

## Comparison of Nestmate Recognition Between Monogyne and Polygyne Populations of *Solenopsis invicta* (Hymenoptera: Formicidae)

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Ann. Entomol. Soc. Am. 83(3): 642-647 (1990)

**ABSTRACT** The occurrence of polygyne and monogyne *Solenopsis invicta* (Buren) populations offers a unique opportunity to test hypotheses related to nestmate recognition. Recognition bioassays were based on the aggressive behavior observed during intraspecific introductions of monogyne and polygyne *S. invicta* workers (intruders) into polygyne and monogyne *S. invicta* colonies (residents) and interspecific introductions into *Solenopsis richteri* Forel colonies. No aggression differences were observed between monogyne and polygyne colony workers that were removed from their colonies, then reintroduced into their parent colony (no aggressive behavior) or when *S. richteri* workers were introduced into monogyne or polygyne colonies (strong aggressive behavior). In all other cases, polygyne workers displayed significantly less aggressive behavior than monogyne workers, as residents and as intruders. Therefore, at the species level, polygyne workers are less able to distinguish nestmates from nonnestmates than monogyne workers. This result fits a theoretical prediction of diminished intraspecific aggression in polygyne populations. These lowered aggression levels are attributed to the polygyne population's exposure to a greater variety of environmental and endogenous stimuli. Although in monogyne *S. invicta*, the queen is not a major contributor to nestmate recognition cues, the role of queens in polygyne situations remains to be determined.

**KEY WORDS** Insecta, nestmate recognition, behavior, *Solenopsis* spp.

NESTMATE RECOGNITION in social Hymenoptera is defined as the ability to discriminate colony members from conspecific noncolony members. Kin recognition is the ability to discriminate different degrees of relatedness among conspecifics. Both occur in ants (see Breed & Bennett [1987] for review). In this paper, unless otherwise specified, we shall consider recognition at the colony level (i.e., nestmate recognition).

It is generally accepted that nestmate recognition is based on a learned "colony odor," or a subset of it (Vander Meer 1988). Nestmate recognition cues can be derived from the individuals, queens, or workers ("discriminators"), or from the environment (Hölldobler & Michener 1980). Because the queen is "the simplest conceivable mechanism" to provide nestmate recognition cues, Hölldobler & Wilson (1977) predicted that intercolony discrimination should be less well developed in polygyne (i.e., multiple queens) colonies than in monogyne (i.e., single queen) colonies. The presence of numerous queens would deny the colony a distinctive odor, thus preventing discrimination among neighboring colonies. A low level of intercolony aggression occurs in several polygyne ant species (see review in Breed & Bennett [1987]). For example, *Monomorium pharaonis* L., which shows a high degree of polygyny, lives in "unicolonial populations" and does not display aggressive be-

havior among neighboring colonies (Petersen-Braun 1982). However, a certain amount of recognition at the supercolony or population level has been reported in polygyne colonies of *Formica polyctena* Forster (Mabelis 1979), *Amblyopone pallipes* (Haldeman) (Traniello 1982), and *Iridomyrmex purpureus* (Smith) (Halliday 1983).

*Solenopsis invicta* Buren is one of the few ant species which has large populations of both monogyne and polygyne forms. The first polygyne colonies of *S. invicta* were discovered 15 yr ago (Glancey et al. 1973), and polygyny now occurs across the entire U.S. range of the ant (Fletcher et al. 1980, Miranda & Vinson 1982, Ross & Fletcher 1985, Glancey et al. 1987). The population dynamics of each form are poorly documented, but we know that monogyne and polygyne populations occur close to each other. Polygyne colonies are typically polydomous (i.e., each colony occupies many mounds connected by subterranean foraging tunnels). In fact, the boundaries of a polygyne colony are not clearly defined. Monogyne *S. invicta* may also occupy more than one mound (Byron & Hays 1986).

The average coefficient of relatedness within monogyne colonies is 0.714 (Ross & Fletcher 1985), indistinguishable from that of 0.75 expected in colonies with one queen inseminated by a single male. In contrast, the within-nest coefficient of related-

ness of workers in polygyne nests does not differ significantly from 0. This reflects the many unrelated matrilines in a single polygyne colony. In monogyne *S. invicta* populations, the contribution of the queen to nestmate recognition cues is much less than are environmentally and worker-derived contributions (Obin 1986, Obin & Vander Meer 1988).

The occurrence of abundant populations of both polygyne and monogyne forms of the same species in the same geographic area make *S. invicta* a perfect model to test Hölldobler and Wilson's prediction about the consequences of polygyny on nestmate recognition. Miranda & Vinson (1982) found that workers from different polygyne *S. invicta* mounds were more tolerant of each other than of monogyne workers when they were allowed to come into contact. However, Miranda & Vinson (1982) studied field-collected colonies maintained in the laboratory, and the uniform environment of the laboratory diminishes the discriminatory abilities of monogyne *S. invicta* (Obin 1986). In our comparison of nestmate recognition in polygyne and monogyne populations of *S. invicta*, we avoided laboratory effects by conducting tests on ants in their nest soil soon after they were collected from the field. We measured the aggressive response of resident polygyne and monogyne colonies to each other, as well as the responses of the polygyne and monogyne intruders. In addition, we tested whether the lower aggressive response of polygyne colonies corresponded to a generally diminished discrimination of nestmate (inter- and intraspecific), or to a phenomenon restricted to the intraspecific level. For this purpose, we compared the responses obtained in the intraspecific tests with those obtained in the interspecific tests with *S. richteri* intruders. We also separately determined if our bioassay could quickly assess whether or not an *S. invicta* colony was monogyne or polygyne.

### Materials and Methods

**Collection and Maintenance of the Ants.** In this paper, a mound will be considered a "colony." Ants from monogyne and polygyne populations were collected in Alachua, Levy, and Marion counties, Fla., in April and June 1987. Mounds were considered monogyne by their size, worker size (Greenberg et al. 1985), previous history of colonies at the collection site, and the presence of only one inseminated female (i.e., queen) during the field collection. Mounds were considered polygyne by the same criteria and by the presence of several inseminated females. Insemination was determined by examining the dissected spermatheca, which is pearl-white and turgid when the female is inseminated.

All *S. invicta* workers were collected by transferring about 300 ml of dirt from each mound to a small ceramic pan (28 by 15 by 5 cm), the sides of which were coated with Fluon (ICI, Wilming-

ton, Del.) to prevent escapes. Each pan represented a colony and contained about 300 workers with some brood. All sexuals were removed immediately. Following the removal of this subsample, the remainder of the mound was searched extensively for queens. Colonies of a particular type collected at a given time came from the same location (within 10,000 m<sup>2</sup>). In the laboratory, a wet cotton ball was placed in each pan, and the ants were left undisturbed for about 24 h before the bioassays began. No food was provided. The room temperature was 24–26°C and the photoperiod varied.

Workers of *S. richteri* for the bioassays came from a monogyne colony collected in Lee County, Miss. They had been maintained for 2 yr in the laboratory as described by Banks et al. (1981). This colony was identified as "pure" *S. richteri* by gas chromatographic analysis of species-specific venom alkaloids and hydrocarbons (Vander Meer et al. 1985).

**Nestmate Recognition Bioassay and Data Analysis.** Nestmate recognition between two colonies was assessed by a bioassay that measured aggressive behavior during nest defense (for a detailed description, see Obin [1986]). Individual workers ("intruders") were introduced into a pan of "resident" ants. The responses of the residents and of the intruders were scored from 0 to 9 by increasing aggressive behavior (Table 1). For each test, the highest aggressive score of the intruder-residents' first 20 interactions was recorded for the intruder and for the residents. The 20 interactions (encounters) provide a better representative sampling of the resident population than, for instance, scoring only the first interaction. After each test, the intruder was removed and discarded. Controls consisted of the removal and reintroduction of workers into their own colonies.

The colonies in each group (P, polygyne; M, monogyne) were assigned the same series of numbers. The sequence in which they were tested was determined by drawing random numbers (i.e., M2 into P5). The same random numbers were used for the reciprocal introductions (i.e., P5 into M2). A colony classified as resident or as providing intruders was never tested twice successively. All colonies were tested once as residents before a colony was tested again as resident. The following day, the same introduction series was performed. The ants received only water between the two test days (body reserves and microarthropods in the nest soil were considered sufficient to maintain the workers for the 2-d test).

Two different sets of colonies were tested: one set of nine P and nine M colonies was collected and tested in April 1987, and a second set of six P and six M colonies was collected and tested in June 1987. Each colony was tested as resident six times with heterocolonial intruders and two times as control during the 2 d. The following types of introductions were tested in addition to the controls ( $n = 40$ ): P into P ( $n = 44$ ), M into M ( $n = 44$ ), P into

**Table 1. Behavioral units and aggression scores used to assess nestmate and species recognition**

Score	Behavior <sup>a</sup>
9	Immediate lunge, grab and stinging.
8	Opponent surrounded and "held" in mandibles, appendages pulled or bitten off, eventual stinging.
7	Opponent held (as in 8) but released, biting, abdomen-curling (stinging position) but no stinging.
6	As in 7, but no abdomen curling.
5	Alarm (running, abdomen elevation and vibration) and recruitment.
4	Mandible gaping, rapid antennation, "sidling" (maintaining a lateral orientation to and slowly circling opponent).
3	Rapid antennation with antennae extended for more than 2 s.
2	Antennation for less than 2 s. If mobile, opponent is followed slowly for several cm; if opponent stationary, worker stops.
1	As in 2, but opponent does not induce following or stop.
0	No interactive behavior displayed.

<sup>a</sup> These behaviors are used for the response of resident to intruder as well as for the response of intruder to resident(s). Residents and intruders are referred to as "opponents."

M ( $n = 40$ ), and M into P ( $n = 40$ ). No significant differences were obtained between the two testing periods; therefore, the data were pooled.

At the end of the April tests, one *S. richteri* worker was tested in each *S. invicta* monogyne and polygyne colony. The results for the intruder were not analyzed statistically, because the aggressive responses of *S. invicta* residents were so intense that the *S. richteri* intruder always scored 0.

The mean ( $\pm$ SD) scores of each group being compared were computed from individual introductions. Wilcoxon two-sample tests were used for comparisons. Although repetitive comparisons can present statistical problems, in all cases where a significant difference was detected, the level of significance was high.

**Blind Tests.** We wished to see whether these tests could determine if an unknown colony is monogyne or polygyne. In June 1987, 16 colonies were collected (eight monogyne and eight polygyne) from a pasture in which separate populations of polygyne and monogyne colonies were known to occur. The colonies were randomly numbered, and the following series of aggression bioassays were run. The observer (L.M.) did not know from which colony the ants were taken. An intruder ant from colony 1 (a monogyne colony) was introduced separately into each of the other 15 colonies. Colony 1 was tested with intruders from colony 16 (a polygyne colony). Predictions based on the level of aggression observed were then compared with the actual type of the colonies, based on the criteria given in the section "Collection and Maintenance of the Ants."

Voucher specimens of the field-collected monogyne *S. invicta* and the laboratory-reared *S. richteri* have been deposited at the Florida State Col-

**Table 2. Responses of monogyne (M) and polygyne (P) *S. invicta* resident ants to intruders in recognition bioassays**

Combination tested <sup>a</sup>		$n$	Aggression level, $\bar{x} \pm$ SD
I	Controls	40	1.15 $\pm$ 0.43
II	M into P	40	2.38 $\pm$ 1.60
III	P into M	40	7.10 $\pm$ 2.22
IV	M into M	44	6.86 $\pm$ 2.13
V	P into P	44	1.45 $\pm$ 1.07
VI	<i>S. richteri</i> into M	9	6.44 $\pm$ 2.18
VII	<i>S. richteri</i> into P	9	7.44 $\pm$ 0.73

<sup>a</sup> Various combinations of I to VII were tested. Statistical comparisons (Wilcoxon test): I versus V ( $P < 0.01$ ); II versus V ( $P < 0.05$ ); III versus IV ( $P > 0.05$ ); III versus VI ( $P > 0.05$ ); IV versus VI ( $P > 0.05$ ); VI versus VII ( $P < 0.01$ ).

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## Results

**Aggressive Response of Resident Ants.** Monogyne and polygyne controls did not differ in their responses; therefore, these data were pooled. The scores elicited by intruders from polygyne colonies into other polygyne colonies were significantly different from the controls, although the low mean scores indicate only investigative activity (Table 2, I versus V). Polygyne residents displayed significantly higher scores to intruders from monogyne colonies than from polygyne colonies (II versus V). There was no significant difference between scores of monogyne residents to monogyne or polygyne intruders (III versus IV), or to *S. richteri* intruders (IV versus VI).

Resident test results fall into three groups: no aggression (monogyne and polygyne controls); awareness (polygyne and monogyne into polygyne); and high aggression (polygyne, monogyne, and *S. richteri* into monogyne and *S. richteri* into polygyne).

**Aggressive Response of Intruder Ants.** Monogyne intruders showed significantly higher aggression when introduced into polygyne colonies than did controls (Table 3, II versus I). With all other

**Table 3. Responses of monogyne (M) and polygyne (P) *S. invicta* intruder workers to residents in recognition bioassays**

Combination tested <sup>a</sup>		$n$	Aggression level, $\bar{x} \pm$ SD
I	Controls	40	1.03 $\pm$ 0.16
II	M into P	40	5.53 $\pm$ 2.11
III	P into M	40	1.20 $\pm$ 0.72
IV	M into M	44	1.53 $\pm$ 1.43
V	P into P	44	1.13 $\pm$ 0.35

<sup>a</sup> Various combinations of I to V were tested. Statistical comparisons (Wilcoxon test): I versus II ( $P < 0.001$ ); II versus III ( $P < 0.001$ ); II versus IV ( $P < 0.001$ ); II versus V ( $P < 0.001$ ); I versus IV ( $P > 0.05$ ).

combinations, no aggressive behavior was displayed by the intruder.

**Blind Tests.** All colonies of unknown type were classified correctly as being monogyne or polygyne (eight of each) based on aggression bioassay results. Workers from each colony were tested twice as either "residents" or "intruders." After the first series, 14 colonies (87.5%) were unambiguously classified; another series of tests was required to classify the remaining two colonies.

### Discussion

Fire ant (*Solenopsis* spp.) workers from monogyne colonies recognize nestmates from nonnestmates at both inter- and intraspecific levels (Obin 1986, Obin & Vander Meer 1988). Nestmate recognition is part of the complex chemical communication system which allows an ant community to maximize the exploitation of its environment and, hence, its survival (Hölldobler & Carlin 1987). The polygyne form of *S. invicta* (Glancey et al. 1973) is found in large populations throughout its current range of infestation in the United States (Fletcher et al. 1980, Mirenda & Vinson 1982, Ross & Fletcher 1985, Glancey et al. 1987). Monogyne and polygyne *S. invicta* populations appear to occupy the same habitats and are found adjacent to each other. Consequently, at least where they interface, the two types must compete for resources. This competition can be mediated by many factors such as foraging strategy, effectiveness of recruitment, recognition of nestmates, and level of aggression. The interactions of neighboring polygyne colonies (mounds) with each other and with monogyne colonies (and vice versa) is important information that will help us understand the dynamics of the two *S. invicta* forms and will provide insight into nestmate recognition mechanisms.

When two polygyne *S. invicta* colonies share the same foraging area in the laboratory, they are tolerant of each other, whereas they are not tolerant of workers from monogyne colonies under similar experimental conditions (Mirenda & Vinson 1982). To minimize possible laboratory effects, bioassays were conducted with worker ants in their nest soil within 2 d of field collection. Although not ideal, this method provides an approximation to field conditions.

Nestmate recognition mechanisms and cue sources have been extensively studied for monogyne *S. invicta*. Workers discriminate nestmates from nonnestmates by matching phenotypic "recognition labels" detected on encountered individuals with a "template" (Obin 1986, 1987). Environmentally derived cues and worker genotypic cues dominate the recognition cue hierarchy with little or no direct involvement of the queen (Obin 1986, Obin & Vander Meer 1988).

In contrast, nestmate recognition is poorly documented in polygyne *S. invicta*. As in monogyne

*S. invicta*, both heritable and environmentally derived cues have been demonstrated to affect nestmate recognition in laboratory-maintained polygyne colonies (M. S. Obin et al., unpublished data). Although the mechanisms of nestmate recognition may be the same in both social forms of *S. invicta*, the role of multiple worker matriline and queens has not been evaluated. In addition, mounds within polygyne populations do not represent a discrete colony. Queens and workers move freely from one mound to another (Glancey & Lofgren 1988), presumably exchanging heritable and environmentally derived nestmate recognition cues.

**Interactions Between Polygyne Workers.** The removal and reintroduction of workers from polygyne colonies back into their own colonies gave the lowest aggression scores, indicating that the colonies were not stressed by their movement (Tables 2 and 3). Although the intercolonial polygyne worker response was greater than intracolony controls, the level of activity corresponded to awareness rather than aggression. This supports the contention that, within polygyne populations, territoriality and competition for resources through aggressive behavior do not exist or are greatly moderated. All workers in a polydomous, polygyne fire ant population are treated as nestmates. Each discrete population probably represents a supercolony or "unicolony" (Hölldobler & Wilson 1977).

Environmental contributors to monogyne *S. invicta* nestmate recognition cues are dampened out by using uniform laboratory conditions, and aggression levels are reduced (Obin 1986). The residual aggression was attributed to heritable factors. Similarly, polygyne *S. invicta* reared in the laboratory were shown to have nestmate recognition cues derived from both environmental and heritable sources (M. S. Obin et al., unpublished data). Interestingly, aggression levels among our polygyne field colonies are lower than that attributed to the heritable cues in monogyne colonies (Obin 1986) or laboratory-reared polygyne colonies (M. S. Obin et al., unpublished data). It appears that in polygyne field populations, the effects of both environmental and heritable cues are dampened. This process cannot be caused by complete mixing of cues, because such a process is unlikely to occur over large areas. If it did occur, the situation would be analogous to that of a monogyne colony, where workers develop a template based on a relatively uniform set of cues characteristic of the colony. Nestmate recognition behavior would then be the same for monogyne and polygyne colonies (polygyne residents would react aggressively to monogyne intruders). We propose, instead, that because polygyne workers contact multiple varieties of nestmate recognition cues, the allowed variability of their template is greater than that of monogyne workers.

Alternatively, polygyne intruders may be recognized as nonnestmates without any modification of the polygyne residents' agonistic behavior. This

hypothesis cannot be tested experimentally (if there are no measurable behaviors) or would require another bioassay. The decreased agonistic behavior of polygyne colonies of *S. invicta* is not because of an impaired ability to display aggressive behavior, for they display all aggressive responses to *S. richteri* intruders.

**Interaction Between Polygyne and Monogyne Workers.** The aggression score of polygyne residents toward monogyne intruders was significantly higher than scores of controls and polygyne workers introduced into polygyne colonies. No true aggressive behavior, such as mandible gaping or biting, was displayed. Instead, the behavior corresponded to "awareness": the monogyne intruder was antennated and followed if mobile. However, the monogyne intruder displayed aggressive behavior, corresponding to alarm and, in some cases, mandible gaping and short bites. This kind of intruder behavior was not observed in the other confrontations.

Polygyne intruders did not interact antagonistically with polygyne residents, and it was common that the intruder resumed activities it was engaged in before the test. In introductions involving monogyne residents or interspecific intruders, the intruder had no opportunity to display aggressive behavior because it was vigorously attacked and usually immobilized. If it was not held by resident(s), the intruder tried to escape or hide (also observed by M. S. Obin, personal communication). In the special situation where the resident colony is polygyne, the monogyne intruder is not attacked and can therefore display its own aggressive behavior. This may have been responsible for the "awareness" behavior observed in polygyne residents with monogyne intruders. Monogyne *S. invicta* recognized an intruder as nonnestmate, whether it came from polygyne colonies, other monogyne colonies, or *S. richteri* colonies. The lack of aggression displayed by polygyne *S. invicta* workers toward other polygyne workers, as well as to monogyne *S. invicta* workers, indicates a lack of conspecific nestmate recognition. In contrast, monogyne *S. invicta* workers recognize both polygyne and other monogyne *S. invicta* colony workers as different. This asymmetry has implications regarding the mechanism of nestmate recognition.

The demonstration that polygyne colonies of *S. invicta* do not discriminate between nestmates or conspecific nonnestmates is in agreement with the results of Miranda & Vinson (1982) in merging laboratory colonies and the reduced aggression prediction of Hölldobler & Wilson (1977). Our data support the proposition of the latter authors that polygyny would yield a confusing amount of odor diversity, which would break down the functionality of heritable cues and erase colony boundaries. However, in the case of *S. invicta*, the heritable cue breakdown is most probably caused by worker discriminators from the multiple matrilines rather than multiple queen discriminators.

Hölldobler & Wilson (1977) also predicted that polygyne colonies would be more aggressive at the interspecific level than monogyne colonies, resulting in a decrease of ant species diversity. Our study showed that statistically polygyne colonies of *S. invicta* are more aggressive than monogyne workers to *S. richteri* intruders. However, how the small difference in aggressive scores relates to field situations is unknown. Other non-*Solenopsis* species also must be tested. It is known that species diversity decreases sharply in areas infested with monogyne *S. invicta* (Whitcomb et al. 1972, Wojcik 1983); however, a comparative study of the two forms has not been made.

For ecological, behavioral, and control purposes, it is important to know if the area is infested with monogyne or polygyne *S. invicta* colonies. A colony is usually identified as polygyne when several inseminated queens can be found. This method requires gross disruption of the mound followed by dissections of queens in the laboratory to check for insemination. Our results with 16 colonies tested blind demonstrate that the recognition bioassay can be used successfully as an alternative method to differentiate monogyne from polygyne colonies with only minor disturbance to the colony.

#### Acknowledgment

We thank L. Davis and K. Plumley for their assistance in field collection and J. Sivinski and A. Undeen for commenting on the manuscript.

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Received for publication 13 March 1989; accepted 26 October 1989.