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REPRINTED FROM:

Interindividual Behavioral Variability in Social Insects

EDITED BY
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Westview Press
BOULDER & LONDON

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Behavioral and Biochemical Variation in the Fire Ant, *Solenopsis invicta*

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The fire ant, Solenopsis invicta Buren, was accidentally introduced into the southern United States in the 1930s from South America. It is most probable that the United States S. invicta population is derived from a limited introduced gene pool, which may dampen within-colony and colony to colony variation (Tschinkel and Nierenberg 1983). Whether this is indeed the case has yet to be determined; however, the fire ant genetic story continues to become more complicated. Prior to S. invicta's introduction a black form had been introduced (early 1900s) from South America. The two forms were originally classified as racial forms of the same species (Wilson 1953); however, each was subsequently given species status (Buren 1972; black form = Solenopsis richteri Forel, red form = S. invicta) based on morphological differences, lack of hybridization in the United States, and phenetic invariability in the two forms. Recently extensive hybridization between the two forms has been detected biochemically (Vander Meer et al. 1985) and confirmed using isozymes (Ross et al. 1987). The hybrid has the color and morphology of S. richteri. As a consequence we cannot be certain of the integrity of the United States S. invicta population. In addition Ross et al. (1985) found a substantial amount of allozyme variability in the United States S. invicta population, which indicates that there may have been multiple introductions. In any event, we do not know the precise history of the introduced

Solenopsis species and we know even less about the ants in their native South America. Based on personal experience and the work of others it is clear that S. invicta has maintained enough variability to add gray hairs to many scientists. The following discussion outlines where variability has been identified.

Female categories within a colony are illustrated in Figure 8.1. Single queen S. invicta colonies are founded independently by either single or multiple newly mated queens, which lead to primary and secondary monogyny, respectively (Hölldobler and Wilson 1977a; Tschinkel and Howard 1983). It should be noted that increasing numbers of polygynous S. invicta colonies have been discovered in recent years (Glancey et al. 1975; Fletcher 1983; Fletcher et al. 1980; Lofgren and Williams 1984). Whether this is a recent phenomenon or a result of heightened awareness is unknown. This paper will not consider polygynous S. invicta colonies, since monogynous colonies are complicated enough. The colony life cycle can be divided into three major stages: (A) colony founding, (B) the ergonomic stage, (C) the reproductive stage (Oster and Wilson 1978). Each of these will be dealt with in the following discussion.

THE COLONY FOUNDING STAGE

At colony founding the newly mated fire ant queen constructs a nuptial chamber and rears the first brood in seclusion and without foraging (claustral colony founding). She relies on food and energy reserves built up prior to her mating flight. In addition, her no longer required wing muscles are histolyzed to provide a needed source of peptides and amino acids for egg production and general maintenance (Toom et al. 1976a). The first pupae that eclose are called nanitic or minim workers, and are the smallest workers produced by a colony (Dumpert 1981; Porter and Tschinkel 1986). It has been assumed that in most social insects the production of many nanitic workers versus a few larger workers has adaptive advantages for successful colony foundation (Oster

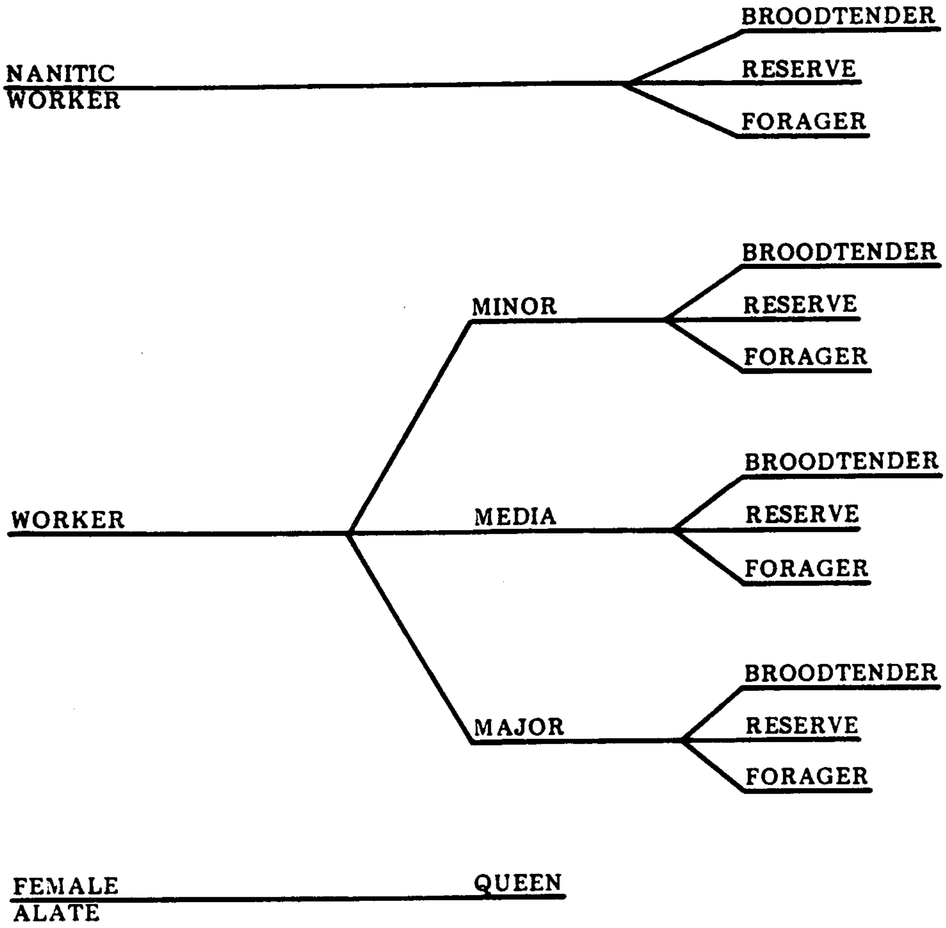

Figure 8.1. *Solenopsis invicta* female castes and sub-castes: sources of variability.

and Wilson 1978). This was demonstrated for *S. invicta* by Porter and Tschinkel (1986), when they showed that founding colonies with nanitic workers produced significantly more brood than modified colonies with equivalent biomasses of larger workers. The number of workers rather than their size was the critical factor influencing brood production (Porter and Tschinkel 1986). Nanitic workers are of uniform size (headwidths are 0.49 ± 0.00 mm [mean ± SD] N = 24) and unlike their counterparts in a mature colony, who have the luxury of undergoing age polyethism (Mirenda and Vinson 1981), they must immediately tend brood, maintain the nest, and forage for food (Oster and Wilson, 1978). It has also been noted (Oster and Wilson, 1978:46) that "one of the most general rules of behavior in all social insects that the members of incipient colonies are more timid than the members of large colonies." The distinct monomorphic size and difference in behavior of nanitic workers compared to mature colony workers suggests that they may be considered a separate caste. This hypothesis was further confirmed by chemical analysis of venom alkaloids (2-alkyl or alkenyl-6-methyl piperidines, Brand et al., 1972) that clearly demonstrated distinct venom alkaloid patterns between nanitic workers and mature colony workers (Vander Meer 1986a; Vander Meer, unpublished data). These differences were demonstrated to be unrelated to worker size. The small size of nanitic workers has been attributed to the poor diet provided by the queen (Dumpert 1981). Experiments designed to test this hypothesis led to the conclusion that nanitic workers are produced regardless of the diet they receive in the incipient colony (Vander Meer, unpublished data). The conclusion is that nanitic workers are a distinct but transient caste, only required during the colony founding stage. Vander Meer (unpublished) has biochemical evidence that nanitic characteristics carry on in the maturing colony for a much longer period of time than defined by the development of a queen's first brood. This has important implications regarding potential variability of colonies and workers for both biochemical and behavioral studies.

THE ERGONOMIC STAGE

After the first workers emerge the colony begins the ergonomic stage, which consists of the buildup of the colony work force. The size of a colony is limited by the egg production of the queen, which is in turn dependent on the rate of food flow supplied to her by the workers (aided perhaps by contributions of the fourth instar larvae). Since food flow is dependent on the size of the worker force, egg production and therefore colony size spiral up to the maximum permitted by the reproductive capacity of the individual queen and extant environmental conditions. The rapid growth of a colony is facilitated by a division of labor strategy (Oster and Wilson, 1978). In _S. invicta_ division of labor is based on a blend of age polyethism and caste based on physical size.

Size Subcastes

After the colony founding stage, worker size distribution changes, with larger workers developing as the colony matures (Wood and Tschinkel 1981). In mature colonies workers exhibit slight polymorphism and occur in a continuous range of sizes; however, minor, media, and major size categories have been arbitrarily assigned to workers based on head width measurements (Wilson 1978). Although worker size distributions are related to colony size, the distribution is not homeostatically regulated (Porter and Tschinkel 1985a). There is a trend toward specialization in the larger size classes. Mirenda and Vinson (1981) showed that worker size was correlated with the size of particle carried (for nest maintenance or food retrieval). The smaller workers of the same age were more involved in brood care than the larger workers. Experiments with artificial monomorphic _S. invicta_ colonies also showed that colonies composed of only large workers produced little brood compared to standard polymorphic colonies, whereas colonies composed only of small workers produced brood at the same rate as standard polymorphic colonies (Porter and Tschinkel 1985b). However, small worker monomorphic colonies were 10% less energy efficient in brood production than corresponding polymorphic colonies (Porter and Tschinkel 1985b). Analysis of venom alkaloids from a range of mature colony worker sizes showed a relationship between the percentage of certain alkaloids and the size of the worker (Vander Meer 1986a; Vander Meer, unpublished data). In addition, the same size categories were analyzed for total alkaloid (Figure 8.2). The data show that although major workers (headwidth = ca. 1.10 mm) are considerably larger than minor

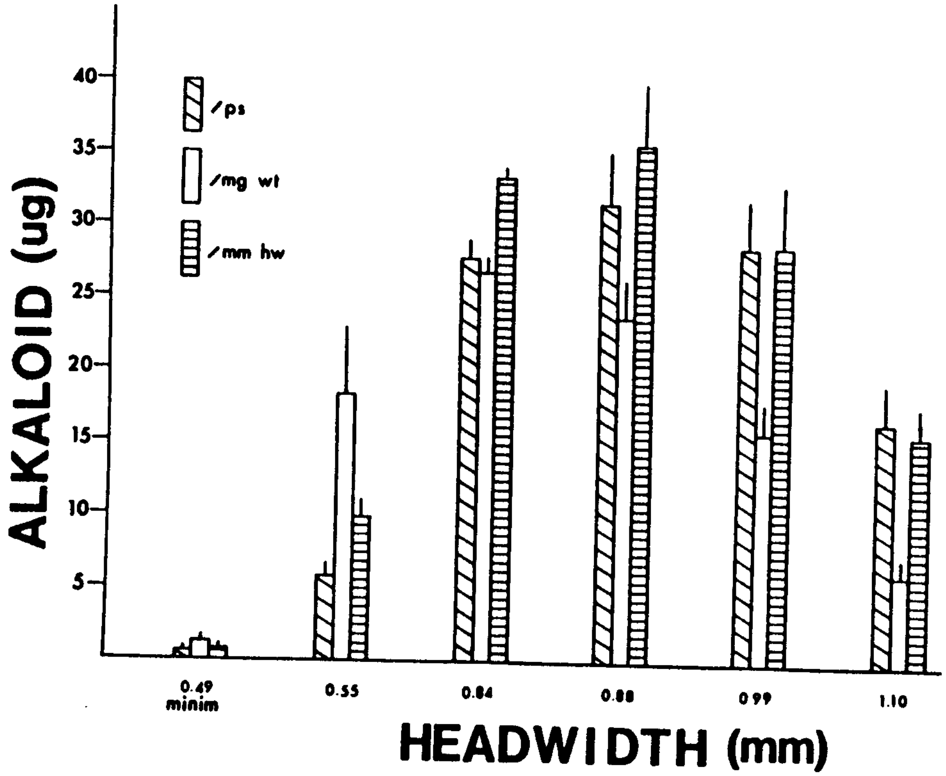

Figure 8.2. The total amount of alkaloid from extirpated glands of various *S. invicta* worker size categories. Analysis by gas chromatography using an internal standard and a Varian 401 data processor.

workers (headwidth = ca. 0.84 mm), they contain less alkaloid. Based on the amount of alkaloid available, major workers are less capable of defending their nest than are minor workers. This was demonstrated behaviorally by Wilson (1978), who found that fire ant aggressive behavior toward introduced foreign objects decreases with increasing size and major workers do not function as a soldier caste. Although S. invicta workers are polymorphic with no distinct morphological castes, worker size represents an important colony variable when considering both biochemical and behavioral studies.

Temporal Subcastes

Nanitic workers (the first adults produced by a colony) must immediately carry out all colony functions; however, mature workers exhibit age related polyethism (Mirenda and Vinson 1981). Age or temporal polyethism is a long established characteristic of eusocial insects (Wilson 1971). Mirenda and Vinson (1981) identified three fire ant subcastes: behaviorally distinct nurses and foragers, and a less distinct intermediate group called reserves. Callow workers spent most of their time near the brood but gradually moved to the periphery of the nest as they aged. Under the laboratory conditions of the experiment, workers that moved to the nest periphery were much less active than those tending brood. These inactive workers were called reserves, and functioned in food transfer from forager to nurse (Sorensen et al. 1985a). Under natural conditions they may be active in nest maintenance and construction. As reserves continued to age they spent increasing amounts of time in the foraging arena until near death, when they were consistently found foraging (Mirenda and Vinson 1981). Although this is complicated enough, the confounding size factor must also be considered. Nurses were primarily mature minor workers with a small proportion of media workers. Some workers, particularly major workers, never tended brood and very quickly moved to the nest periphery with the reserves. Some of these major workers may serve as repletes (Glancey et al. 1973). Mirenda and Vinson (1981) found that although there were significant average differences in task performance due to age, interindividual variance was the largest contributor to the total variance in time spent in certain locations and performing certain behavior. This type of individual variation can be due to differences in an individual's past experience, genetics, or other unknown factors. Although time is a convenient measure of the progression of a worker from nurse to forager, it is not accurate due to the large individual variation. Future efforts at devising methods for measuring an individual ant's physiological rather than temporal age could have a significant impact on our understanding of social insect behavior. This has been successfully done in the beetle, *Oryctes rhinoceros* L. (Vander Meer 1987), in which several behavioral acts (first flight and feeding) were strongly correlated with a beetle's weight at the time of the behavioral act and its adult emergent weight. In contrast, time was a poor predictor. Ants also have a fixed exoskeleton, which might make them amenable to a similar analysis.

The context in which a worker finds herself is another potentially confounding factor. Sorensen et al. (1985b) found that *S. invicta* nurses, reserves, and foragers exhibited a high degree of behavioral flexibility when posed with artificial elimination of all but their own subcaste in a colony.

One bright note of consistency was found amid the experimenter's nightmares discussed above. Quantitative and qualitative analyses of the venom alkaloids from the three defined temporal castes were not significantly different from each other when ants of approximately the same size were used in the analysis (Table 8.1). This means that, at least in terms of this particular biochemical character, fire ant workers are consistent over time. This has made venom alkaloids an important chemotaxonomic tool (Vander Meer 1986a; Vander Meer et al. 1985). Nurses have as much venom alkaloid capacity as foragers (Table 8.1), which are responsible for prey capture and colony defense because of the multiple functions of the

Table 8.1
Comparison of *Solenopsis invicta* temporal caste venom alkaloids[a,b]

Temporal caste	$C_{11:0}$	$C_{13:1}$	$C_{13:0}$	$C_{15:1}$	$C_{15:0}$	Total alkaloid (μg)
Brood tender	0.44 ±0.05	33.75 ±2.69	12.83 ±0.67	41.08 ±0.70	12.17 ±1.42	8.35 ±2.16
Reserve	0.33 ±0.01	31.42 ±1.61	13.38 ±0.49	42.44 ±0.87	12.52 ±0.86	6.30 ±1.76
Forager	0.88 ±0.30	34.96 ±1.15	12.29 ±0.27	41.39 ±0.77	10.84 ±0.37	7.80 ±1.23

[a] Mean percent total alkaloid ± SD; $N = 5$.

[b] No significant differences between the temporal castes for percent alkaloid or total alkaloid (Wilcoxon's 2-sample test for unpaired observation $P > .05$).

poison sac contents and the sting apparatus. The venom alkaloids have a wide variety of physiological effects, such as hemolysis (Adrouny et al. 1959), histamine release from mast cells (Lind 1982), and antibiotic activity (Blum et al. 1958; Jouvenaz et al. 1972). Obin and Vander Meer (1985) discovered a basic gaster vibration behavior used by S. invicta nurses and foraging workers. The effects of sting extension, venom release, and gaster vibration are to disperse fine droplets of venom into the surrounding environment. For a forager this can have a repellent effect on an antagonist, preventing direct confrontation, as reported for other ant species (Holldobler 1982; Adams and Traniello 1981). For a brood tending ant this mechanism allows the dispersal of minute amounts of the antibiotic alkaloids on the brood and within the nest to help defend against omnipresent soil bacteria and fungi (Obin and Vander Meer 1985). Consequently, regardless of a worker's position within a colony (nurse or forager), there is a continuous requirement for the production and dispersal of venom alkaloids.

Changes in behavioral sensitivity. Over many years our laboratory has investigated and developed S. invicta bioassays for queen-produced pheromones (Vander Meer et al. 1980; Glancey et al. 1982), brood tending pheromones (Glancey et al. 1970), and trail pheromones (Jouvenaz et al. 1978; Vander Meer et al. 1981). The isolation of pheromones requires a bioassay that offers a quick, reliable, and definitive answer. Consequently, for pheromone isolation we modified the bioassays until the worker ant response was optimized. Interestingly, brood tending workers gave the most consistent results in many of the bioassays. We have recently systematically investigated the responsiveness of nurses, reserves, and foragers to several pheromone systems (Glancey et al., unpublished data). Response to the queen attractant at five concentrations was measured in an olfactometer bioassay (Vander Meer et al. 1980). The results show that the proportion of brood tenders responding was significantly greater than reserves, which responded significantly better than foragers. These results can be readily rationalized, since brood tending workers are in closer association with the queen than are reserves or foragers, which could result in the sensitization of brood tenders to queen-produced pheromones. Based on our previous temporal caste definitions, reserves would be expected to fall somewhere between brood tenders and foragers, and they do. Foragers are the furthest away from the influence of the queen and should be the least sensitive to the queen-produced pheromones.

A second bioassay measured the time it took an individual worker placed on a pile of brood to pick up a piece of brood. The results showed significant differences between each of the three subcastes. Brood tenders responded more quickly than the other two subcastes. These results are not surprising, since again brood tending workers interact directly with the brood and might be expected to be sensitized to brood pheromones. As the workers age and move through the reserve and forager subcaste they would be expected to be less sensitive to brood pheromones because of being further away from brood interactions in both physical distance and time.

Another bioassay involved worker attraction to the recruitment part of the trail pheromone as measured by the response of worker ants to Dufour's gland volatiles in a Y-tube olfactometer (Vander Meer et al., in press). The results were similar to those obtained in the previous two bioassays. Brood tenders are significantly more sensitive to the trail recruitment pheromone than are reserves and foragers. Previous arguments were based on the assumption that association with a particular pheromone system promotes an increase in sensitivity to that pheromone. The expected order of responsiveness then would be forager greater than reserve, greater than brood tender. On the other hand, it could also be argued that continual contact with a particular pheromone system could lead to a decreased response due to habituation (Shorey 1976). This hypothesis would predict the experimental order of responsiveness for the trail pheromone, but the opposite results in the other two bioassays. The data for the three bioassays are consistent. Brood tenders are the most sensitive temporal subcaste in all bioassays, and the order of decreasing sensitivity is in the direction of increasing age. The most plausible explanation is also the least complicated: as workers age they become less sensitive to all pheromone systems as a consequence of that catchall term, senescence. The experimental results may be a reflection of deterioration of the physiological and/or physical systems (see Porter and Jorgensen 1981). The conclusion from these experiments is that all worker ants in a colony are not equal in their behavioral responses to pheromones and perhaps other stimuli. The responsiveness of workers to pheromone systems in general diminishes with the physiological age of the individual.

Variation in trail formation ability. The fire ant is noted for its efficient foraging strategy, which involves a combination of search behavior, homing mechanisms, and the use of trail pheromones for recruitment and trail orientation (Wilson 1962). One of the most important elements of this strategy is the homing and subsequent trail formation to the food source. The majority of competition for food resources comes from other fire ant colonies and other ant species. We measured the initial trail formation abilities of several S. invicta laboratory colonies (all laboratory colonies are derived from field colonies or from newly mated queens collected from the field). Colonies of approximately equal size were transferred to clean trays. After one to three hours a cockroach was placed 25 cm from the colony cell and the time required for formation of a discernable worker trail was recorded. This bioassay measured a combination of (A) the foraging worker's ability to find its way back to the colony, (B) the foraging worker's ability to deposit a chemical trail, and (C) the responsiveness of reserve workers or other foraging workers to the recruitment and orientation pheromones (Vander Meer 1986b). Table 8.2 shows the remarkable variability we found in a colony's trail formation ability. Within colony variation was small compared with colony to colony differences. In the laboratory the time it takes to recruit workers to a food source is not important to the colony's survival, since there is no intraspecific or interspecific competition. However, in a field situation, SNAIL, the slowest colony to respond, would have a difficult time competing for resources with LIGHTNING, the quickest to respond, or any of the other colonies. The moral of these results is that at any given time colony behavioral responses are not equal. In addition to the general within colony differences in pheromone responsiveness associated with age polyethism, we have the further confounding colony to colony variation, which, in the case of initial trail formation, is considerable.

THE REPRODUCTIVE STAGE

Female alates are another female caste, morphologically and chemically different from

Table 8.2
Comparison of initial trail formation response times for nine _Solenopsis invicta_ laboratory colonies

Colony name	Mean response (min)	SD	SE	Comp.[a]
Snail	21.28	2.98	1.49	A
Tortoise	13.40	4.71	2.35	B
Molasses	10.74	2.06	1.03	BC
Slowpoke	10.10	2.04	1.02	BCD
Mediocre	7.58	2.94	1.47	CDE
W.E. Coyote	6.83	1.71	0.85	DEF
Road-runner	4.78	1.76	0.88	EFG
Secretariat	2.88	0.53	0.27	G
Lightning	2.16	0.21	0.11	G

[a] Colonies with different letters are significantly different from each other ($\underline{P} < .05$, $\underline{N} = 4$, Newman-Keuls test).

workers (Brand et al. 1973). The size of alates, measured by headwidth, is constant whether they are from the laboratory or field (Table 8.3). This indicates that the fixed morphology of the adult female sexual caste is not influenced by diet. However, the weight of alates increases as they mature and store the energy and crop reserves required for colony founding (Toom et al. 1976b). Invariably, spring-reared alates captured when about to fly from their nest are of uniform weight; however, overwintering alates captured when about to leave on mating flights weighed one-third less (Fletcher and Blum 1983a). A comparison of mating and colony founding success for these two groups has not been done, however it would be predicted that the overwintering alates would be less fit for colony founding. This would definitely be true for haplometrotic colony founding (founding by individuals) but maybe not so critical in pleometrosis (founding in groups). Perhaps there is a connection between the development of polygynous S. invicta colonies (Lofgren and Williams 1984) and the initial interdependency of the founding queens. This interdependency may occur in colonies started from overwintered newly mated queens. An alate's behavior depends on its physiological state, and unless colonies in the field or laboratory are

Table 8.3
Solenopsis invicta female sexual head width measurements

		Head width (mm)		
Type	Source	Mean	SD	N
Alate	Laboratory	1.43	±0.00	3
Alate	Laboratory	1.44	±0.01	3
Alate	Field	1.43	±0.01	3
Alate	Field	1.44	±0.06	10
Queen	Field	1.42	±0.02	3

closely monitored it may be difficult to non-destructively (that is, without checking for ovariole development) determine when an alate is mature or whether it is an overwintering or spring type. The specific behavior associated with mating flights requires the correct environmental factors as well as alates in the right physiological state (weight, in this case, appears to be an indicator of physiological state).

Biochemical Changes

Insemination brings about dramatic physiological, biochemical, and behavioral changes that are not immediate, but occur over time. For example, concomitant with wing muscle histolysis (Toom et al. 1976a) and ovariole development, the crop contents are forced into the esophagus which expands to form a thoracic crop (Vander Meer et al. 1982; Glancey et al. 1980). By 24 days the majority (90 percent) of the triacylglycerols, originally stored in the crop, are utilized. However, hydrocarbons in the crop and esophagus did not follow the movement of the triacylglycerols and remained at low levels throughout the 120 days of the experiment (Vander Meer et al. 1982). The postpharyngeal gland opens into the pharynx and is most highly developed in *S. invicta* female sexuals (Phillips and Vinson 1980a). Hydrocarbons are the major lipid class in the postpharyngeal gland and have been identified as a mixture of five normal, methyl, and dimethyl branched heptacosane hydrocarbons (Thompson et al. 1981). These compounds are species specific, are ubiquitous in *S. invicta*, and can be used as taxonomic characters (Vander Meer et al. 1985; Vander Meer 1986a). Shortly after (about 20 days) insemination there is a dramatic spurt of hydrocarbon accumulation or biosynthesis in the gland (Vander Meer et al. 1982), which decreases to starting amounts after 120 days. Coupled with the total quantitative changes is a qualitative change in the hydrocarbon pattern, where the proportion of two of the five components are greatly reduced. The significance of these changes is not known. Phillips and Vinson (1980b) studied the function of the gland in S. invicta workers and concluded that it functions as a cephalic caecum and that the major lipid components come from the food of the adult ant. The postpharyngeal gland of queens, however, probably has as yet undetermined functions.

Pheromone Production

Two S. invicta queen pheromone systems develop as part of the dramatic physiological and biochemical changes that occur after insemination. A queen attractant pheromone is stored in the poison sac of the queen and is dispensed through the sting apparatus (Vander Meer et al. 1980). This gives the queen control over release of the pheromone at whatever time and whatever quantity a particular situation dictates. Interestingly, queen pheromone production requires worker stimulation, since queens removed from their colonies for more than 30 minutes are no longer attractive (Lofgren et al. 1983). Biosynthesis of this pheromone occurs 9 to 12 days after dealation and is independent of insemination (Glancey et al. 1981). Several bioassays (Lofgren et al. 1983; Glancey et al. 1982) were used to isolate and identify the active pheromone components (Rocca et al. 1983a, 1983b). Although quantitative studies on queen attractant pheromone variation have not been completed, it is apparent that the queen's control of pheromone release makes the related behavioral response highly context dependent.

A second pheromone system inhibits dealation and oogenesis in fire ant female alates (Fletcher and Blum 1981a). The pheromone is produced by the colony queen and acts directly on the alates. Since uninseminated dealates produce queen pheromones and unfertilized eggs, they would represent considerable competition for colony resources. Therefore, it is to a queen's advantage to inhibit the tendency of female sexuals to dealate. Similar to the queen attractant pheromone, the dealation inhibitory pheromone is produced within 10 days of dealation (Fletcher 1986). A bioassay for detecting this primer pheromone was used to determine that the queen's abdomen was the site of release (Fletcher and Blum 1981b). In addition, the inhibitory capability of a mated queen increases with its fecundity (Fletcher and Blum 1983b). Investigation of the quantitative variation of this pheromone system awaits the isolation and identification of the active components.

Queen fecundity, worker stimulation, queen age, and situational context are some of the factors that affect variation in the release of these two important social regulatory pheromones.

NESTMATE RECOGNITION

In this section I would like to look specifically at the behavioral and chemical variability of recognition in fire ants although some statements will apply to nestmate recognition in general. Colony odor is a composite of exogenous (environmentally derived) and endogenous (includes genetic factors that are and are not influenced by the environment) odors. Exogenous odors are made up of atmospheric, soil, food, and other odors not produced or modified by an individual. Endogenous odors are comprised of cuticular lipids, exocrine products, excretory products, regurgitory products, and other odors produced or modified by an individual and released to the outside. This set of definitions applies to all social insect systems and simply defines in general terms the sources of potential recognition cues. Odors responsible for nestmate recognition represent a subset of colony odor and may be composed of any possible combination of the components that make up the exogenous and/or endogenous components of colony odor. Examples of the importance of exogenous (Jutsum et al. 1979, for *Acromyrmex octospinosus* [Reich]) and endogenous (Hölldobler and Wilson 1977b for *Oecophylla longinoda* Latreille; Mintzer and Vinson 1985 for *Pseudomyrmex ferruginea* F. Smith) colony odor recognition factors have been reported in the literature.

Hubbard (1974) studied the influence of nest material and colony odor on the digging behavior of S. invicta and found that workers preferentially dug in nest materials from their own nests rather than that of non-nested soil or nest material from other S. invicta colonies. He concluded that since laboratory colony diets were identical, ant derived odors were being transferred to the soil. Colony odor cannot be thought of as a unidirectional acquisition toward colony members. An individual's exogenous and endogenous odors can be transferred to the environment, both passively from the cuticle and actively from exocrine sources. For example, species-specific cuticular hydrocarbons have been found in S. invicta nest soil (Vander Meer, unpublished data). There is a continual flow of exogenous odors onto the individual's cuticle and there is flow of both exogenous and endogenous factors back to the environment in which the individual resides. The flow of colony odor to the environment may be important in territorial recognition, and it would not be surprising if territory and nestmate recognition cues were identical (see Jaffé 1986). More important for nestmate recognition is that exogenous and endogenous odors are passed from individual to individual through grooming and trophallaxis, so these factors are distributed throughout a colony. Odors that originate from the environment but are now passed from individual to individual are still exogenous odors. Similarly, endogenous odors produced by an individual then passed to others or the environment should be considered endogenous regardless of where they are found. The point of origin is the critical factor.

The surface of an insect's cuticle is coated with lipids synthesized by cells located near the integument (Blomquist and Dillwith 1985). The cuticle and associated lipids are ideal for the absorption of both exogenous and endogenous odors. It is appealing to think of the individual ant as enveloped in chemicals that identify that individual at both species and colony levels (Vander Meer 1983). This follows Wilson's (1971) statement that in all social insects, recognition of a nestmate only involves a pause and sweep of the antennae over the other's body. Consequently, the search for potential nestmate recognition cues has been directed at the analysis of cuticular components, particularly hydrocarbons.

Cuticular Hydrocarbons

I would like to emphasize that it is not possible to obtain a cuticular rinse that only contains chemicals from the cuticle. Regardless of the length of rinse time, contamination from exocrine products, crop and postpharyngeal gland contents, fecal material, infrabuccal pocket pellets, etc. is always a problem with which to contend (Vander Meer 1986a; Vander Meer, unpublished data). These potential contaminants must be taken into consideration whenever chemical and/or behavioral studies are conducted on solvent rinses or soaks of whole individuals.

Hydrocarbons are inert and chemically not very interesting; however, they have been reported to elicit several kinds of physiological activity in insects; that is, sex attraction (Conner et al., 1980), alarm (Lofquist, 1976), and parasite attraction (Vinson et al. 1975). In addition they have been implicated in species and caste recognition in termites (Howard et al. 1982; Blomquist et al. 1979). In *S. invicta* hydrocarbons comprise about 75 percent of the cuticular lipids and the five major components have been identified as normal, methyl, and dimethyl branched compounds (Lok et al. 1975; Nelson et al. 1980). These hydrocarbons are species specific and have been used as species markers in several studies (Vander Meer 1986a; Vander Meer et al. 1985). They are found everywhere in the ant, from postpharyngeal gland to the queen's ovaries (Vander Meer et al. 1982; Vander Meer, unpublished data). Although there is no direct evidence that *S. invicta* hydrocarbons play a role in nestmate recognition, there is a relationship between the integration of a myrmecophilous beetle, *Myrmecophodius excavaticollis* L. into fire ant colonies and the passive acquisition of the species-specific hydrocarbons of the host (Vander Meer and Wojcik 1982). In addition, *S. richteri* workers treated with *S. invicta* hydrocarbons survive longer than untreated *S. richteri*, when placed with *S. invicta* workers (Glancey, unpublished data). Obin (1986) found that suppression of environmental differences in *S. invicta* laboratory reared colonies dampened but did not eliminate aggression between workers from those colonies. He concluded that both endogenous and exogenous cues were important in *S. invicta* nestmate recognition. Obin (1986) also found that cuticular hydrocarbon patterns were not well correlated with the measured aggressive response of laboratory colonies on the same diet versus field colonies, indicating that aggression at this level was keyed to exogenous odors.

Several important questions arise when considering hydrocarbons as potential nestmate recognition cues for *S. invicta*: (1) Are cuticular hydrocarbons a part of endogenous colony odor? Answer: Yes. They are biosynthesized by the ants and are released to the cuticle (Blomquist and Dillwith 1985). (2) Are cuticular hydrocarbons species-specific? Answer: Yes. Analysis of four *Solenopsis* species in the United States and several others from South America demonstrated that this biochemical character is species-specific (Vander Meer, unpublished data). (3) Are cuticular hydrocarbons nestmate recognition cues for *S. invicta*? Answer: Unknown. There has been no direct evidence linking cuticular hydrocarbons to *S. invicta* nestmate recognition. They may or may not be involved. (4) Are cuticular hydrocarbons readily analyzed? Answer: Yes and no. The chemical separation and subsequent gas chromatographic analysis is readily accomplished, but the differences in chromatogram patterns may not be great and the analysis of the data usually requires sophisticated pattern recognition techniques (Jurs 1986). (5) Can cuticular hydrocarbons act as a model for the fate of both exogenous and endogenous nestmate recognition cues? Answer: Yes. Assuming that nestmate recognition cues are resident on the cuticle, then whether or not hydrocarbons are involved in nestmate recognition, they suffer (or enjoy) the same fate as all other potential nestmate recognition cues (both endogenous and exogenous) on the cuticle.

Hydrocarbon Pattern Variability

Recently we have analyzed the cuticular hydrocarbons of *S. invicta* workers (reserve subcaste) by gas chromatography. Analyses of the data by several pattern recognition techniques (Jurs 1986) all clearly grouped the data according to colony. The variation within colonies was less than that between colonies. Using SIMCA pattern recognition methodology (Wold and Sjostrom 1977) a classification success rate of 100 percent was achieved. Therefore, colonies can be statistically distinguished by their cuticular hydrocarbon patterns.

Surprisingly, investigation of changes in colony hydrocarbon patterns with time (one to three month sampling intervals) showed that cuticular hydrocarbon patterns change with time. Replicates within a time period showed little variation compared to variation from time period to time period for a given colony. Hydrocarbon patterns, which at least represent what is occurring on the cuticle, are dynamically changing.

Along with changing hydrocarbon patterns, evidence for continuous mixing of colony hydrocarbons comes from a myrmecophile integration mechanism (Vander Meer and Wojcik 1982) and from the creation and chemical analysis of interspecific *Solenopsis* colonies (Vander Meer, unpublished data). There are at least three scenarios that explain hydrocarbon mixing and time dependent pattern changes. Scenario 1: Each individual produces a constant pattern through time but individuals differ, therefore the mean colony profile changes with time as new individuals (interindividual variation) enter the work force. Scenario 2: Individuals undergo continous random change within a specific genetic "window" of variability. Here the pattern variability is derived from both interindividual and intraindividual variation. Scenario 3: Individuals all produce the same pattern which synchronously changes with time. Scenario 3 does not require intimate mixing of hydrocarbons throughout the individuals of the colony. At this time we do not have enough information to distinguish the possibilities. If we consider that cuticular hydrocarbons at least act as a model of nestmate recognition cues, then all nestmate recognition cues found on the cuticle (exogenous and endogenous) are mixed throughout the colony, and they are dynamically changing. The cumulative evidence favors a type of Gestalt model (Crozier and Dix, 1979) for *S. invicta*.

Recognition Cue Imprinting

In general it is thought that there is a short (in time) critical sensitive period in a newly eclosed worker's life in which it experiences the colony's odor and imprints or learns the nestmate recognition cues (Morel 1983; Le Moli and Mori 1984). What are the implications of the above results on the learning hypothesis of nestmate recognition? (1) If colony cuticular hydrocarbon patterns change with time, then it is possible that other endogenous colony odor factors also change with time. (2) No one would argue against the statement that colony odors derived from the environment (exogenous) are dynamically changing with time. Therefore, nestmate recognition cues (a subset of colony odor) are continously changing over time, regardless of their source. Most importantly, recognition cues cannot be learned by callow workers as a fixed pattern but require continuous updating through an *iterative learning process*. A similar process was proposed by Wallis (1963), who worked with two *Formica* species. He suggested that each worker ant was probably "continually habituating to slight variations in the odour of its nestmates".

Nestmate recognition in social insects has attracted a great deal of attention, especially in the last few years. As a consequence of the inherent complexities of the potential mechanisms involved there is a plethora of terminology. The above discussion attempts to address the need to re-evaluate what has been done and evolve a more streamlined and self-consistent lexicon for nestmate recognition. Even the term nestmate recognition may be misleading, since the ants may in fact be recognizing a difference in non-nestmates rather than a similarity in nestmates.

CONCLUSION

Life within a fire ant colony is extremely complex. Ideally, an experimenter would like to control morphological caste, worker size, worker age (preferentially a worker's physiological age), colony to colony variation (we need genetically engineered clones), colony age, the bioassay context, the season of the year, and other variables. Control of these variables is often not practical or possible, but to be aware that they exist helps to avoid some dangerous traps associated with social insect research. This variation makes working with fire ants both interesting and challenging.

SUMMARY

Fire ants, especially _Solenopsis invicta_, have been studied intensively for the past thirty-five years. Variability in behavior and biochemistry has been detected at every stage of colony development. Nanitic workers, the first adults produced by colony founding queens, differ behaviorally and chemically from their mature colony counterparts. As a colony matures the worker size distribution changes and certain behavior patterns are preferentially performed by specific size categories. In addition, workers undergo age related polyethism, moving from nurse to forager as they become older. Venom alkaloids (2-alkyl or alkenyl 6-methyl piperidines) vary both qualitatively and quantitatively with the size of the worker, but there are no differences between temporal castes of the same size. Adult workers require the venom alkaloids regardless of their function; nurses use it to disinfect the brood and nest, while foraging workers use it to secure prey and defend the colony. The responsiveness of workers to pheromone systems in

general diminishes with the physiological age of the individual. Also, the behavioral responsiveness of colonies often shows considerable variation, for example in initial trail formation. Female sexuals are very complicated in terms of their sexual maturity and the events, both behavioral and biochemical, that take place after mating. Nestmate recognition factors, as modeled by the cuticular hydrocarbons, have been shown to be statistically different from colony to colony and in a dynamic state of flux. In conjunction with evidence for continuous mixing of colony odor, these data suggest that individual workers continually update their perception of colony odor and, therefore, nestmate recognition cues.

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