A BIOGEOGRAPHIC COMPARISON OF THE BEES, SPHECID WASPS, AND MEALYBUGS OF THE CALIFORNIA CHANNEL ISLANDS (HYMENOPTERA, HOMOPTERA)

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INTRODUCTION

We have three main goals in this paper: 1) to describe the distribution patterns of three diverse groups of insects, 2) to compare these patterns and determine if there are general statements that apply to all three groups, and 3) to test the hypothesis that certain inter-island similarity relationships can be predicted based on knowledge of geological and climatological history. Bees, sphecid wasps (Hymenoptera: Apoidea and Sphecidae) and mealybugs (Homoptera: Pseudococcidae) have different biologies and species dispersal patterns, and they have an array of life-history strategies. On the islands these insects display a diversity of distribution patterns from widespread taxa that occur on each island and on the mainland, to island endemics restricted to one or a few of the islands.

Our analysis is based primarily on museum specimens, but we have relied on literature records where there is little question of the correct identity of the species. We have examined most specimens available for study that have been collected on the islands.

Unfortunately, our analysis must be considered preliminary for the following reasons. In many cases collecting by a specialist on a particular island has been restricted to a single, short duration survey. Based on the rare occasions when we have been able to revisit an island, we frequently have collected species that were not encountered previously. This is especially true when subsequent visits have been during other seasons of the year, but even at the same time of the year some obvious differences have been apparent. Most island collecting has been in the spring and early summer leaving a conspicuous void in mid summer, late summer, fall and winter. Finally, species determinations in a few genera of each family have been difficult or impossible with the currently available systematic information. For these reasons we believe that additional species in each of the groups will be found on the islands, including more insular endemics.

It is important to realize that this paper is written in a descriptive mode. Similarity of island biotas is expressed in terms of the total number of shared taxa without consideration of phylogenetic relationships.

PREVIOUS WORK ON ISLAND BEES, SPHECID WASPS AND MEALYBUGS

Bees:

Fowler (1899) was the first to report on bees of the California Channel Islands. He described Habropoda depressa (now in Emphoropsis) as a new species from the southern California mainland and Santa Catalina Island. T. D. A. Cockerell (1901, 1903) subsequently

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described Anthophora catalinae (= urbana Cresson) and Halictus catalinensis (= tripartitus Cockerell) from Santa Catalina Island. He continued to publish on Channel Island bees for the next 37 years, although P. H. Timberlake and G. A. Sandhouse also made early contributions (see Miller and Menke 1981 for citations). In 19 papers Cockerell gave new records for island bees and described 24 new species and 12 new subspecies. Many of his supposed endemics have been reduced to synonyms of mainland forms by authors of generic revisionary works (see Rust 1984 for citations). Only 15 bee endemics are currently recognized (see list in S. Miller's introduction paper in this volume).

Sphecid wasps:

About 20 species of sphecid wasps have been recorded in the literature from the Channel Islands, and most of these are fairly large, common species easily caught by nonspecialist collectors. Intensive collecting by specialists during the past 20 years has more than quadrupled this figure to 90 (subspecies excluded). Very few papers of substance have been published on island sphecids, and most contain only collection records. As might be expected, the largest wasps have gained the most attention, and the first publication on island sphecids was that of C. L. Fox (1923) who described Bembix hamata from San Miguel and B. hamata lucida from Santa Cruz. Cockerell (1938, 1940) described B. nicolai from San Nicolas and B. sanctaerosae from Santa Rosa, respectively. Sand wasps of the genus Bembix (subfamily Nyssoninae) are common, conspicuous insects on most of the islands, and distinctive populations have evolved on some of the Channel Islands. Specialists have differed in their treatments of these island endemics. Evans and Matthews (1968) recognized one species of Bembix on the islands with two subspecies: B. hamata hamata (including lucida and sanctarosae as synonyms) restricted to San Miguel, Santa Rosa, and Santa Cruz, and B. hamata nicolai known only from San Nicolas. More recently, Bohart and Horning (1971) treated these two taxa as subspecies of the common mainland wasp, americana Fabricius. These authors had much more island material than Evans and Matthews which permitted them to analyze the insular populations more critically. Bohart and Horning also recorded populations of americana on Anacapa and Santa Catalina which they assigned to the subspecies B. a. comata Parker, a common form on the adjacent mainland. An undescribed endemic population of americana is present on San Clemente (see description in appendix).

Other common, large, conspicuous island wasps belong in the subfamily Sphecinae. Bohart and Menke (1961) described the insular endemic Palmodes insularis from San Miguel, Santa Rosa, Anacapa and San Clemente, and Menke (1967) described the endemic subspecies Ammophila azteca clemente from San Clemente. Fernald (1927) recorded Podalonia valida from Santa Rosa, but fairly extensive collecting on that island has not confirmed the presence of this large, conspicuous wasp which is a very common and presumably relictual species on San Miguel, Santa Cruz and San Clemente.

Coville (1979) described the presence of a second midtibial spur, an aberrant condition, in some Santa Cruz Island specimens of Trypoxylon tridentatum. Bohart and Grissell (1975) gave island records for many species of the subfamily Philanthinae.

Mealybugs:

Published studies of mealybugs on the islands generally are restricted to miscellaneous collection records. Eriococcus catalinae (= Amonostherium lichtensioides (Cockerell)) was described by Ehrhorn (1906) and mention was made of two other scales that he collected on Santa Catalina Island. Cockerell (1938) stated that he found a "mealy-bug on San Miguel Island on Astragalus miquelensis". McKenzie (1967) recorded Rhizoecus falcifer Kunckel d'Herculais from Catalina and treated Eriococcus artemisiae var. catalinae as a junior synonym of Amonostherium lichtensioides. Hambleton (1976) gave island records for Rhizoecus nakaharai Hambleton, R. gracilis McKenzie, and R. bicirculus McKenzie. Beginning in 1971 Miller published a series of three papers on island mealybugs including the faunas of Santa Cruz Island (1971), San Miguel Island (1973), and San Clemente Island (1974b), and described a San Clemente Island endemic (Miller 1974a). Heterococcus arenae Ferris was recorded by Miller (1975) from Santa Cruz and San Miguel Islands.

DISPERSAL MECHANISMS AND REQUIREMENTS

Bees and sphecid wasps are similar to one another in that their dispersal stage must be a gravid female or individuals of both sexes because of the haploid-diploid sex system in Hymenoptera. However, there is an important difference in their trophic placement. Sphecid wasps are predators that provision their nest with various insect groups and spiders, or occasionally are parasitic on other members of the family (Bohart and Menke 1976). Bees are herbivores that collect nectar and pollen from flowering plants or are parasitic on other bee species (Stephen, Bohart and Torchio 1969). Successful colonization for bees and sphecid wasps necessitates the presence of the "correct" prey or pollen and nectar source. Several genera of both sphecid wasps and bees nest in holes in various types of plant materials, and rafting dispersal of immatures is possible (Krombein 1967; Stephen, Bohart, and Torchio 1969). The transport by man of reeds, sticks and logs containing nests is another dispersal mechanism.

Mealybugs, like typical scale insects, are sucking herbivores that are sedentary throughout most of their life cycle. Dispersal can be achieved in several ways. First instars undergo short-ranged dispersal by walking short distances from the mother and settling. This instar is also commonly dispersed passively by wind (McClure 1977, Washburn and Washburn 1984, Willard 1974), and likely this mechanism is the most effective for natural, long-ranged dispersal. As small, wax covered propagules on vegetation, all instars of scale insects are potential waifs in rafting dispersal, and first instars also are potential stowaways on birds and mammals. Man's transportation of ornamental plants also frequently brings about inadvertent introduction of scale insects as plant contaminants. As with other oligophagous or monophagous herbivores, it is important that suitable host plants occur in the area to be colonized. Although parthenogenesis is common in scale insects (Nur 1971), most scales probably require introduction of at least one gravid female or nearly simultaneous introduction of several colonizing propagules of both sexes.

GEOLOGICAL HISTORY

The past 30 million years (my) of geological history of the California Borderland containing the California Channel Islands began with a fundamental change in crustal behavior from a convergent plate tectonic regime to one of right-lateral shear (Vedder and Howell 1980). The Oligocene-Miocene (24-20 my ago) transition was a period of volcanism that peaked during mid Miocene (16-12 my ago) and terminated toward the end of the epoch. Island shorelines presumably were much expanded during the late Miocene and Pliocene (see figs. 7, 8 in Corey 1954). The Pliocene (5-2 my ago) was a time of rapid sediment accumulation in near-shore basins and accelerated tectonism. These phenomena reached maximum intensity during the Pleistocene and formed large areas of high relief. It is possible that a Pliocene land bridge could have connected the northern island group with the mainland (Corey 1954, Green 1976); however, it is unlikely that either the San Clemente Ridge or the Santa Cruz-Catalina Ridge were emergent. The Pleistocene was a period of crustal deformation and eustatic sea level changes. These activities repeatedly increased and decreased island size with the advance and retreat of polar ice caps. Minimum sea level about 17,000 to 18,000 years ago united the northern four islands forming the super island "Santarosae" (Orr 1968, Johnson 1983). There is neither geological nor geophysical evidence of any Pleistocene bridges between the mainland and the northern islands or between the northern and southern island groups of the southern California Borderland (Vedder and Howell 1980).

ISLAND FLORAS

Axelrod (1967), using paleoclimatic and fossil evidence, suggested that the flora of the California Channel Islands resulted from successive waves of migration from different source areas. The floristics of the California Channel Islands have been treated by Power (1976), Philbrick (1972), Thorne (1967, 1969), Raven (1963) and Foreman (1967) (see Table 1). More recently (Philbrick 1980) treated the endemic species, and Philbrick and Haller

Table 1. Physical and biotic parameters for the California Channel Islands.

Island	Size in sq km	Distance from mainland in km	Maximum elevation in m	Plant species[1]	Number of plant communities[2]	Index of topographic diversity[3]
San Miguel	37	42	253	149	4	0.76
Santa Rosa	217	44	475	229	11[4]	1.14
Santa Cruz	249	30	753	367	10	1.45
Anacapa	2.9	20	283	157	3	0.46
Santa Barbara	2.6	61	194	68	2	0.58
San Nicolas	58	98	277	94	4	0.85
Santa Catalina	194	32	632	396	10	0.83
San Clemente	145	79	599	239	7	1.22

1. Data from Power 1976 (San Miguel, Santa Rosa, Santa Cruz and Anacapa), Philbrick 1972 (Santa Barbara), Thorne 1967, 1969 (Santa Catalina, San Clemente), Raven 1963 (San Clemente) and Foreman 1967 (San Nicolas).
2. Data from Philbrick and Haller 1977.
3. Data from Weissman and Rentz 1976. Equals the number of arroyos per kilometer of coastline.
4. Only 10 plant communities were used in the regression analysis. We excluded the Torrey pine community because of its extremely limited area.

Table 2. Number of bee, sphecid wasp and mealybug species on the California Channel Islands.

Island	Bees	Sphecids	Mealybugs
San Miguel	35	12	13
Santa Rosa	39	32	19
Santa Cruz	85	78	25
Anacapa	27	2	1
Santa Barbara	13	1	1
San Nicolas	19	11	10
Santa Catalina	62	35	18
San Clemente	23	17	18

Table 3. F test statistic (2-way) and coefficient of determination (r^2), as F/r^2 for 6 independent variables regressed against the three taxa. Sphecid wasps and mealybugs df = 1, 4; bees df = 1, 6.

Independent variable	Bees	Sphecid wasps	Mealybugs
Island size	4.968/0.45	11.403/0.74	12.184*/0.75
Island distance	3.310/0.36	5.282/0.57	3.387/0.46
Island elevation	8.908*/0.60	9.378/0.70	16.531*/0.81
Plant species	23.597**/0.80	10.328/0.72	18.647*/0.82
Plant communities	10.343*/0.63	11.638/0.74	13.519*/0.77
Topographic diversity	2.407/0.29	3.382/0.46	6.130/0.61

*$p < 0.05$, **0.01

(1977) discussed the vegetation of the California Channel Islands. Philbrick and Haller recognize 12 plant communities on the islands of which 11 is the maximum found on any one island, Santa Rosa (Table 1). The island chaparral (Crossosoma californicum, Eriodictyon traskiae, Prunus ilicifolia, etc.) and island woodland (Quercus agrifolia, Heteromeles arbutifolia, Marah macrocarpus, etc.) may represent the oldest island communities. Their modern relatives occur today in the temperate highlands of Mexico and may reflect Pliocene relicts, preserved by the more equitable insular climate (Philbrick and Haller 1977). The maritime cactus scrub community (Cereus emeryi, Lycium californicum, Opuntia littoralis, etc.) found on Santa Catalina Island and San Clemente Island presumably expanded onto the islands during the recent xerothermic (10,000-3,000 years ago). The coastal sand dune, coastal bluff, native grassland and Bishop pine forest communities show a more northerly coastal association possibly reflecting the more moderate temperatures and higher humidities on the islands than on the adjacent southern California mainland. Island chaparral, woodland, Torrey pine forest, and coastal bluff communities contain the greatest diversity of insular endemics. Recently, grazing by both domestic and feral mammals has altered the composition and distribution of the island plant communities (Johnson 1980, Hobbs 1980, Coblentz 1980). Because of the extremely small Torrey pine forest community on Santa Rosa (0.04+ Hectares, Philbrick and Haller 1977), we eliminated it from the regression analysis, and recognized only 10 island plant communities.

DESCRIPTIVE BIOGEOGRAPHY

To date, 153 bee, 90 sphecid wasp and 43 mealybug species have been collected from the eight California Channel Islands (see Tables 2, 6-8). Although the three groups are present on all islands, the sphecid wasp and mealybug faunas on Anacapa and Santa Barbara Islands have not been surveyed by respective specialists. Thus we regard these two groups as insufficiently known for inclusion in our analysis. The island species represent 14% of the mealybugs, 7% of the sphecid wasps and 5% of the bee species known to occur in North America north of Mexico based on data given by McKenzie (1967), Krombein (1979), and Hurd (1979), respectively. They represent 22% of the mealybug species, 16% of the sphecid wasp species and 10% of the bee species known from the California mainland.

Endemism:

Sixteen bee taxa, two sphecid wasps and three mealybugs are endemic to the California Channel Islands. Only mealybugs of the genus Phenacoccus, bees of the genus Dialictus, subspecies of the bee Anthophora urbana and the wasp Bembix americana contain sufficient numbers of island taxa for phylogenetic interpretations of endemic relatedness. Such studies of these groups would be of considerable interest.

Physical and biotic variables/number of taxa:

Using log-log regression analysis, the number of sphecid wasps on the six islands studied were not significantly correlated with any of the physical or biotic variables examined.

The mealybugs alone showed a significant increase in species number with increasing island size ($F= 12.1844$, $df= 1, 4$) (Fig. 1, Table 3); the value of z is 0.36. The bees and mealybugs both were significantly correlated with island elevation (Fig. 3), number of plant species (Fig. 4) and number of plant communities (Fig. 5). The bees and mealybugs showed no correlation with mainland distance (Fig. 2, Table 3) or with topographic diversity as quantified by Weissman and Rentz (1976), i.e. average number of arroyos per kilometer of coastline.

The number of island endemics showed no significant relationship to island size, island-mainland distance, island elevation, topographic diversity, number of plant species or number of plant communities.

Plant-insect associations:

Thirty-two species of island bees (21%) are parasitic on other bee species, and 3 sphecid wasps (3%) are parasitic on other island sphecids. Of the 121 pollen-nectar col-

lecting bees, only 13 (11%) are considered oligolectic in their foraging behavior (Hurd 1979). Five of the specialist bees are in the genus Diadasia. Thus, the vast majority of bees on the California Channel Islands are generalists in foraging for pollen and nectar.

Within the mealybugs, most species on the California Channel Islands are found on over five genera of hosts and are found on the same host plants as the mainland populations. Of the 40 species of mealybugs on the islands that are not endemics, four are recorded from one host genus (10%), four are known from two host genera (10%), eight from three host genera (20%), two from four host genera (5%), two from five host genera (5%), and 20 island mealybug species are recorded from more than five host genera (50%). There are, however, two notable examples of niche expansion. On San Miguel Island Pseudococcus maritimus is recorded from nine genera of plants (four families); all are new host records for the species. Although this mealybug is recorded from over 50 genera of host plants, most of which are ornamentals, it is never found as abundantly on the mainland as on San Miguel Island and it is unusual for it to be found on such a diversity of native plants. Second, Spilococcus keiferi on San Clemente Island is found on five genera (four families), while on the mainland it is restricted to three genera (two families) (McKenzie 1967).

Inter-island relatedness:

To study inter-island "relatedness" based on the total number of shared taxa, we have compared the island faunas in two ways. First, to examine the relatedness of island faunas using the criteria of inter-island distance, island size ratios, and relatedness of island plant communities, we calculated an index of shared species per island pairs using Sorensen's coefficient (Brower and Zar 1977): $CC_S = \frac{2C}{A + B}$, where A is the species number on one island, B is the species number on the other island, and C is the number of shared species. Sorensen's coefficient was also used for the shared plant communities per island pairs. All possible island pairs were analyzed: $\binom{8}{2}$ or 28 for bees and $\binom{6}{2}$ or 15 for sphecid wasps and mealybugs. Sorensen's coefficients were then correlated with inter-island distance. We expected that closest islands would share more species and have greater correlation than widely separated islands. For island size ratio, shared faunas of island pairs with low size ratios should have more shared species than islands with high ratios. Islands that share more plant communities should share more insect species. For bees, sphecid wasps and mealybugs, there was no significant relationship between shared faunas and inter-island distance; for bees and mealybugs there was no relationship between shared faunas and shared plant communities, or between shared faunas and island size ratio (Table 4). Sphecid wasps showed a highly significant relationship with shared plant communities, and a significant relationship with island size (Table 4).

A second method of examining island-fauna relatedness was by calculating the difference between observed and expected shared species using Chi-square analysis (Zar 1974). For mealybugs, two island pairs (SM-SR, SM-SN) had significantly more shared species than expected (Table 5). Three island pairs (SM-SR, SR-SN, SN-SCl) had significantly more sphecid wasps than expected. Seven island pairs (SM-SR, SM-A, SR-A, A-SB, SB-SN, SB-SCl, SN-SCl) had significantly more bees than expected, and (SCr-SCa) had significantly fewer bees than expected (Table 5). All other island pairs for the three taxa showed no significant differences between observed and expected shared species.

HISTORICAL PATTERNS

Historical climatological and geological events could have had profound effects on the biogeography of bees, sphecid wasps, and mealybugs. Because of the submergence of most of the islands under high seas during the Middle Pleistocene and concomitant mass extinction of the biota, we will begin our historical analysis with events that have taken place since that period. Two series of events are examined: 1) the emergence of the super island Santarosae without an emergent connection to the mainland, and 2) the dramatic change in the adjacent mainland climate from Late Pleistocene mild winters and cool, moist summers to post Pleistocene xeric periods with long summer drought conditions.

Santarosae:

If Santarosae existed and its components have been continuously emergent since

Table 4. F test statistic (2-way) and coefficient of determination (r^2), as F/r^2 for three independent variables regressed against the index of shared species per island pairs. Percent data arcsin transformed for analysis. Sphecid wasps and mealybugs df = 1, 13; bees df = 1, 26.

Independent variable	Bees	Sphecid wasps	Mealybugs
Inter-island distance	2.828/0.09	1.580/0.05	0.082/0.00
Island size ratio	1.587/0.05	12.836*/0.33	0.213/0.01
Index of shared plant communities	2.444/0.08	19.003**/0.42	0.627/0.04

*p < 0.05, **0.01

Table 5. Chi-square analysis of shared species per island pairs, df = 1 (X^2 = 3.841, p < 0.05; X^2 = 10.828, p < 0.01).

Island pair	X^2 value	observed	expected
	Bees		
Miguel-Rosa	5.607	15	9.0
Miguel-Anacapa	11.090	10	6.2
Rosa-Anacapa	8.024	11	6.9
Cruz-Catalina	5.349	24	33.3
Anacapa-Barbara	22.501	9	2.3
Barbara-Nicolas	29.748	9	1.6
Barbara-Clemente	19.809	7	1.9
Nicolas-Clemente	11.537	9	2.8
	Sphecid wasps		
Miguel-Rosa	17.553	12	4.7
Rosa-Nicolas	14.118	10	3.9
Nicolas-Clemente	7.103	6	2.2
	Mealybugs		
Miguel-Rosa	6.306	10	5.7
Miguel-Nicolas	4.521	7	3.6

that time, and if the other islands have remained distinct and separate during the same period, we would expect the super-island components, i.e., San Miguel, Santa Rosa, Santa Cruz, and Anacapa, to share more species among themselves than would be shared by the four southern islands. This phenomenon is hypothesized primarily because we believe that when the islands were connected, exchange of biotas was extensive. An unusually high number of shared taxa also might reflect the larger number of total species that inhabited Santarosae because, with the concurrent lower sea level, it was closer to the mainland (as little as 6 km according to Johnson 1983) and had a considerably greater area than the combined land masses of the present day islands at the current sea level.

To test this hypothesis Chi-square analysis was used to compare observed to expected numbers. Mealybugs shared on both the northern and southern island groups were not significantly different from chance. Sphecid wasps on the northern islands were highly significantly different from expected (X^2 = 24.330, df = 7, $p < 0.01$), but the southern island sphecid wasps were not. Bees on both northern and southern island groups were highly significantly different from chance (X^2 = 30.3 and X^2 = 26.21, df = 7, $p < 0.01$).

Disjunctions:

With dramatic, fluctuating changes in the climate during the Pleistocene, disjunctions would be anticipated on the California Channel Islands. With the moderate climates of the islands, relictual populations should remain that are geographically separate from mainland populations that have become extinct or have been forced to retreat to areas that are more favorable to their survival. Two major disjunctions were observed in our groups: a northern Californian, and an eastern desert/Great Basin. The northern Californian disjunction probably reflects a shift to a hotter-drier climate along the adjacent California mainland with extinction or northern movement of the biota that was unable to tolerate the more xeric climate. Because the California Channel Islands remained relatively cool and moist due to the annual fog patterns, the organisms unable to survive on the adjacent mainland persisted on the cooler islands. The northern disjunct mealybugs include seven of the 43 species (Anisococcus quercus (SCr), Discococcus simplex (SCr, SR, SCa, SCl), Pseudococcus longisetosus (SCr), Radicoccus kelloggi (SCa, SCl), Rhizoecus bicirculus (SCr, SR, SN, SCa, SCl), Rhizoecus subcyperalis (SCl), and Triomymus caricis (SCr)). The sphecid wasp Prionyx canadensis (SCr, SR) was the only northern disjunction in the two Hymenoptera groups.

The eastern desert disjunction is a xeric one with an intervening mesic area on the mainland. It is represented by the mealybug Rhizoecus subcyperalis (SCl) and the sphecid wasp Podalonia valida (SM, SR, SCr, SCl). The nearest mainland populations of the sphecid wasp and mealybug are in the Great Basin and northern and central Arizona. Although not a disjunction, the mealybug, Heliococcus clemente, a San Clemente Island endemic, appears to be most closely related to Heliococcus deserticola and H. atriplicis from eastern Mojave Desert locations. California Channel Island bee species do not show disjunctions.

DISCUSSION

One of the most surprising results of this paper is that sphecid wasps show no correlation with any of the variables studied. Bees and mealybugs, in contrast, are correlated with at least three variables. The reason for this basic difference is not understood. Sphecid wasps seem to be as well collected on the islands as bees and probably are better collected than mealybugs. Within the two hymenopterous groups, there do not appear to be any unique characteristics that would affect the amount of collecting. Both contain species that are large and conspicuous and are frequently taken by general collectors, and both contain smaller, less obvious species that are unlikely to be collected by anyone other than specialists. Wasp specialists have collected on the islands approximately as much total time as bee specialists. The number of sphecid species on the islands is 16% of the total sphecid fauna on the California mainland, whereas, the number of bees on the islands comprises only 10% of the California mainland fauna. These figures may reflect some inherent difference in the ability of bees and sphecid wasps to colonize islands, but we suspect that these data at least partially relate to the relative completeness of the survey of the two groups. A possible explanation for

the difference in sphecid wasps may be related to their feeding habits. The other insect groups that have been studied on the islands are totally or predominantly herbivorous; the sphecid wasps, on the other hand, are entirely predaceous. It is easy to invoke a scenario centered around the theme that suitable hosts are much less abundant for insect predators than for herbivores, but this thought must remain as speculation until other predaceous groups are studied.

A positive, significant correlation was expected between the number of bee, sphecid wasp and mealybug species compared with the number of plant species; a similar correlation was expected with the number of plant communities. Excluding the sphecid wasps, our results support this relationship, but our findings are not surprising. We would expect the number of taxa of any natural group to better reflect the complexity of factors affecting distribution patterns compared with the analysis of one or a few of these factors. The distribution of plant species and plant communities is a result, not a cause; the factors suggested by MacArthur and Wilson (1967) such as island area are a cause, not a result.

We anticipated poor correlation between the number of species in the three insect groups and such single factors as maximum elevation, island area, and distance from the mainland. Maximum elevation was significantly correlated with the number of species of bees and mealybugs and seems to be the best descriptor of the physical variables examined. Island size was correlated with species number in the mealybugs only. The lack of correlation with topographic diversity is interesting. We expected that an index of the average number of arroyos per kilometer of coastline would be a reasonable estimate of the true topographic diversity since this index appears indirectly to consider total island elevation not just highest elevation. Unfortunately, this variable was a poor descriptor of species number on the islands. It is unclear whether this lack of correlation is caused because our groups are unaffected by topographic diversity or because the index is not a true measure of topographic diversity.

It is not surprising that all three groups show no significant correlation between species numbers and distance of an island from the mainland. This distance is arbitrarily the shortest measure to the mainland which is not necessarily correlated with dispersal routes. In the case of the California Channel Islands, major wind and ocean current patterns may have a far more significant effect on how insects reach the islands (Owen 1980, Kanter 1980). These patterns are complex and differ drastically between the northern and southern islands. In terms of wind and ocean currents off Point Conception, California, San Miguel Island is the closest to the mainland of the four northern islands. The wind and current patterns around the southern islands probably do not affect the mainland-island distance as much as the northern ones, but there is a distinct south to north movement which may be responsible for some of the unusual island pair patterns that we have shown, e.g., SCr-SCa, A-SB, SR-SN, and SM-SN.

It is not surprising that the numbers of island endemics show no particular pattern. If the sea level during the Middle Pleistocene inundated all but small areas of the highest islands, we would not expect the evolution of large numbers of distinctive endemics <u>in situ</u> in such a short period of time. If autochthonous endemics do exist on the islands, they should be recently derived, and many should be very similar in appearance to sister taxa. We suspect that many autochthonous taxa remain undetected in insect groups because entomological research has been neglected on the islands and search for cryptic species has not been intensive. We suspect that most distinctive island endemics are relictual in nature and simply are remnants of species that once were widespread but now have become extinct on the mainland.

Results are mixed, at best, for the analysis using Sorensen's coefficient of the number of shared species on each island pair in comparison with inter-island distance, island size and shared plant communities. If dispersal is the sole mechanism for colonization of the islands, then islands closest to each other and closest to the same mainland source should share more species than distant islands. This assumption was not borne out by any of the three insect groups. There was no correlation between inter-island distance and the number of shared species on island pairs.

With all other variables constant, correlation would be anticipated between shared species and island size if all or most species within a group were best suited to living on islands of a particular size. Such correlation was found only in the sphecid wasps; how-

ever, it would be premature to suggest that sphecid wasps clearly were island-size oriented since all other variables are not constant.

Correlation between Sorensen's coefficient of shared plant communities with Sorensen's coefficient of shared insect species would be expected if both plant communities and insect species are sensitive to the same factors, e.g., island size, inter-island distance, etc. Bees and mealybugs did not show such an association, but sphecid wasps were highly correlated. One scenario for this correlation is that island size may have a major influence on sphecid wasps and plant community distribution on the islands. Only certain species of wasps and certain plant communities are able to inhabit small, medium or large islands.

Results were mixed for the analysis designed to test the hypothesis that Santarosae components should share more species among themselves than are shared by other California Channel Islands. Mealybugs showed no unusual affinities; bees showed greater numbers of shared species than expected on Santarosae components, but also had higher numbers of shared species than expected on the other islands as well; sphecid wasps were the only group that had unusually high Santarosae affinities without concomitant southern island high similarity indices.

It is interesting to note that the mealybugs on the islands include a much higher percentage of the total number of species known from North America north of Mexico or from California in comparison with the same figures for either bees or sphecid wasps. It also is of interest that mealybugs are distributed randomly when comparing inter-island shared similarity between the northern and southern groups. These two pieces of evidence suggest that there may be some basic differences in mealybugs' ability to colonize the islands compared with bees and wasps. We suspect that the difference at least partially my be attributable to the primary methods of long-range dispersal. Mealybugs as components of aerial drift would seem to have a marked advantage over bees and wasps at reaching the islands.

Polyphagous species as island colonists would seem to have an advantage over specialist species because of the increased likelihood that the generalist will locate a suitable host after reaching an island. Therefore, it is not surprising that most species in all three groups are generalists or feed on hosts that are widespread throughout the islands.

SUMMARY

Bees and mealybugs on the California Channel Islands are responding in similar ways to such biogeographic factors as island-mainland distance, island elevation and diversity of island plant species and communities. Sphecid wasps show no correlation with any of the variables examined. Evidence is given suggesting that sphecid wasps are sensitive to island size; some species occur on small islands, others inhabit large islands. More importantly, the three groups do not represent the same inter-island affinities regime on the islands. Mealybugs basically show a random assortment on the islands, whereas bees and sphecid wasps show faunal relatedness on the four northern California Channel Islands, and bees also show a relatedness on the four southern island faunas. These patterns of similarity most likely result from geological events and floral movements during the past 10,000 years, but we suspect that the effects of these events have been significantly modified in the mealybugs because of their high vagility as first instars.

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Table 6. Distribution of bee species on the Channel Islands (L refers to unconfirmed literature records).

BEE SPECIES	ISLANDS SM	SR	SCr	A	SB	SN	SCa	SCl
Colletidae								
Colletes hyalinus gaudialis Cockerell	X	X	X	X		X	X	
Hylaeus polifolii (Cockerell)		X	X				X	
Andrenidae								
Andrena gnaphilla (Cockerell)							X	
Andrena submoesta Viereck	X			X	X	X		X
Andrena auricoma Smith		X					L	
Andrena caerulea Smith	L	X	X					
Andrena chlorura Cockerell								L
Andrena nigrocaerulea Cockerell			X					
Andrena suavis Timberlake			X					
Andrena escondida Cockerell							L	
Andrena cerasifolii Cockerell							L	
Andrena perimelas Cockerell	X		X	X			X	
Andrena sola Viereck		X	X					
Andrena chlorogaster Viereck			X					
Andrena piperi Viereck			X					
Andrena oenotherae Timberlake			L					
Andrena prunorum prunorum Cockerell			X	X				
Andrena hypoleuca Cockerell			X					
Andrena candida Smith			X				X	
Andrena (Euandrena) sp.							X	
A. (Melandrena) sp.			X					
A. (Simandrena) sp.			X					
Andrena sp. 1			X					
A. sp. 2		X					X	
A. sp. 3	X							
A. sp. 4							X	
A. sp. 5			X					
A. sp. 6			X	X				
Panurginus armaticeps Cockerell			X					
Panurginus gracilis Michener			X					
Pterosarus californicus (Cresson)		X					X	X
Perdita layiae layiae Cockerell	X		X					
Perdita sp.		X						
Halictidae								
Augochlorella pomoniella (Cockerell)		L	X			L	X	
Agapostemon texanus Cresson	X	X	X	X	X	X	X	X
Halictus tripartitus Cockerell		X	X	X			X	
Lasioglossum pavonotum (Cockerell)	X	X						
Lasioglossum sisymbrii (Cockerell)				X			X	
Lasioglossum titusi (Crawford)				X				
Lasioglossum sp. nr. trizonatum (Cresson)		X	X					
Evylaeus argemonis (Cockerell)			X					
Evylaeus avalonensis (Cockerell)							L	L
Evylaeus hammondi (Cockerell)	L							
Evylaeus kincaidii (Cockerell)			X					
Evylaeus miguelinsis (Cockerell)	X	X	X				X	

Table 6 continued.

BEE SPECIES	ISLANDS SM	SR	SCr	A	SB	SN	SCa	SCl
Evylaeus nigrescens (Crawford)		X	X				X	X
Evylaeus ovaliceps (Cockerell)			X				X	
Dialictus cabrilli (Cockerell)	L							
Dialictus californiae (Ellis)			X				X	
Dialictus diversopunctatus (Ellis)			X	X	X	X		
Dialictus grinnelli (Cockerell)	L							
Dialictus incompletus (Crawford)							L	
Dialictus megastictus (Cockerell)	X						X	
Dialictus microlepoides (Ellis)			X					
Dialictus nevadensis (Crawford)	L				X	L	X	X
Dialictus perichlarus (Cockerell)	X	X	X	X	X	X		
Dialictus pilosicaudus (Cockerell)	X					X		
Dialictus punctiferellus (Cockerell)	X							
Dialictus tegulariformis (Crawford)						L	L	
Dialictus sp. 1			X					
Dialictus sp. 2		X						
Dialictus sp. 3	X							X
Dufourea californica (Michener)							X	
Dufourea dentipes Bohart		X						
Sphecodes nigricans miguelensis Timberlake	L							
Sphecodes sp. 1			X					
Sphecodes sp. 2		X						
Sphecodes sp. 3		X						
Sphecodes sp. 4							X	
Sphecodes sp. 5						X		
Sphecodes sp. 6						X		
Megachilidae								
Anthidium collectum Huard		X	X		L			X
Anthidium emarginatum (Say)							X	
Anthidium maculosum Cresson			X	X				
Stelis sp.			X					
Dioxys pomonae cismontanicus Hurd			X				L	
Chelostomopsis rubifloris (Cockerell)			X					
Hoplitus hypocrita (Cockerell)							X	
Anthocopa copelandica albomarginata (Cockerell)			X					
Ashmeadiella cactorum basalis Michener			X					
Ashmeadiella californica californica (Ashmead)				X	X	X		
Ashmeadiella timberlakei timberlakei Michener			X					
Ashmeadiella sp.		X	X					
Osmia albolateralis Cockerell	X	X	X					
Osmia californica Cresson			L					
Osmia calla Cockerell			X				L	
Osmia clarescens Cockerell			X					X
Osmia gabrielis Cockerell			X					
Osmia kincaidii Cockerell		X	X					
Osmia nemoris Sandhouse	L	X	X					
Osmia nigrobarbata Cockerell	L							
Osmia trevoris Cockerell	X	X						
Osmia tristella Cockerell			X					
Megachile brevis Say			X					

Table 6 continued.

BEE SPECIES	ISLANDS SM	SR	SCr	A	SB	SN	SCa	SCl
Megachile coquilletti Cockerell		X	X				X	
Megachile parallela Smith							L	
Coelioxys octodentata Say							L	
Anthophoridae								
Epeolus minimus (Robertson)	X	X	X	X				
Epeolus sp.			X				X	
Triepeolus heterurus (Cockerell & Sandhouse)			X	X			X	
Nomada avalonica Cockerell							L	
Nomada edwardsii edwardsii Cresson	X							
Nomada hesperia Cockerell		X	X		X		X	
Nomada semisuavis Cockerell		L	L				L	
Nomada suavis Cresson			X				X	
Nomada formula Viereck	L	L	X	X		X	X	X
Nomada sp. 1			X					
Nomada sp. 2			X					
Nomada sp. 3			X					
Nomada sp. 4			X					
Nomada sp. 5			X					
Nomada sp. 6			X					
Nomada sp. 7			X					
Nomada sp. 8			X					
Nomada sp. 9			X					
Nomada sp. 10			X					
Nomada sp. 11			X					
Exomalopsis cockerelli Timberlake							X	
Exomalopsis mitens Cockerell							X	
Diadasia bituberculata (Cresson)			X					X
Diadasia enavata (Cresson)							L	
Diadasia ochracea (Cockerell)							L	
Diadasia opuntiae Cockerell				X			L	
Diadasia rinconis Cockerell		X	X			X	X	X
Synhalonia actuosa (Cresson)		X	X	X	X	X		X
Synhalonia amsinckiae Timberlake			X					
Synhalonia edwardsii (Cresson)	X	X	X	X				
Synhalonia frater (Cresson)	X		X	X				
Synhalonia lunata Timberlake							X	X
Synhalonia pagosana (Cockerell)						X		
Synhalonia tricinctella Timberlake								L
Melissodes agilis Cresson							X	
Melissodes lupina Cresson		X	X	X	X		L	
Melissodes scotti Cockerell								L
Anthophora bomboides Kirby							L	
Anthophora californica Cresson	X	X		X			L	
Anthophora edwardsii Cresson	X	X	X	X	X	X	X	X
Anthophora urbana Cresson	L		X		X	X	X	X
Emphoropsis depressa (Fowler)							L	
Emphoropsis miserabilis (Cresson)	X							
Emphropsis sp.								X
Melecta separata Cresson								X
Xeromelecta californica (Cresson)				X	X			X

Table 6 continued.

BEE SPECIES	ISLANDS							
	SM	SR	SCr	A	SB	SN	SCa	SCl
Centris pallida Fox							L	
Ceratina acantha Provancher			X	X				
Ceratina nanula Cockerell							X	
Apidae								
Bombus californicus Smith	X	X					L	
Bombus crotchii Cresson		L		X				
Bombus edwardsii Cresson			L	X			L	
Bombus nevadensis Cresson	L							
Bombus sonorus Say							L	
Bombus vosnesenskii Radoszkowski	L						L	
Apis mellifera Linnaeus			X			L	X	L
Totals:	35	39	85	27	13	19	62	23

Table 7. Distribution of sphecid wasp species on the Channel Islands (species arrangement follows Bohart and Menke, 1976).

WASP SPECIES	ISLANDS SM	SR	SCr	A	SB	SN	SCa	SCl
Sceliphron caementarium (Drury)		X	X				X	X
Sphex lucae Saussure			X				X	
Isodontia elegans (Smith)							X	
Palmodes californicus Bohart & Menke			X					
Palmodes dimidiatus (DeGeer)							X	
Palmodes insularis Bohart & Menke	X	X	X	X				X
Prionyx canadensis (Provancher)	X	X	X					
Prionyx thomae (Fabricius)								X
Podalonia communis (Cresson)		X	X					
Podalonia compacta Fernald	X	X						
Podalonia mexicana (Saussure)	X	X				X		X
Podalonia valida (Cresson)	X	?*	X					X
Ammophila azteca azteca Cameron	X	X	X					
Ammophila azteca clemente Menke								X
Ammophila mcclayi Menke			X				X	X
Ammophila nearctica Kohl		X	X					
Ammophila parapolita (Fernald)			X					
Ammophila parkeri Menke		X	X					
Ammophila placida Smith			X					
Mimesa cahuilla Finnamore		X	X			X		
Diodontus occidentalis Fox	X	X	X				X	
Passaloecus armeniacae Cockerell							X	
Stigmus fulvipes Fox			X				X	
Stigmus inordinatus Fox			X			X	X	
Spilomena sp.			X					
Diploplectron peglowi Krombein		X	X			X		X
Astata bechteli Parker			X		X			X
Astata nubecula Cresson		X	X					
Astata occidentalis Cresson			X					
Dryudella caerulea (Cresson)		X	X				X	
Dryudella rhimpa Parker		X	X			X	X	X
Liris argentatus (Palisot de Beauvois)			X			X		X
Liris beatus (Cameron)			X				X	X
Liris mescalero (Pate)			X				X	
Ancistromma bradleyi (Bohart & Bohart)			X					
Tachytes californicus Bohart			X					
Tachysphex alpestris Rohwer			X					
Tachysphex amplus Fox			X					
Tachysphex apicalis Fox			X					
Tachysphex clarconis Viereck	X	X				X		
Tachysphex mundus aequalis Fox			X					
Tachysphex pauxillus Fox		X	X					
Tachysphex tarsatus (Say)	X	X	X			X		
Tachysphex texanus (Cresson)		X	X				X	X
Tachysphex sonorensis (Cameron)		X	X					
Plenoculus davisi Fox							X	
Solierella albipes (Ashmead)			X					
Solierella arcuata Williams			X				X	

* Unconfirmed record of Fernald (1927).

Table 7 continued.

WASP SPECIES	ISLANDS SM	SR	SCr	A	SB	SN	SCa	SCl
Solierella bicolor Williams			X					
Solierella blaisdelli (Bridwell)		X	X				X	
Solierella clypeata Williams ?							X	
Solierella levis Williams			X					
Solierella peckhami (Ashmead)			X				X	
Solierella sayi (Rohwer)		X	X				X	X
Solierella sp.							X	
Miscophus californicus (Ashmead)	X	X	X			X	X	X
Miscophus cyanurus (Rohwer)			X				X	
Miscophus texanus (Ashmead)		X	X					
Pisonopsis birkmanni Rohwer			X					
Trypoxylon tridentatum (Packard)			X					
Trypoxylon sp.			X					
Oxybelus californicus Boh. & Schlinger			X					
Oxybelus uniglumis (Linnaeus)	X	X	X			X	X	
Lindenius tecuya Pate			X					
Crossocerus chromatipus Pate			X					
Crossocerus insolens (Fox)			X					
Crossocerus maculipennis (Smith)			X					
Crossocerus nigricornis (Provancher)			X					
Crabro villosus Fox			X				X	
Ectemnius spinifer (Fox)			X				X	
Didineis nodosa Fox		X	X			X	X	
Nysson pumilus Cresson		X	X					
Hyponysson bicolor Cresson		X	X				X	
Foxia secunda (Rohwer)			X					
Ochleroptera bipunctata (Say)			X				X	
Harpactus clypeatus (Bohart)			X					
Harpactus pictifrons (Fox)		X	X					
Gorytes angustus (Provancher)			X				X	
Gorytes provancheri Handlirsch			X				X	
Microbembex californica Bohart								X
Bembix americana comata J. Parker				X			X	
Bembix americana hamata C. Fox	X	X	X					
Bembix americana nicolai Cockerell						X		
Bembix americana dugi Menke								X
Steniolia scolopacea Handlirsch			X					
Philanthus multimaculatus Cameron		X	X				X	
Philanthus pacificus Cresson		X	X					
Clypeadon utahensis (Baker)							X	
Cerceris acanthophila Cockerell			X					
Cerceris sp. near aequalis Provancher			X					
Cerceris convergens Viereck & Cockerell			X					
Cerceris finitima Cresson			X					
Cerceris minax Mickel			X				X	
Cerceris sextoides Banks			X					
Totals:	12	32	78	2	1	11	35	17

Table 8. Distribution of mealybug species on the Channel Islands

MEALYBUG SPECIES	ISLANDS SM	SR	SCr	A	SB	SN	SCa	SCl
Amonostherium lichtensioides (Cockerell)	X	X	X				X	
Anisococcus adenostomae (Ferris)		X					X	
Anisococcus quercus (Ehrhorn)			X					
Chorizococcus abroniae McKenzie	X	X	X			X		X
Discococcus simplex Ferris		X	X				X	X
Discococcus spectabilis McKenzie			X					
Distichlicoccus salinus (Cockerell)	X	X	X					X
Ferrisia virgata (Cockerell)						X		X
Heliococcus clemente Miller								X
Heterococcus arenae Ferris	X		X				X	
Miserococcus arenarius (Doane & Steinweden)			X				X	X
Paludicoccus distichlium (Kuwana)	X		X				X	X
Phenacoccus artemisiae Ehrhorn		X						
Phenacoccus colemani Ehrhorn	X	X	X					
Phenacoccus eriogoni Ferris			X					
Phenacoccus eschscholtziae McKenzie			X					X
Phenacoccus gossypii Townsend & Cockerell	X	X	X			X	X	
Phenacoccus solani Ferris		X	X			X		X
Phenacoccus n. sp. 1			X					
Phenacoccus n. sp. 2		X						
Pseudococcus beardsleyi Miller & McKenzie			X					
Pseudococcus longisetosus Ferris			X					
Pseudococcus maritimus (Ehrhorn)	X	X						X
Pseudococcus obscurus Essig							X	X
Pseudococcus sp. nr. *dispar* McKenzie		X						
Pseudococcus sp. 1			X					
Pseudococcus n. sp. 1		X						
Puto yuccae (Coquillett)	X	X	X	X	X	X	X	X
Radicoccus kelloggi (Ehrhorn)							X	X
Rhizoecus bicirculus McKenzie		X	X			X	X	X
Rhizoecus gracilis McKenzie	X	X	X			X	X	
Rhizoecus nakaharai Hambleton			X					
Rhizoecus subcyperalis Hambleton								X
Scaptococcus n. sp.						X		
Spilococcus corticosus McKenzie								X
Spilococcus implicatus Ferris		X						
Spilococcus keiferi McKenzie	X	X	X				X	X
Spilococcus pressus Ferris						X	X	
Tridiscus distichlii (Ferris)	X					X	X	
Trionymus caricis McConnell			X					
Trionymus frontalis McKenzie							X	
Trionymus smithii (Essig)	X	X					X	X
Trionymus utahensis (Cockerell)			X				X	
TOTALS	13	19	25	1	1	10	18	18

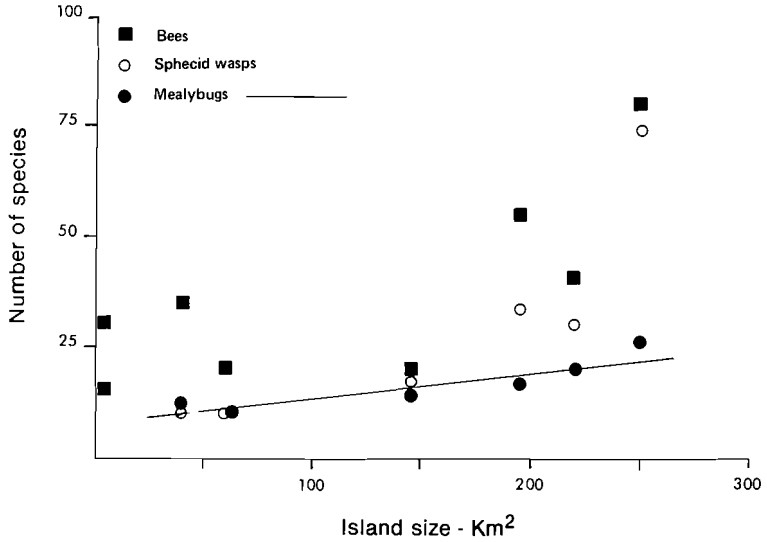

Figure 1. The relationship of island area to number of mealybug, sphecid wasp, and bee species on the California Channel Islands. Regression lines are significantly different from zero.

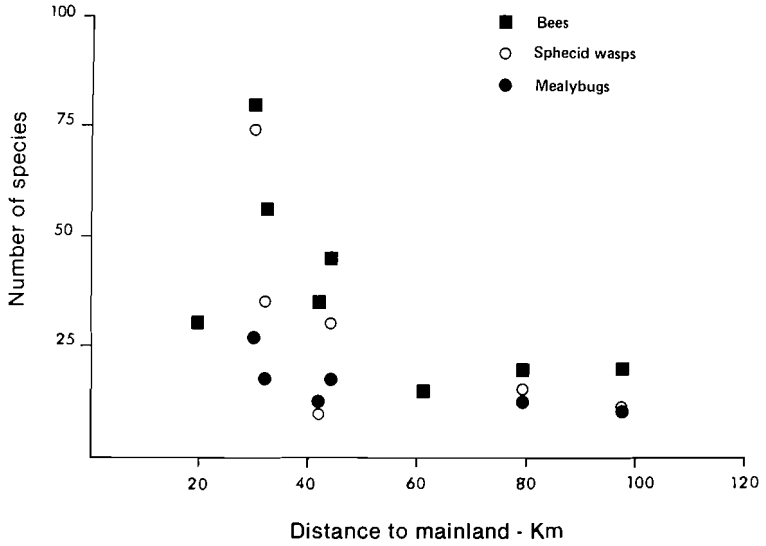

Figure 2. The relationship of island distance to the mainland to the number of mealybug, sphecid wasp, and bee species on the California Channel Islands.

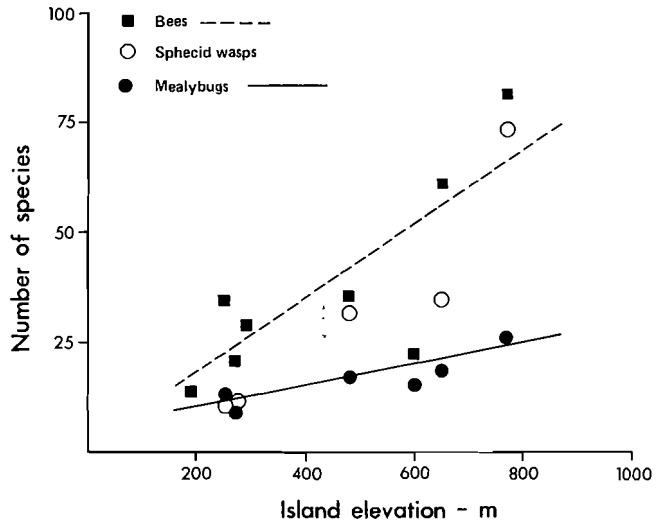

Figure 3. The relationship of island elevation to the number of mealybug, sphecid wasp and bee speces on the California Channel Islands. Regression lines are significantly different from zero.

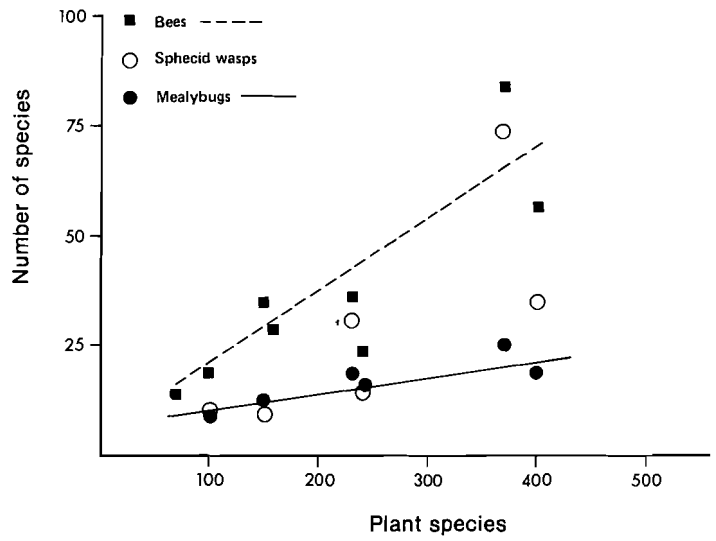

Figure 4. The relationship of island plant species to number of mealybug, sphecid wasp, and bee species on the California Channel Islands. Regression lines are significantly different from zero.

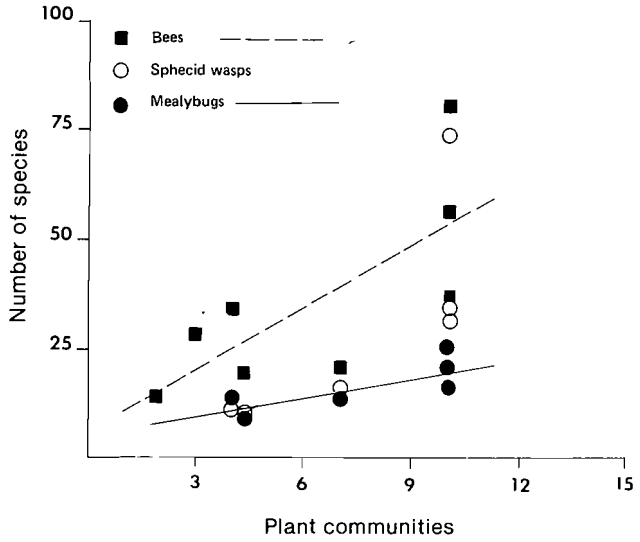

Figure 5. The relationship of island plant communities to number of mealybug, sphecid wasp, and bee species on the California Channel Islands. Regression lines are significantly different from zero.

APPENDIX*

NOTES ON CHANNEL ISLAND SPHECIDAE

Arnold S. Menke

Included here are differences between insular and mainland populations of some species, notes on synonymy, wasp habitats, and biological observations. The description of a new subspecies of Bembix americana from San Clemente I. is included and a key to the Channel Island subspecies of this wasp is appended. Only a few of the 90 species listed in Table 7 will be discussed here. Unless otherwise indicated, the material upon which these notes are based is in the National Museum of Natural History, Washington, DC.

Podalonia mexicana (Saussure)

In December, 1981, on San Clemente I., four females of this wasp were dug up at West Cove. They were clustered in a cell at the end of a burrow. The wasps were in very fresh condition which suggests that they had recently emerged from their cells and presumably were overwintering. The weather was cold and no wasps were seen flying.

Podalonia valida (Cresson)

This is one of the largest sphecid species on the islands and it is a common wasp on San Miguel, Santa Cruz and San Clemente. In 1973 I caught two females transporting prey over the ground, venter up, head forward, on San Clemente I. at Eel Point and West Cove. Prey were the densely spiny caterpillars of the arctiid moth, Apantesis proxima (Guérin-Méneville)(det. D. Ferguson). Setose caterpillars are generally avoided by ammophiline wasps, and I assumed at the time that valida was simply using the only suitable prey available, although naked noctuid caterpillars, the common prey of most species of Podalonia, occur on San Clemente. However, Steiner (1974) observed valida in Arizona provisioning with hairy arctiid larvae of Estigmene acraea (Drury). Thus my observations confirm that valida prefers setose arctiid caterpillars for prey.

Ammophila azteca azteca Cameron

Scott Miller caught a female flying with prey, a geometrid caterpillar, near Cabrillo Monument on San Miguel I., May 25, 1984.

Ammophila azteca clemente Menke

I caught two females of this all black San Clemente endemic flying with prey at Eel Point. One taken in May 1973 had a looper of the geometrid subfamily Larentiinae (det. Roger Heitzman), and the other, taken in June 1978, had a lycaenid caterpillar, probably Strymon melinus Hübner (det. Robert Robbins).

Ammophila mcclayi Menke

Several nests of this wasp were excavated near Boulder on San Clemente in May 1973. Nest architecture and number of prey per cell were not recorded but prey consisted of the noctuid larvae, Peridroma saucia (Hübner) and Autographa sp. (det. D. Weisman).

Dryudella rhimpa Parker

A female was caught on San Nicolas with prey, a nymph of the bug subfamily Pentatominae (det. Tom Henry).

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* Literature cited here will be found under "Literature Cited" following the main part of the paper.

Liris argentatus (Palisot de Beauvois)

A female collected on San Nicolas I. has been seen (CIS) that is pinned with prey, an immature cricket of the genus Gryllus (det. D. Nickle).

Tachysphex clarconis Viereck

This western U. S. species usually has a red abdomen in the female, but a black abdomen occurs in populations in the northern part of the wasp's range, and also in some specimens from high altitudes. The male is often completely black, although occasionally the abdomen is all red in southern California. Intergrades between black and red occur and some populations have mixtures of black and red forms. Tachysphex clarconis occurs on San Miguel, Santa Rosa, and San Nicolas. Specimens from San Miguel (1 male, 2 females) are completely black in both sexes. Those from San Nicolas (17 specimens, CIS, SBMNH) are black except terga IV-VI are partly red in 7 of the 8 females. Only three females have been seen from Santa Rosa and the abdomen is mostly red (the sterna and tergum I are suffused with black).

Tachysphex sonorensis (Cameron)

Mainland specimens of this species have a red abdomen in both sexes except in some mountain populations where it may be black according to W. J. Pulawski (pers. comm.). Tachysphex sonorensis occurs on Santa Cruz and Santa Rosa (46 specimens) and on the last island the male (39) is consistantly all black. No males have been seen from Santa Cruz.

Tachysphex tarsatus (Say)

This common transcontinental species usually has a red abdomen on the mainland which may be black at the tip. However, specimens from coastal northern California sometimes have a black abdomen according to W. J. Pulawski (pers. comm.). Tachysphex tarsatus occurs on San Miguel, Santa Rosa, Santa Cruz, and San Nicolas Is. Specimens from Santa Rosa (84) and Santa Cruz (3) have a red abdomen, but those from San Miguel (63) and San Nicolas (95, USNM, CIS) are completely black.

A nest was excavated on San Nicolas in June 1978. What appeared to be one cell contained 4 immature acridid grasshoppers of the species Camnula pellucida (Scudder) (det. D. Nickle).

A female of tarsatus was caught as prey by the beetle Cicindela haemorrhagica LeConte (det. C. Nagano). on San Nicolas I.

Tachysphex texanus (Cresson)

A female was caught on Santa Cruz I. with its acridid prey, an immature Encoptolophus robustus Rehn & Hebard (det. D. Nickle).

Genus Solierella

Because of their small size and tendency to stay close to the ground, these wasps are often overlooked by collectors. They are fairly common on some of the islands however, and I have been able to recognize 9 apparent species in the material available. In some cases these taxa are represented by only one specimen or by a few of one sex. Also some island populations vary somewhat from mainland material. Williams (1950, and in several subsequent short papers) reviewed the California species of Solierella, but his work is unsatisfactory in some respects: male/female associations are not clear for all species, and extralimital taxa usually were ignored. In his defense, however, species discrimination in some sections of the genus is difficult. I studied type material of a number of taxa in an effort to accurately identify the island species, but the proper names for some are unresolved. The results of some of these studies are recorded below.

Solierella peckhami (Ashmead)

Plenoculus peckhami Ashmead, 1897. Psyche 7:130. Lectotype male, Hartland (as "Haitland"), Wisc., present designation, type in U. S. National Museum.
Niteliopsis kansensis Williams, 1914. Univ. Kansas Sci. Bull. 18:178. Holotype female, Norton Co., Kansas, type in Univ. of Kansas. NEW SYNONYMY.

In addition to the type material of peckhami and kansensis, I studied the types of nigra (Ashmead), arenaria Krombien, and rohweri (Bridwell)(all USNM), and can confirm that these last three have been treated correctly as synonyms of peckhami (Bohart and Menke 1976, Krombein 1979). Two male syntypes of peckhami exist in the National Museum of Natural History, and I have labeled one as lectotype. My examination of the type of kansensis has revealed that it is the opposite sex of peckhami.

Solierella peckhami is transcontinental on the mainland and is adventive in Hawaii and the Marshall Is. (Krombein 1979). It and blaisdelli, which is known only from the western U.S., are very similar in clypeal details and male antennae. The free margin of the male clypeus has a spike-like median process (see fig. 185 in Williams), and the last male flagellomere is very long (Williams fig. 143). The female clypeus is depicted by Williams (1950, compare figs. 96-97, his "nigra" = peckhami).

I have been unable to find characters that consistently separate peckhami and blaisdelli and possibly they represent one variable species. On the mainland, females generally can be separated by the following features: color (metanotum black: peckhami, with yellow crossband: blaisdelli); sculpture of the hypoepimeron (usually completely punctate but sometimes with small impunctate area next to scrobe: peckhami, lower half or more of hypoepimeron impunctate, shining: blaisdelli); and tergal punctation (punctures of terga I-II deep, round: peckhami, punctures shallow, like pinpricks: blaisdelli). These characters don't hold up well for males. Solierella nigrans Krombein, which is intermediate between peckhami and blaisdelli to some extent, may be a synonym of one of these species.

Both peckhami and blaisdelli nest in hollow plant stems on the mainland (Krombein 1979).

Solierella sayi (Rohwer)

Niteliopsis sayi Rohwer, 1909. Trans. Amer. Ent. Soc. 35:114. Lectotype female, Florissant, Colo., present designation, type in U. S. National Museum.

Rohwer based sayi on one female and four male syntypes (USNM). I have selected and labeled the female as lectotype. The clypeus of sayi has a small, somewhat truncate median lobe which has a rounded median prominence (see figs. 155-156 in Williams). The male antenna has a short terminal flagellomere (similar to fig. 172 in Williams). Specimens of sayi from San Clemente are atypical in being shinier and less coarsely sculptured than material from Santa Cruz and Santa Catalina whose populations are like mainland specimens. I have seen only 3 females and 3 males from Santa Rosa I. and 5 of them (one male the exception) are melanic. The fore and midfemora lack the yellow apical spots typical on the mainland, and the mandible is black almost to the tip instead of being yellow.

Miscophus californicus (Ashmead)

On the mainland this species varies in color from all black (except yellowish mandibles and clypeal edge, and brownish tarsi) to forms in which the legs, gaster, scape, mandible, clypeal margin, pronotal lobe and tegula are red. Various intergrades occur. Dark specimens of californicus seem to occur randomly (e.g., Lassen Co., Corona del Mar in California, Florissant, Colorado), but bicolored specimens predominate.

In contrast, color patterns of californicus on the Channel Islands are consistent within each insular population (only 1 specimen each from Santa Cruz and San Miguel). This wasp is known from six of the Channel Islands, and it is essentially completely black on 5 of them: San Miguel, Santa Rosa (11 specimens), Santa Cruz, San Nicolas (57, USNM,

CIS), and Santa Catalina (85, USNM, CIS). These black forms usually have brownish tarsi and mandibles. The single specimen from Santa Cruz (BV) has yellowish mandibles.

The 96 specimens (USNM, CIS) seen from San Clemente are consistently bicolored: gaster (except apex usually black), legs, tegula, scape, mandible and clypeus or clypeal margin red. The rest of the body is black. It is surprising to find bicolored californicus on an island that tends to have melanic forms in some species of Sphecidae. Likewise it is odd that Catalina has the melanic form instead of the bicolored type. Sphecid wasps from both Catalina and Santa Cruz tend to resemble mainland populations.

A female was caught with prey, an immature salticid spider of the genus Habronattus (det. J. Coddington), at Middle Ranch on Catalina.

Miscophus cyanurus (Rohwer)

On the mainland this species has two color forms: body black, or body black with red abdomen. All black specimens occur in northern California. Those with red abdomens are widespread in southern Calfornia, and all material seen from Catalina I. (11 specimens) are bicolored. An intermediate color form is known on Santa Cruz according to Joanne Slansky Wasbauer (personal comm.).

Oxybelus uniglumis (Linnaeus)

I have seen this common mainland species from San Miguel, Santa Rosa, Santa Cruz, San Nicolas and Santa Catalina. On the mainland uniglumis is transcontinental and there is some sculptural and other variation over its range. Specimens from the California mainland tend to have deep, round punctures on terga I-II of the male and they are crowded, less than a diameter apart. Female tergal punctures are often finer, shallower, almost resembling pin pricks, and are sometimes separated by up to a puncture diameter. Specimens of uniglumis from Santa Cruz and Santa Catalina (only 2 female specimens from this island, USNM, CIS) are essentially like the mainland forms.

However, in the populations on San Miguel (18 specimens, USNM, UCD), Santa Rosa (1), and San Nicolas (172, USNM, CIS) the tergal punctures are finer, shallower and sparser in both sexes, so fine in some males and all females that they resemble pin pricks. The tergal surface is highly polished in these populations.

The San Nicolas population is additionally peculiar in that the yellow maculations of the body of the male are more extensive than they are on the other islands or the mainland. The pronotal collar and lobe are yellow, and the scutellum usually (66 of 75 specimens) has a pair of yellow spots or even one large spot. The legs are more extensively yellow also. Females usually have some yellow on the pronotum but none on the scutellum. The high degree of yellow maculation in the Nicolas population of uniglumis is unexpected in view of the melanistic tendencies of some other wasps on the island. Furthermore, yellow on the pronotal collar and scutellum of males appears to be very rare in mainland material.

Bembix americana dugi Menke, new subspecies

Description:

Color: Body black, maculated with or entirely lemon yellow as follows: labrum, clypeus, lower frons, lower surface of scape, flagellum beneath in some females (flagellum dirty yellow beneath in males and some females), thin stripe along outer orbit, mandible except apex; spot on pronotum near propleuron (occasionally absent), posterior edge of propleuron beneath pronotal lobe; small spot on tegula (usually), outer margin of post-tegula, base of forewing costal vein; apical half of femora; foretibia yellow except for small linear black spot usually present (13 of 22 males, 21 of 23 females) on outer surface, and inner surface with elongate black spot; mid and hindtibiae yellow (except small or faint black spot sometimes on inner surface); tarsi yellow except claws; male tergum I with uninterrupted yellow band that is narrowed toward midline, that of female broken at midline, sometimes narrowly so; terga II-V with broad uninterrupted yellow bands that have anterolateral U-shaped notches, apical half of tergum VI yellow, large apical spot on VII yellow (male); male sterna II-III usually with uninterrupted apical yellow

bands, that of II covering apical half of median process, bands containing two black spots (4 of 22 males have band on III reduced to three large yellow spots); female sternum II usually (16 of 23 females) with complete yellow band enclosing 2 black spots, female sterna III-V (most) or II-V, and male sterna IV-V with three large posterior yellow spots that are usually thinly connected along posterior margin; apical half of male sternum VI yellow (black beneath median process), female sternum VI occasionally with yellow spot.

Structure: forebasitarsus with 6 or 7 rake spines in male, with 7 or 8 rake spines in female, basalmost one sometimes small (11 females had 7 spines on each leg, 6 had 8, and 6 had 7 on one leg and 8 on the other); median process of male sternum II thornlike, its base stout, roughly circular in cross-section, tapering to a sharp, posteriorly directed point; male sternum VI with elevated flattened median process and lateral angular swelling; length 19-20 mm. (males), 18-20 mm. (females).

Types:

Holotype male: CALIFORNIA, Los Angeles Co., San Clemente I., Eel Point, June 18, 1978 (A. S. Menke, R. W. Rust, D. R. Miller). Paratypes: 21 males, 23 females, same data as holotype except dates are June 13, 15, 18-19.

The holotype is deposited in the National Museum of Natural History, Washington DC. Paratypes will be deposited there and also at the following institutions: University of California, Davis; University of California, Berkeley; California Academy of Sciences, San Francisco; Santa Barbara Museum of Natural History, Santa Barbara; and the Natural History Museum of Los Angeles County, Los Angeles.

Etymology:

It is with great pleasure that I dedicate this distinctive island form to its discoverer, Douglass R. "Dug" Miller. Dug claimed to have seen a Bembix at Eel Point during our first trip to the island in May 1973, but it was not until June 1978 that he was vindicated by the actual capture of specimens. During the five year interval Dug received considerable kidding about the phantom Bembix he had "seen".

Habitat:

Despite fairly intensive collecting by hymenopterists over the entire island, Bembix americana dugi is known only from one restricted site, namely Eel Point on the western side of San Clemente. The neck of this point is quite sandy and a large nesting population of dugi was found on the south side, an area of about one acre. Wasps were only seen in the immediate vicinity of Eel Point; none were seen at the large sand hill located on the coast about one half mile to the south. Other choice sites for Bembix such as the extensive sand dune area southeast of West Cove, and the extensive sandy areas around China Point, were devoid of these wasps. It seems likely however, that Bembix will be found at these or other sites when they are visited at the right time of the year. For example, Microbembex californica was not detected for some years despite intensive collecting on San Clemente. It was discovered in 1978 as an abundant inhabitant of the sand dunes south east of West Cove, an area that had been scoured by many hymenopterists.

Biology:

Four females were captured with prey: Syrphidae (det. F. C. Thompson), Copestylum lentum Williston (2), C. satur (O.S.); and Tachinidae (det. N. E. Woodley), Reinhardiana sp. nr. petiolata (Townsend). One nest was excavated. It was about 11 inches long, and the cell was about 5 inches from the soil surface. The cell was stocked with the following Diptera: Syrphidae (det. Thompson), Allograpta micrura (O.S.) (1), A. obliqua (Say) (1), Copestylum avidum (O.S.) (2), C. satur (O.S.) (1); Sarcophagidae (det. Woodley), Sarcophaginae (1); Calliphoridae (det. Woodley), Phormia regina (Meigen) (1); and an unidentifiable bombyliid.

Discussion:

The extensive lemon yellow banding of the abdomen in both sexes, especially ventrally, is a distinctive feature of dugi. Females of Bembix a. comata on nearby Catalina are similarly colored dorsally, but the sterna are not yellow crossbanded. The

male of comata has whitish abdominal markings. The thorax of comata is more extensively yellow marked than that of dugi. Only a pair of comata from Anacapa I. have been available for study (SBMNH), but no differences from the Catalina population are evident.

Structurally dugi is more closely allied to the melanistic nicolai from San Nicolas. Males of dugi and nicolai have a similar thorn-like process on sternum II, although in the latter subspecies it tends to be somewhat laterally compressed in most specimens. In small males of nicolai the process is sometimes reduced to a median carina, with intermediate conditions expressed in some examples. Both dugi and nicolai have prominent lateral swellings on sternum VI in addition to the large central process. Males of comata from Catalina have a keel-like process on sternum II which is strongly laterally compressed. In small males of comata the process may be reduced to a carina. Also male sternum VI in comata lacks the angular lateral swelling found in dugi (and nicolai).

Differences in the number of rake setae on the female forebasitarsus between subspecies of americana were discussed by Bohart and Horning (1971). Most females of dugi have 7 rake setae on at least one foreleg (17 out of 23 specimens), a few have 8. Of 32 females of nicolai examined for this feature, 23 had 7 rake setae on both legs, 3 had 6, 1 had 8, 3 had 6 on one leg and 7 on the other, and 2 had 7 on one leg and 8 on the other. Of 33 females of comata examined from Catalina, 16 had 6 rake setae on both legs, 12 had 7, and 5 had 6 on one leg and 7 on the other. Thus dugi is closest to nicolai, both tending to have 7 rake setae on the female foreleg, while females of comata tend to have 6.

Bembix a. dugi is fairly constant in body length (18-20 mm.) based on the sample available (45 specimens), but nicolai and comata vary considerably. Both sexes of nicolai range from 11 to 19.5 mm. with the norm around 18 mm. Bembix a. comata on Catalina is smaller than dugi and nicolai. Females range from 10 to 17 mm., and males from 12 to 16.5 mm. The norm for comata is around 15.5 mm. A larger sample of dugi may indicate more variability in size and male sternal features than is currently apparent.

The three northernmost islands, San Miguel, Santa Rosa and Santa Cruz, are inhabited by Bembix americana hamata. This subspecies differs from dugi as noted in the accompanying key. Both subspecies have similar male sternal features, although hamata displays considerable plasticity in the development and form of these secondary sex characters. In hamata the process on sternum II is often thorn-like as in dugi, but usually it is somewhat laterally compressed. In hamata the median process of sternum VI tends to be broader than in dugi but both subspecies share the lateral angular swellings. However, in males of hamata from Santa Cruz these lateral swellings are often weak. The Santa Cruz I. population of hamata tends to be less melanistic than those on San Miguel and Santa Rosa. For example, the outer surface of the midtibia is usually entirely yellow, and the clypeus rarely has black pigment adjacent to the frontoclypeal suture. Most specimens of hamata from San Miguel and Santa Rosa have a linear black spot on the outer surface of the midtibia, and the clypeus is often bordered by black along the frontoclypeal suture. Thus, the Santa Cruz population of hamata approaches the subspecies comata in several characteristics. Further study of hamata may indicate the desirability of resurrecting the name lucida as a subspecies for the population on Santa Cruz I.

Prey records for Channel Island Bembix

Bembix americana comata:

Four females were caught with prey on Catalina: Muscidae (det. R. Gagne), Spilogona n. sp.; Stratiomyidae (det. N. E. Woodley), Stratiomys maculosa Loew; and Syrphidae (det. F. C. Thompson), Copestylum avidum (O.S.), Eristalis stipator O.S. A nest that was excavated on Catalina contained the following species: Syrphidae (det. Thompson), Allograpta micrura (O.S.) (1), Copestylum avidum (O.S.) (3), C. satur (O.S.) (1); Tachinidae (det. Woodley), Peletieria sp. (4); Calliphoridae (det. Woodley), Phaenicia sericata (Meigen) (2), Muscidae (det. Woodley), Stomoxys calcitrans (Linnaeus) (1), Musca domestica Linnaeus (1); and Sarcophagidae (det. Woodley), one unidentifiable species in Sarcophaginae.

Bembix americana hamata:

One female (CIS) was caught with prey on Santa Cruz, the syrphid Copestylum avidum (O.S.) (det. Thompson).

Bembix americana nicolai:

One nest was excavated and found to contain the following flies: Syrphidae (det. Thompson), Eupeodes volucris O.S. (2), E. (Metasyrphus) sp. (1), Platycheirus sp. (1); Tachinidae (det. Woodley), Peleteria sp. (1); and an unidentifiable bombyliid.

Key to island subspecies of Bembix americana

1. Females 2
- Males 5
2. Gastral terga black except for small yellow spots laterally that usually are not visible from above except on IV-V; San Nicolas I. ..... nicolai Cockerell
- Gastral terga II-V with whitish to lemon yellow cross bands that are not interrupted .. 3
3. Tergal bands whitish, contrasting with yellow of mid and hindlegs; midtibia with black stripe on outer and inner surfaces (sometimes only on inner surface - Santa Cruz I.); San Miguel, Santa Rosa, Santa Cruz Is. ..... hamata C. Fox
- Tergal bands yellow, not paler than yellow of mid and hindlegs (although may be of different hue); midtibia completely yellow or with inner black spot 4
4. Pronotal lobe yellow, this color extending onto collar and ventrad; scutal spot next to tegula yellow; sterna II-V black in middle, with lateral yellow spot (rarely tiny yellow spot at middle of II-III - Catalina); Anacapa and Santa Catalina Is. .... comata J. Parker
- Pronotal lobe and collar, scutum, black; sternum II usually with yellow band enclosing two black spots (sometimes reduced to 3 large yellow spots), III-V each with three yellow spots (one median); San Clemente I. ..... dugi Menke
5. Gastral terga completely black; clypeus and labrum mostly or all black; San Nicolas I. .. .. nicolai Cockerell
- Gastral terga with transverse whitish or yellow bands or spots; clypeus and labrum completely yellowish or nearly so 6
6. Clypeus pale yellow, contrasting with darker lemon yellow of legs; San Miguel, Santa Rosa, Santa Cruz Is. ..... hamata C. Fox
- Clypeus same lemon yellow as legs 7
7. Tergal bands whitish; sternum II process (when well developed*) laterally compressed, keel-like, its apex not extending posterad much past base; sternum VI without lateral angular swelling; sterna II-VI each with lateral whitish spot; Anacapa and Santa Catalina Is. ..... comata J. Parker
- Tergal bands lemon yellow; sternum II process thornlike, roughly circular in cross-section basally, attenuating to apex which extends posterad well beyond base; sternum VI with lateral angular swelling; sterna II-VI with lemon yellow maculations, those on II and usually III band-like, enclosing 2 small black spots .... dugi Menke

* In some small males the process is reduced to a median, longitudinal carina.

NOTES ON CHANNEL ISLAND MEALYBUGS

Douglass R. Miller

3 This section is written to draw attention to changes in the names of certain mealybugs discussed in previous papers on the pseudococcids of the California Channel Islands.

A recent study (Miller et al. 1984) has demonstrated that the correct name of Pseudococcus obscurus Essig, 1909 is P. affinis (Maskell), 1894. This research also gave detailed information on the characters that distinguish between P. affinis and P. maritimus (Ehrhorn).

Island specimens of these species always have been problematical and often have been misidentified. In many cases the problem has been caused by the occurrence of several discoidal pores near the eyes, a character previously believed to be diagnostic of P. affinis. It now is obvious that this character cannot be used indiscriminantly, and that many specimens previously believed to be P. affinis actually are P. maritimus. The specimens recorded from Santa Cruz Island as P. obscurus are neither it nor P. maritimus, but are a new species similar to the latter.

In Miller (1974) mention was made of a possible island endemic known only from immatures. It was quite unusual because it possessed quinquelocular pores, structures that occur only in a small group of mealybugs. Since the original discovery of this species I have been able to collect adults and immatures at the same time and have found them to be Misericoccus arenarius (Doane and Steinweden). This species is unusual in that it is the first pseudococcid known to have quinquelocular pores as immatures, but not in the adult. Misericoccus arenarius is not an endemic, in fact, it is recorded throughout the state of California and is known also from Utah.