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Distribution of the Introduced Argentine Ant (*Iridomyrmex humilis*) in Natural Habitats of the Lower Sacramento Valley and Its Effects on the Indigenous Ant Fauna

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ABSTRACT

This study was designed to determine the extent to which the introduced Argentine ant (*Iridomyrmex humilis*), a pest in urban and agricultural environments, has invaded natural habitats in the lower Sacramento Valley, and its effects on the native ant fauna. Of four natural habitats surveyed (valley riparian woodland, foothill riparian woodland, blue oak-digger pine woodland, and chaparral), at 46 sites in Yolo and Solano counties, only valley riparian woodland was found to have been colonized by *I. humilis.* Riparian woodland sites occupied by *I. humilis* have permanent sources of water and tend to be environmentally degraded. Populations of *I. humilis* are common but patchily distributed along four principal riparian systems in Yolo and Solano counties (Ulatis Creek, Putah Creek, Cache Creek, and the Sacramento River). Observations indicate that patches of semidisturbed riparian woodland provide refuges from which populations of *I. humilis* may invade adjacent agricultural land, and vice versa. The species richness of native ants is markedly reduced at riparian woodland sites occupied by *I. humilis.* Among the common native ants, epigaeic (aboveground foraging) species are more susceptible to displacement by *I. humilis* than are hypogaeic species. The three most adversely affected species (*Liometopum occidentale, Tapinoma sessile,* and *Formica occidua* [= *moki*]), which are absent from sites colonized by *I. humilis*, are dominant epigaeic ants; two of the three least displaced species (*Stenamma diecki* and *S. californicum*) are timid, cryptobiotic ants that forage in soil and leaf litter.

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Distribution of the Introduced Argentine Ant (*Iridomyrmex humilis*) in Natural Habitats of the Lower Sacramento Valley and Its Effects on the Indigenous Ant Fauna[1]

INTRODUCTION

SINCE ITS INTRODUCTION into North America about 95 years ago, the Argentine ant (*Iridomyrmex humilis* Mayr) has spread widely in the southern half of the continent, particularly in agricultural and urban habitats (Barber 1916; Smith 1965). First recorded from California in 1907 (Woodworth 1908), *I. humilis* is now found in disturbed habitats at lower elevations throughout much of the state and is a significant pest in homes and orchards (Eckert and Mallis 1937; Flanders 1945; Markin 1970). The foraging and honeydew-gathering activities of *I. humilis* workers disrupt biological control of scales and other homopterous insects on citrus (Flanders 1945, 1958; DeBach 1951). Less attention has been focused on the degree to which *I. humilis* has been able to invade nonurban and nonagricultural habitats in California or its effects on the indigenous insect fauna (but see Erickson 1972; Tremper 1976).

This study is concerned with the distribution and abundance of *I. humilis* in natural habitats in California's lower Sacramento Valley, a region in which the species is well entrenched in certain environments modified by humans. The study addresses three questions: (1) To what extent has *I. humilis* colonized natural habitats in this region? (2) What factors are associated with the invasion of such habitats by *I. humilis?* (3) What effects does the presence of *I. humilis* have on the diversity and composition of the native ant fauna? The results of such an investigation can be expected to provide information about potential natural refuges of *I. humilis* and to give insight into the factors that limit spread of this species.

A "natural habitat" is here defined as a community whose flora and fauna consist largely of indigenous species and whose composition and physiognomy approach the condition presumed to occur before human (or European) settlement. In effect, this study involved sampling the ant communities of woodland and shrub habitats in the lower Sacramento Valley, although it is recognized that none of these natural areas exists in an entirely unaltered state. In particular, riparian woodland, the focus of most of this study, is represented by fragmented and variably disturbed remnants (Roberts, Howe, and Major 1980).

MATERIALS AND METHODS

This study was carried out in Yolo and Solano counties, in an area bounded by latitudes 38°10′N and 38°55′N, and by longitudes 121°30′W and 122°20′W (fig. 1).

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The basic sampling was conducted in 1984 and 1985, with some replicate samples and spot checks being taken in 1986. Four broad habitat categories were recognized and surveyed in detail for the presence of *Iridomyrmex humilis:* (1) valley riparian woodland, (2) foothill riparian woodland, (3) blue oak-digger pine woodland, and (4) chaparral. Habitat classification follows Küchler (1977) except that two types of riparian woodland are recognized: (1) valley riparian woodland, occurring on the valley floor and containing such trees as *Populus fremontii, Acer negundo, Juglans hindsii,* and *Quercus lobata,* and (2) foothill riparian woodland, representing an extension of the same system into the adjacent foothills and characterized by steeper banks and surrounding slopes, and by the appearance or increased importance of such trees as *Acer macrophyllum, Aesculus californica,* and (where water flow is permanent) *Alnus rhombifolia,* in lieu of *Acer negundo* and *Quercus lobata.*

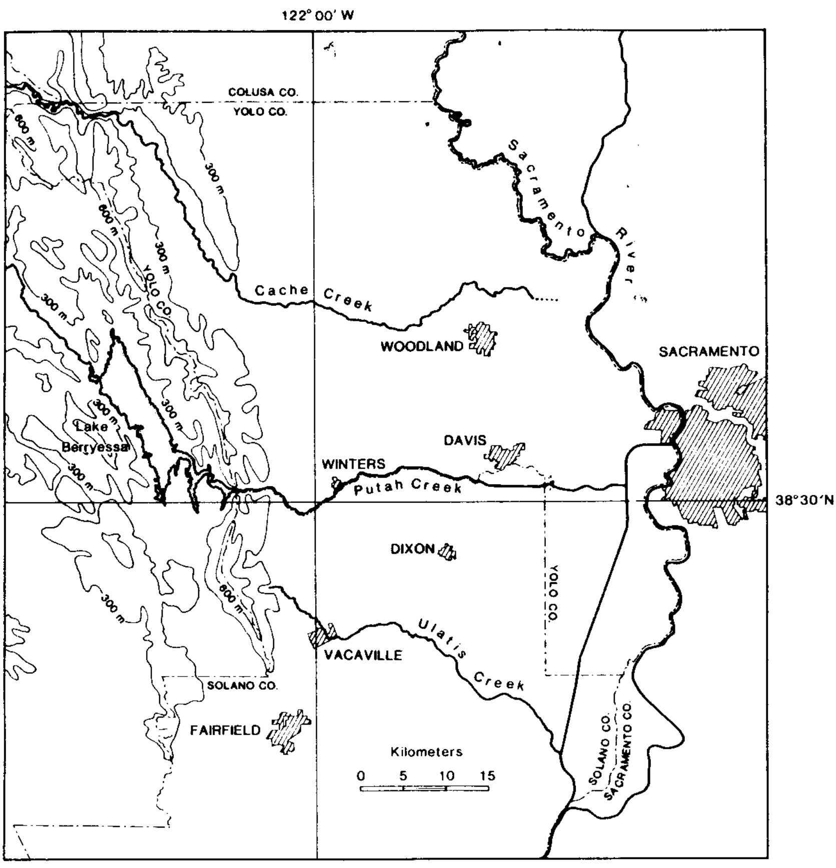

Fig. 1. Map of study area, showing principal riparian systems, urban localities, and topography.

Forty-six study sites were selected from throughout both counties (table 1), with the intention of providing broad geographic and ecological coverage of the region. Initially, eight locations were chosen for each habitat type, with fourteen additional valley riparian sites being added as information accumulated on habitat preferences of *I. humilis.*

At each site an ensemble of three sampling methods was used to determine the presence of *I. humilis* and to assess the species richness and composition of the native ant fauna.

(1) Ant workers were collected from moist ground litter (leaf mold, rotten wood) using Winkler litter-sifting and arthropod-extraction devices (Hildegard Winkler, Dittesgasse 11, A-1180, Vienna, Austria). This method was used to survey the hypogaeic ant fauna—that is, those species that forage below the ground surface, although some surface foragers also appeared in the samples. At each study site, handfuls of moist leaf mold and rotting wood were gathered diffusely from the ground, over an area of approximately 1,000 m^2, and sifted through a wire sieve of square, 0.8-cm mesh, up to a total quantity of 6 L of sifted litter. This standard 6-L sample was returned to the laboratory, and the litter ants were extracted in a Winkler funnel. The funnel consists of an enclosable cloth bag, the lower portion of which tapers to a cup of alcohol. It functions like a Berlese-Tullgren funnel, except that the sifted litter is held vertically inside the cloth bag in several flat, loosely hanging, mesh sacks, and the litter dries passively without aid of a heat source. Arthropods that attempt to leave the dessicating litter fall to the bottom of the bag where they are funneled into the cup of alcohol. The litter was allowed to dry at room temperature over a 3-day period, since exhaustive extractions showed that, on average, 98 percent of the ant species and 85 percent of the individual worker ants were removed from the litter in the first 3 days of drying. All litter collections were made in February, March, or April.

(2) Foraging worker ants were attracted to tunafish bait. This was designed to sample the epigaeic (aboveground foraging) ant fauna. At each site an 80-m line transect was set out, consisting of 20 bait stations, each 4 m apart. At each bait station, about 1 g of tunafish (in oil) was placed on a plastic petri dish cover, of 5.6-cm diameter. After 2 hours, collections were made of all worker ants on the petri dish covers. Bait transects were put out in March, April, or May, on clear, sunny days with ambient temperature $\geq 15°C$.

(3) Ant foragers and ant nests were sampled using time-honored general collecting techniques. At each study site, 1 person hour was devoted to turning stones, examining fallen logs and dead branches on trees, and searching for soil-excavated ant nests and foraging workers.

Thus, a complete "sample" of the ant fauna at any given site was based on three different kinds of collections. These collections were used primarily to provide presence/absence data on *Iridomyrmex humilis* and other ant species, although the number of individual ants of each species in litter and bait samples was also recorded. For each site, the following measures of ant species richness were used:

S_L: number of native ant species in litter collection

S_B: number of native ant species in bait collection

S_T: total number of native ant species recorded from site, based on all three sampling methods

TABLE 1. INTENSIVELY SURVEYED SITES IN YOLO AND SOLANO COUNTIES (SEE ALSO FIGURE 3)

Site no.	Habitat	County/location	Altitude (*m*)
1	Valley riparian woodland	Solano: Vacaville	40
2	Valley riparian woodland	Solano: 8km NW Vacaville	110
3	Valley riparian woodland	Solano: Lake Solano Park	40
4	Valley riparian woodland	Solano: S end, Lake Solano	40
5	Valley riparian woodland	Solano: E end, Lake Solano	40
6	Valley riparian woodland	Solano: 5km NE Lake Solano	40
7	Valley riparian woodland	Solano: 2km E Winters	35
8	Valley riparian woodland	Solano: 13km NW Dixon	35
9	Valley riparian woodland	Solano: 10km NNW Dixon	25
10	Valley riparian woodland	Yolo: Putah Crk. Reserve, Davis	15
11	Valley riparian woodland	Yolo: Spieth Reserve, Davis	10
12	Valley riparian woodland	Yolo: Olive Drive, Davis	10
13	Valley riparian woodland	Yolo: Rd. 103, Davis	10
14	Valley riparian woodland	Yolo: 9km N Davis	10
15	Valley riparian woodland	Yolo: Bryte	5
16	Valley riparian woodland	Yolo: 9km NW Bryte	5
17	Valley riparian woodland	Yolo: 12km SE Knights Landing	10
18	Valley riparian woodland	Yolo: 4km E Yolo	15
19	Valley riparian woodland	Yolo: 8km W Woodland	30
20	Valley riparian woodland	Yolo: Capay	60
21	Valley riparian woodland	Yolo: 6km W Capay	90
22	Valley riparian woodland	Yolo: Guinda	110
23	Foothill riparian woodland	Solano: Gates Canyon	330
24	Foothill riparian woodland	Solano: Mix Canyon	150
25	Foothill riparian woodland	Solano: Cold Canyon	120
26	Foothill riparian woodland	Yolo: 10km NW Winters	80
27	Foothill riparian woodland	Yolo: 4km SSW Brooks	130
28	Foothill riparian woodland	Yolo: 5km SW Guinda	530
29	Foothill riparian woodland	Yolo: 4km NW Rumsey	150
30	Foothill riparian woodland	Yolo: 6km WNW Rumsey	190
31	Oak-pine woodland	Solano: 2km NW Rockville	85
32	Oak-pine woodland	Solano: 9km NNW Vacaville	240
33	Oak-pine woodland	Solano: Cold Canyon	120
34	Oak-pine woodland	Yolo: Capay	100
35	Oak-pine woodland	Yolo: 4km SSW Brooks	170
36	Oak-pine woodland	Yolo: 3km SW Guinda	150
37	Oak-pine woodland	Yolo: 4km NW Rumsey	680
38	Oak-pine woodland	Yolo: 5km NW Dunnigan	60
39	Chaparral	Solano: 2km SE Mt. Vaca	680
40	Chaparral	Solano: Mix Canyon	790
41	Chaparral	Solano: 3km NW Mt. Vaca	800
42	Chaparral	Solano: Cold Canyon	420
43	Chaparral	Yolo: 2km NNW Berryessa Pk.	755
44	Chaparral	Yolo: 4km SW Guinda	380
45	Chaparral	Yolo: 3km NE Guinda	410
46	Chaparral	Yolo: 6km WNW Rumsey	370

Iridomyrmex humilis was the only nonnative ant species encountered in this survey, except for *Tetramorium caespitum* which was recorded from two sites only. To assess the consistency of this sampling procedure, replicate samples comprising litter, bait, and general collections were taken from twelve sites: nine randomly chosen valley riparian sites, and one randomly chosen site from each of the three other habitats.

At the valley riparian sites, the following habitat variables were recorded:

(1) Distance, in kilometers, to the nearest urban area (Vacaville, Winters, Davis, West Sacramento, or Woodland) along the same or closest riparian corridor;

(2) Seasonality of stream flow (continuous or intermittent, assessed in late summer);

(3) Encroachment by nonnative trees, principally *Eucalyptus* and *Ailanthus* (recorded as present or absent);

(4) Overall disturbance, measured on a scale of 0 to 8; this was a composite index, based on a summation of the following four factors, each assessed subjectively on a scale of 0 to 2: absence or scarcity of large, vigorous native trees; replacement of native understory plants by adventive species; presence of human garbage and waste materials; and disturbance of soil by human activities.

In addition to intensive sampling of 46 sites as described above, spot sampling for the presence of *Iridomyrmex humilis* and other epigaeic ants was carried out at 68 additional sites located along four valley riparian systems, and at 14 disturbed sites located along roadsides and irrigation ditches. These spot samples entailed about 30 minutes of general collecting per site.

Voucher specimens of ants recorded during this survey have been deposited in the Bohart Museum, Department of Entomology, University of California at Davis (UCD).

RESULTS

Sampling Efficacy

Replicate sampling of twelve sites suggested that, collectively, the three sampling methods give reliable, repeatable results with respect to detection of *Iridomyrmex humilis* and assessment of the native ant fauna.

Estimates of ant species richness, as indicated by the total number of native ant species recorded at a site (S_T), are highly positively correlated between replicates ($r = 0.87$, $p < .001$; see figure 2). Species richness is also significantly correlated between replicate litter collections ($r = 0.60$, $p < .05$) and replicate bait collections ($r = 0.58$, $p < .05$), although less strongly so.

Iridomyrmex humilis had been detected at four of the twelve sites in 1984-85 during the original survey of those sites. Application of the same sampling procedures to the twelve sites a year later revealed *I. humilis* at all four previously recorded sites, and at none of the eight null sites, with one exception (table 2). In the exceptional case, *I. humilis* occupied the margins of a riparian site (site 21, 6km W Capay, Yolo County) from which it had not been previously recorded. Circumstantial evidence, discussed in further detail below, indicates that this population is recently established.

Finally, with respect to detecting the presence of native ant species, replicate between-year samplings show high concordance, despite the possible obscuring influence of

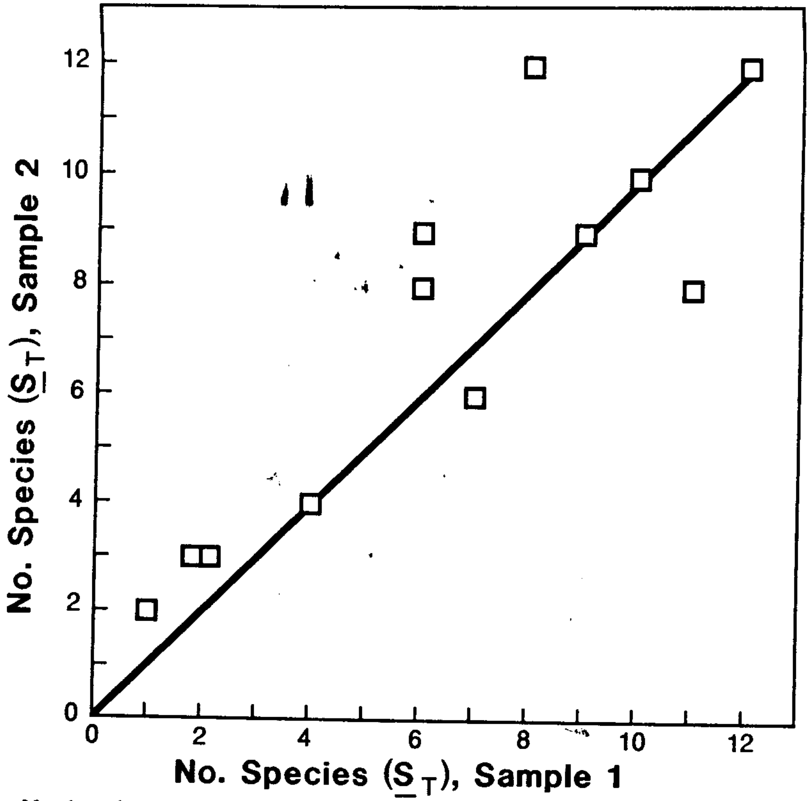

Fig. 2. Number of native ant species recorded in replicate samples from 12 sites. Line is drawn through points of equal value.

year-to-year fluctuations in abundance. Table 2 gives the results for the five most common ant species at the twelve sites. There is presence/absence agreement between years for 53 out of 60 site by species comparisons.

Habitat Preferences of *I. humilis*

Of the four types of natural habitat surveyed, only valley riparian woodland was found to contain populations of *I. humilis.* Ten out of 22 such sites were occupied by *I. humilis.* Detailed sampling of the other habitats (eight sites each of foothill riparian woodland, oak-pine woodland, and chaparral), and much additional general collecting outside the prescribed sampling program, failed to detect *I. humilis* in foothill habitats in the lower Sacramento Valley.

Iridomyrmex humilis was found to be rather widely distributed and locally abundant in valley riparian woodland (fig. 3). A consideration of the features of riparian sites with, and without, *I. humilis* populations (table 3) reveals the following:

(1) *Iridomyrmex humilis* is almost exclusively confined to sites with permanent

TABLE 2. OCCURRENCE OF *I. HUMILIS* AND FIVE COMMON NATIVE ANT SPECIES AT 12 SITES IN YOLO AND SOLANO COUNTIES*

	Site†											
Native ant species	**4**	**5**	**8**	**9**	**11**	**15**	**16**	**19**	**21**	**23**	**33**	**41**
Iridomyrmex humilis, sample 1	−	+	−	+	−	+	+	−	−	−	−	−
sample 2	−	+	−	+	−	+	+	−	+	−	−	−
Tapinoma sessile, sample 1	+	−	+	−	+	−	−	+	−	−	+	+
sample 2	+	−	+	−	+	−	−	+	−	−	+	+
Liometopum occidentale, sample 1	+	−	+	−	+	−	−	+	+	+	−	+
sample 2	+	−	+	−	+	−	−	+	−	+	+	+
Prenolepis imparis, sample 1	−	+	+	+	+	+	−	+	+	+	+	+
sample 2	+	+	+	+	+	+	−	+	+	+	+	+
Formica occidua, sample 1	+	−	+	−	+	−	−	+	+	+	+	−
sample 2	+	−	+	−	+	−	−	+	+	−	+	+
Stenamma diecki, sample 1	−	+	−	−	+	−	−	+	+	+	+	+
sample 2	−	+	+	−	+	−	−	+	−	+	+	+

*Sample 1 was taken during the original survey of the sites in 1984-85; sample 2 involved the application of identical sampling procedures to the same sites in 1986.

†Presence is indicated by plus (+) sign; absence is indicated by minus (−) sign.

sources of water. Small tracts of riparian woodland traversed by seasonally intermittent streams were not found to be colonized by *I. humilis,* with the exception of one disturbed site in Davis (site 12), adjacent to a building complex with irrigated landscaping. The aversion of *I. humilis* to summer-dry riparian sites is demonstrated by its distribution along Putah Creek (fig. 3). A section of this creek near Davis has been diverted from its original course, leaving fragments of riparian woodland (e.g., sites 11 and 13) without permanently flowing water. *Iridomyrmex humilis* has not occupied these areas, despite adjacent populations in urban Davis and along the current course of the creek.

(2) There is a suggestion from the data in table 3 that riparian sites with *I. humilis* populations are more likely to be close to urban areas. The difference in distances between the two kinds of sites approaches statistical significance (Mann-Whitney U-test, $p \approx 0.080$).

(3) Valley riparian sites occupied by *I. humilis* tend to be environmentally degraded. There is more frequent encroachment by nonnative trees (6 out of 10 *I. humilis* sites; 2 out of 12 other sites; G-test, $p < .05$), and the mean estimated overall disturbance is greater for *I. humilis* sites (t-test, $p \approx 0.046$).

Distribution of *I. humilis*

Iridomyrmex humilis was found in remnant riparian woodland along four stream systems: Ulatis Creek, Putah Creek, Cache Creek, and the Sacramento River. Spot checks elsewhere in Yolo and Solano counties confirmed that populations of this species are also widespread in urban and agricultural locations (fig. 3).

Extensive spot sampling was also used to examine the microgeographic distribution of *I. humilis* along the four principal corridors of riparian woodland. The results

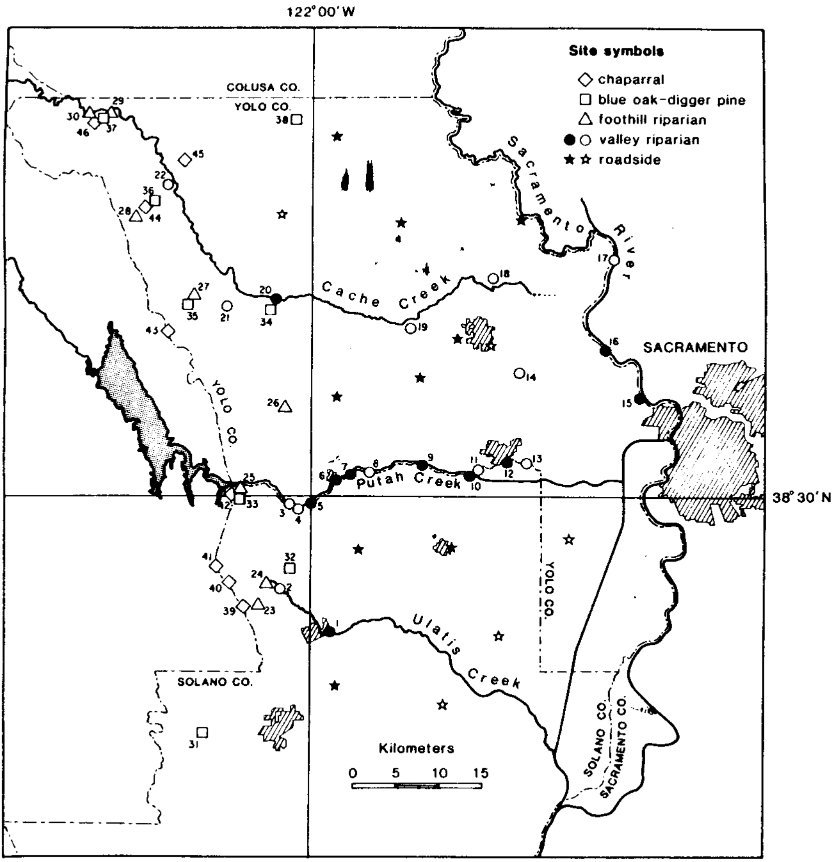

Fig. 3. Location of 46 intensively surveyed sites (representing four natural habitats) and 14 roadside spot samples. Closed symbols: *I. humilis* present; open symbols: *I. humilis* absent.

(fig. 4) indicate the following:

(1) The *I. humilis* populations are patchily distributed. Areas with dense populations often alternate with sites devoid of *I. humilis.* This is particularly evident along Putah Creek and sections of Cache Creek.

(2) Extensive, uninterrupted populations occur in some places, for example along Ulatis Creek, where it transects urban Vacaville, and along the Sacramento River.

(3) The distribution of *I. humilis* in riparian woodland along Putah Creek is correlated with the occurrence of this species in adjacent agricultural land. At 19 riparian sites along Putah Creek (12 with *I. humilis,* 7 without) spot samples were also taken in nearby (50 to 100 m distant) agricultural land. For 9 of the 12 riparian sites occupied by *I. humilis,* this species was also present in adjacent farmland. Conversely, no *I. humilis* were detected in agricultural areas next to uninfested riparian sites. The

TABLE 3. FEATURES OF VALLEY RIPARIAN SITES WITH AND WITHOUT POPULATIONS OF *I. HUMILIS*

Site	Distance to nearest urban area (*km*)	Stream flow*	Encroachment by nonnative trees†	Overall disturbance (0-8 scale)
I. humilis present				
1	0.0	1	+	2
5	3.1	1	−	3
6	0.1	1	+	4
7	1.5	1	+	2
9	6.9	1	+	4
10	2.8	1	+	4
12	0.0	0	+	5
15	2.0	1	−	4
16	9.0	1	−	3
20	21.9	1	−	3
I. humilis absent				
2	5.5	0	−	2
3	5.0	1	−	1
4	4.5	1	−	1
8	3.6	1	−	2
11	2.0	0	+	4
13	1.7	0	+	3
14	4.4	1	−	2
17	17.8	1	−	4
18	4.5	0	−	4
19	6.0	0	−	3
21	27.5	0	−	1
22	38.1	0	−	2

*1 = permanent; 0 = intermittent

†Presence is indicated by plus (+) sign; absence is indicated by minus (−) sign.

nonindependent occurrence of *I. humilis* in the two environments (table 4) suggests that one might serve as a reservoir for populations to invade the other.

(4) Spot samples also indicate that indigenous species of ants are conspicuous in *I. humilis*-free patches and are underrepresented at sites occupied by *I. humilis.* Because ants were incompletely surveyed in spot samples, this pattern is analyzed in further detail below, using data from the 22 valley riparian sites that were intensively sampled with the full ensemble of collecting methods.

TABLE 4. PATTERN OF OCCURRENCE OF *I. HUMILIS* AT PAIRED SITES, ONE IN RIPARIAN WOODLAND AND THE OTHER IN ADJACENT AGRICULTURAL LAND*

		Riparian woodland sites			
		Present	Absent	Total	
Adjacent agricultural land	Present	9	0	9	$G = 12.79$
	Absent	3	7	10	$p < .001$
	Total	12	7	19	

*Based on spot samples taken at 19 pairs of sites along Putah Creek.

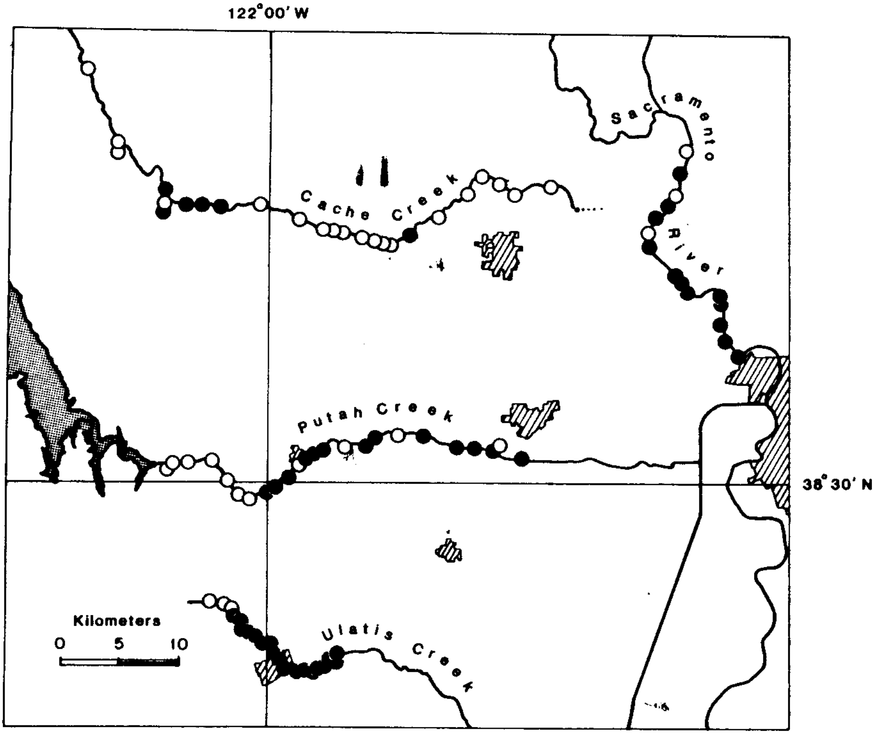

Fig. 4. Detailed distribution of *Iridomyrmex humilis* along corridors of riparian vegetation in Yolo and Solano counties. Closed circles: *I. humilis* present; open circles: *I. humilis* absent.

Effects of *I. humilis* on Native Ant Fauna

This analysis is necessarily confined to the ant fauna of valley riparian woodland, because no other natural habitats were found to be invaded by *I. humilis.* A total of 27 native ant species were recorded in valley riparian woodland during this survey. By all three measures of species richness—the number of ant species in litter collections (S_L), in bait collections (S_B), and recorded in total for the site (S_T)—sites occupied by *I. humilis* have significantly more depauperate ant faunas than those unoccupied by this species (table 5). In fact the ranges in S_T do not even overlap for the two kinds of sites (1 to 5 species in *I. humilis* sites; 6 to 12 species in unoccupied sites).

Because *I. humilis* appears to occupy riparian sites with certain features (that is, disturbed sites with permanently flowing water), it might be possible to attribute the differences in species richness to those variables rather than to the presence or absence of *I. humilis.* However, separate analyses of variance show no significant effects of stream flow or encroachment by nonnative trees on S_T (including no significant interaction effects with site type). Moreover, an analysis of covariance, with site type

TABLE 5. ANT SPECIES RICHNESS (NUMBER OF NATIVE ANT SPECIES) IN RIPARIAN WOODLAND SITES WITH AND WITHOUT POPULATIONS OF *I. HUMILIS*

Site	S_L	S_B	S_T	No. hypogaeic spp.	No. epigaeic spp.
I. humilis present					
1	3	3	5	4	1
5	4	1	4	2	2
6	2	1	3	2	1
7	0	1	3	0	3
9	2	1	2	1	1
10	2	0	3	2	1
12	2	1	3	1	2
15	0	1	2	0	2
16	0	0	1	1	0
20	4	1	5	3	2
Mean (± s.d)	1.9 ± 1.5	1.0 ± 0.8	3.1 ± 1.3	1.6 ± 1.3	1.5 ± 0.8
I. humilis absent					
2	3	4	7	2	5
3	4	5	11	3	8
4	4	2	9	3	6
8	2	4	10	1	9
11	10	2	11	6	5
13	6	2	9	5	4
14	3	6	10	3	7
17	4	2	7	0	7
18	10	3	12	7	5
19	5	2	6	2	4
21	3	2	6	2	4
22	5	3	6	2	4
Mean (± s.d)	4.9 ± 2 6	3.1 ± 1.4	8.7 ± 2.2	3.0 ± 2.0	5.7 ± 1.7
t-test on means					
t-statistic	3.219	4.194	7.073	1.881	6.954
probability	0.004	0.000	0.000	0.075	0.000

(presence or absence of *I. humilis*) as the grouping variable, and estimated overall disturbance as the covariate, reveals no effect of disturbance on S_T ($p \approx 0.891$), but a highly significant effect of site type ($p \approx 0.000$). This indicates that it is the presence of *I. humilis* itself, rather than site disturbance or stream flow, that is primarily responsible for the drastic decline in ant species richness in patches of riparian woodland colonized by *I. humilis.*

Litter and bait collections were designed to provide information on hypogaeic and epigaeic ants, respectively. However, ants extracted from litter include some species which also forage extensively aboveground, and at many sites some of the epigaeic species detected by general collecting methods did not come to bait. To more accurately assess the effect of *I. humilis* on these two groups of ants, each of the ant species recorded from valley riparian woodland was classified as epigaeic or hypogaeic according to the following criteria: hypogaeic species were considered to be those which occurred

TABLE 6. OCCURRENCE OF ANT SPECIES IN RIPARIAN WOODLAND SITES WITH AND WITHOUT POPULATIONS OF *I. HUMILIS**

	Sites with *I. humilis*										Sites without *I. humilis*											
Species	1	5	6	7	9	10	12	15	16	20	2	3	4	8	11	13	14	17	18	19	21	22
Epigaeic																						
Pogonomyrmex subdentatus	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−
Aphaenogaster occidentalis	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−
Pheidole californica	−	−	−	−	−	−	+	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−
Crematogaster hespera	−	−	−	−	−	−	−	−	−	−	+	−	+	−	−	−	+	−	−	−	−	−
Monomorium sp.cf. *minimum*	−	−	−	+	−	−	−	−	−	+	−	+	+	+	−	+	−	−	−	−	−	+
Solenopsis xyloni	−	+	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−
Leptothorax rugatulus	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−
Tetramorium caespitum†	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	−	−
Liometopum occidentale	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+
Conomyrma insana	−	−	−	+	−	+	−	−	−	−	−	+	+	+	−	−	−	−	−	−	−	−
Tapinoma sessile	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	−	+	+	−	+	−	+
Camponotus essigi	−	−	−	−	−	−	−	+	−	−	+	−	−	+	−	−	+	+	+	−	−	−
Camponotus semitestaceus	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−
Lasius alienus	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	−	−
Prenolepis imparis	+	+	+	+	+	−	+	+	−	+	+	+	−	+	+	+	+	−	+	+	+	+
Formica aerata	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+	−	−	−	−
Formica occidua (= *moki*)	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+	+	+	+	+	+	−
Polyergus breviceps	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−
Hypogaeic																						
Amblyopone pallipes	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−
Proceratium californicum	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−
Hypoponera opacior	−	−	−	−	−	−	−	−	−	−	+	−	−	−	+	+	−	−	+	−	−	−
Hypoponera sp.cf. *opacior*	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−
Stenamma californicum	+	+	+	−	+	+	−	−	−	+	−	+	−	−	+	+	−	−	+	+	+	+
Stenamma diecki	+	+	+	−	−	+	+	−	−	+	−	−	−	−	+	+	−	−	+	+	+	+
Stenamma punctatoventre	−	−	−	−	−	−	−	−	−	−	−	−	+	−	+	+	−	−	+	−	−	−
Solenopsis molesta	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+	+	+	−	+	−	−	−
Leptothorax andrei	+	−	−	−	−	−	−	−	−	−	+	+	+	+	−	−	+	−	+	−	−	−
Leptothorax nitens	+	−	−	−	−	−	−	−	−	+	−	−	+	−	−	−	+	−	−	−	−	−

*Presence is indicated by plus (+) sign; absence is indicated by minus (−) sign.

†Nonnative species.

predominantly or exclusively in litter samples and were seldom (or never) observed foraging in exposed situations; epigaeic species were those which commonly foraged aboveground (some of these were also found in litter and soil).

Using this classification, the two groups of ants are shown to be differentially affected by the presence of *I. humilis* (table 5). While the mean number of epigaeic species is strongly reduced at sites with *I. humilis* (t-test, $p \approx 0.000$), the difference in the mean number of hypogaeic species at the two kinds of sites is much less marked and not statistically significant (t-test, $p \approx 0.075$).

The specific composition of the ant fauna of these sites is given in table 6, and reveals further differential sensitivity to the presence of *I. humilis*. For the six most common ant species, the results are as follows: Three epigaeic species (*Liometopum occidentale, Tapinoma sessile,* and *Formica occidua*) are very adversely affected by the presence of *I. humilis,* being absent from all sites where it occurs while present in most unoccupied sites (G-tests, $p < .001$ in all three cases). One epigaeic species (*Prenolepis imparis*) and two hypogaeic species (*Stenamma diecki* and *Stenamma californicum*) appear to be much less influenced by *I. humilis* insofar as they are equally present in the two kinds of sites. An analysis of the abundance of these three species, based on the numbers of *P. imparis* workers at tunafish bait and the numbers of *S. diecki* and *S. californicum* workers in litter samples, shows no significant differences between the two kinds of sites (table 7); results, however, suggest that larger sample sizes might reveal a negative effect of *I. humilis* on the abundance of *P. imparis.*

The remaining 22 species of ants are less common and more locally distributed in general, so that it is more difficult to assess the impact of *I. humilis* on their occurrence. It is striking, however, that 14 of these 22 species were recorded only from *I. humilis*-free sites; no species was confined to sites occupied by *I. humilis.*

The preceding analyses are based on the results of surveys undertaken in 1984-85. One of the valley riparian sites (site 21, 6km W Capay, Yolo County), recorded as unoccupied by *I. humilis* during the original survey, was found to contain colonies of *I. humilis* in 1986. The colonization appears to be recent. Nests occur along a roadside margin and workers have been observed foraging in dense files on valley oaks (*Quercus lobata*) at the edge of the small tract of riparian woodland, but not in the center. An adjacent, irrigated almond orchard is heavily infested with *I. humilis* and may represent the source population. *Liometopum occidentale,* abundant at the riparian site in 1984, has now disappeared. At the time of this writing (October 1986) the epigaeic species, *Formica occidua* and *Prenolepis imparis,* are still present and common.

TABLE 7. ABUNDANCE OF *PRENOLEPIS IMPARIS, STENAMMA DIECKI,* AND *S. CALIFORNICUM* AT RIPARIAN SITES WITH AND WITHOUT *I. HUMILIS**

Sites		*P. imparis*	*S. diecki*	*S. californicum*
With *I. humilis*	Mean no. workers	104.6	4.9	1.8
(n = 10)	Range	0-503	0-12	0-8
Without *I. humilis*	Mean no. workers	220.8	8.8	3.9
(n = 12)	Range	0-619	0-32	0-22
Mann-Whitney U test, probability (one-tailed)		.073	.472	.431

*Abundance at a site is measured by the number of workers at tunafish bait (*P. imparis*) or in litter samples (*Stenamma* spp.).

DISCUSSION

In the study area (Yolo and Solano counties) in the lower Sacramento Valley, the only natural habitat colonized by *Iridomyrmex humilis* is riparian woodland on the valley floor. The absence of this species from chaparral and oak-pine woodland may be partly a function of extreme summer aridity. *Iridomyrmex humilis* has invaded disturbed chaparral, coastal scrub, and other nonriparian habitats in the San Francisco Bay region (Tremper 1976; Ward, unpublished) where the climate is cooler and more humid.

It is not immediately clear what, if anything, prevents *I. humilis* from penetrating foothill riparian woodland in Yolo and Solano counties, along permanently flowing creeks (Putah Creek, Cache Creek), especially since the species occurs in comparable habitat along the Russian River in Mendocino and Sonoma counties (Ward, unpublished). However, upstream dispersal in *I. humilis* may be slow since the species reproduces by colony fission (budding), not by aerial dispersal of queens (Newell and Barber 1913; Skaife 1961). Moreover, unlike the situation along the Russian River, there are no significant concentrations of urban or agricultural land in the western foothills of the lower Sacramento Valley from which introduced innoculi of *I. humilis* might spread.

The present study documents an association between the presence of *I. humilis* in riparian woodland and its occurrence in adjacent agricultural land. Observations suggest that the interchange of populations can occur both ways. Thus, valley riparian woodland harbors populations of *I. humilis,* with the potential of invading adjacent farmland; at the same time, irrigated agricultural land (particularly orchards) may provide source populations which invade nearby natural areas. The latter process appears to have occurred recently at site 21, near Capay, Yolo County.

The preference shown by *I. humilis* for partially disturbed habitats is consistent with observations made elsewhere in the United States (Barber 1916; Smith 1965). In fact, the present study indicates that the ability of *I. humilis* to invade riparian woodland in California and displace native ant species is partly related to the degree of disturbance of the site, in addition to the presence of a permanent water source. However, it is unclear why some far-from-pristine patches of riparian woodland along Putah Creek, Cache Creek, and the Sacramento River remain unoccupied by *I. humilis.* Are the native ants resisting invasion, or is the absence of *I. humilis* from some sites merely a reflection of stochastic aspects of colonization or lack of source populations? This problem could be addressed by experimental manipulation of *I. humilis* populations, and by detailed observations on interactions between native ants and *I. humilis* at the margins of its local distribution.

The displacement of both indigenous and introduced ant species by *I. humilis* has been widely reported (Wheeler 1906; Skaife 1961; Haskins and Haskins 1965; Crowell 1968; Pasfield 1968; Fluker and Beardsley 1970; Lieberburg, Kranz, and Seip 1975; Bond and Slingsby 1984). Erickson (1972) documented the replacement of three native ants, *Pogonomyrmex californicus, Pheidole grallipes* (= *vistanus*), and *Messor pergandei,* by *I. humilis* in an old field in southern California. Tremper (1976) found little coexistence between *I. humilis* and other ants in the San Francisco region. *Iridomyrmex humilis* workers have been observed aggressively attacking a variety of native California ants including *Tapinoma sessile, Conomyrma bicolor, Formica occidua, Pogonomyrmex californicus, P. subdentatus, Messor andrei,* and *Neivamyrmex cal-*

ifornicus (Woodworth 1910; Shapley 1920; Mallis 1938; Michener 1942; Ward unpublished).

What does not appear to have been previously documented, perhaps because of exclusive concentration on conspicuous epigaeic species, is the *differential* displacement of indigenous California ants by *I. humilis*, a pattern that is quite pronounced, at least in the riparian woodland habitat investigated in this study. Thus, whereas most epigaeic species disappear from sites invaded by *I. humilis, Prenolepis imparis* is equally distributed between occupied and unoccupied sites, and the same is true of several hypogaeic species, notably *Stenamma diecki* and *S. californicum.* Two of the three most adversely affected ant species (*Liometopum occidentale* and *Tapinoma sessile*) are taxonomically and ecologically similar to *Iridomyrmex humilis* in that they are members of the same subfamily (Dolichoderinae) and they are dominant, opportunistic, epigaeic ants, with propensities to establish dense foraging trails, to tend homopterans, and to move nest sites readily. *Tapinoma* nests are polygynous (multiple-queened), like those of *I. humilis,* and this is probably also the case for *Liometopum.* Moreover, these two species forage under the same ambient conditions as *I. humilis,* that is, throughout the summer and during warmer winter weather. In contrast *Prenolepis imparis* tends to be active under cooler (and wetter) conditions and ceases foraging during summer months, a behavior that may reduce the frequency of its interactions with *I. humilis.*

Sixteen out of 27 native ants recorded from riparian woodland in the Sacramento Valley, including rare hypogaeic species such as *Amblyopone pallipes* and *Proceratium californicum,* were found only in sites unoccupied by *I. humilis.* Some of these species are confined to riparian woodland in California and face the danger (at least locally) of extinction in the face of an onslaught by *I. humilis.* The effects of this species on other indigenous insects remain largely unexplored. By excluding such dominant ant species as *Liometopum occidentale* and *Formica occidua, I. humilis* may significantly alter the homopteran and cynipid communities on oaks and other plants. Attention should also be directed to its effects on the valley elderberry longhorn beetle, (*Desmocerus californicus dimorphus*) (Coleoptera: Cerambycidae), a federally listed threatened (sub)species confined to riparian habitats in the Central Valley of California (Anon. 1980).

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LITERATURE CITED

ANONYMOUS
1980. Two California beetles listed as threatened. Endangered Species Tech. Bull. 5:6-7.
BARBER, E. R.
1916. The Argentine ant: distribution and control in the United States. U.S. Dept. Agr., Bull. 377:1-23.

BOND, W., and P. SLINGSBY
1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. Ecology 65:1031-37.
CROWELL, K. L.
1968. Rates of competitive exclusion by the Argentine ant in Bermuda. Ecology 49:551-55.
DeBACH, P.
1951. The necessity of an ecological approach to pest control on citrus in California. J. Econ. Entomol. 44:443-47.
ECKERT, J. E., and A. MALLIS
1937. Ants and their control in California. Univ. Calif. Agric. Exp. Station Circ. 342:1-37.
ERICKSON, J. M.
1972. The displacement of native ant species by the introduced Argentine ant *Iridomyrmex humilis* Mayr. Psyche 78:257-66.
FLANDERS, S. E.
1945. Coincident infestations of *Aomidiella citrina* and *Coccus hesperidium,* a result of ant activity. J. Econ. Entomol. 38:711-12.
1958. The role of the ant in the biological control of scale insects in California. Proc. 10th Int. Congr. Entomol. 4:579-82.
FLUKER, S. S., and J. W. BEARDSLEY
1970. Sympatric associations of three ants: *Iridomyrmex humilis, Pheidole megacephala* and *Anoplolepis longipes* in Hawaii. Ann. Entomol. Soc. Amer. 63:1290-96.
HASKINS, C. P., and E. F. HASKINS
1965. *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda—equilibrium or slow replacement? Ecology 46:736-40.
KÜCHLER, A. W.
1977. Appendix: the map of the natural vegetation of California. *In* Barbour, M. G., and J. Major (eds.). The terrestrial vegetation of California. New York: Wiley and Sons, pp. 909-38, and accompanying map.
LIEBERBURG, I., P. M. KRANZ, and A. SEIP
1975. Bermudian ants revisited: the status and interaction of *Pheidole megacephala* and *Iridomyrmex humilis.* Ecology 56:473-78.
MALLIS, A.
1938. Army ants in California. Sci. Monthly 47:220-26.
MARKIN, G. P.
1970. The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera, Formicidae) in southern California. Ann. Ent. Soc. Amer. 63:1238-42.
MICHENER, C. D.
1942. The history and behavior of a colony of harvester ants. Sci. Monthly 55:248-58.
NEWELL, W., and T. C. BARBER
1913. The Argentine ant. U.S. Dept. Agr. Bull. 122:1-98.
PASFIELD G.
1968. Argentine ants. Aust. Nat. History 16:12-15.
ROBERTS, W. G., J. G. HOWE, and J. MAJOR
1980. A survey of riparian forest flora and fauna in California. *In* Sands, A. (ed.). Riparian forests in California, their ecology and conservation. A symposium sponsored by the Institute of Ecology and the Davis Audubon Society. Univ. Calif. Berkeley, Div. Agric. Sci. Publ. 4101, pp. 3-19.
SHAPLEY, H.
1920. Notes on Pterergates in the California harvester ant. Psyche 27:72-74.
SKAIFE, S. H.
1961. The study of ants. London: Longmans Green and Co.
SMITH, M. R.
1965. House-infesting ants of the eastern United States, their recognition, biology, and economic importance. U.S. Dept. Agr., Tech. Bull. 1326:1-105.
TREMPER, B. D.
1976. Distribution of the Argentine ant, *Iridomyrmex humilis* Mayr, in relation to certain native ants of California: ecological, physiological, and behavioral aspects. Ph.D. Thesis, Univ. Calif., Berkeley.
WHEELER, W. M.
1906. On certain tropical ants introduced into the United States. Entomol. News 17:23-26.
WOODWORTH, C. W.
1908. The Argentine ant in California. Univ. Calif. Agric. Exp. Sta. Circ. 38:1-11.
1910. The control of the Argentine ant. Univ. Calif. Agric. Exp. Sta. Bull. 207:53-82.