs were not active, and twenty-one functional queens were recovered. Many other authors have reported on nests of various *Vespula* spp. with cell number ranging from approximately 50,000 to 100,000 (see Table 1. Ross and Matthews, 1982; Ross and Visscher, 1983; Ratnieks et al., 1996; Vetter and Visscher, 1997). Tissot and Robinson (1954) recorded a *V. squamosa* comparable in external dimensions (about 3 m tall and 3 m in circumference) to the nest reported here, but with only 39 combs. Gambino (1991), reported a nest of *V. pensylvanica* (introduced to Hawaii) with 546,260 small cells and 47,229 large cells, but the methods by which the cell counts were reached were not reported.

Multi-season nests are common for some North American vespines, and *Vespula*

Table 1. Colony size by estimated cell number of various *Vespula* spp. reported in the literature, sorted by colony size. The colony attributed to Gambino (1991) was discovered in Hawaii, where *V. pensylvanica* is invasive.

Colony Size	Species	Authors
9,802	<i>Vespula squamosa</i>	Akre et al. 1981
10,456	<i>Vespula pensylvanica</i>	Duncan 1939
56,359	<i>Vespula pensylvanica</i>	Vetter and Visscher 1997
65,970	<i>Vespula pensylvanica</i>	Ratnieks et al. 1996
90,000–100,000	<i>Vespula squamosa</i>	Ross and Matthews 1982
100,120	<i>Vespula maculifrons</i>	Ross and Visscher 1983
120,130	<i>Vespula squamosa</i>	Akre et al. 1981
230,000	<i>Vespula vulgaris</i>	Akre et al. 1993
477,000	<i>Vespula squamosa</i>	This study
593,489	<i>Vespula pensylvanica</i>	Gambino 1991

*squamosa* nests are sometimes maintained over many years in the southern coastal plain areas (Akre et al., 1981). We report such a colony, the largest North American vespid colony to date.

#### MATERIALS AND METHODS

The nest was discovered outside Ft. Myers, Florida by a construction surveyor in an area of typical glade and scrub vegetation. The surveyor contacted Dr. Henry Hermann, who subsequently contacted JWW.

The nest (see Fig. 1) had been constructed underground, beside the hollowed bole of a decaying, broken pine tree. The nest subsequently grew up through and extended above the broken stump and into the fronds of a cabbage palm tree, and down around the outside of the pine stump. The fronds were 213.4 cm tall. The trunk of the pine was decayed and composed of a hollow cylinder of bark with a small central core of heartwood, with a radius of 2 cm to 6 cm of empty space separating these through most of the nest. The base of the trunk was 35.6 cm in diameter, and the majority of the trunk's middle section was surrounded in comb. This nest was divided into upper and ground sections, both of which incorporated many twigs and branches from surrounding vegetation, and altogether it resembled a large mushroom.

The upper section of the nest began at the base of the fronds and gradually flared out into a more or less spherical shape, reaching a maximum diameter of 114.3 cm. This upper section of the nest extended from the trunk 33.0 cm in radius at its widest point, and 39 stacked, circular combs filled the trunk of the pine stump. The lower portion of the upper section contained no combs and was composed of close but separate, broad laminar sheets of paper (*sensu* Wenzel, 1991), while the uppermost envelope of both the upper and ground sections of the nest was imbricate (*sensu* Wenzel, 1991: like the tiles of a roof) and heavily reinforced with oral secretion. The ground section of the nest, resting to the side of the pine stump and connecting to it underground, reached 114.3 cm at its maximum diameter. Both sections of the nest were active.

Our initial intention was to collect the nest at night, after enclosing it in a mesh

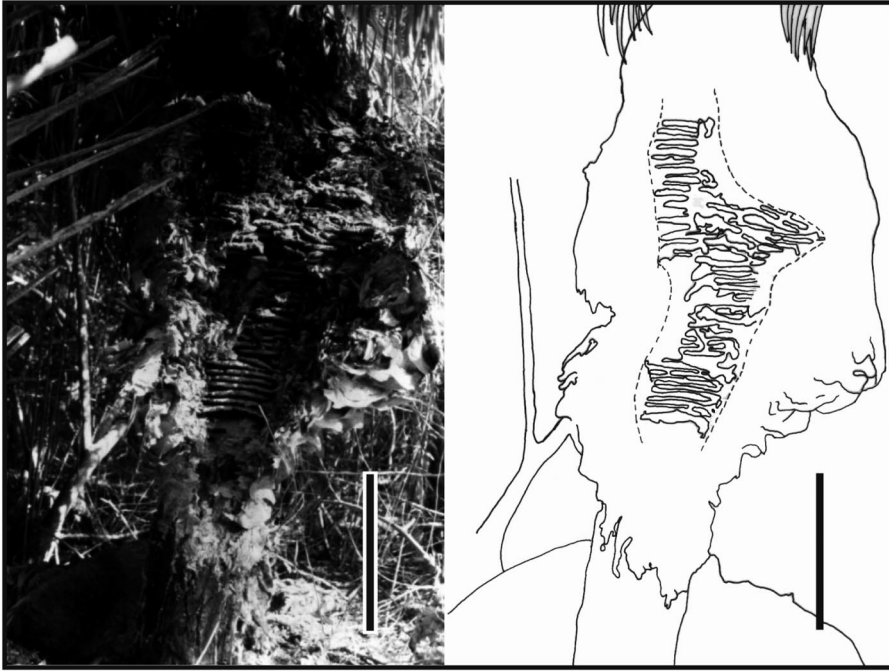


Fig. 1. Photograph of the bisected nest, prior to collection, and a schematic of the photo, drawn for clarity. The nest is shown in two connected parts, the hemispherical lower portion erupting from the soil and the upper portion dependent upon the hollow tree trunk and overhanging palm leaf. The extremities of both lower and upper portions are not shown. Dashed lines represent regions of the nest cut away to reveal the comb. Scale bar = 0.5 m.

sheet. This way, we might be able to count virtually all the individuals in the colony. However, due to its size, and because the nest incorporated many branches from nearby trees and shrubs, this was not possible. Instead, we collected the nest during the day and opted to estimate the productivity of the colony indirectly using cell number.

**Areas of dead and live comb.** Some active brood areas of nest were separated from one another by many dead combs. The presence of meconium in the cells of these dead combs revealed that they had once been active. Therefore, we collected these combs along with the active comb for estimation of cell number and production of individuals.

#### METHODS OF ESTIMATING CELL NUMBER, BROOD, AND ECOLOGICAL IMPACT

It was not possible to carry all the combs back to The Ohio State University for exact analysis of cell number. All combs we did not bring back with us were traced onto sheets of white paper. Each tracing was marked either "live" or "dead." A sample of the live comb was weighed in Florida at the American Entomological

Institute for a measure of the weight of the comb prior to desiccation of the brood biomass. A sample of dead comb, the previously weighed live comb, and all combs attached to the heartwood of the tree were taken to Columbus, OH and further analyzed at the OSU Museum of Biological Diversity.

**Estimation of cell number.** The 39 combs inside the bark of the tree, attached to the heartwood, were circumscribed with a metal wire. The wire shape was then traced on paper, and the diameter of the heartwood subtracted. Projecting from the outside of the bark of the tree were two lobes of comb. One of these lobes contained 10 combs and projected farther than the other smaller lobe, which contained 4 combs. These two sections were also circumscribed with a metal wire, and the wire shapes were traced onto paper.

Several square feet of paper were weighed to derive a value of the weight of the paper per unit area. All tracings were cut from the paper with a razor. Tracings were weighed on a Mettler PM400, and many tracings per measure were combined to reduce error. Three separate exact counts were performed on dead combs and two counts on live combs to derive a value for the number of cells per unit area. Thus, the weight of the tracings can be used to evaluate the area of the combs they represent, and this total area can be translated to cell number based on the counts for representative combs. Several calculations were made for comparison. These calculations were used to estimate the total cell number for the entire colony using the following formula:

*Formula 1*

$(g. \text{ of comb tracings}) (cm^2/g \text{ of tracing paper}) (cell \text{ no./cm}^2) = \text{total cell number}$

**Estimation of brood mass.** Using paper tracings of live and dead comb and the known mass of representative combs to standardize area, we estimated the total mass of larvae. By subtracting the mass per unit area of dead comb from that of live comb, we derived an estimate of mass of larvae per unit area of live comb. This estimate is then extrapolated to the total area of live comb using the following formula:

*Formula 2*

$[(g/cm^2 \text{ live comb}) - (g/cm^2 \text{ dead comb})] [(g \text{ live comb tracings}) (cm^2/g \text{ tracing paper})] = g \text{ larvae}$

**Ecological impact.** Assuming the weight of an adult is 45 mg, the mass of larvae was used to determine the mass of arthropod prey consumed by the colony. The prey consumed by the entire colony was estimated under the conservative assumption that every cell was used only once.

## RESULTS

**Estimation of cell number.** The cell density of dead comb (cell number/unit area) was 4.9 cells/cm<sup>2</sup> (1,689 cells counted) using one measurement and 5.0 cells/cm<sup>2</sup> (2,508 cells counted) on a second measurement. For the dead comb brought back to OSU we counted one row of cells and measured how much linear distance they extended, giving 5.2 cells/cm<sup>2</sup>. Comb that was active at the time of capture was

measured at 6.3 cells/cm<sup>2</sup> (650 cells counted) using one measurement and 6.1 cells/cm<sup>2</sup> (892 cells counted) in another measurement. These values were averaged, giving 5.03 cells/cm<sup>2</sup> for dead combs, and 6.2 cells/cm<sup>2</sup> for live combs. The total weight of comb tracings was 375.26 g and 199.26 for dead and live combs, respectively. As the paper tracings were measured at 152.8 cm<sup>2</sup>/g, following Formula 1 (see Methods), the total cell number estimate was 476,982.15 cells.

**Estimation of brood mass.** Eleven pieces of dead comb (124.861 g) and their paper tracings (4.749 g) were multiplied by the area per unit mass of the paper (152.8 cm<sup>2</sup>/g) giving a dead comb mass per unit area of 0.17 g/cm<sup>2</sup>. The paper tracings of the live combs were used similarly to obtain a live comb mass per unit area of 0.53 g/cm<sup>2</sup>. The mass per unit area of dead comb was then subtracted from the mass per unit area of live comb giving the mass per unit area of the actual larvae in the combs. This value, 0.36 g/cm<sup>2</sup>, was then multiplied by the product of the combined weight of the paper tracings of the live combs and the area per unit mass of the paper giving 10,960.89 g of larvae (see Formula 2 in Methods).

**Ecological impact.** The estimated cell number is 476,982.15. If each cell produced an adult wasp of 45 mg, then the total mass of the arthropod prey consumed by the colony equals (476,982.15 cells)(.045 g/cell)(10), or 214.64 kg of arthropod prey. If the average vespine worker kills only 2 prey animals that are half its own size per larva reared to adulthood, then this would approximate 5 million prey insects taken by this colony. The actual number would seem to be much larger.

**Queen number and ovarian development.** During nest collection, 38 putative egg-laying queens (easily identified by their size and orange coloration) were retrieved and ovarian development was examined in a sample of 20. Of these all had ovarian development of some degree. Twenty workers were sampled, dissected and examined for ovarian development. One worker, collected from deep within a "dead" region of comb during nest collection, contained two large eggs.

#### DISCUSSION

The large size of this *V. squamosa* nest is not unusual in the glade regions of Florida, and the surveyor who found the nest offered to show us other comparable nests. A number of studies report what the authors consider to be unusually large vespine nests from North America (Akre et al., 1981; Ross and Matthews, 1982; Ross and Visscher, 1983; Akre et al., 1993; Ratnieks et al., 1996), but what is shown by the scientific literature, as well as annual reports in local newspapers, is that large, polygyne colonies of *Vespula* spp. are, in fact, not rare. These colonies attain large sizes because in warm environments they can persist for many years, often with queens overwintering in the nest itself (Vetter and Visscher, 1997). In our study, it seems unlikely that a nest of this size could have been constructed during a single season. Also, many regions of comb were no longer being used for egg laying, and inspection of these cells revealed many layers of meconia (up to 4 layers in some cells), suggesting that the cells had been used in previous seasons.

In the colony presented here, it seems the proximate mechanism permitting multiple queens to inhabit the colony was the manner in which brood regions were separated from each other by regions of dead comb. We believe that traffic across these dead comb regions was rare, as stepwise dissection of some parts of the nest

often elicited no reaction from other regions of the nest. These conditions, we believe, led to a situation in which a form of supercolony, as is known in ants, was maintained over several years. The size of the nest and the number of fertile queens suggest that queen pheromones were dilute in peripheral portions of the nest, which gave rise to queen development and, subsequently, local isolation of workforces in those regions. As the nest continued to grow, this phenomenon resulted in the multiplication of queens and local sub-nests.

As Ratnieks et al. (1996) observed, there is no obvious reason why polygyny should not be a stable strategy in *Vespula*, as it is in polistines. Indeed, there are hundreds of polygyne species of Polistinae, and the largest colonies recorded can achieve tens of millions of cells and include thousands of queens (Zucchi et al., 1995; Sakagami et al., 1996; Baio et al., 1998). It should not be surprising if some *Vespula* form polygyne colonies, and the many reports scattered over the decades taken together support the contention that polygyny may be more than accidental (Akre et al., 1981; Ross and Matthews, 1982; Ross and Visscher, 1983; Gambino, 1991; Akre et al., 1993; Ratnieks et al., 1996). Ratnieks et al. (1996) proposed three adaptive explanations as to why polygyny should be rare in *Vespula*. Two of these—increased potential for diseases and inclusive fitness considerations—apply equally to *Vespula* and swarm founding polistines of the tribe Epiponini, but in epiponines polygyny is the rule. The third reason is that their native range is mild temperate, which would seem to preclude perennial colonies. Yet, many *Vespula* spp. live in regions of North America that provide enough year-round warmth to accommodate perennial polygyny. Additionally, *Vespula squamosa* nests can be polygynous in the Midwestern United States as well (two queens in a nest in Hocking Co., Ohio, unpubl. data.).

*Vespula squamosa* is distinctive in being either a free-living or a temporary, facultative parasite of other *Vespula* (MacDonald and Matthews, 1975). We propose a connection between parasitic habit and polygyny. In both cases, fertile females may enter a queenright nest to begin laying eggs. The difference between them is that females who enter nests of other species are considered parasitic, while females who enter conspecific nests may be usurpers if the queens are incompatible. Thus, polygyny may represent a form of autoparasitism. There is evidence that conflict among *V. squamosa* queens can be common, and MacDonald and Matthews (1984: 144) reported a nest with 25 dead queens and another with 13 dead queens. Considering these and other data, they concluded that there is intense intraspecific queen competition. We propose that if the female returns to her natal nest she might be recognized as kin, greeted tolerantly, and subsequently tolerate other active queens. Perhaps, once a perennial colony is very large, several queens could coexist with little contact, increasing the likelihood that polygyny would be stable regardless of relatedness. Although the colony reported here had many queens in each of the thriving regions of growing brood, the active pieces of nest were separated by abandoned areas. Conspecific usurpation is common in yellowjackets, reported in at least 14 species (Carpenter, pers. comm.), and seems to provide the origin of parasitic habit. It is possible that stable polygyny represents queens aggressively joining colonies so large that queens rarely interact.

Large polygynous colonies of *Vespula* appear to be more common than traditional interpretation permits. We propose that polygynous colonies of *Vespula squamosa*

may not be anomalous, but rather may represent a southern, perennial correlate of more northern, annual parasitic habit. If our interpretation is correct, then social parasitism and polygyny may not be far apart evolutionarily.

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