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25. This is a contribution to the Hubbard Brook Ecosystem Study. Financial support was provided by the National Science Foundation. We thank R. H. Whittaker for comments and suggestions on the manuscript.

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Vespula squamosa: A Yellow Jacket Wasp Evolving Toward Parasitism

Abstract. *Evidence from behavior and from nest architecture implicates* Vespula squamosa *as a temporary, apparently facultative social parasite of* V. maculifrons. *Analysis of 66* V. squamosa *nests collected in northern Georgia revealed that 54 were initially built by* V. maculifrons. *Three very young* V. maculifrons *nests, each with a* V. squamosa *queen and workers of both species, confirmed the parasitic propensity.*

Social parasitism, in which the young of one species are actively raised by another, has arisen repeatedly among such divergent animal groups as birds and insects. It is widespread in the eusocial Hymenoptera, particularly among the ants, among whom it occurs repeatedly in quite unrelated stocks; among eusocial wasps, however, only four genera are known to contain social parasites (*1, 2*). Among the three dozen species of socially parasitic wasps, most have a relationship involving obligatory and permanent coexistence between intruder and host; the parasite queen usurps the host queen's position but produces no worker caste and depends on host workers to rear her reproductive forms (*3*). However, this common and rather extreme form of parasitic dependence (inquilinism) tells us little of the evolutionary pathways by which it was achieved. We now report on a notable exception, a temporary and apparently facultative social parasite—the yellow jacket wasp *Vespula squamosa* (Drury)—that seems to be crossing the evolutionary threshold from a free-living existence to parasitism.

Over most of its range, *V. maculifrons* is sympatric with *V. squamosa*. Although *V. squamosa* is common and widely distributed throughout eastern North America from New York to southern Mexico (*4*), few biological data exist for this species, except for reports of unusual nests and various miscellaneous observations (*5*). The only previous indication of its possible parasitic propensity is the single report that a queen was found in West Virginia in a *V. vidua* (Saussure) nest (*6*). In 1974, however, in collecting 66 *V. squamosa* and 63 *V. maculifrons* (Buysson) colonies from northern Georgia for analysis of nest architecture and population structure, we found evidence that *V. squamosa* queens regularly usurp established colonies of *V. maculifrons*.

A number of characteristics easily distinguish nests of the two species, especially nonoverlapping differences in the size of worker cells, and envelope paper—*V. maculifrons* nests are always tan and of a fragile, flaky texture, but *V. squamosa* makes a much tougher gray paper. In 54 (82 percent) of the outwardly typical *V. squamosa* nests, we found distinguishable central cores of smaller tan cells in the initial worker combs. Remains of a tan, fragile envelope covered the top of the oldest comb (Fig. 1). Supports between combs in the oldest part of the nest had the grainy, brittle, sawdust texture of *V. maculifrons* nests, in contrast to the hard, glossy gray *V. squamosa* supports in the rest of the nest. Typically, the number of *V. maculifrons* cells was low compared with the number of *V. squamosa* cells, which indicated that usurpation occurred quite early in the nesting season. Excluding two unusual nests (*7*), an average of 278 *V. maculifrons* cells (range, 58 to 479) occupied the central core of initial combs of usurped nests, only 1 to 19 percent of the total worker cells ($\bar{X}$ = 6 percent).

Direct behavioral confirmation of usurpation was obtained in June 1975, when two *V. maculifrons* nests were discovered into which individuals of both species carried provisions and pulp loads. Upon dissection, one nest the size of a baseball was found to contain 16 *V. maculifrons* workers, 58 *V. squamosa* workers, and a single *V. squamosa* queen, with no trace of the host queen. Cells of the three combs were all small and tan; the predominantly tan nest envelope contained gray bands intermixed in the most recently constructed portions. The smaller second nest that was usurped contained 245 tan cells and harbored seven *V. maculifrons* workers, 35 *V. squamosa* workers, and a single *V. squamosa* queen, again with no trace of the host queen. A third usurped *V. maculifrons* nest, transplanted into an observation nest box, contained an estimated 330 tan cells and harbored only 13 host workers, one newly eclosed parasite worker, and the parasite queen; but again there was no host queen.

The above evidence indicates a socially parasitic existence for *V. squamosa*, in which a fertile overwintered queen searches out and invades an established young colony of *V. maculifrons* and somehow eliminates the host queen. Laying her own eggs within the nest, the *V. squamosa* queen relies on *V. maculifrons* workers to raise her first brood of workers. After a week or so, since no further *V. maculifrons* eggs are being laid, host workers begin to dwindle in number, and eventually a "pure" *V. squamosa* colony results, with parasite workers and finally with reproductives. This relationship is termed temporary social parasitism; the only other vespid wasp at a similar evolutionary level is a hornet, *Vespa dybowskii* Andre, a facultative temporary social parasite of two other Oriental species of *Vespa* (*8*).

While over four-fifths of our *V. squamosa* nests constituted unequivocal cases of usurpation, 12 nests showed no trace of a *V. maculifrons* heritage. These may repre-

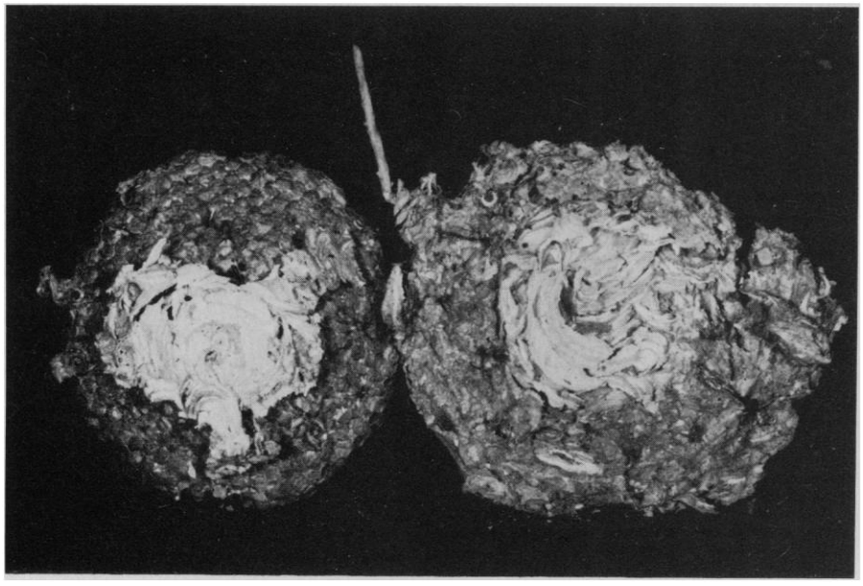

Fig. 1. Portion of a subterranean nest of *Vespula squamosa*. A typical mature nest would contain a stack of four to eight horizontal combs with cells opening downward, these being enclosed by a multilayered paper envelope. Nest expansion occurs laterally and downward, and the cavity is enlarged by workers as more space is needed. The dorsal surface of the oldest worker comb (left) and the inside of the envelope that covered it (right), which has been folded away from it, clearly show the lighter color and different texture of *V. maculifrons* paper in the center. This nest is approximately the size of a softball.

sent nests initiated by *V. squamosa* queens, in which case the parasitism is facultative. Since the smallest unequivocally usurped nest contained at least twice as many cells as a typical queen nest (*9*), *V. squamosa* queens may not discover host nests until after the first host workers become active. Alternatively, usurpation might occur so early in some colonies that it cannot be detected by study nest architecture. A precedent for the latter exists in another host-parasite *Vespula* pair; the inquiline *V. arctica* Rohwer queen and *V. arenaria* (F.) host queen are present together very soon after nest building and before emergence of host workers (*10*). Thus, the question of whether the socially parasitic behavior of *V. squamosa* queens is obligatory or facultative cannot be conclusively determined at this time (*11*).

Emery's rule, a general axiom regarding social parasitism, states that the closest relative of a social parasite tends to be the free-living species from which the parasite stock was derived (*1*, p. 360). According to one classification of Nearctic *Vespula*, *V. squamosa* and *V. maculifrons* are not closely related but are assigned to different species groups (*12*). Moreover, *V. squamosa* appears wrongly placed in the same species group with *V. vidua* (*13*). Thus, if reported parasitism of *V. vidua* by *V. squamosa* (*6*) in fact occurs, it seems that two distantly related species may be parasitized by a species not closely related to either host. This apparent violation of Emery's long-standing generalization suggests that pressures leading to the evolution of temporary, apparently facultative parasitism by *V. squamosa* may have been quite different from other cases of social parasitism, in which close association between two species would seem facilitated by common communicative channels and other shared behavioral patterns.

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References and Notes

1. E. O. Wilson, *The Insect Societies* (Harvard Univ. Press, Cambridge, Mass., 1971).
2. The four genera include *Polistes*, *Mischocyttarus*, *Vespa*, and *Vespula*. *Vespula* is divided into two subgenera based on adult morphology and nesting habits; *V. (Dolichovespula)* construct aerial nests and *V. (Vespula)* construct subterranean nests.
3. Among Nearctic *Vespula*, obligatory permanent social parasites include *V. (D.) arctica* Rohwer in nests of *V. (D.) arenaria* (L.) and *V. (V.) austriaca* (Panzer), whose Nearctic host has not been documented but which parasitizes *V. (V.) rufa* (L.) in Europe (*1*, p. 378).
4. C. D. F. Miller, *Can. Entomol. Suppl.* **22**, 1 (1961).
5. A. N. Tissot and F. A. Robinson, *Fla. Entomol.* **37**, 73 (1954); A. T. Gaul, *Bull. Brooklyn Entomol. Soc.* **42**, 87 (1947). Our study finds that *V. squamosa* colonies persist late into autumn and typically consist of 2000 to 4000 workers. Mature nests contain up to 10,000 cells.
6. L. H. Taylor, *Ann. Entomol. Soc. Am.* **32**, 304 (1939).
7. One nest contained 1360 tan cells, the other 2186 (31 percent and 48 percent of the total worker cells, respectively). Thus, although most nest usurpation seems to occur early in the season, *V. squamosa* queens are apparently able to invade even well-established *V. maculifrons* colonies. Moreover, repeated usurpations of the same nest may occur; three nests collected in late July and early August 1974 contained from 3 to 25 *V. squamosa* queen carcasses in the nest cavity together with a live queen in each. Similarly, June excavations of very young *V. maculifrons* nests in 1975 suggest conspecific supersedure, the first stage in the evolution of social parasitism as postulated by Taylor (*6*); from one to three freshly killed *V. maculifrons* queens were found beneath nests of some *V. maculifrons* colonies.
8. S. F. Sakagami and K. Fukushima, *Insectes Sociaux* **4**, 1 (1957).
9. Documented queen nest sizes of the subgenus *Vespula* are few, but most have contained 20 to 40 cells [J. P. Spradbery, *Wasps* (Univ. of Washington Press, Seattle, 1973)].
10. H. E. Evans, *Insect World Dig.* **2**, 6 (1975).
11. Obligatory, temporary social parasitism between species, so common in the ants, has not been documented in the social wasps (*1*, *6*).
12. J. C. Bequaert, *Entomol. Am.* **12**, 78 (1931). The subgenus *Vespula* is divided on the basis of adult morphology and biology into at least two species groups, *V. vulgaris* (L.) and *V. rufa* (L.).
13. Comparative nest architectural, behavioral, morphological, and electrophoretic data currently under study strongly indicate that *V. squamosa* is wrongly aligned with the *V. rufa* group to which *V. vidua* is assigned.

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On Evoked Potentials, Cognition, and Memory

Begleiter and Porjesz (*1*) report a study of the effects of decision-making processes on event-related brain potentials (ERP) recorded at the vertex. They have obtained data which "demonstrate the relationship between specific components of the ERP to a sensory stimulus and a cognitive decision about the physical attributes of that stimulus." From this finding they derive the suggestion "that these patterns of neural activity might reflect the activation of memory traces about the specific experience." The relation between evoked potential components and cognitive activity which Begleiter and Porjesz report is well known. The data they present suggest that the principal decision-related ERP component they record is the P300 component. This being the case, the conclusions that they draw concerning memory are unwarranted.

A brief survey of the literature will put matters in perspective. In *Science* alone there have appeared in the last decade numerous reports (*2–4*) which have unequivocably established "a relationship between specific components of the ERP to a sensory stimulus and a cognitive decision . . ." (*1*). The component of the evoked response to which these reports refer is a positive-going potential, with a peak latency in the range of 250 to 350 msec. This component, often labeled P300 or P_3, is currently the focus of much active research. A recent bibliography by Price and Smith (*5*) contains 145 items. Considerable detail has accumulated on the relationship of P300 to cognitive activity and has been published in several major journals (*6–10*). Of this vast literature Begleiter and Porjesz cite a single paper—Sutton *et al.* (*3*).

Had they considered the relevant literature Begleiter and Porjesz would have realized that most, if not all, of the enhanced