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Nestmate Recognition in Fire Ants: Monogyne and Polygyne Populations

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INTRODUCTION

Nestmate recognition in ants is defined by the ability of workers to discriminate colony members from non-colony members among conspecifics. This is a well documented behavioral phenomenon (see Breed and Bennett 1987 for review). It is generally accepted that nestmate recognition is based on learned "chemical cues," a subset of overall colony odor (Vander Meer 1988). These cues can be derived from individuals, queens and/or workers ("discriminators") or from the environment (Hölldobler and Michener 1980). The recognition process has two elements: chemical cues on the intruding ant's surface and the resident worker's "neural imprint" or sensory template. If the intruder's cues match the template of the resident no aggression occurs; however, agonistic behaviors may ensue if they do not match.

S. invicta from the United States exist in both monogyne and polygyne forms. Polygyne *S. invicta* colonies were first reported by Glancey et al. (1973). Surveys indicate extensive polygyne populations in most of the 11 infested states of the south and southeast (Fletcher et al. 1980; Mirenda and Vinson 1982; Ross and Fletcher 1985; Glancey et al. 1987). Although the population dynamics of each form are poorly documented, monogyne and polygyne *S. invicta* occur in close proximity to each other. Hölldobler and Wilson (1977) predicted that the multiple matriline and patriline in a single polygyne nest would lead to reduced intraspecific aggression compared to a typical monogyne situation. For example, the highly polygyne *Monomorium pharaonis*, lives in "unicolonial populations," and does not display aggressive behavior between neighboring colonies (Petersen-Braun 1982). In addition, Hölldobler and Wilson (1977) predicted polygyne colony workers would be more aggressive at the interspecific level than monogyne workers, resulting in decreased ant species diversity.

This paper reviews studies aimed at elucidating the nestmate recognition mechanism of *S. invicta* in both monogyne and polygyne forms. Since both polygyne and monogyne *S. invicta* occur in the same species and the same geographic area, this ant makes a good model to test Hölldobler and Wilson's (1977) predictions. Recognition test comparisons for the two forms also provide insight into the potential practical application of the recognition process.

ENVIRONMENTAL VS HERITABLE CUES

Environmental

Heritable (Mintzer and Vinson 1985) and/or environmental (Jutsum et al. 1979) odors have been reported as ant nestmate recognition cues. Obin (1986) reared *S. invicta* workers from different colonies under identical laboratory conditions and found that they respond less aggressively to non-nestmate laboratory conspecifics than they do to field collected conspecifics. The almost 100 percent recognition of field collected non-nestmates by laboratory reared workers eliminates the possibility that laboratory rearing produced less aggressive workers.

The reduced aggression level observed among laboratory reared colonies supports the hypothesis that environmental odors play a role in *S. invicta* nestmate recognition (Obin 1986). Environmental odor sources include foods, soil and the atmosphere. These odors are passively absorbed unto the ant's lipophilic cuticle through simple contact, social interactions and trophallaxis. The continuously changing odors will be more or less uniformly distributed throughout the colony (Vander Meer 1988).

Heritable

The response of resident lab-reared workers to lab-reared intruders from monogyne colonies was significantly greater than the resident response to nestmates, despite over 18 months of uniform laboratory conditions (Obin 1986). By providing a uniform environment (lab-rearing), the effects of environmental cues can be nullified. The remaining aggression must be due to heritable cues. Although quantitative, the bioassay cannot determine the relative contributions of environmental and heritable cues to the recognition process (see next section).

THE HIERARCHY OF RECOGNITION CUES

Genetically correlated cues may be produced by any colony member; e.g., workers or the queen (Hölldobler and Michener 1980). The rapid distribution of cuticular compounds to other colony members has been demonstrated by: a) mixing of species-specific cuticular compounds in laboratory colonies with two different species (Errard and Jallon 1987; Vander Meer unpublished, b) rapid distribution of radiolabeled markers in fire ant colonies (Sorensen et al. 1985) and c) transfer of species-specific fire ant hydrocarbons to a myrmecophilous beetle (Vander Meer and Wojcik 1982). Transferable queen discriminators have been demonstrated for laboratory colonies of *Camponotus* spp. (Carlin and Hölldobler 1983).

Since aggression persists between non-nestmate *S. invicta* workers reared under identical laboratory conditions, heritable cues derived from either workers or queen are involved. Several experiments designed to test the hypothesis that queen discriminators influence nestmate recognition have been carried out. Addition of an alien queen to small, queenless subcolonies did not significantly increase aggression between recipient and non-recipient subcolonies derived from the same parental colony (Obin and Vander Meer 1988). In addition, parent colony response to intruders from queenless

subcolonies was not significantly different from parent colony response to queenright nestmates; the response of parent and corresponding subcolony to non-kin was not different (Obin and Vander Meer 1989a). These data argue against the involvement of queen produced discriminators which, by elimination, leaves worker discriminators as the source of heritable nestmate recognition cues in *S. invicta*.

The aggression observed when colonies are held under uniform environmental conditions is investigative or challenging, rather than attack. This does not mean that environmental cues cause the most aggressive response in *S. invicta*. Until heritable cues can be nullified without affecting environmental cues, the relative contributions of the two cue sources cannot be determined; nor can any synergistic effects. Therefore, the question of cue hierarchy remains unanswered in *S. invicta*.

THE CHEMISTRY OF NESTMATE RECOGNITION

Researchers generally accept that nestmate recognition involves detection of specific chemicals on the cuticle (Wilson 1971). As already mentioned *S. invicta* utilizes environmental and heritable cues. Dietary effects (an environmental component) on nestmate recognition have been clearly demonstrated (Obin 1986, Obin and Vander Meer 1988, Obin and Vander Meer 1989c); however, the heritable part has been much more elusive. Cuticular hydrocarbons, potential heritable cues, have been associated with nestmate recognition in *Camponotus vagus* (Bonavita-Cougourdan et al. 1987) and with the integration and survival of a myrmecophilus beetle in fire ant nests (Vander Meer and Wojcik 1982). Undue excitement, regarding nestmate recognition, surrounds cuticular hydrocarbons as cues because they are readily analyzed and if studied using pattern recognition techniques, individual colonies are distinguishable. This may mean nothing to the ants.

In any event, the hydrocarbons are a part of the heritable component of colony odor and can be used as a general model for heritable nestmate recognition cues. For example they were recently used to investigate the transfer of colony odor, and therefore recognition cues, to a myrmecophilous wasp that parasitizes fire ants (Vander Meer et al. 1989a). While, *S. invicta* colony hydrocarbon patterns are distinctive from colony to colony for a given sampling time, they also change continuously within a colony over time (Vander Meer et al. 1989b). Assuming that all heritable cues are also dynamic rather than static, a worker must, during its lifetime, continually update its perception (template) of colony odor and nestmate recognition cues (Vander Meer et al. 1989b).

The experiment that unambiguously links cuticular chemistry with an aggression bioassay has yet to be done for any ant species.

POLYGYNE VS MONOGYNE RECOGNITION

Polygyne *S. invicta* colonies are polydomous, i.e. each colony occupies several mounds connected by subterranean foraging tunnels. Consequently, a colony's boundaries are not clearly defined. The average coefficient of relatedness within monogyne colonies is indistinguishable from the theoretical 0.75 expected in colonies with one queen inseminated by a single male. In contrast, within-nest coefficient of relatedness in polygyne populations is not

significantly different from 0. This is due to the large number of different matrilinies in a single polygyne colony (Ross and Fletcher 1985).

Mirenda and Vinson (1982) found that, in the context of colony fusion, laboratory reared *S. invicta* polygyne nests tolerated neighboring mounds to a greater extent than monogyne mounds. However, we know overall discrimination is greatly diminished by the laboratory's uniform environment (Obin 1986, unpublished). To alleviate this problem we compared nestmate recognition in polygyne and monogyne *S. invicta* populations with aggression bioassays conducted on ants in their nest soil, soon after collection from the field (Morel et al. in press, unpublished).

No aggressive behavior was observed in intercolonial introductions, although there was a heightened awareness (rapid antennation) compared to intracolony controls. This supports the contention that territoriality within polygyne populations is almost nonexistent and that all workers are treated as nestmates. Thus polygyne *S. invicta* populations fall under Hölldobler and Wilson's (1977) definition of a super- or unicolony.

Polygyne workers are also non-aggressive toward monogyne workers whether or not they are intruder or resident. But the monogyne workers were highly aggressive toward polygyne workers. However, *S. richteri* intruders were vigorously attacked by polygyne workers indicating that polygyne workers' potential aggressivity was not diminished.

Environmental cues can be dampened through uniform conditions, but apparently in natural *S. invicta* polygyne populations, both environmental and heritable cues are dampened. It is reasonable to assume that nestmate recognition cues would spread throughout a population by social interactions and unchallenged movement of workers. However, an area-wide uniform cue pattern would be unreasonable to expect. Instead we propose that since polygyne workers contact a large number of different cues, environmental and heritable, the observed lack of aggression is due to a much less discriminating template rather than uniform cue profile. The asymmetry in aggressive behavior of monogyne and polygyne *S. invicta* supports this hypothesis. Just as for monogyne workers, at any point in time each polygyne worker has a distinct cue pattern; however, the polygyne worker template is broadly defined compared to that of monogyne workers.

HYBRID VS PARENTS

Hybridization between *S. invicta* and *S. richteri* was first reported by Vander Meer et al. (1985). It was later found to be reproductively viable (Ross et al. 1987) and to occupy an extensive range in northeastern Mississippi, northern Alabama and northwestern Georgia (Diffie et al. 1988). Within this range it borders both parental types only in northeastern Mississippi. The most plausible explanation for this asymmetric distribution is hybrid superiority in habitats intermediate to those favoring parental forms (Moore's [1977] "bounded hybrid superiority"). Ross et al. (1987a,b) found greater heterozygosity values for the hybrid than parental forms, which supports hybrid superiority.

Competition for territory and resources is significantly mediated by competitor-enemy recognition (see Hölldobler and Carlin 1987 for review). Intraspecific and interspecific aggression bioassays were used to measure the

ability of the two parental fire ant species and their hybrid to detect intruders (Obin and Vander Meer 1989b).

All aggression bioassays were done with laboratory colonies reared under identical conditions, thus the results were largely due to heritable nestmate recognition cues. Within the resolution of the bioassay, there were no significant differences for between population aggression scores; therefore, in the context of interspecific recognition no inferiority or superiority can be inferred.

Among the two parental forms, intraspecific aggression was significantly lower than interspecific; however, the scores for the hybrid were not significantly different. These data support the hypothesis that variability of heritable recognition cues is greater for hybrids than for either of the parents, as well as the suggestion (Ross et al. 1987) that fire ant hybrid zone stability may be a consequence of greater genetic diversity.

The intraspecific aggression scores suggest the following hierarchy of heterozygosity: *S. invicta* < *S. richteri* < hybrid (Obin and Vander Meer 1989b), which differs from the order determined by Ross et al. (1987) using isozymes. Thus, the data do not support an asymmetric "wave of advance" (see Barton and Hewitt 1985) in which the hybrid's movement is northward to a competitively inferior *S. richteri*. The extent that the aggression scores or for that matter isozymes reflect overall genetic heterozygosity is unknown, since each is looking at only a small part of the genome.

CONCLUSION

An understanding of the nestmate recognition process in fire ants has applications in many areas of study other than those discussed above. For example, differences in monogyne versus polygyne intraspecific aggression provide a facile way to determine if a nest is polygyne or not, without disruption of the mound (Morel et al. in press). The lack of intraspecific aggression in polygyne *S. invicta* gives a behavioral bioassay for determining if suspected South American *S. invicta* populations are the same as in the United States (Vander Meer and Patterson unpublished). Recognition of an intruder as non-nestmate initiates a host of non-chemical and semiochemical defenses, whether the intruder is another ant, parasitoid or parasite. Our understanding of nestmate recognition provided insights into myrmecophile integration mechanisms (Vander Meer and Wojcik 1982; Vander Meer et al. 1989a). Other areas of research for the future include the definition of recognition cue chemistry (their environmental and genetic bases) and the use of nestmate recognition differences to gain a better understanding of *S. invicta*'s transition from monogyne to polygyne.

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