

Flight Phenology of Sympatric Populations of *Reticulitermes* (Isoptera: Rhinotermitidae) in Northern California: Disparate Flight Intervals Indicate Reproductive Isolation Among Cuticular Hydrocarbon Phenotypes

MICHAEL I. HAVERTY,¹ GAIL M. GETTY,² LORI J. NELSON, AND VERNARD R. LEWIS²

Chemical Ecology of Forest Insects, Pacific Southwest Research Station, USDA Forest Service, P.O. Box 245, Berkeley, CA 94701

Ann. Entomol. Soc. Am. 96(6): 828–833 (2003)

ABSTRACT The diurnal flights of *Reticulitermes* spp. have been reported to occur in the spring and early fall in northern California. From the spring of 1994 until the fall of 2001, we collected hundreds of alates of *Reticulitermes* spp. cuticular hydrocarbon phenotypes CA-A/A' and CA-D during flights from multiple locations in the San Francisco Bay Area. As predicted, there were two flight seasons: one in the spring from February to May and one in the fall from October to December. The flights in the spring were made only by phenotypes CA-A/A'; those in the fall exclusively included phenotype CA-D. These disparate flight times indicate that reproductive isolation is complete and provide further biological evidence that phenotypes CA-A and CA-A' are variants of one taxon and are distinct from CA-D.

KEY WORDS chemotaxonomy, colony founding, *Reticulitermes hesperus*, speciation, subterranean termite

STUDIES OF *Reticulitermes* spp., a Holarctic genus of ecologically and economically important subterranean termites, are constrained by the antiquated state of the taxonomy of this genus. Much of the taxonomic and biogeographical information on *Reticulitermes* spp. was developed early in the last century (Banks and Snyder 1920, Light 1934, Pickens 1934a, b, Banks 1946, Miller 1949, Snyder 1954), and there is agreement that the genus needs revision (Weesner 1970, Nutting 1990, Scheffrahn and Su 1994, Thorne 1999).

Termite taxonomy is a complex issue (Clément et al. 2001). Termites often lack features that facilitate specific diagnoses, are extremely plastic, and exhibit considerable morphological variation (Light 1927). Determination of species of *Reticulitermes* based on morphology has proven difficult for our studies in northern California (Haverty et al. 1996a, 1999a–c, 2000, Haverty and Nelson 1997, Getty et al. 2000a). According to the published descriptions, keys, and bionomic information relevant to alates of *R. hesperus* and *R. tibialis*, the main distinguishing characteristics are body and wing membrane coloration (Banks and Snyder 1920, Pickens 1934b, Weesner 1965, Nutting

1990) and the shape of the post clypeus and color of the tibiae (Clément 1978). To quote Pickens (1934b), "the reproductives are even more difficult to recognize, although on comparison *R. tibialis* is found to be a deeper black." Wing coloration is characterized as either brownish gray, or colorless or tinged with brown (Nutting 1990).

No objective character state or discrete or continuous measurement is presented to unequivocally identify a given specimen to species. Vague and subjective color differences may be more apparent to some observers than others. Furthermore, geographical distribution may not be meaningful as part of the description of a species so easily transported by human activity. It is hoped that more reliable and definable characters can be found by using a variety of methods to differentiate the insects and to determine whether or not they can be named as distinct species. That is our goal in using chemical and behavioral characters to study *Reticulitermes*. Such characteristics might also be more biologically meaningful.

To make progress in our studies of *Reticulitermes* spp. and circumvent the difficulty with keys, our group has used characterization of cuticular hydrocarbons to help delineate taxa. There is a growing body of evidence suggesting that termites have species-specific mixtures of cuticular hydrocarbons (Page et al. 2002). Repeatable chemical phenotype groups and support-

¹ E-mail: mhaverty@fs.fed.us.

² Division of Insect Biology, Department of Environmental Science, Policy, and Management, 210 Wellman Hall, University of California, Berkeley, CA 94720.

ing biological information are needed to confirm that cuticular hydrocarbon phenotypes represent distinct taxa (Haverty et al. 1999a,b, Clément et al. 2001, Nelson et al. 2001). Until taxonomic descriptions are published and new species named, we must rely on the assignment of cuticular hydrocarbon phenotype labels to *Reticulitermes* spp. in California (Haverty and Nelson 1997).

Biogeographical information describes *R. hesperus* Banks as the predominant species in northern California. *R. hesperus* has been reported to occur along the Pacific coast and throughout the northern portion of California into the Sierra Nevada, as well as in portions of Oregon, Washington, Idaho, and Nevada (Light 1934, Pickens 1934a, Weesner 1970). Pickens (1934a, b) claimed that *R. hesperus* coexists with *R. tibialis* Banks in the inland valleys of California and is displaced by *R. tibialis* in the desert areas of California and the Great Basin. We feel this information is outdated, and the distribution of these and other species of *Reticulitermes* has undoubtedly changed dramatically since these descriptions were published.

Recent chemosystematic studies of *Reticulitermes* indicated five cuticular hydrocarbon phenotypes occur in northern California (Haverty and Nelson 1997). Characterization of the soldier defense secretions of these phenotypes corroborates the status of three of them (CA-B, CA-C, and CA-D) as distinct taxa, whereas CA-A and CA-A' seem to be variants of the same taxon but different from CA-B, CA-C, and CA-D (Nelson et al. 2001). The three most common phenotypes, CA-A, CA-A', and CA-D, are sympatric in the San Francisco Bay Area (Haverty and Nelson 1997).

The diurnal flights of *R. hesperus* have been reported to occur in the spring and early fall. Spring flights have been reported to be diffuse and usually follow periods of rainfall on clear, sunny afternoons. In contrast, the fall flights are purported to be very conspicuous, with thousands of alates emerging from many colonies simultaneously (Pickens 1934a, Weesner 1956, 1970). There is no indication in the literature that these two flight seasons might involve different species of *Reticulitermes*. The only clue to confusion of species status involved difficulties in assigning alates collected in Nevada to either *R. hesperus* or *R. tibialis* (Weesner 1970).

We report here the results of characterization of the cuticular hydrocarbons of *Reticulitermes* alates collected from 1994 to 2001 during flights in northern California from the San Francisco Bay Area east to Placerville in the foothills of the Sierra Nevada and north to Cloverdale. Our results provide further support for the hypothesis that the cuticular hydrocarbon phenotypes CA-A and CA-A' of *Reticulitermes* represent a distinct taxon, or species, that is distinguishable from CA-D.

Materials and Methods

Collection of Termites. From the spring of 1994 until the fall of 2001, we opportunistically collected *Reticulitermes* spp. alates during flights at residences in

Table 1. Date and locality of collections of alates of *Reticulitermes* spp. phenotypes A and A' from northern California

Date	Locality
Phenotype A	
4/19/94	Placerville, CA-IFG monitoring station-Wc7
4/24/96	Placerville, CA-IFG monitoring station-Wg36
5/8/96	Cloverdale, CA-9.8mi fr. Hwy101 on Hwy128
5/8/96	Placerville, CA-pine log
3/23/99	Sacramento, CA-Sacramento Housing Authority
3/25/99	Sacramento, CA-Sacramento Housing Authority
3/30/99	Larkspur, CA-private residence
4/13/99	Davis, CA-private residence
4/19/99	South Davis, near Yolo-Solano Co. border
4/20/99	Walnut Creek, CA-private residence
4/22/99	Lafayette, CA-private residence
4/7/00	Lafayette, CA-Carol Lane @ Moraga Blvd.
3/7/01	Placerville, CA-IFG Monitoring station-Yr19
4/5/01	Walnut Creek, CA-private residence
4/17/01	Lafayette, CA-private residence
4/17/01	Willow Slough, Yolo County, CA
Phenotype A'	
3/20/96	Novato, CA-St. Francis monitoring station St 57
3/29/96	Novato, CA-St. Francis monitoring station St 60
3/25/97	Novato, CA-St. Francis monitoring station St 57
4/16/98	Novato, CA-St. Francis monitoring station St 63
3/12/99	San Rafael, CA-private residence
4/20/99	Novato, CA-private residence
2/8/00	San Rafael, CA-private residence

the greater San Francisco Bay Area and in the general vicinity of Cloverdale, Sacramento, Davis, and Placerville, CA (Tables 1 and 2). On several occasions we made collections from multiple sites on the same residential property on the same date; we consider these collections as one collection. Occasionally, we were able to collect *Reticulitermes* spp. alates from monitoring stations or from laboratory cultures that we used in studies of the foraging ecology, agonistic behavior, or baits for control of *Reticulitermes* spp. (Lewis et al. 1998, Haverty et al. 1999a, b, 2000, Getty et al. 2000a, b). After collection, alates were frozen, air-dried, and sent to our laboratory in Albany, CA, for characterization of the cuticular hydrocarbons.

Characterization of Cuticular Hydrocarbons. Cuticular hydrocarbons were characterized by extract-

Table 2. Date and locality of collections of alates of *Reticulitermes* spp. phenotype D from northern California

Date	Locality
11/2/95	Novato, CA-St. Francis monitoring station-St 3
11/21/95	Novato, CA-St. Francis monitoring station-St 21
11/20/96	Novato, CA-9/94 lab culture-St 7
10/25/98	Lafayette, CA-private residence
10/7/98	Novato, CA-St. Francis monitoring station-St 116, 314
11/23/98	Novato, CA-7/98 lab cultures-St 21, 35, 116, 125
12/5/98	San Francisco, CA
12/15/98	Berkeley, CA
10/19/99	San Rafael, CA-private residence
10/20/99	San Rafael, CA-private residence
10/28/99	San Rafael, CA-private residence
11/18/99	Novato, CA-St. Francis monitoring station-St 63
9/4/00	Lafayette, CA
10/10/00	Albany, CA
10/27/00	Lafayette, CA-private residence
10/27/00	Novato, CA
9/19/01	Novato, CA

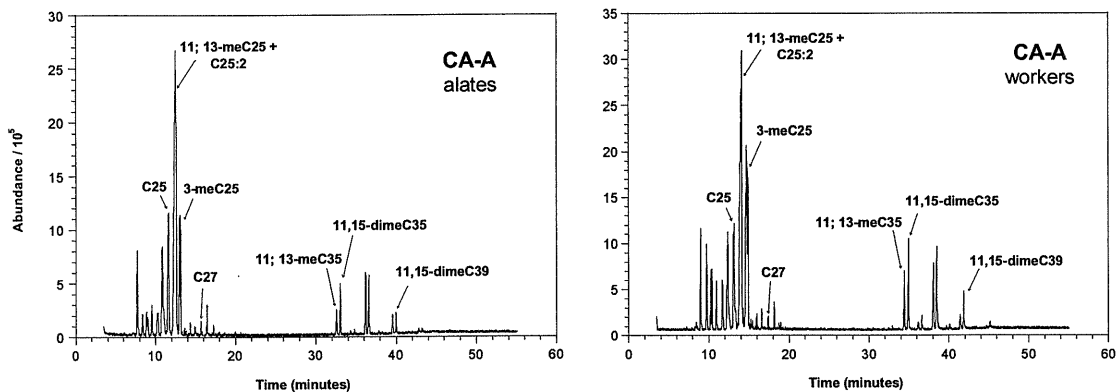


Fig. 1. Total ion chromatograms of *Reticulitermes* spp. cuticular hydrocarbon phenotype CA-A alates from Lafayette, CA, and workers from Placerville, CA.

ing samples of 20–30 *Reticulitermes* spp. alates that had been dried again at 70°C for up to 1 h. We identified all cuticular hydrocarbons in each collection by GS-MS; extraction, separation, characterization, and labeling of cuticular hydrocarbons were identical to that reported for *Reticulitermes* spp. workers from northern California (Haverty and Nelson 1997). Each collection was assigned to a phenotype previously described for *Reticulitermes* spp. (Haverty and Nelson 1997). Voucher specimens for each hydrocarbon phenotype were previously deposited in the Essig Museum, University of California, Berkeley (Haverty et al. 1999a).

Display of Flight Patterns. The number of collections, by phenotype, was charted as a function of month of the year. To provide a smoothed representation of the flight dates, a kernel in the shape of a normal distribution with an SD of 7.5 d was placed over each observed flight date (Silverman 1986). The contributions from each flight date were averaged for each day in the 8-yr period. The choice of the SD was arbitrary, but it was chosen so that the middle 95% of the normal kernels would cover ≈ 30 d, which corresponds approximately to ± 2 SD.

Results and Discussion

We made 40 separate location/date collections (Tables 1 and 2). Only three cuticular hydrocarbon phenotypes were found: CA-A, CA-A', and CA-D (Figs. 1–3). The cuticular hydrocarbon mixtures of the alates are qualitatively identical to those of the workers as reported by Haverty and Nelson (1997). Alates have not yet been collected from the less common phenotypes, CA-B and CA-C, found in the Sierra Nevada (Haverty and Nelson 1997).

There were two flight seasons: a spring flight from early February to early May and a fall flight from early October to mid-December. The flights in the spring were comprised exclusively of phenotypes CA-A and CA-A'; flights in the fall only included phenotype CA-D (Fig. 4; Tables 1 and 2).

Cuticular hydrocarbon mixtures of alates have been reported to be qualitatively similar to those of pseudergates or workers of *Neoterme mona* (Banks) (Haverty et al. 1997), *Zootermopsis nevadensis* (Hagen) (Haverty et al. 1988), *Coptotermes formosanus* Shiraki (Haverty et al. 1996b), and *Nasutitermes acajutlae* (Holmgren) (Haverty et al. 1996c, 1997) collected

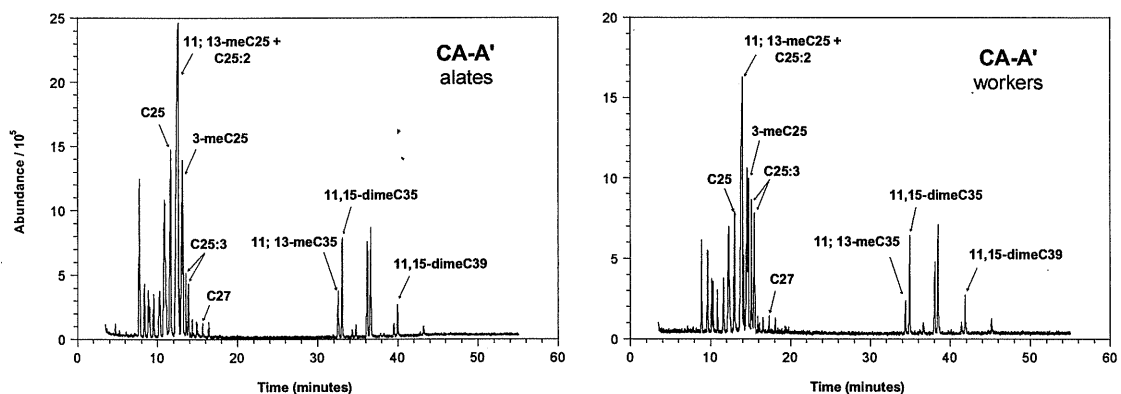


Fig. 2. Total ion chromatograms of *Reticulitermes* spp. cuticular hydrocarbon phenotype CA-A' alates from Novato, CA, and workers from Novato, CA.

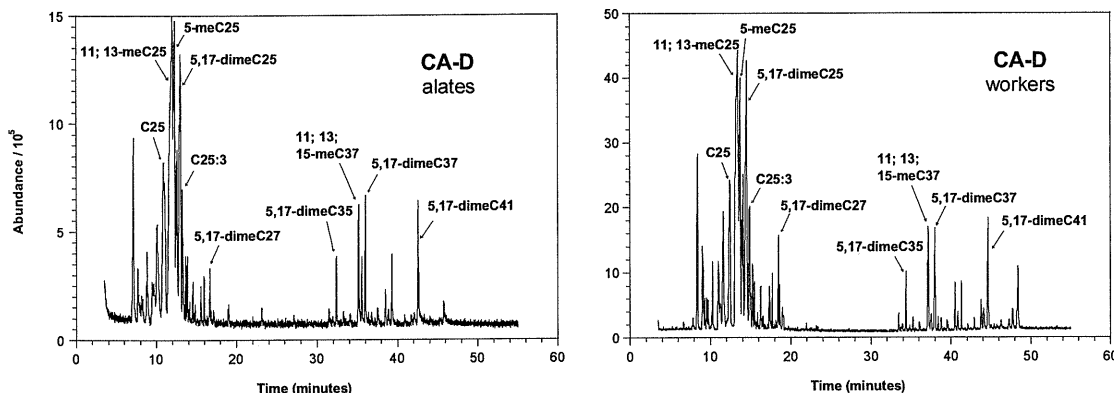


Fig. 3. Total ion chromatograms of *Reticulitermes* spp. cuticular hydrocarbon phenotype CA-D alates from Novato, CA, and workers from Novato, CA.

from the same colonies. Therefore, it is reasonable to assign alates of *Reticulitermes* spp. collected in flight to a particular phenotype or taxon, especially when the hydrocarbon mixtures are qualitatively identical.

Six species of *Reticulitermes* are currently recognized in the Nearctic (Snyder 1954, Weesner 1970, Nutting 1990). All are diurnal fliers, but the time of year when they fly is stated to "vary somewhat from species to species, from area to area, and from year to year" (Weesner 1970). Both *R. hesperus* and *R. tibialis* were reportedly observed flying at the same time in the San Joaquin Valley in California (Pickens 1934b). Weesner (1970) addresses the variability of flight times in both *R. hesperus* and *R. tibialis* and concedes the difficulty of assigning species identity to insects collected outside their accepted territory. The limits of the territories are said to overlap in the inland valleys of California, but one can conclude that the limits are not clearly defined and are unlikely to be static.

According to Weesner (1956), flights of *R. hesperus* in the San Francisco Bay Area usually occur both immediately after the initial fall rains and in the early spring. Pickens (1934a) further specified that flights

characteristically occur on the first clear day that follows rain, under conditions of high soil moisture and warm air temperatures. This agrees with our observations, except we see distinct groupings of taxa in spring and fall. Other species of *Reticulitermes* have disparate flight seasons. Weesner (1970) reported that outdoor flights of *R. flavipes* occur in the spring, most frequently in April and May, whereas the flights of the sympatric species *R. virginicus* or *R. hageni* occur later under similar conditions. Nutting (1969) found that *R. tibialis* in Arizona flies during summer above 4,000 ft in elevation and during the winter below this elevation. These disparate flight seasons reported for *R. tibialis* by Nutting (1969) probably reflect the behavior of different taxa (Haverty et al. 1999c).

Nutting (1969) suggested a parallel between termite colonies and sessile organisms; wings have been retained by the sexual adults of one caste for a single, seasonal migration, or dispersal flight, much like the dispersal of seeds by plants. Alates seem ready for flight within a few days after molting into adults, yet flight is essentially a seasonal phenomenon. Flights occur during the season of the year and time of day when conditions are most favorable for colony establishment (Nutting 1969). Elevated soil moisture is distinctly advantageous to the dealated adults of subterranean termites because it expedites excavation of their nuptial chamber and provides moisture during the critical period of the incipient colony (Nutting 1969). In the primitive termites, specifically the Kalotermitidae and Termopsidae, alates may be present in the nests continuously throughout the year. Species of these families usually nest entirely within a single piece of wood, enter the wood through beetle exit holes or cracks and crevices, and do not rely heavily on moisture. There may be periodic peaks, but flights by these species are not precisely synchronized with seasonal changes (Nutting 1969).

Mayr (1942) introduced the biological species concept. He defined species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." Currently, the biological species concept is the most

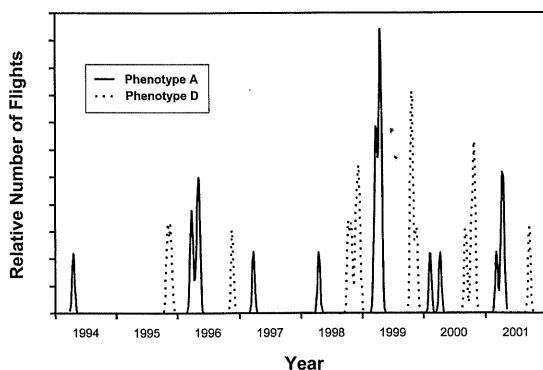


Fig. 4. Collections of alates of *Reticulitermes* spp. phenotypes CA-A, CA-A', and CA-D flying from 1994 through 2001 in northern California.

widely used definition of species. Populations or groups of populations are reproductively isolated if gene flow between them is prevented by biological differences, or barriers to gene flow, called isolating mechanisms (Futuyma 1998). Reproductive isolation is most convincing if the populations are sympatric (Freeman and Herron 1998). What could be more demonstrative of reproductive isolation or species status than the temporal isolation of adults of sympatric populations? Seasonal isolation is the most common prezygotic barrier to gene flow (Futuyma 1998).

These disparate flight intervals provide a reproductive isolating mechanism and further evidence that phenotypes CA-A and CA-A' constitute a taxon distinct from CA-D. This information, along with supporting data on distinct cuticular hydrocarbon and soldier defense secretion profiles and agonistic behavior toward different phenotypes (Haverty et al. 1999a, Getty et al. 2000b, Nelson et al. 2001) convinces us that CA-A/A' and CA-D represent different species. There is no evidence of hybridization among these cuticular hydrocarbon phenotypes. Reproductive isolation seems to be complete.

We do not know what situation or situations caused the populations to become reproductively isolated (allopatric or sympatric speciation) or to curtail gene flow that eventually led to the divergent behavior and reproductive isolation. There is always the possibility that one of these species is exotic. Certainly hundreds or thousands of small populations of *Reticulitermes* have been introduced to new habitats around the world in the last 150 yr because of the activities of humans (Freeman and Herron 1998). The success of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, testifies to the potential for invasion of exotic species of subterranean termites. However, there must be a precise fit for species with seasonally defined dispersal periods. If critical factors, such as ample soil moisture, are not present at the time of alate dispersal, the exotic is not likely to succeed.

At first it may seem that the *Reticulitermes* samples collected in northern California since the days of Banks and Snyder (1920) are a single, morphologically uniform species. Now we know that these *Reticulitermes* include two or more populations that occupy the same area but do not interbreed. Until a detailed, modern morphological study is completed, these phenotypes might be considered sibling species. Variations in ecology or behavior are usually the first indications of sibling species (Futuyma 1998), and we hope that morphological differences will be found later by which they can be distinguished. The evidence is mounting that these *Reticulitermes* from this general locality comprise two species. They have two distinct states (i.e., cuticular hydrocarbon phenotypes CA-A/CA-A' and CA-D) but no intermediates. Like most features, cuticular hydrocarbon mixtures are polygenically inherited (Coyne et al. 1994, Dallerac et al. 2000, Takahashi et al. 2001). However, because the two phenotypes differ in a number of other bimodally distributed features (soldier defense secretions and flight times) and the characters are consistently cor-

related, our suspicion that these are two species grows stronger as the number of such distinguishing features increases (Futuyma 1998). Based on the characterization of the cuticular hydrocarbons from collections of topotypes from the type locality, Little Bear Lake (now called Lake Arrowhead) in the San Bernadino Mountains of California (Snyder 1949), we will designate CA-A as *R. hesperus* (M. I. H. and L. J. N., unpublished data).

Acknowledgments

The authors made many of the collections used in this study. However, the authors thank all cooperating homeowners and organizations that provided samples. We also thank J. Baldwin for help in graphically displaying *Reticulitermes* spp. flight patterns.

References Cited

- Banks, F. A. 1946. Species distinction in *Reticulitermes* (Isoptera: Rhinotermitidae). MS Thesis. University of Chicago, Chicago, IL.
- Banks, N., and T. E. Snyder. 1920. A revision of the Nearctic termites. Bull. U. S. Natl. Mus. 108: 1-228.
- Clément, J.-L. 1978. Nouveaux critères taxinomiques dans le genre *Reticulitermes* (Holmgren) [Isoptera] description de nouveaux taxons français. Ann. Soc. Entomol. Fr. 131: 131-139.
- Clément, J.-L., A.-G. Bangères, P. Uva, L. Wilfert, A. Quintana, J. Reinhard, and S. Dronnet. 2001. Biosystematics of *Reticulitermes* termites in Europe: morphological, chemical and molecular data. Insectes Sociaux. 48: 202-215.
- Coyne, J. A., A. P. Crittenden, and K. Mah. 1994. Genetics of a pheromonal difference contributing to reproductive isolation in *Drosophila*. Science. 265: 1461-1464.
- Dallerac, R., C. Labeur, J.-M. Jallon, D. C. Knipple, W. L. Roelofs, and C. Wicker-Thomas. 2000. A $\Delta 9$ desaturase gene with a different substrate specificity is responsible for the cuticular diene hydrocarbon polymorphism in *Drosophila melanogaster*. Proc. Natl. Acad. Sci. USA. 97: 9449-9454.
- Freeman, S., and J. C. Herron. 1998. Evolutionary analysis, 2nd ed. Prentice Hall, Upper Saddle River, NJ.
- Futuyma, D. J. 1998. Evolutionary biology, 3rd ed. Sinauer, Sunderland, MA.
- Getty, G. M., M. I. Haverty, K. A. Copren, and V. R. Lewis. 2000a. Response of *Reticulitermes* spp. (Isoptera: Rhinotermitidae) in northern California to baiting with hexaflumuron with Sentricon Termite Colony Elimination System. J. Econ. Entomol. 93: 1498-1507.
- Getty, G. M., M. I. Haverty, and V. R. Lewis. 2000b. Agonistic behavior between recently collected and laboratory cultured *Reticulitermes* spp. (Isoptera: Rhinotermitidae) from northern California. Pan-Pacific Entomol. 76: 243-250.
- Haverty, M. I., and L. J. Nelson. 1997. Cuticular hydrocarbons of *Reticulitermes* (Isoptera: Rhinotermitidae) from northern California indicate undescribed species. Comp. Biochem. Physiol. 118B: 869-880.
- Haverty, M. I., M. Page, L. J. Nelson, and G. J. Blomquist. 1988. Cuticular hydrocarbons of dampwood termites, *Zootermopsis*: intra- and intercolony variation and potential as taxonomic characters. J. Chem. Ecol. 14: 1035-1058.
- Haverty, M. I., B. T. Forschler, and L. J. Nelson. 1996a. An assessment of the taxonomy of *Reticulitermes* (Isoptera:

- Rhinotermitidae) from the southeastern United States based on cuticular hydrocarbons. *Sociobiology*. 28: 287–318.
- Haverty, M. I., J. K. Grace, L. J. Nelson, and R. T. Yamamoto. 1996b. Intercaste, intercolony, and temporal variation in cuticular hydrocarbons of *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae). *J. Chem. Ecol.* 22: 1813–1834.
- Haverty, M. I., B. L. Thorne, and L. J. Nelson. 1996c. Hydrocarbons of *Nasutitermes acajutlae* and comparison of methodologies for sampling cuticular hydrocarbons of Caribbean termites for taxonomic and ecological studies. *J. Chem. Ecol.* 22: 2081–2109.
- Haverty, M. I., M. S. Collins, L. J. Nelson, and B. L. Thorne. 1997. Cuticular hydrocarbons of termites of the British Virgin Islands. *J. Chem. Ecol.* 23: 927–964.
- Haverty, M. I., K. A. Copren, G. M. Getty, and V. R. Lewis. 1999a. Agonistic behavior and cuticular hydrocarbon phenotypes of colonies of *Reticulitermes* (Isoptera: Rhinotermitidae) from northern California. *Ann. Entomol. Soc. Am.* 92: 269–277.
- Haverty, M. I., G. M. Getty, K. A. Copren, and V. R. Lewis. 1999b. Seasonal foraging and feeding behavior of *Reticulitermes* spp. (Isoptera: Rhinotermitidae) in a wildland and a residential location in northern California. *Environ. Entomol.* 28: 1077–1084.
- Haverty, M. I., L. J. Nelson, and B. T. Forschler. 1999c. New cuticular hydrocarbon phenotypes of *Reticulitermes* (Isoptera: Rhinotermitidae) from the United States. *Sociobiology*. 34: 1–21.
- Haverty, M. I., G. M. Getty, K. A. Copren, and V. R. Lewis. 2000. Size and dispersion of colonies of *Reticulitermes* spp. (Isoptera: Rhinotermitidae) in a wildland and a residential location in northern California. *Environ. Entomol.* 29: 241–249.
- Lewis, V. R., M. I. Haverty, G. M. Getty, K. A. Copren, and C. Fouche. 1998. Monitoring station for studying populations of *Reticulitermes* (Isoptera: Rhinotermitidae) in California. *Pan-Pacific Entomol.* 74: 121–133.
- Light, S. F. 1927. A new and more exact method of expressing important specific characters of termites. *Univ. Calif. Publ. Entomol.* 4: 75–88.
- Light, S. F. 1934. The termite fauna of North America with special reference to the United States, pp. 127–135. In C. A. Kofoid, S. F. Light, A. C. Horner, M. Randall, W. B. Herms, and E. E. Bowe (eds.), *Termites and termite control*, 2nd ed. University of California Press, Berkeley, CA.
- Mayr, E. 1942. *Systematics and the origin of species*. Columbia University Press, New York.
- Miller, E. M. 1949. *A handbook of Florida termites*. University of Miami Press, Coral Gables, FL.
- Nelson, L. J., L. G. Cool, B. T. Forschler, and M. I. Haverty. 2001. Correspondence of soldier defense secretion mixtures with cuticular hydrocarbon phenotypes for chemotaxonomy of the termite genus *Reticulitermes* in North America. *J. Chem. Ecol.* 27: 1449–1479.
- Nutting, W. L. 1969. Flight and colony foundation, pp. 233–282. In K. Krishna and F. M. Weesner (eds.), *Biology of termites*, vol. I. Academic, New York.
- Nutting, W. L. 1990. Insecta: Isoptera, pp. 997–1032. In D. L. Dindal (ed.), *Soil biology guide*. Wiley, New York.
- Page, M., L. J. Nelson, B. T. Forschler, and M. I. Haverty. 2002. Cuticular hydrocarbons suggest three lineages in *Reticulitermes* (Isoptera: Rhinotermitidae) from North America. *Comp. Biochem. Physiol. B*. 131: 305–324.
- Pickens, A. L. 1934a. The biology and economic significance of the western subterranean termite, *Reticulitermes hesperus*, pp. 157–183. In C. A. Kofoid, S. F. Light, A. C. Horner, M. Randall, W. B. Herms, and E. E. Bowe (eds.), *Termites and termite control*, 2nd ed. University of California Press, Berkeley, CA.
- Pickens, A. L. 1934b. The barren-lands subterranean termite, *Reticulitermes tibialis*, pp. 184–186. In C. A. Kofoid, S. F. Light, A. C. Horner, M. Randall, W. B. Herms, and E. E. Bowe (eds.), *Termites and termite control*, 2nd ed. University of California Press, Berkeley, CA.
- Scheffrahn, R. H., and N.-Y. Su. 1994. Keys to soldier and winged adult termites (Isoptera) of Florida. *Fla. Entomol.* 77: 460–474.
- Silverman, B. W. 1986. *Density estimation for statistics and data analysis*. Chapman & Hall, London, United Kingdom.
- Snyder, T. E. 1949. Catalog of the termites (Isoptera) of the world. *Smithsonian Misc. Coll.* 112: 1–490.
- Snyder, T. E. 1954. Order Isoptera. The termites of the United States and Canada. National Pest Control Association, New York.
- Takahashi, A., S.-C. Tsaui, J. A. Coyne, and C.-L. Wu. 2001. The nucleotide changes governing cuticular hydrocarbon variation and their evolution in *Drosophila melanogaster*. *Proc. Natl. Acad. Sci. USA*. 98: 3920–3925.
- Thorne, B. L. 1999. Biology of subterranean termites of the genus *Reticulitermes*, pp. 1–30. In B. L. Thorne and B. T. Forschler (eds.), *NPMA research report on subterranean termites*. National Pest Management Association, Inc., Dunn Loring, VA.
- Weesner, F. M. 1956. The biology of colony formation in *Reticulitermes hesperus* Banks. *Univ. California Publ. Zool.* 61: 253–314.
- Weesner, F. M. 1965. The termites of the United States. A handbook. The National Pest Control Association, Elizabeth, NJ.
- Weesner, F. M. 1970. Termites of the Nearctic Region, pp. 477–525. In K. Krishna and F. M. Weesner (eds.), *Biology of termites*, vol. II. Academic, New York.

Received for publication 26 February 2003; accepted 8 August 2003.

