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# Reproductive partitioning in *Vespula squamosa* (Hymenoptera: Vespidae)

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**Abstract**

The yellowjacket, *Vespula squamosa* (Drury) (Hymenoptera: Vespidae), is the only eusocial wasp that commonly has 2 social forms (monogyne and polygyne nests), has annual and perennial nests, facultatively usurps the nests of conspecifics, and parasitizes other vespine species. Thus, *V. squamosa* is ideally suited for examining various phenotypic and genetic variables as they relate to different social alternatives in the context of kin selection theory. In this study, we compared various metrics relating to reproduction for queens in monogyne versus polygyne nests including queen abdominal weight, fertility, egg number, egg size, and worker relatedness. Monogyne nests (*N* = 7) and polygyne nests (*N* = 5) were collected from Georgia and Florida, USA. Examination of nest comb material indicated all polygyne nests were perennial; the number of workers in these nests varied from approximately 700 to 36,379. All monogyne nests were annual and had fewer than 1,500 workers. Single queens were more physogastric than their polygyne counterparts and had significantly more mature eggs per ovary. Polygyne queens, however, had significantly larger eggs but produced smaller workers. Twelve percent of the queens in polygyne nests were either devoid of sperm or did not have full spermathecae (*n* = 142), whereas the spermathecae of single queens (*n* = 7) were replete with spermatozoa. Mean genetic relatedness among workers in perennial, polygyne nests suggests these nests include multiple egg-laying queens.

Key Words: southern yellowjacket; reproduction; polygyne

**Resumen**

La avispa chaqueta amarilla, *Vespula squamosa* (Drury) (Hymenoptera: Vespidae), es la unica avispa eusocial que normalmente tiene dos sistemas sociales, monogyne (colonias con una reina) y polygyne (colonias con reinas múltiples), tiene avisperos anuales y perennes, es un parásito de avisperos de otras especies de chaquetas amarillas, y desplaza reinas de la misma especie por medio de usurpación. Por estas razones, *V. squamosa* es una especie apropiada e ideal para examinar variables genéticos y fenotípicos en relacion a diferentes alternativas sociales dentro de la teoria de selección de parentesco. En este estudio comparamos varias métricas en cuanto a la reproducción de reinas que provienen de avisperos con una o varias reinas incluyendo el peso del abdomen, la fertilidad, el número y tamaño de huevos y el parentesco de avispas obreras. Se recolectaron avisperos con una reina (*N* = 7) y con reinas multiples (*N* = 5) en los estados de Georgia y Florida, E.E.U.U. La examinación del material del avispero indicó que todos los nidos polygynes eran perennes; el número de trabajadores en estos últimos varió de aproximadamente 700 a 36.379. Todos los nidos monogynes eran anuales y tenían menos de 1.500 trabajadores. Las reinas solas eran más físogástricas que sus contrapartes polygynes y tenían huevos significativamente más maduros por ovario. Las reinas polygynes, sin embargo, tenían huevos significativamente más grandes, pero produjeron trabajadores más pequeños. El doce por ciento de las reinas de los nidos polygynes estaban desprovistos de espermatozoides o no tenían espermatecas completas (*n* = 142), mientras que los espermatecas de reinas solas (*n* = 7) estaban repletos de espermatozoides. El promedio de la relación genética entre los trabajadores en los avisperos perennes, polygynes sugiere que estos nidos incluyen reinas múltiples que ponen huevos.

Palabras Clave: avispa chaqueta amarilla del sur; reproducción polygyne

*Vespula squamosa* (Drury) (Hymenoptera: Vespidae) is unusual among vespine wasps in its distribution and repertoire of life history strategies. Unlike hornets and other yellowjackets in the western hemisphere, which are primarily distributed in temperate zones, *V. squamosa* has a primarily southern distribution extending as far south as Honduras (Akre et al. 1980; Hunt et al. 2001; Landolt et. al. 2009). It is also the most common species of vespine wasp in southeastern USA, particularly in Florida. Queens of this species commonly usurp interspecific and conspecific nests (MacDonald & Matthews 1984), which subsequently develop into annual or perennial nests (Akre et al. 1980; Ross & Matthews 1982). *Vespula squamosa* queens are also unusual in that they exhibit one of the highest frequencies of multiple mating observed among the social Hymenoptera (an effective mate number of 3.33, Strassmann 2001). Thus, *V. squamosa* offers a good model system for not only examining possible ecologic and genetic determinants of alternate life history strategies but also for addressing the theoretical challenges inherent in eusocial systems with varying degrees of genetic relatedness among individuals in a nest with the concomitant conflicts associated with multiple reproductive interests.

Studies on the biology of *V. squamosa* have primarily focused on its distribution, nest size, general phenology, and breeding system (Akre et al. 1980; Ross & Matthews 1982; MacDonald & Matthews 1984; Ross 1986), but there has not been a study comparing the reproductive morphology of monogyne versus polygyne nests with estimates of worker relatedness to assess the possibility of multiple-egg layers in the latter and relative nest fertility.

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## Materials and Methods

Five polygyne nests and 7 monogyne nests of *V. squamosa* were collected from 4 counties in Florida (Alachua, Bradford, Putnam, and St. Lucie) and 1 county in southern Georgia (Glynn) during the months of Jun and Jul. Yellowjackets were collected in mesh bags with a vacuum system, and nests were subsequently unearthed and examined for queens, workers, males, and comb. Comb with the following characteristics was considered evidence of a perennial nest (in its 2nd year, at least): discolored cells devoid of brood and eggs and including organisms associated with decomposition (mites, cockroaches, fungi), and sections of old, papered-over, fully formed brood cells. All material used for DNA analysis and dissections was stored at −80 °C.

### REPRODUCTIVE STATUS

The abdomen of each queen was weighed and dissected in insect Ringer's solution to detect the presence of spermatozoa and to ascertain the developmental status and number of mature eggs in the ovaries. Ovarian development was estimated by randomly selecting 1 of the 7 ovarioles from each ovary and counting the number of mature eggs. In addition, the most distal egg of both ovarioles was measured for length and width (distance across the widest portion of an egg). Eggs were teased out of ovarioles with jeweler's forceps and measured with an ocular micrometer. Eggs were considered mature if they were elongate, completely filled with yolk, and completely opaque (Cumber 1949; Spradbery 1973). Undeveloped eggs were more spherical in shape, granular in appearance, and translucent. Insemination of queens was determined by removing the single spermatheca into a drop of saline and crushing the contents with a coverslip. Spermathecal contents were examined under a compound microscope at 400× magnification. The amount of sperm in a spermatheca was categorized as full (3/4 to completely full), half-full (1/2 to 3/4 full), quarter-full (up to 1/2 filled), and empty. These categories were established by comparing the relative size of the sperm mass within spermathecae of queens. A sperm mass that completely occupied the lumen of a spermatheca was considered full, a sperm mass occupying about half the spermathecal lumen was considered half-full, etc.

The total number of mature eggs in each ovary was estimated by multiplying the mean number of developed eggs of 1 ovariole by 7 (total number of ovarioles per ovary). The mean number of eggs for queens from each nest was determined for the right and left ovaries and a paired *t*-test used to compare both mean values within each colony. Mean values for right and left egg lengths and widths were also computed for each nest and compared by paired *t*-test for significance. A 1-way ANOVA and Duncan multiple range test for each of the variables compared (abdomen weight, egg number, egg length, and egg width) tested for significance among multiple queen nests and single queen colonies.

### GENETIC ANALYSIS

In order to estimate genetic relatedness among workers in multiple queen nests, we screened 8 random workers for polymorphism at 7 enzyme loci and in 2 buffer systems (HAD, 3-hydroxybutyrate dehydrogenase, EC 1.1.1.30; PGM, phosphoglucomutase, EC 5.4.2.2; IDH, isocitrate dehydrogenase, EC 1.1.1.42; PGI, phosphoglucoisomerase, EC 5.3.1.9; αGDH, alpha-glycrophospahte dehydrogenase, EC 1.1.1.8; HBDH, hydroxybutyrate dehydrogenase, EC 1.1.1.30; GOT, glutamic-oxaloacetic transaminase, EC 2.6.1.1). Four workers and 1 queen from each nest were screened for polymorphism based on 14 microsatellite primer pairs developed by Thoren et al. (1995) for *Vespula rufa* (L.) (Hymenoptera: Vespidae). DNA samples were tested with 2 PCR temperature profiles, and amplicons were examined on 6% acrylamide sequencing gels according to the protocols of Ausubel et al. (1992) and Promega Silver Sequence™ (Promega Corp., Madison, Wisconsin) staining protocols. Silver-stained plates were video-scanned into files on an ATI Video Player and analyzed with SCION Image software (Informer Technologies, Inc., Madrid, Spain). A combination of M13 sequenced virus and internal controls were used as standard markers for identifying alleles. Mean genetic relatedness within multiple queen nests was estimated from the genotypes of 20 workers by using the Relatedness software program by Goodnight & Queller (1996). All nests were weighted equally in estimating mean nest relatedness, and standard errors were estimated by jackknifing over loci.

## Results

Whereas monogyne colonies were exclusively annual nests, all polygyne nests were deemed perennial by the criteria outlined in the methods section. The number of queens in polygyne nests ranged from 21 to 46 individuals (Table 1). No queen cells were observed in any of the 5 polygyne nests sampled, but 2 of these nests had live males. Monogyne nests appeared to be only 1 season old and contained fewer than 1,500 individuals; the number of individuals in perennial nests ranged from 741 to 36,379.

### REPRODUCTIVE STATUS

Queens from polygyne nests were not physogastric relative to their counterparts in monogyne nests, and this observation was confirmed by significant differences in the mean abdominal weight of queens from both social forms (Table 2). The abdominal weights ranged from 0.22 to 0.31 g for monogyne queens and from 0.11 to 0.25 g for polygyne queens.

There were no significant differences between left and right ovaries for mean egg number ($t$cal = −0.55, $P > 0.1$), mean egg length ($t$cal = 0.22, $P > 0.4$), and mean egg width ($t$cal = −0.44; $P > 0.2$) among queens in monogyne nests or among queens in the 5 polygyne nests. All 3 metrics were significantly different, however, between monogyne and polygyne nests (Tables 3 and 4). The width and length of eggs in polygyne nests were significantly greater than that of eggs in monogyne nests ($F = 1.7$, df = 5,137 and $F = 4.8$, df = 5,137, respectively), but the latter queens contained significantly more eggs ($F = 39.5$, df = 5,141). There were significant differences in mean egg length and mean egg number among polygyne nests but no significant difference in mean egg width (Table 4). All ($n = 7$) single queens and 97.8% of gynes from polygyne nests ($n = 137$) contained mature eggs. Only 1 polygyne queen was found with no mature eggs.

All queens in monogyne colonies ($n = 7$) and 97.8% of queens from polygyne nests ($n = 138$) had sperm in their spermathecae. All monogyne queens ($n = 7$) had spermathecae with full quantities of spermatozoa, but 12% of polygyne queens ($n = 142$) had partially empty spermathecae: 10.6% were half full and 1.4% were a quarter full with spermatozoa.

**Table 1.** Collection sites for 5 polygyne nests of *Vespula squamosa*.

| Nest designation | Collection location (State, County, Town) | No. of gynes collected |
|---|---|---|
| Pol1 | Florida, Alachua, Newnans Lake | 21 |
| Pol2 | Florida, Bradford, Starke | 21 |
| Pol3 | Georgia, Glynn, Brunswick | 23 |
| Pol4 | Florida, Putnam, Bostwick | 46 |
| Pol5 | Florida, St. Lucie, Port St. Lucie | 32 |

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**Table 2.** Mean (± SE) abdomen weights for gynes from 7 monogyne and 5 polygyne nests of *Vespula squamosa*.

| Nest | Gynes (*n*) | Mean weight (g)[a] |
|---|---|---|
| Monogyne | 7 | 0.26 ± 0.013a |
| Pol1 | 21 | 0.17 ± 0.003bc |
| Pol2 | 20 | 0.18 ± 0.005b |
| Pol3 | 23 | 0.18 ± 0.005b |
| Pol4 | 46 | 0.16 ± 0.003c |
| Pol5 | 32 | 0.16 ± 0.003c |

[a]Means followed by a different letter are significantly different (ANOVA & Duncan multiple range test, $P < 0.05$).

**Table 4.** Mean (± SE) egg length and width for gynes from 7 monogyne and 5 polygyne nests of *Vespula squamosa*.

| Nest | Gynes (*n*) | Egg length (mm)[a] | Egg width (mm)[a] |
|---|---|---|---|
| Monogyne | 7 | 1.84 ± 0.019a | 0.72 ± 0.009a |
| Pol1 | 18 | 1.96 ± 0.009b | 0.81 ± 0.006b |
| Pol2 | 19 | 2.09 ± 0.012cd | 0.81 ± 0.006b |
| Pol3 | 23 | 2.09 ± 0.008d | 0.80 ± 0.004b |
| Pol4 | 45 | 1.97 ± 0.009b | 0.79 ± 0.004b |
| Pol5 | 31 | 2.02 ± 0.006bc | 0.80 ± 0.003b |

[a]Means followed by a different letter are significantly different (ANOVA & Duncan multiple range test, $P < 0.05$).

### GENETIC ANALYSIS

None of the 7 enzyme loci tested in 2 buffer systems was polymorphic. Of the 14 microsatellite loci examined, only 3 (RUFA5, RUFA15, and RUFA18) had suitable numbers of alleles (10, 8, and 15, respectively) and levels of heterozygosity useful for estimating genetic relatedness (direct count heterozygosity of 0.82, 0.64, and 0.87, respectively). Thus, mean heterozygosity for all 3 loci was 0.779 ± 0.069. RUFA5 and RUFA18 primers amplified dinucleotide repeats producing amplicons approximately 180 bp long whereas RUFA15 primers amplified a trinucleotide repeat of amplicons approximately 100 bp long. Mean genetic relatedness among workers for each of the polygyne nests ranged from −0.005 ± 0.033 SE to 0.257 ± 0.195 SE (Table 5).

## Discussion

Although the existence of 2 social forms had been observed in previous studies of the biology of *V. squamosa* (Akre et al. 1980), there has been no attempt to correlate both social forms with nest longevity. This study appears to show that polygyne nests are exclusively perennial and that polygyne nests probably originate as single queen colonies but convert to a perennial and polygyne form, most likely during the fall mating season. Consistent with this hypothesis is the absence of records regarding aggregations of queens founding new nests in the spring or of young nests (less than 1 yr) containing more than 1 queen. On the contrary, queens of *V. squamosa* are known to parasitize the nests of other queens, especially those of *Vespula maculifron*s (Buysson) (Hymenoptera: Vespidae), and to kill the resident queen (MacDonald & Matthews 1984). Perennial nests in this study were always found with tiers of nest cells from the previous year that had been papered over or partially destroyed and were in decay. As queen cells were not observed in any of the perennial nests, these particular tiers were probably destroyed by workers prior to the months of Jun and Jul, when the nests in this study were collected. The origin of perennial nests, therefore, is most likely due to queens returning to their natal nests after mating flights in the fall or joining other already established perennial nests. Four out of the 5 polygyne nests examined had mean relatedness values of less than 0.25, which is the relatedness expected for workers in a monogyne nest where the queen has mated with multiple males (Table 5). The mean genetic relatedness of polygyne nests in this study ranged from −0.005 ± 0.033 SE to 0.257 ± 0.195 SE. These values suggest that all queens in polygyne nests are not necessarily sisters, particularly because 1 polygyne nest had a mean relatedness among workers that was not significantly different from 0. Polygyne nest SL1P, however, had a mean relatedness that was not significantly different than that expected for a monogyne queen mated to multiple males (a relatedness of 0.25). It would appear, then, that some polygyne nests can have a single queen dominating most of worker production though this outcome may be relatively uncommon.

**Table 3.** Mean (± SE) egg numbers for gynes from 7 monogyne and 5 polygyne nests of *Vespula squamosa*.

| Nest | Gynes (*n*) | Mean egg number[a] |
|---|---|---|
| Monogyne | 7 | 48.5 ± 2.6a |
| Pol1 | 20 | 10.3 ± 1.9b |
| Pol2 | 19 | 19.2 ± 1.5c |
| Pol3 | 23 | 15.6 ± 1.8c |
| Pol4 | 46 | 9.7 ± 1.1b |
| Pol5 | 32 | 10.1 ± 1.0b |

[a]Means followed by a different letter are significantly different (ANOVA & Duncan multiple range test, $P < 0.05$).

Social forms of *V. squamosa* do not simply differ in the number of queens or workers present in a nest; a number of important differences may indicate some of the reproductive costs and benefits of either type of nest. Queens from polygyne nests, for example, were not physogastric and had significantly fewer developed eggs per ovary. These eggs, however, were significantly larger than the eggs produced by monogyne queens. Larger egg size in insects often correlates with an increase in size, survival, and reproductive success of the resulting adult (Krebs & Davies 1993), but this outcome does not seem to hold for *V. squamosa* worker offspring. Although polygyne queens invest more energy into each egg, the mean size of workers in polygyne colonies is actually significantly smaller than the mean size of workers in monogyne colonies (Deets & Fritz 2001). If small worker size has a fitness cost (e.g., smaller workers might have reduced load capacity for carrying food or be less effective in warding off nest predators and parasites), then this difference suggests perennial nests are developmentally more constrained by the availability of food resources than single queen nests. This constraint may be the result of the food requirements that these oftentimes enormous nests require (G. N. F. has collected nests as large as 3 m high by 1.5 m in diameter containing over 14 kg of individuals including the presence of numerous non-foraging males and multiple queens). Though an average queen from a monogyne nest may contain close to 50 mature eggs per ovary at any time, a polygyne colony with only 30 queens will have close to 8 times that number of mature eggs.

*Vespula squamosa* exhibits a variety of possible life history options that include usurping interspecific and conspecific nests (MacDonald & Matthews 1984) and establishing single or multiple queen colonies that are either annual or perennial. Each set of options probably generates specific costs and benefits associated with particular environmental contexts. In this study, costs of joining other queens to establish a polygyne perennial nest are a relatively low reproductive output and small worker size; alternatively, a benefit of polygyny is a guarantee of some reproductive success relative to single queens that may suffer high mortality rates due to predation and conspecific usurpation.

This study provides evidence that polygyne colonies of *V. squamosa* are truly multiple queen colonies (more than 1 diploid-egg layer). Not only are

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**Table 5.** Mean relatedness (r ± SE) for workers (*n*) from 5 polygyne nests of *Vespula squamosa*.

| Nest | *n* | r |
|---|---|---|
| Pol1 | 20 | 0.182 ± 0.068 |
| Pol2 | 20 | −0.005 ± 0.033 |
| Pol3 | 20 | 0.134 ± 0.012 |
| Pol4 | 20 | 0.096 ± 0.049 |
| Pol5 | 19 | 0.257 ± 0.195 |

most queens in polygyne nests storing sperm, almost all have developed eggs. Furthermore, the mean relatedness of workers in nests is consistent with there being more than 1 egg-laying queen whose progeny survive to adulthood (absence of selective culling by workers). Several queens in polygyne nests had small amounts of spermatozoa in their spermathecae, and 1 queen had no detectable sperm; in contrast, all single queens were replete with spermatozoa. Ross & Mathews (1982) collected a polygyne nest of *V. squamosa* in Jan 1981 that had 114 gynes. Of these gynes, 57.9% had been inseminated, and 88.6% had developed ovaries; all gynes appeared to be young based on the integrity of their wings. It appears, then, that insemination is not a requirement for ovarian development. The low rate of insemination in the nest recorded by Ross & Matthews (1982) and the high rate of insemination reported for perennial nests in this study suggest that mating may occur beyond the fall season for gynes in such nests. Certainly, males are available all year round as evidenced by some nests in this study and that reported on by Ross & Matthews (1982).

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