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Agonistic Behavior Among Colonies of the Formosan Subterranean Termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae), from Florida and Hawaii: Lack of Correlation with Cuticular Hydrocarbon Composition

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Cuticular hydrocarbon patterns of the Formosan subterranean termite, Coptotermes formosanus Shiraki, were similar among colonies from the same geographical location. Hydrocarbon patterns of Florida colonies were easily distinguished from those of Hawaii colonies by using canonical discriminant analysis. Groups of termites from the same colony did not fight one another when placed in an arena. Intercolonial aggression was not recorded among C. formosanus *populations from Florida but three colonies from Hawaii fought with the other Hawaiian and three Florida colonies. Of the 12 colonies (six each from Florida and Hawaii) tested, 3 Florida colonies did not direct or receive aggression from any other colony. Cuticular hydrocarbon patterns were not correlated with agonistic behavior.*

KEY WORDS: aggression; nestmate recognition; *Coptotermes*; Isoptera; cuticular hydrocarbons; intercolonial differences.

INTRODUCTION

Intra- and interspecific aggression within the Isoptera has been reported in the literature numerous times (Binder, 1988; Haverty and Thorne, 1989; Pearce *et al.*, 1990). Recognition of alien and conspecific termites has been attributed to, or correlated with, the composition of cuticular hydrocarbons on the epicuticle

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(Howard and Blomquist, 1982; Clément, 1986; Haverty and Thorne, 1989). Aggressive behavior is often used by termite researchers to delimit boundaries among colonies of the same species (Nel, 1968; Thorne, 1982; Levings and Adams, 1984; Clément, 1986; Jones, 1987; Adams and Levings, 1987). Lack of aggression among conspecific colonies may be much less common, as this phenomenon has only recently been reported in the literature (Clément, 1986; Haverty and Thorne, 1989; Pearce *et al.*, 1990).

During the course of studies of foraging territories of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, in Florida and Hawaii, varying degrees of agonistic behavior among colonies were observed (N.-Y. Su, unpublished observations). Agonistic behavior varied from no apparent aggression to fierce combat. Colonies of *C. formosanus* from Hallandale, Florida, never displayed any aggression toward other colonies from the same location. Therefore, intercolonial aggression cannot be used to delimit colony foraging territory of *C. formosanus* in southern Florida. Instead, release and recapture of marked foragers must be used (Su and Scheffrahn, 1986). Two of these Florida colonies have even been shown to fuse to form a larger colony (Su and Scheffrahn, 1988). Colonies from the campus of the University of Hawaii were variable in their agonistic responses toward other colonies of *C. formosanus* from the same location (N.-Y. Su, unpublished observations).

We suspected that the reason for these differences in aggressive responses in *C. formosanus* from the two locations was associated with the relatedness of the colonies: closely related colonies were less likely to fight. Colonies from Florida probably resulted from a single introduction, and are therefore closely related. On the other hand, *C. formosanus* was established in Hawaii before 1911 (Swezey, 1914) and was probably reintroduced numerous times (Tamashiro *et al.*, 1987). Thus colonies in Hawaii are less likely to be related than those found in southern Florida.

We decided to reexamine aggressive responses of *C. formosanus* from Florida and Hawaii to determine the degree of variation in agonistic behavior within and among colonies of this species from these two locations. Furthermore, since cuticular hydrocarbons have been implicated in intraspecific and interspecific recognition in termites (Howard and Blomquist, 1982), we attempted to determine whether the cuticular hydrocarbon patterns of individual colonies were associated with aggressive behavior.

MATERIALS AND METHODS

Termites

Termites were collected in October 1987, from Hallandale, Florida, and Honolulu, Hawaii. Foraging parties from colonies were collected from soil in Florida as described by Su and Scheffrahn (1986) or in Hawaii as described by

Tamashiro *et al.* (1973). The six different colonies from Florida all came from a single location (up to 5 km apart) in Hallandale. The six colonies from Honolulu were from the University of Hawaii campus. Florida termites were transported to Hawaii for bioassay.

Agonistic Behavior Bioassay

To determine the origin of aggressive or fleeing behavior, bioassay with dyed and undyed termites were used (Binder, 1988). Half of the collected termites from each colony were confined in a glass petri dish (9 cm in diameter by 2 cm high) and allowed to feed on filter papers stained with 1% (w/w) Sudan red 7B for 24 h (Su *et al.*, 1988). Eight unstained termites (seven workers and one soldier) were introduced into a glass petri dish (5 cm in diameter by 1.5 cm high) containing a moistened filter paper and an equal number of stained termites. For each colony, two groups of stained individuals were paired with a separate group of unstained individuals from each of the 12 colonies, including unstained individuals from the same colony. This resulted in four replicates each of all possible combinations of the 12 colonies, except when termites were paired with members of their own colony. These combinations were replicated only twice.

Initial agonistic responses were recorded with a video cassette recorder for 1 min. Tests were conducted in a laboratory maintained at about 27°C with fluorescent lighting. After the initial 1-min encounter, termites were held in the same containers in an incubator at 28°C for 24 h, and the number of survivors (stained and unstained) was counted.

The video tapes were reviewed later. When there were indications of agonistic behavior, the 1-min bout was reviewed 16 times to record the behavior of all individuals in the arena. A sheet of clear plastic was placed over the television screen and the positions of each of the 16 termites at time 0 were marked on the plastic sheet. The agonistic response (aggressive behaviors including chasing, mandible flares, mandible insertion, and biting and defensive behaviors including fleeing and being attacked) of each individual was traced and recorded.

Characterization of Cuticular Hydrocarbons

Termites were separated from debris and subsequently dried in a desiccator. They were held dry at room temperature until hydrocarbons were extracted. Cuticular lipids were extracted by immersing 100 termites, as a group, in 10 ml of hexane for 10 min. For each colony, one group of 100 workers and one group of 100 soldiers were used to quantify the hydrocarbon composition for the colony. After the termites were extracted, hydrocarbons were separated from other components and identified by gas chromatography–mass spectrometry (GC-MS) (Page *et al.*, 1990). Routine quantification of cuticular hydrocarbon

components was achieved with a Hewlett Packard 5890 gas chromatograph; all operating conditions were the same as described by Haverty *et al.* (1990).

Cuticular hydrocarbon patterns of the Hawaiian and Florida populations were compared by stepwise discriminant analysis to select the discriminating variables (percentage of a given hydrocarbon), followed by canonical discriminant analysis to provide one-dimensional displays of the chosen variables. The purpose of the discriminant analysis was to define a subset of hydrocarbon components that best revealed the differences between the two populations for workers and soldiers. The program that we used (STEPDISC) employs stepwise selection of variables (SAS Institute, Inc., 1985). Canonical discriminant analysis is a dimension-reduction technique that derives a linear combination of quantitative variables (percentage of hydrocarbon components) that summarizes between-class variation. The program that we used (CANDISC) computes and tests Mahalanobis distances for pairwise comparisons of the populations (SAS Institute, Inc., 1985). We assume that these distances are indicative of the degree of hydrocarbon similarity between populations.

Data Analysis

For each encounter of all possible caste and colony combinations, the difference in percentage proportion of each of the 14 cuticular hydrocarbons was correlated to the presence or absence of agonistic responses. A stepwise multiple regression analysis (STEPDISC) was done to establish relations between cuticular hydrocarbon proportion (independent variables) and the agonistic response (dependent variable). Cuticular hydrocarbons that contributed to the significance level of more than 0.15 were added into the model (SAS Institute, Inc., 1985). A similar analysis was conducted to explore the relationship between differences in the percentage of each cuticular hydrocarbon and mortality (number dead) at 24 h.

RESULTS AND DISCUSSION

Agonistic Behavior

The summary of the agonistic responses resulting from pairings of six colonies each from Hallandale, Florida, and Honolulu, Hawaii, is presented in Table I. Agonistic behavior was never observed when eight-member groups of the same colony were paired. No combination of termites from Florida showed aggressive behavior toward any other colony from Florida. When colonies from Hawaii were paired, 13 of 36 pairings resulted in aggressive responses. Colonies A, B, and C did not fight among themselves; the same was true for colonies D and E. Colony F never attacked another colony and was attacked only by

Table I. The Agonistic Responses of Individuals During 1-min Encounters Between Groups of *Coptotermes formosanus* from Hallandale, Florida, and Honolulu, Hawaii[a]

	Unstained colony											
	Florida						Hawaii					
Stained colony	1	2	3	4	5	6	A	B	C	D	E	F
							Florida					
1	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	10 → 15	3W → 7W	0	0	0
3	0	0	0	0	0	0	0	2W → 4W	6 ↔ 6	0	0	0
4	0	0	0	0	0	0	2S → 6W	0	S → 7	0	S → 5W	0
5	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0
							Hawaii					
A	0	0	0	2W ← 2S	0	0	0	0	0	0	8 ← 7	0
B	0	3W ← W	W ← W	0	0	0	0	0	0	3W ← 2W	5W ← W	0
C	0	S → S	4W ← 4W	2 → 2W	0	3 → 6	0	0	0	10 ↔ 11	7 ← 9	5 → 9W
D	0	0	0	0	0	0	5 → 6	9 → 15	10 → 14	0	0	0
E	0	0	0	2 → 2W	0	0	7 → 8	8 → 10	14 → 14	0	0	0
F	0	0	0	0	0	0	0	0	7 ← 7	0	0	0

[a]Each number is the aggressive responses of 8 unstained and 8 stained termites from each colony. Letters (S = soldiers, W = workers) depict which caste is the aggressive or fleeing caste. If both castes were involved, no letter is given. Arrow points right (→) if aggression from stained colony, left (←) if from unstained colony.

colony C. Colonies D and E consistently fought with colonies A, B, and C (except when a stained colony A was mixed with an unstained colony D). These observations indicate that there were two distinct groupings among the six colonies we tested from Hawaii (A, B, and C vs D, E, and F).

When colonies from Florida were paired with colonies from Hawaii, no aggressive responses were observed between any of the pairings of colonies 1, 5, and 6 (the one exception was the pairing of unstained 6 vs stained C). Likewise, Hawaiian colonies A, D, E, and F never displayed agonistic behavior against Florida colonies except 4 vs A or E.

It is obvious that geographical location did not correlate with agonistic behavior between colonies from Florida and Hawaii. Although there are numerous small but consistent exceptions, the agonistic responses indicated that the 12 colonies that we tested can be divided into two gross groups; namely A, B, C, 1, 5, and 6 and D, E, F, and all Florida colonies as shown in Fig. 1.

Of the 117 initially peaceful encounters, only 5 pairings (indicated by a "z" in Table II) resulted in ≥ 3 dead individuals of 16 total termites. Of the 27 aggressive encounters, 12 pairs resulted in a mortality of ≥ 3 (indicated by "x" in Table II), while 15 pairs produced insignificant levels (≤ 2) of mortality (indicated by a "y" in Table II). By comparing agonistic responses and mortality data, we conclude that an initially peaceful encounter generally does not result in mortality, nor does an initially aggressive encounter always result in appreciable mortality.

Therefore, even though termites may display aggressive behavior when first placed in the vicinity of "alien" conspecifics (the aggressive responses in Table I), they either continue their aggressive behavior, habituate to the aggression-

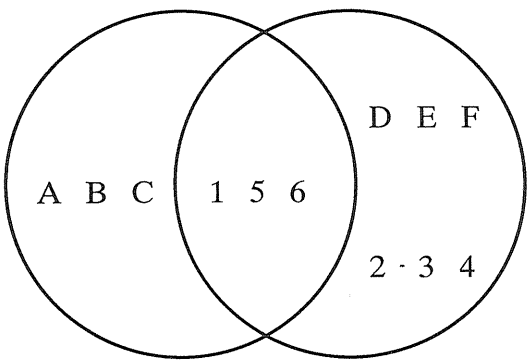

Fig. 1. *C. formosanus* populations collected from six colonies each from Hallandale, Florida (1–6), and Honolulu, Hawaii (A–F), are divided into two groups based on agonistic responses. In general, no agonistic response was observed from populations enclosed in the same circle.

Table II. Mortality Associated with Agonistic Behavior During 24-h Exposures of Two Eight-Member Groups of *Coptotermes formosanus* from Six Colonies Each from Hallandale, Florida, and Honolulu, Hawaii[a]

	Unstained colony[b]											
	Florida						Hawaii					
Stained colony	1	2	3	4	5	6	A	B	C	D	E	F
						Florida						
1	0/0	0/0	0/0	0/0	0/0	0/0	3/0z	3/0z	0/0	1/0	0/0	0/0
2	0/0	0/0	0/0	1/0	0/0	0/0	0/0	12/0x	0/0y	0/0	0/0	0/0
3	0/0	0/0	0/0	0/0	0/0	0/0	0/0	13/0x	1/0y	2/0	1/0	2/0
4	0/0	0/0	0/0	0/0	1/0	1/0	0/0y	0/0	0/0y	0/0	6/0x	0/0
5	0/0	0/0	0/0	0/0	0/0	0/0	0/1	2/0	0/0	2/0	0/0	0/0
6	0/0	0/0	0/0	0/0	0/0	0/1	0/0	2/0	2/0	1/0	2/0	1/0
						Hawaii						
A	0/1	0/0	1/0	1/0y	1/0	0/0	0/0	2/0	0/0	1/1	4/0x	1/0
B	2/0	1/0y	0/0y	1/0	2/1	1/0	1/0	0/0	5/0z	0/0y	0/0y	0/0
C	0/0	0/0y	0/0y	0/1y	0/0	3/0z	1/0	0/0	0/0	9/1x	12/0x	4/0x
D	0/0	1/0	0/0	0/0	0/0	0/0	6/0x	0/0y	17/0x	0/0	0/0	1/0
E	0/0	2/0	1/0	2/0y	0/1	0/0	5/0x	3/0x	27/2x	0/0	0/0	1/0
F	0/0	0/0	0/0	1/0	0/0	0/0	4/0z	0/0	0/0y	1/0	0/0	1/0

[a] In each cell, the number on the left represents the number of workers that died during the 24-h period; the number on the right represents dead soliders.
[b] x, agonistic encounter resulted in ≥ 3 mortality; y, agonistic encounter resulted in < 3 mortality; z, peaceful initial 1-min encounter resulted in ≥ 3 mortality at 24 h.

inducing stimulus, or become passive again because they were only "on alert" to the new situation of being placed in the test arena. This would indicate that there is a stimulus causing initial aggression, but for aggressive behavior to continue, it must be reinforced by another stimulus. Without the reinforcing stimulus, initial agonistic encounters would result in insignificant mortality (Tables I and II). This could also explain the mortality from pairings that were initially passive. In some cases we saw no initial agonistic behavior but we observed significant mortality after 24 h (Tables I and II). Presumably, after the termites from different colonies had had time to examine one another closely, the next level of aggression was released while the termite groups were forced to cohabit the small petri dish for the entire 24-h period.

The direction of the aggression in the agonistic encounter was also fairly persistent. Mutual fighting (indicated by ↔ in Table I) was observed only twice in the 29 agonistic encounters. Of the 27 unidirectional aggressive encounters (as indicated by → or ←), the direction of the attacks was persistent in eight pairs (or 16 encounters). This observation leads to a hypothesis that there are multiple factors involved in recognition and agonistic behaviors: previous hypothesis suggested cuticular hydrocarbons as recognition cues (Howard and Blomquist, 1982; Howard *et al.*, 1980). For example, if colony I uses factors α and β as cues but colony II uses only α, then colony II would not recognize colony I as "alien," while the lack of factor β would enable colony I to recognize II as nonnestmate. In this hypothetical encounter, therefore, termites from colony I would be the attacker while colony II would remain passive.

Cuticular Hydrocarbons

Cuticular hydrocarbons were identified from workers and soldiers from each of six colonies from Florida and Hawaii (Figs. 2 and 3). The hydrocarbon components we identified were qualitatively identical and quantitatively similar to those reported earlier for this species (Haverty *et al.*, 1990). The major components were 2-methylpentacosane (HC3), *n*-heptacosane (HC8), an isomeric mixture of 9-; 11-; 13-methylheptacosane (HC9), a mixture of 2-methylheptacosane and 9, 13-dimethylheptacosane (HC10), 3-methylheptacosane (HC11), and an isomeric mixture of 9-; 11-; 13-; 15-dimethylnonacosane (HC14).

Cuticular hydrocarbon patterns were similar within geographic locations but different between geographic locations. Except for soldiers of colony 3, the isomeric mixture 9-; 11-; 13-methylheptacosane (HC9) is the most abundant hydrocarbon component extracted from the epicuticle of *C. formosanus* collected from Florida, while cuticular hydrocarbon patterns of Hawaiian colonies (except for workers of colony F) are characterized by the dominance of the 2-methylheptacosan + 9, 13-dimethylheptacosane (HC10) (Figs. 2 and 3).

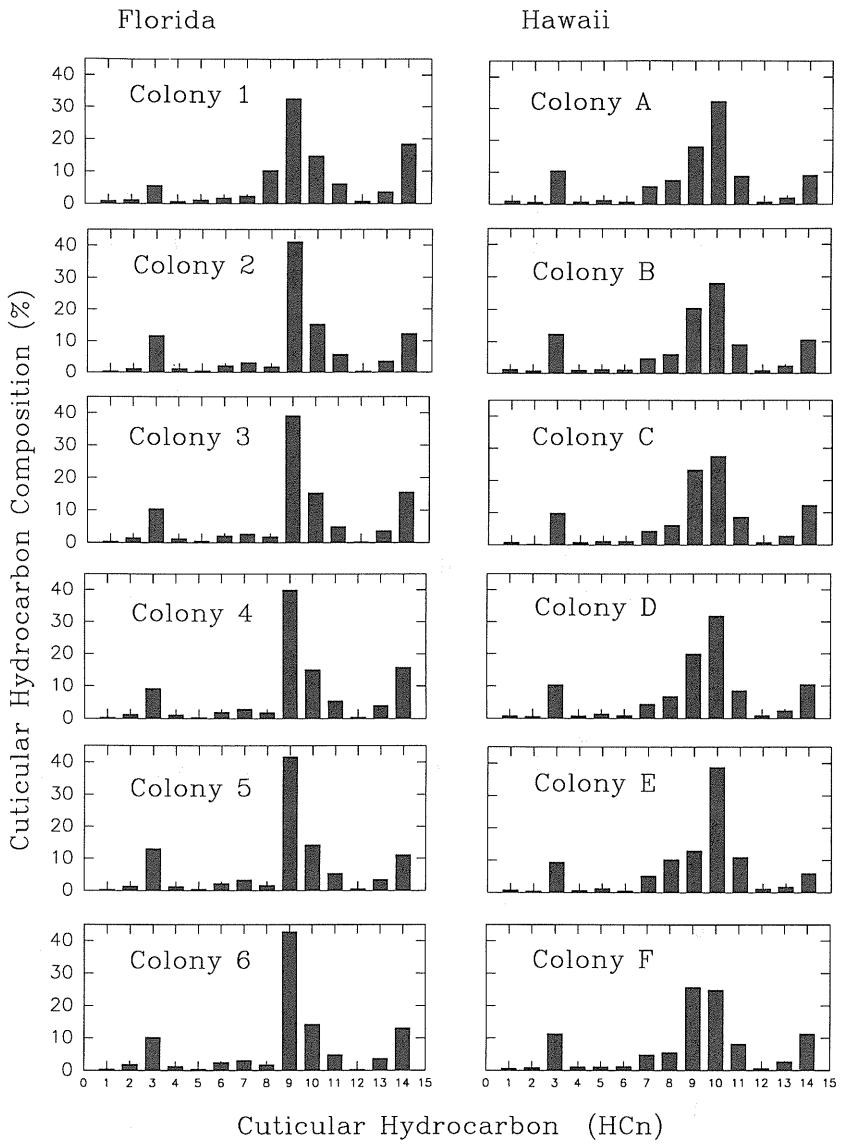

Fig. 2. Percentage of 14 hydrocarbon peaks extracted from the cuticle of workers from each of six colonies from Hallandale, Florida (1–6), and Honolulu, Hawaii (A–F). Hydrocarbon peaks are the same as those reported by Haverty *et al.* (1990). Peak components are as follows: HC1, *n*-C_{25}; HC2, 9-;11-MeC_{25}; HC3, 2-MeC_{25}; HC4, 3-MeC_{25}; HC5, *n*-C_{26}; HC6, 9-;11-;13-MeC_{26}; HC7, 2-MeC_{26}; HC8, *n*-C_{27}; HC9, 9-;11-;13-MeC_{27}; HC10, 2-MeC_{27} + 9, 13-DimeC_{27}; HC11, 3-MeC_{27}; HC12, *n*-C_{28}; HC13, 9-;11-;13-;15-MeC_{28}; HC14, 9-;11-;13-;15-MeC_{29} + 13, 15-DimeC_{29}. These abbreviations use a descriptor for the location of the methyl groups (*X*-Me or *X*, *Y*-Dime) and the total numbers of carbons (CXX) in the hydrocarbon component, excluding branch(es). Some peaks are a mixture of positional isomers; in others two or more components coelute.

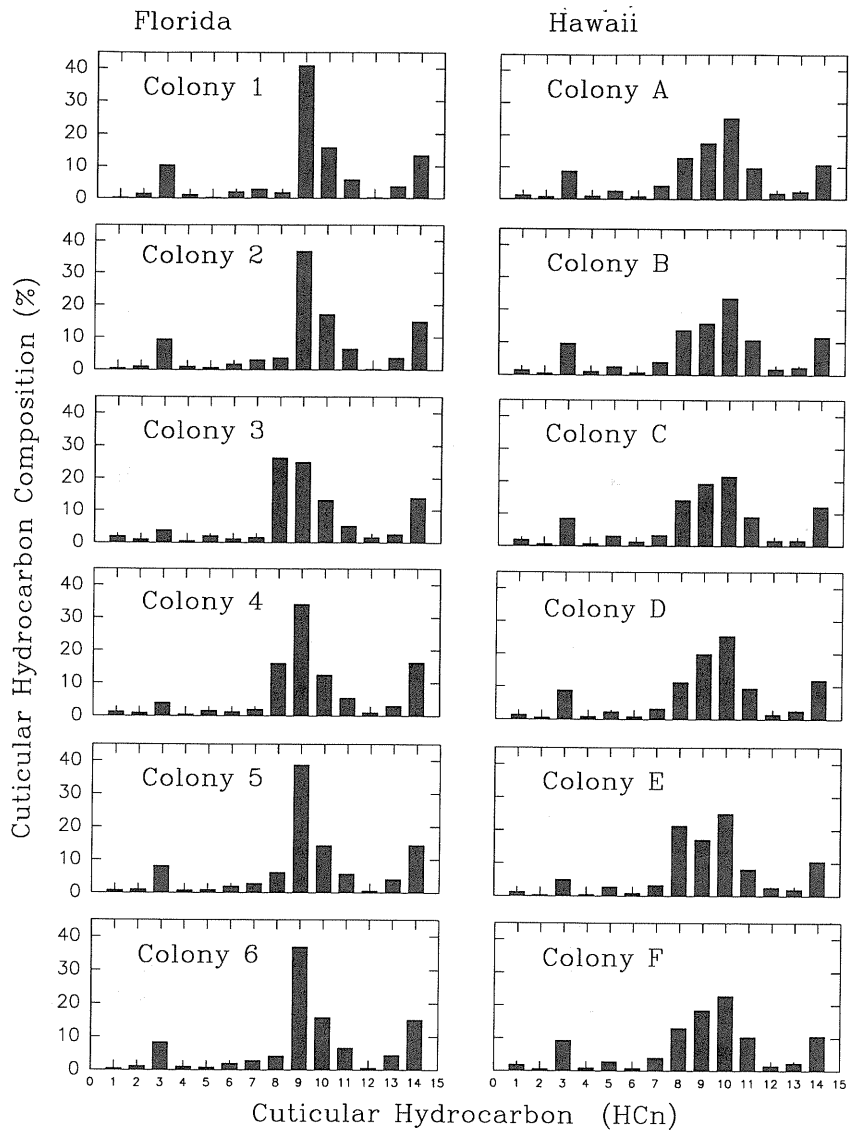

Fig. 3. Percentage of 14 hydrocarbon peaks extracted from the cuticle of soldiers.

The locationwise similarity in cuticular hydrocarbon patterns is also demonstrated by discriminant analysis. This analysis identified three hydrocarbon components (or correlating mixtures) that reasonable separate the two populations: *n*-hexacosane (HC5), *n*-heptacosane (HC8), and 3-methylheptacosane

(HC11) for workers and *n*-hexacosane (HC5), *n*-heptacosane (HC8), and a co-eluting mixture of 2-methylheptacosane + 9, 13-dimethylheptacosane (HC10) for soldiers. With these hydrocarbon variables we were able to display the differences with plots of hydrocarbon proportions along one axis of canonical discriminant space (Fig. 4) and test the similarity between locations. The estimated Mahalanobis distance was 11.1 for workers and 21.3 for soldiers; both estimates were statistically different from zero at the 0.0001 level. In other words, colonies of *C. formosanus* from Hallandale, Florida, can be separated from colonies from Honolulu, Hawaii, on the basis of relative concentrations of three cuticular hydrocarbon components or coeluting mixtures.

Correlation Between Cuticular Hydrocarbon Patterns and Agonistic Behavior

Cuticular hydrocarbon patterns did not appear to correlate with agonistic response. For example, colonies C and D persistently fought (Table I), which resulted in a high mortality (Table II), yet cuticular hydrocarbon patterns of these two colonies were fairly similar in both workers (Fig. 2) and soldiers (Fig. 3). On the other hand, pairing of colonies 5 and E never resulted in fighting or appreciable mortality (Tables I and II), but the cuticular hydrocarbon patterns were distinctly different between these two colonies in both castes (Figs. 2 and 3).

The apparent lack of correlation between cuticular hydrocarbon patterns and agonistic behavior was further demonstrated by the stepwise multiple regression analysis. After nine cuticular hydrocarbons were added to the regression model, no increase was observed in r^2 value, when the presence or absence of the agonistic behavior was correlated with the cuticular hydrocarbon patterns

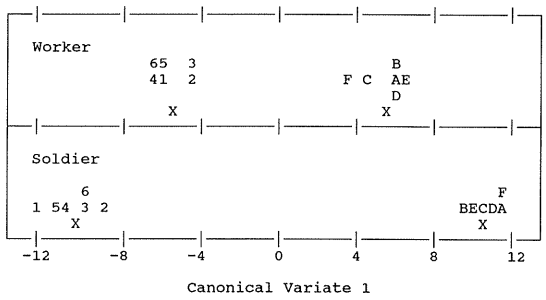

Fig. 4. Plot of colonies of *C. formosanus* from two locations along one axis of canonical discriminant space. Numbers 1 through 6 represent colonies from Florida; A through F represent colonies from Hawaii. X indicates the mean value of each population of the same location.

(Table III). Even with the inclusion of these nine cuticular hydrocarbon groups (HC1–HC4, HC6, HC7, HC9, HC11, and HC12), the highest correlation coefficient (r^2) was 0.106. Likewise, little correlation was established between cuticular hydrocarbon patterns and 24-h mortality, which is considered the end result of agonistic encounters. The highest r^2 for the model correlating five cuticular hydrocarbons (HC6, HC10, HC11, HC13, and HC14) and mortality was 0.045.

Even though other investigators have suggested that hydrocarbons are responsible for, or correlated with, recognition of alien and conspecific termites (Blomquist and Howard, 1979; Howard *et al.*, 1980, 1982; Howard and Blomquist, 1982; Clément, 1986; Haverty and Thorne, 1989), we conclude from our data that there was no apparent relation between cuticular hydrocarbon patterns and agonistic behavior in the *C. formosanus* populations we examined. Reasons for this inconsistency may simply be species differences. Future studies to identify recognition cues for *C. formosanus* should examine factors other than cuticular hydrocarbons. These might include mandible gland exudates,

Table III. Summary of Stepwise Multiple Regression, with Difference in Proportion for Each Cuticular Hydrocarbon as the Independent Variable and the Presence or Absence of Agonistic Response or 24-h Mortality as the Dependent Variable

Step	Cuticular hydrocarbon[a]	Partial r^2	Model r^2	$C(p)$	F	P
			Agonistic behavior			
1	HC2	0.024	0.024	44.43	13.99	0.0002
2	HC6	0.020	0.044	33.81	11.97	0.0006
3	HC11	0.025	0.069	20.24	15.13	0.0001
4	HC12	0.008	0.076	17.45	4.69	0.0308
5	HC7	0.008	0.084	14.50	4.88	0.0276
6	HC3	0.005	0.089	13.51	2.95	0.0863
7	HC4	0.009	0.098	10.11	5.39	0.0207
8	HC1	0.004	0.102	9.41	2.69	0.1013
9	HC9	0.004	0.106	8.92	2.49	0.1151
			Mortality			
1	HC6	0.013	0.013	21.79	7.82	0.0053
2	HC10	0.015	0.029	14.51	9.09	0.0027
3	HC13	0.007	0.036	12.18	4.27	0.0394
4	HC14	0.005	0.041	11.05	3.10	0.0788
5	HC11	0.004	0.045	10.58	2.45	0.1183

[a] HC1, *n*-C_{25}; HC2, 9-;11-MeC_{25}; HC3, 2-MeC_{25}; HC4, 3-MeC_{25}; HC5, *n*-C_{26}; HC6, 9-;11-;13-MeC_{26}; HC7, 2-MeC_{26}; HC9, 9-;11-;13-MeC_{27}; HC10, 2-MeC_{27} + 9,13-$DimeC_{27}$; HC11, 3-MeC_{27}; HC12, *n*-C_{28}; HC13, 9-;11-;13-;15-MeC_{28}; HC14, 9-;11-;13-;15-MeC_{29} + 13,15-$DimeC_{29}$. These abbreviations use a descriptor similar to that in Figs. 1 and 2.

polar cuticular compounds, behavioral (tactile) differences, and volatile digestive compounds.

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