SOCIAL PARASITISM IN YELLOWJACKETS

(VESPULA)

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SUMMARY

Laboratory studies of competition between queens of two species of yellowjackets, *Vespula squamosa* and *V. maculifrons*, reveal that queens fight intensely over viable nests. Residents are more likely to win over intruders, despite unequal body sizes. The losing queen is fatally stung, but workers are killed by biting. Results are consistent with game theory which predicts intense contests for valuable resources (viable nests). Since orphaned workers may gain the opportunity to lay their own eggs their aggressive participation in queen battles may be interpreted as selfish. Data are presented on queen abundance, seasonal occurrence and habitat preferences based on sightings and Malaise trap collections. The possibility that social parasitism contributes to cyclical fluctuations in yellowjacket populations is considered.

RESUMEN

El parasitismo social en las avispas (Vespula)

Estudios en el laboratorio de competencia entre reinas de dos especies de *Vespula, V. squamosa* y *V. maculifrons*, revelan que las reinas pelean intensamente por nidos viables. Las reinas residentes frecuentemente ganan sobre las intrusas a pesar de un desigual tamaño del cuerpo. Tanto las obreras de nidos con reina como las que nos poseen reina, participan avidamente en las batallas. En este trabajo se presentan también datos de campo sobre la abundancia de las reinas, sobre su ocurrencia estacional y sus habitats preferidos, basados en observaciones y colectas con trampas Malayas.

INTRODUCTION

Four evolutionary «stages» of socially parasitic behavior have been hypothesized for yellowjackets (*Vespula* spp.) by Taylor (1939). The most advanced state is termed inquilinism, the case where host and parasite queen coexist for a period of time in the same nest and the parasite queen depends upon the host workers to rear its reproductives. An intermediate stage in the hypothetical evolutionary progression is represented by *Vespula squamosa* Drury, a common and widespread species in southeastern U.S. This species was regarded as a facultative temporary parasite of *Vespula maculifrons* Buysson (MacDonald and Matthews, 1975). I now believe that queens of *V. squamosa* are obliged to locate an embryonic nest of their host and usurp it, immediately killing the host queen (Matthews and Matthews, 1979). Ultimately, the host worker force is replaced by *V. squamosa* workers so that by mid-summer the colony becomes «pure» *V. squamosa*, having progressed through a temporary period when workers of both species coexisted. Facultative intraspecific usurpation also regularly occurs in both species.

Over the past few years I have been investigating the dynamics of *Vespula* queen behavior in Athens, Georgia, incorporating both field and laboratory studies. In the field, efforts have focused on determining queen abundance, queen flight seasons, nest initiation times and nest distribution over different habitats. Queen interactions in staged laboratory contests have provided insights into the behaviors of parasite and host. This paper presents some results of these studies.

METHODS

Field studies were conducted from late March through June annually from 1976 through 1979 in a municipal park in Athens, Georgia. A 300 m stretch of meandering stream flowing through a mature deciduous forest with an extensively cleared understory was the principal study area. The site was visited from one to three hours at least once daily, between 1000 and 1400 hrs and counts of all queens displaying typical nest searching behavior in the study area were made. Because none were marked, it is possible that some queens were sighted and counted more than once. An independent measure of queen abundance and activity was obtained by sampling with 3 Malaise traps (non-attractant collection devices that intercept flying insects), noted for their ability to catch Hymenoptera (Matthews and Matthews, 1970). One trap was placed in each of 3 contrasting habitats and emptied every other day. Habitats trapped included the municipal park, a botanical garden forest and a suburban back yard.

Embryo nests of *V. maculifrons* were excavated from their natural sites and reestablished in observation boxes in the laboratory. The plywood nest boxes (35 x 35 x 4 cm) were fitted with removable glass bottoms and fronts. Adjustable mirrors positioned below the nest boxes allowed the observation of nest activities with minimal interference. Following a confinement period of 24 to 48 hr during which honey was provided, nest inhabitants were allowed access to the outside via flexible transparent tubing. Wasps reoriented readily and soon resumed normal foraging and nesting activities. Nests were maintained at room temperatures, humidity in the nest boxes was increased by the addition of a dish of saturated sand in one corner.

Field-caught searching queens of both species (each distinctively marked with paint) were introduced into nest boxes having reestablished colonies. Most experiments were conducted the same day that the introduced queen was caught, but in a few cases the introduced queen was chilled overnight. Introductions were made by placing the marked queen into a specially constructed plexiglass chamber connected midway along the entrance tube. A pair of one-way gates detained the queen and prevented her from escaping. Eventually the introduced queen found her way into the nest box and discovered the host nest more or less naturally. Interactions between residents and intruders were recorded on videotape for subsequent analysis.

RESULTS

Field studies. Queen occurrence and abundance

Table I gives the results of the Malaise trap collections of *Vespula* queens for 3 successive seasons. Although total numbers trapped are low, they suggest that queens of *V. squamosa* may be more restricted to disturbed and open habitats such as typified by suburban back yards. No *V. squamosa* were captured in the undisturbed forest of the botanical garden during the 3 years. In contrast, *V. maculifrons* queens were trapped in all habitats sampled and were about equal in abundance to *V. squamosa* in the suburban yard samples. Over the 3 seasons 544 *V. maculifrons* queens were sighted at the semi-natural municipal park study site compared to 50 *V. squamosa* queens (based on 188 observations hrs.), corroborating the Malaise trap findings.

Seasonal abundance of the two species based on Malaise trap collections is depicted in Fig. 1. Queens of *V. maculifrons* appear about one week earlier in the spring and are very abundant in early April with only an occasional queen taken later. In contrast *V. squamosa* queens appear later and exibit no clearly defined abundance peaks. An independent sample of queens from the spring of 1976 (Fig. 2) taken at a research station in Eatonton, Georgia (about 50 miles south of Athens) using Manitoba horse fly traps

Table I – Summary of *Vespula* queens captured by Malaise traps over three successive spring flight seasons in same locations in Athens, GA.

Tabla I – Resumen de reinas de *Vespula* capturadas con trampas Malayas durante 3 sucesivas estaciones de vuelo primaverales en las mismas localidades en Athens, GA.

Habitat	1976 Apr. 1 - July 4	1977 Mar. 15 - June 24	1978 Apr. 3 - May 30	Total
Municipal Park				
V. maculifrons	-	9	7	16
V. squamosa	-	1	1	2
Botanical Garden				
V. maculifrons	29	4	26	59
V. squamosa	0	0	0	0
Suburban Yard				
V. maculifrons	18	5	8	31
V. squamosa	20	6	1	27

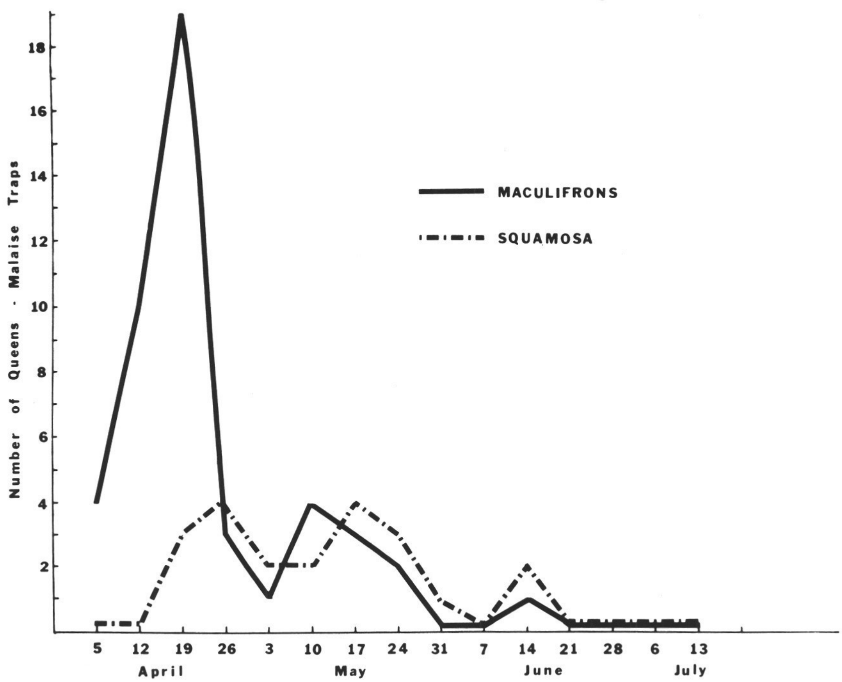

Fig. 1 – Seasonal abundance of *Vespula squamosa* and *V. maculifrons* queens throughout the queen flight season based on collections of Malaise traps in Athens, GA.

Fig. 1 – Abundancia estacional de las reinas de *Vespula squamosa* y *V. maculifrons* durante su vuelo estacional, basada en colectas con trampas Malayas en Athens, GA.

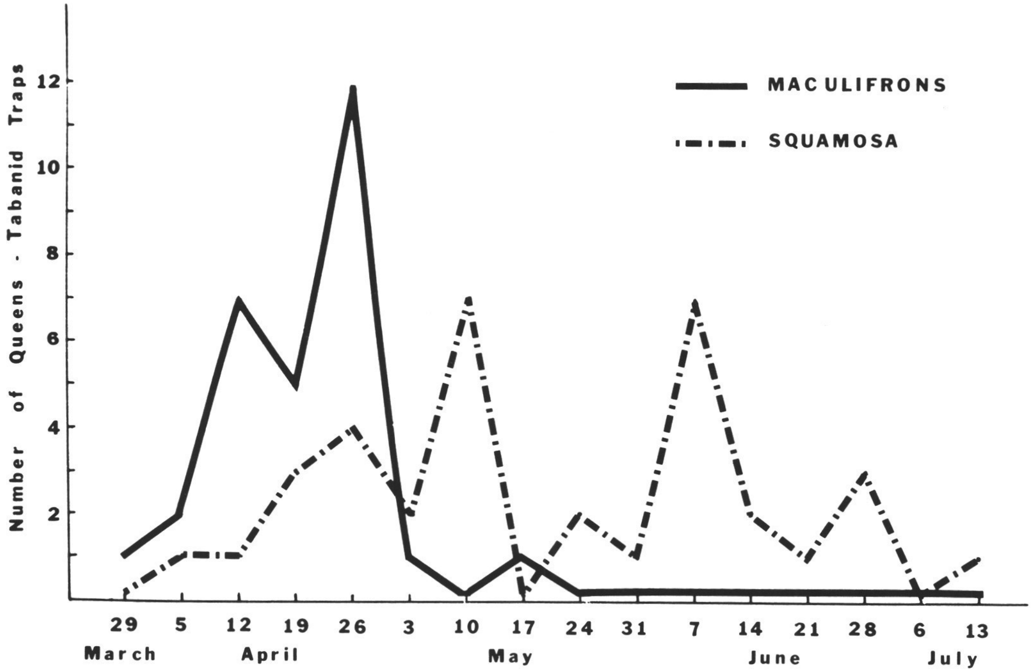

Fig. 2 – Seasonal abundance of *Vespula squamosa* and *V. maculifrons* queens taken in horse fly traps (see Thorsteinson et al., 1965) in Eatonton, GA.

Fig. 2 – Abundancia estacional de las reinas de *Vespula squamosa* y *V. maculifrons* colectadas en trampas para tábanos (ver Thorsteinson et al., 1965) en Eatonton, GA.

corroborates the Malaise collections. Additionally these data suggest that *V. squamosa* has a slightly longer flight season than does *V. maculifrons*.

Laboratory studies

Behaviors observed during agonistic interactions of *Vespula* queens included : search, approach, touch, bite, kick, sting, akinesis, retreat, and tumble. The sequence of these acts was highly variable and unpredictable in any queen contest. Workers (when present) also entered the fray and displayed a similar behavioral repertoire. Indeed, when workers were present they were usually the first to encounter an invading queen (Fig. 3). Invading queens did not use their stings in these encounters with workers, dispatching them instead by biting. The result was that workers were often dismembered in these battles, and as many as 20 have been observed killed by an invading queen. Queens typically did not confront one another or fight for sometimes several hours after the alien entered the nest. The final confrontation typically took place inside the nest making it difficult to observe. On some occasions the embattled queens fell from the nest where they continued to grapple. Eventually one successfully stung her opponent, and the battle ended abruptly with the stung queen instantly paralyzed. Escalated contests also resulted in physical injury to one or both participants (see photos in Matthews and Matthews, 1979).

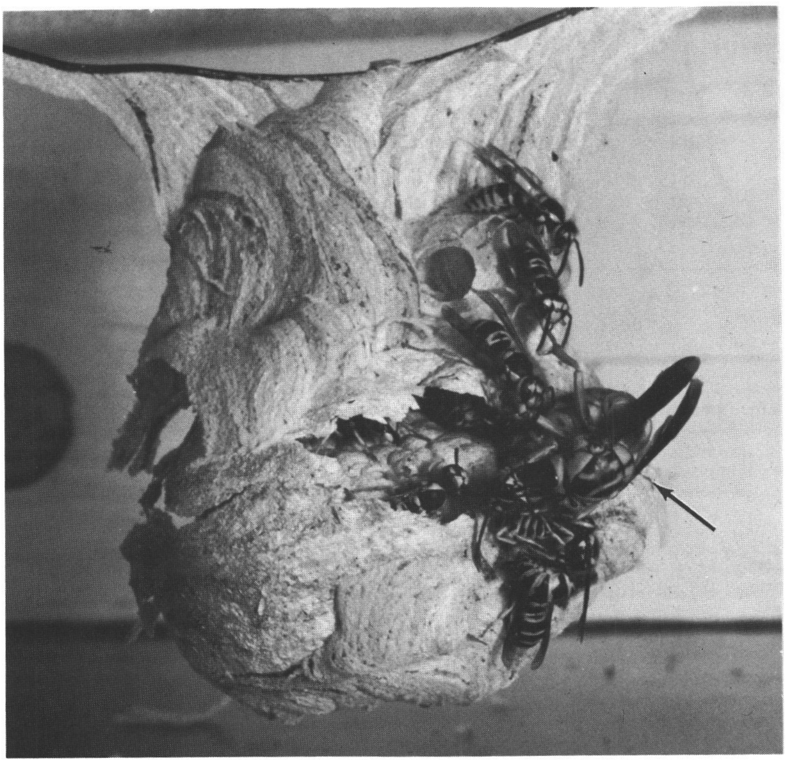

Fig. 3 – Orphaned workers of *Vespula maculifrons* mobbing an introduced *V. squamosa* queen (arrow) who has just invaded their nest in a laboratory nest box

Fig. 3 – Obreras sin reina de *Vespula maculifrons* atacando una reina de *V. squamosa* introducida (flecha) que ha recientemente invadido su nido, bajo condiciones de laboratorio.

Possible parameters thought to affect the outcome of queen contests included : (1) home bias, (2) relative size of combatants, (3) duration of interaction, and (4) presence of workers. Although sample sizes were small, home bias appeared to be the major determining factor (Table II). In 13 of 16 trials, regardless of species combinations, the resident queen prevailed. This difference is significant (p = .002, Fisher's Exact Probability Test). Despite the greater size of *V. squamosa, V. squamosa* queens won in only-third of its' contests. Workers in orphaned nests were highly aggressive toward intruders. Introduced queens were quickly mobbed by the workers who attempted to bite and sting, sometimes in a battle so intense that the nest was severely damaged. In only 4 of 13 trials did the introduced queen ultimately prevail (Table III).

Table II – Results of 16 staged *Vespula* queen contests using queen-right colonies

Tabla II – Resultados de 16 experimentos de introducción de una nueva reina de *Vespula* en colonias con reina.

Intruder Species	Fate of Intruder Queen	Opponent Resident Species		
		V. maculifrons	*V. squamosa*	Totals
V. maculifrons	Wins	0	0	0
(n = 6)	Loses	5	1	6
V. squamosa	Wins	2	1	3
(n = 10)	Loses	4	3	7

Table III – Results of 13 trials using orphaned colonies with variable numbers of workers present in which either conspecific queens or queens of a different species were introduced.

Tabla III – Resultados de 13 experimentos usando colonias huérfanas con número variable de obreras, en las cuales fueron introducidas reinas conespecíficas o reinas de una especie diferente.

Outcome	Intruder		
	Conspecific	Different species	Totals
Intruder wins	3	1	4
Intruder loses	6	3	9

Not revealed in these data is the fact that even the «winners» were sometimes ultimately losers ! Two successful defenders and two successful usurpers subsequently died of battle injuries, which under natural conditions would leave orphaned colonies, which, unless subsequently adopted, would be destined to die prematurely. Thus, there exists a small but measurable probability that any usurpation attemps will result in an orphaned nest.

DISCUSSION

Yellowjacket queen competition is essentially a contest situation which is *asymmetric* in the sense of Maynard Smith and Parker (1976). The payoff – possession of an established nest – has greatly different values for each contestant. The resident queen stands to lose her entire (and considerably greater) investment if she is defeated. The intruder on the other hand stands to gain a great deal by taking over, and (providing she survives to try again) will be little worse off in losing than if she had made no attemps at all. Under such asymmetric payoff conditions, Maynard Smith and Parker predict an intense «escalated» contest carrying the possibility of serious injury, even death, to one or both contestants. This is exactly the case in *Vespula* queen interactions. For yellowjacket queens the situation is exacerbated since contestants would seem to have no means of accurately assessing the fighting ability or resource holding power (RHP) of opponents in conventional ways. Animals fighting over territories are, for example, able to assess one another by various sorts of displays made in close proximity, but without physical contact. For example, fumel web spiders assess RHP of opponents via tactile stimuli perceived at a distance through the web. Most intense fights occur between roughly equal-sized individuals (Reichert, 1978). Decisions to escalate or withdraw can be made at a safe distance and escalated contests occur only when opponents are about evenly matched. This is not the case for *Vespula* queens who would seem to have no obvious way of predicting the situation underground in advance.

The staged laboratory queen contest outcomes suggest that the resident queen will usually hold the advantage. The relatively few documented cases of usurpation in nature (Mac Donald and Matthews, 1981) corroborate these data, suggesting that home bias may be an important factor under natural conditions as well. However, sighting records and queen trapping results from the field presented here suggest that there are seasonal as well as spatial aspects to queen competition which were not mimicked in the laboratory. Also, previous field studies showed that successful *V. squamosa* usurpation did not occur until after several *V. maculifrons* workers were present, with usurped nests averaging over 200 cells (Mac Donald and Matthews, 1975). Laboratory contests were staged with smaller nests containing up to about 60 cells and at most 15 workers.

Workers, being reproductively sterile, might be predicted to have little interest in a contests'outcome. Indeed, at first, I postulated that workers (particularly those in orphaned nests) should readily accept an invading queen since her presence would likely assure the perpetuation of an otherwise doomed colony. Experiments showed otherwise (Table III). A possible explanation of worker pugnacity was suggested when some queenless nests began to produce males. In such nests, workers have a «once in a lifetime» chance to contribute their genes directly to the next generation. Acceptance of a foreign queen forfeits this opportunity. Hence from the workers standpoint, hostility toward invading queens is to be expected, even in queen-right colonies, though not necessarily for altruistic reasons. Conceivably some worker-derived males could live to mate.

On a larger time scale the aggressive interactions of queens may help to explain the cyclical nature of yellowjacket population fluctuations. Every year certain regions report high densities of yellowjacket populations (Akre and Reed, 1981) while in the subsequent year or two they seem to be hardly noticeable. Factors causing tremendous population fluctuations of yellowjackets are undoubtedly multiple and complexly interrelated (also reviewed by Spradbery, 1973 and Archer, 1980b). However, the results of this study suggest that queen warfare may play a larger role in population fluctuations than generally thought. The following scenerio is suggested. Consider first the situation where populations are high, and large numbers of fertile queens are produced to overwinter. Assuming that mortality due to overwintering is density independent (Archer, 1980b, gives a figure of 98 % winter mortality), the following spring the incidence and intensity of queen interactions would be relatively high, with a concommitant increase in nest failure rate due to repeated queen usurpation attempts (both intra-and-interspecific) each carrying the risk of severe damage and the possibility of being orphaned. Conversely, when overwintering populations are relatively low there would be a reduced probability of repeated nest disturbance by intruding queens the following spring, and hence a greater likelihood that a given nest will survive beyond the critical embryonic stage. Thus in seasons following low population densities, the fewer surviving queens may enjoy a greater probability of successful nest establishment and hence yellowjacket populations begin to build. Archer (1973, 1980a, b) has made a similar suggestion based upon his long term studies of British yellowjackets. Thus, the biggest single factor determining yellowjacket nesting success may not be the number of available nest sites or favorability of hibernating conditions or spring weather, but rather the abundance and behavior of other queens. To be sure, the vagaries of spring weather also impose their effect and impede our ability to accurately predict yellowjacket populations (Akre and Reed, 1981).

Clearly, the ability of a yellowjacket queen to initiate and defend a nest carries a very large risk. Perhaps, as Evans (1975) has said «... too much has been made of the sting as a defense against vertebrate enemies, and too little made of the sting as a means of repelling foreign queens».

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