The Microlepidoptera Fauna of Santa Cruz Island is Less Depauperate than that of Butterflies and Larger Moths

Jerry A. Powell[1] and David L. Wagner[2]
[1]Department of Entomological Sciences, University of California, Berkeley, CA 94720
[2]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269

Abstract – Surveys of Lepidoptera on Santa Cruz Island, California, indicate that the fauna of small to minute leaf mining moths from six families are proportionately better represented relative to the nearby mainland fauna, than are larger microlepidopterans (Tortricoidea and phycitine Pyralidae) or macrolepidopterans (Papilionoidea, Hesperioidea, Arctiidae and ennomine Geometridae). Collectively, 71% of the central coast leaf mining species occur on Santa Cruz Island; whereas in the other 5 groups surveyed 30-62% of the mainland fauna are resident. Species with small adults or with larvae that feed internally occur in higher proportion than do large and external feeding Lepidoptera. In three well-sampled host plant genera (*Ceanothus*, *Quercus* and *Salix*) used by both leaf miners and butterflies, 87% of the mainland leaf miner species are recorded for Santa Cruz Island, whereas only 35% of the butterflies are present. We postulate that this disharmony in species richness is due to the smaller areas required to maintain effective populations of leaf mining moths, which enhances the survival rates of these minute insects in small patches of host plant.

Introduction

Two of the most consistent and conspicuous features of island biotas are that they have fewer species than comparable mainland areas, and those present comprise an unequal taxonomic representation of mainland communities. Such unbalanced or disharmonious faunas and floras are most pronounced on distant oceanic islands where the species are derived almost exclusively from long-distance dispersal events (Carlquist 1974). However, impoverished species numbers and disharmonic biotas also occur on islands situated near the mainland (Pielou 1979; MacArthur & Wilson 1967). Some organisms are obviously underrepresented in island faunas, for example, large vertebrates that require expansive home ranges, particularly predators, are rare or absent; and organisms that are poor dispersers, such as fresh water vertebrates, wingless insects and plants having propagules that are neither able to float for long periods nor adapted for transport by birds are lacking from distant islands (Thorne 1963; Williamson 1981).

A question that has not received much attention in island biogeography is the one we pose here: Is species richness uniformly depressed across taxa of similar biological roles, such as phytophagous insects within one Order? On nearby continental islands of moderate size, such as Santa Cruz Island (SCrI), the representation often seems sporadic and absences require subtle explanation. For example, the butterflies are the best surveyed group of insects on the California Islands; there have been only two additions to the SCrI faunal list during the past 15 years and both of these are widespread species which are characteristic of weedy habitats and are believed to have colonized recently (Powell 1981; Miller 1985). There are 34 species recorded on SCrI, approximately half the number of resident species in a region of equivalent area and elevational range on the adjacent Santa Barbara coast (Miller 1985).

We expected commensurate levels of depauperateness for other groups of Lepidoptera (Powell 1985). However, after our fieldwork in 1984, which added 80 species to

Table 1. Species accumulation during recent surveys of Santa Cruz Island. Taxa arranged from largest mean size of individuals at top, to smallest at bottom of column.

Taxa	Total Species	Species Added 1979*	Species Added 1984*	% Added after 1978
Bombycoidea & Sphingoidea	7	0	0	0
Hesperioidea & Papilionoidea	34	1	0	3
Noctuoidea	116	8	5	11
Geometroidea	69	4	3	10
Pyraloidea & Pterophoroidea	74	0	5	7
Tortricoidea *etc.***	80	3	8	14
Gelechioidea	102	1	34	34
Tineoid & primitive leaf miners (includes *Marmara*, 3 spp.)	73	2	29	40

* 1979: UCB, Feb.; SBMNH, May; LACM, June (5 days, 1 collector each)
1984: UCB, May (5 days, 3 collectors).
** Tortricidae (n = 46), Cossidae (2), Carposinidae (1), Sesioidea (3), Yponomeutoidea (7), Copromorphoidea (1), Tineidae (14), Incurvariidae (6).

the inventory (15% of the total), we realized that species representation in small microlepidoptera seemed to be proportionately richer than the island macrolepidoptera fauna. This was because we found no new butterflies and few larger moths, while the roster of Gelechioidea and leaf mining taxa increased dramatically (Table 1). The relative richness of species on the island is especially striking for leaf mining taxa. Here we compare the fauna of SCrI to that of the mainland for selected groups of Lepidoptera, emphasizing butterflies and primitive and tineoid leaf miners.

Methods

To obtain an adequate census of Lepidoptera, three general approaches were employed: 1) observation and net collection during the daytime for butterflies and diurnally active moths, which are occasional members of all superfamilies; 2) nocturnal sampling at lights (incandescent and ultraviolet fluorescent), which attract larger moths more effectively than small microlepidoptera, especially in cooler climates such as prevail much of the time in maritime areas and 3) by searching for larvae and rearing them to adults in the lab. The last usually is the most efficient way to collect leaf miners and other small microlepidoptera, because the adults come to lights only sporadically, and often the taxonomic state of species is too poor to allow identification of moths that have not been associated with their host plants.

Lepidoptera that feed in the larval stage between the upper and lower epidermis of a single leaf are termed leaf miners. Mining occurs in a wide diversity of families, at least in the early instars, and several families are characterized by having larvae that are strongly modified morphologically for this mode of life and are unable to survive outside the mine.

Survey for the presence of leaf miner genera is enhanced by the characteristic form of the mine. Most species are host specific, and on any given plant species the mines are consistently distinguishable for each moth species. Often occurrence of leaf miner species can be censused throughout the season by the characteristic 'calling card' left by the larva. By contrast, most other Lepidoptera are effectively collected only during a particular, often quite brief season, when either the larvae or adults are active.

For purposes of this analysis, we defined central coastal California as the coastal plain, foothills and contiguous valleys, up to 650 m elevation, from Big Sur (Monterey Co.) south

Table 2. Seasonal distribution of Lepidoptera sampling on Santa Cruz Island, 1934-1984.

Jan.	1-15	YU '73	Jul.	1-15	—
	16-31	—		16-31	YU '67, '68, '70, '75
Feb.	1-14	UC '79*	Aug.	1-15	LA '39; YU '68
	15-28	—		16-31	LA '39; YU '71, '74
Mar.	1-15	UC '69*; YU '70	Sep.	1-15	—
	16-31	LA '41; YU '70; UC '76		16-30	UC '78
Apr.	1-15	YU '70	Oct.	1-15	—
	16-30	JG '34; UC '66; YU '70		16-31	YU '72
May	1-15	UC '66,'76,'77*; YU '70	Nov.	1-15	—
	16-31	YU '70; SB '79; UC '84*		16-30	—
Jun.	1-15	UC '66; YU '70	Dec.	1-15	—
	16-30	GG '78; LA '79		16-31	—

* = visits in which leaf miner survey was emphasized
Specimen sources: GG = G.A. Gorelick collection; JG = J. Garth (Hancock Foundation); LA = Los Angeles County Natural History Museum; SB = Santa Barbara Museum of Natural History; UC = Essig Museum, University of California, Berkeley; YU = Peabody Museum, Yale University.

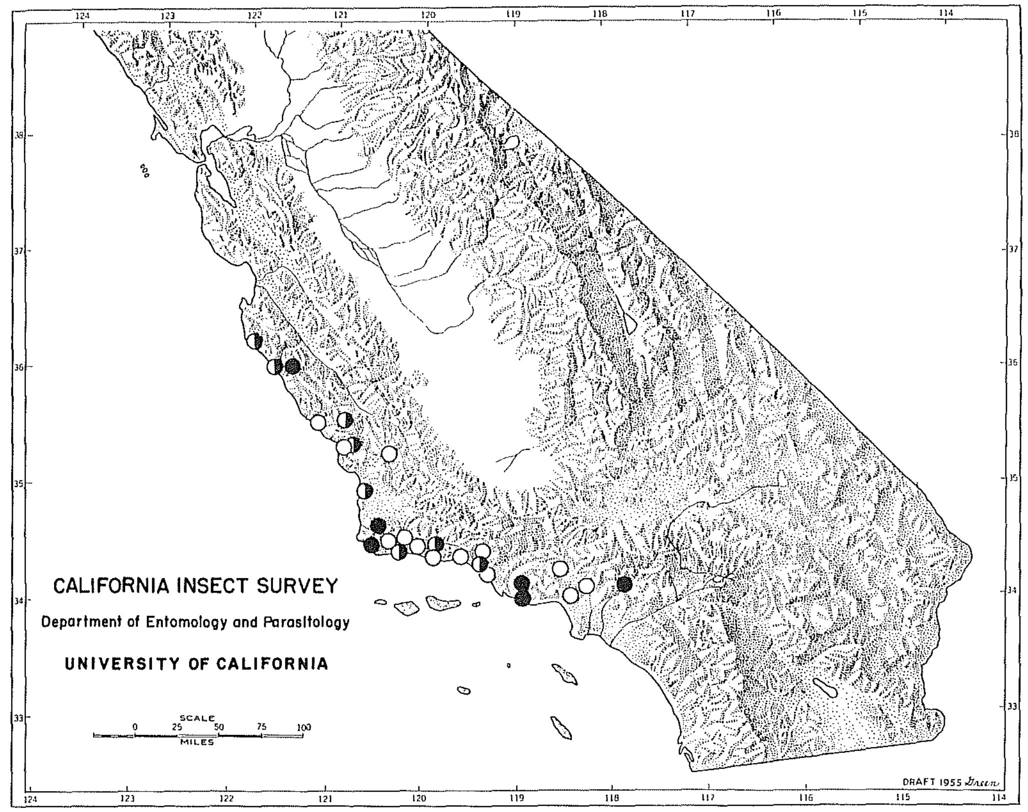

Figure 1. Distribution of localities in the central coast of mainland California that have been sampled for moths, 1962-1987. Open symbols = diurnal and/or nocturnal (blacklight) surveys for adults; closed symbols = leaf miner and other larval surveys; half-closed symbols = sampling for both adults and larvae, including abandoned leaf mines.

to Palos Verdes Point (Los Angeles Co.) In southern California this zone extends inland to include the lower parts of the Santa Monica Mountains and other ranges in Ventura County and the western San Gabriel Mountains (Fig. 1). The limits of this range were in part defined by localities which have been sampled for Lepidoptera during the past 25 years.

Butterfly data are compiled from Burns (1964), Emmel & Emmel (1973), MacNeill (1964), Miller (1985), J. Emmel (in litt.), W. Swisher (in litt.) and University of California, Berkeley (UCB); records for pyralids and larger moths were provided by Heinrich (1956), McFarland (1965), Rindge (1949, 1964, 1966, 1970, 1974a, 1974b, 1975, 1976), R. Leuschner (in litt.), Los Angeles County Museum of Natural History (LACM) and UCB; tortricid records were from Powell (1964), R. Priestaf (in litt.) and UCB (open and half-closed symbols, Fig. 1). Leaf miner localities originated from D.L. Wagner and UCB (closed and half-closed symbols, Fig. 1).

Status of Lepidoptera Faunal Survey

Santa Cruz Island: Santa Cruz Island is the largest and biologically most diverse of the California Islands. It is linear, situated on an east-west axis, about 38 km long and 11 km across at its widest point and comprises 249 km^2. The physiography is dominated by a central valley and two parallel ridges that reach elevations of 460 and 740 m. The history and status of Lepidoptera surveys on the California Islands have been reviewed elsewhere (Powell, 1985). The flora of SCrI was perturbed by feral sheep and pigs for 100 years prior to any recorded collections of Lepidoptera, which are several butterflies taken by John Garth in April, 1934. An attempt at comprehensive census was made by the LACM Channel Islands Biological Survey in 1939-1941, but SCrI was relatively neglected, considering its size and physiographic diversity, with only a one-week visit in August by 3 entomologists, and a 5-day visit in March, by a lepidopterist, with limited collecting by 2 other biologists (Comstock, 1939, 1946). These efforts produced records of about 90 species of butterflies and moths (Powell, unpubl. data). In 1966 California Insect Survey (University of California) trips to SCrI began, and a series of visits by C. L. Remington (Yale University) commenced in 1967. We estimate that >90% of available records date from the era since 1965.

The seasonal distribution of Lepidoptera sampling on SCrI is summarized in Table 2. One or more collectors have worked on the island in 15 of the 24 half-months, including about 26 separate expeditions. Most of these efforts have been during the spring months, when most Lepidoptera are active, either as adults or as larvae during the period of concentrated foliation. The weakest coverage has been during the fall, the activity period for some univoltine species. However, one 5-day visit in late September by four University of California collectors produced records of about 200 species. We feel that the lack of visits in November-December is of minor concern because this is the season of dormancy for most species and few are active only during this period.

While some visits depicted in Table 2 have been limited to butterfly inventory, our efforts (UC) have emphasized various sampling methods, including larval collections. We have documented the larval mines and/or reared larvae of about 130 of the SCrI species, nearly 25% of the Lepidoptera fauna.

Searching for leaf miners has been carried out primarily from February to May (Table 2), when immatures of most species are present. A few additional species are expected later in the season. Several potential host plants that occur in wet canyons of the north slope and other remote areas, which we did not visit, need to be surveyed. Additional nocturnal sampling should be done in the mesic pine forest on the western part of the island. Nonetheless, we feel that the butterfly and moth fauna of SCrI has been sufficiently surveyed to allow meaningful biogeographic comparisons.

To date we have recorded about 550 species of Lepidoptera on ScrI. This total is approximately equivalent to those compiled during 8-year surveys in suburban areas of Walnut Creek (Contra Costa Co.) and at the Big Creek Reserve (coastal Monterey Co.), the only other places in California where comprehensive lists have been compiled (Powell, unpubl. data). Similarity in proportions in taxa of larger moths at Walnut Creek and Big Creek with SCrI, together with the modest species accumulation in these groups during recent island surveys (Table 1), suggests that butterflies and families of larger moths are >90% known. Smaller moth taxa are more difficult to assess because recent investigations have discovered many previously undetected species; however, on the basis of known potential host plants, we estimate that 70-80% of the extant microlepidoptera fauna is recorded.

Mainland Lepidoptera: An important question in any attempt to assess an island fauna is, what area of the mainland should we use for comparison? Logically the 'comparable' area might be a portion of the nearest coastal mainland of the same size and elevational range. However, even if we had a coastal area of California with the same elevational characteristics as SCrI, the two would not be equivalent biologically because one is surrounded by ocean, while the other has climatic and biogeographic influences of the mainland interior. Moreover, in Lepidoptera we do not have a comprehensive census of any one mainland region of the central coast, such that the kind of comparison made by Miller (1985) for butterflies can be extrapolated for moths. Therefore, we elected to contrast the fauna of a lengthy strip of the coastal mainland. There are biological considerations, in addition to pragmatic ones, for such a comparison. Raven (1967) estimated that at least 10% of the species of vascular plants of the California Islands have mainland distributions not adjacent to the islands, and the majority of those are northern species. A similar proportion of moths show this kind of distributional affinity, with about 14% of SCrI species having disjunct ranges to the north (Powell 1985). Thus there is a justification to include coastal areas to the north in the comparison.

Table 3. Representation of primitive and tineoid leaf mining Lepidoptera on Santa Cruz Island (total number of records in parentheses).

Taxa	No. Species on Central Coast Mainland (330)	No. Species on SCrI (224)	% Species on SCrI
Eriocraniidae	6	4	66.7
Nepticulidae	20	15	75.0
Tischeriidae	9	7	77.8
Heliozelidae	7	5	71.4
Lyonetiidae	12	10	83.3
Gracillariidae*	44	29	65.9
TOTALS	98	70	71.4

* Excludes *Marmara*.

No locality on the mainland has been thoroughly sampled. The best surveyed are Big Creek (Monterey Co., *ca.* 30 collector-day/nights, March to October); Santa Maria dunes (San Luis Obispo Co., >30 collector-days, 8 collector-nights, February to early October); Goleta-Santa Ynez Mountains (Santa Barbara Co., >30 collector days/nights, March to July) and the Santa Monica Mountains north of Beverly Hills (Los Angeles Co., macro moths only, 5 years continuous survey). These totals and the percent comparisons with the island fauna are based on data accumulated through March, 1987. We believe that the pooled data for all the central coastal region represents a comparable census to that of SCrI (*i.e.*, >95 % complete for butterflies and large moths, >90% for Geometridae, 80-90% for Pyralidae and Tortricidae and perhaps 70-80% for leaf mining families).

Results

Faunal Comparisons: For purposes of this discussion we limited the comparison of leaf miners to six families: four are primitive moth

Table 4. Proportional relationship of the Santa Cruz Island fauna to that of the central coast of mainland California, in selected Lepidoptera. Taxa are arranged from largest mean size of individuals at top, to smallest at bottom.

Taxa	No. Species on Central Coast	No. Species on SCrI	% Species on SCrI
Hesperioidea & Papilionoidea	82	34	41.5
Arctiidae	24	13	54.2
Geometridae: Ennominae	85	26	30.6
Pyralidae: Phycitinae	53	33	62.3
Tortricidae	98	40	40.8
Tineoid leaf miners	56	39	69.6
Primitive leaf miners	42	31	73.8
TOTALS	440	216	49.1

taxa, within the Suborder Glossata (Kristensen, 1984), Eriocraniidae, Nepticulidae, Tischeriidae and Heliozelidae; while two are families of the more derived Tineoidea (Suborder Ditrysia), Lyonetiidae and Gracillariidae. From the last we excluded stem miners of the genus *Marmara* from consideration because the taxonomic status of the species is so preliminary that the degree of host specificity is unknown, and therefore the mines cannot be used as reliable species indicators as in leaf miners.

Among these six families, there are 98 species recorded in central coastal California, represented by 330 collection records (species/locality/hostplant). Of these, 70 have been discovered on SCrI (71.4% of the mainland total; Table 3).

By contrast, Miller (1985) listed 71 species of butterflies in the Santa Barbara region, in an area of comparable size and elevational range to SCrI. Three are vagrants or intermittent colonists (*Pholisora catullus*, *Phoebis sennae* and *Nymphalis californica*). Thus the 34 species reported on SCrI (Langston 1981; Miller 1985) represent 50% of the resident fauna of the adjacent mainland.

In a few instances the missing butterflies are attributable to the lack of particular food plants on the island, but for most species the absence is not readily explained. For instance, the Western Tiger Swallowtail (*Papilio rutulus* Lucas) and the Lorquin's Admiral (*Limenitis lorquini* Bdv.), larvae of which feed on willows (*Salix*), are two of California's most conspicuous butterflies. They are prevalent along watercourses throughout coastal and foothill parts of the State, but neither occurs on any of the California Islands; nor do the ubiquitous species, *Phyciodes mylitta* (Edw.), a small nymphalid that feeds on thistles and the grass-feeding satyrid, *Coenonympha california* Westw., both of which fly throughout the season in low elevation, often in disturbed habitats of the coastal mainland.

To examine this discrepancy further, we compared four additional taxa of Lepidoptera that represent a range in size of individuals and larval biologies. The groups characterized below were selected because each is relatively speciose in the region and the taxonomy is sufficiently well known that reliable identifications can be obtained.

Arctiidae (Noctuoidea): Most species are nocturnal and attracted to lights, but some are diurnal; both kinds are popular with collectors and hence well sampled. The larvae ('wooly bears') are free-living, external feeders on foliage and often are polyphagous; members of one genus specialize on lichens.

Geometridae, Ennominae (Geometroidea): Nearly all are nocturnal, attracted to lights and have been collected extensively in central coastal California by specialists. The larvae are free-living, external feeding caterpillars ('inchworms'), most of which are believed to be relatively host specific.

Pyralidae, Phycitinae (Pyraloidea): Mostly nondescript, gray, nocturnal moths that are attracted to lights and collected primarily by specialists. A few species are concealed feeders on foliage in tough, silken shelters; but the larvae of most species feed internally. SCrI species feed in flower heads, seed pods, cones of conifers, or roots of angiosperms, or in wood-rot fungus (Xylariaceae), scale insects, nests of social Hymenoptera and decaying fruit (Heinrich 1956; Powell 1967, 1981; UCB).

Table 5. Species richness of butterflies and leaf mining Microlepidoptera on Santa Cruz Island and the central coast of mainland California, compared by host plants used by three or more species.

	No. Host Plants*	No. Lepidoptera Mainland	No. Lepidoptera SCrI	% on SCrI
Butterflies	12	53	23	43.4
Leaf miners	7	49	45	91.8

*Species, species-pairs or genera in dicots; Poaceae in monocots.

Table 6. Species richness of butterflies and leaf mining Microlepidoptera on Santa Cruz Island and the central coast of mainland California, compared by shared host plant genera.

Plants	Butterflies Mainland	Butterflies SCrI	Butterflies %	Leaf miners Mainland	Leaf miners SCrI	Leaf miners %
Salix	4	1	25.0	7	6	86.0
Ceanothus	6	3	50.0	8	5	62.5
Quercus	7	2	28.6	23	22	96.0
TOTALS	17	6	35.3	38	33	86.8

Tortricidae (Tortricoidea): Mostly smaller, nocturnal moths that are attracted to lights and collected primarily by specialists. Larvae of *ca.* 55% of the species on SCrI feed on foliage of flowering plants, concealed in silken shelters, such as a leaf roll; the remainder are borers in flower heads, stems, roots or galls. Most are host specific; about 12% are polyphagous.

A comparison of species numbers on the central coastal mainland with those on SCrI (Table 4), reveals an insular representation of 30-54% among butterflies (Papilionoidea and Hesperiioidea) and larger moths, which develop from free-living, external feeding larvae, significantly lower than that of leaf miners (71%). The two remaining groups show intermediate (62% in Phycitinae) and poor representation (41% in Tortricidae).

We believe the figures for butterflies and Arctiidae are nearly complete. One or two species may be added on either the mainland or SCrI, but probably the relative proportion of insular species will not change appreciably. In Geometridae, we expect that 30% is a low estimate because seasonal sampling by specialists on the mainland has been more comprehensive.

The remaining groups probably are incompletely surveyed and we expect that additional species will be discovered both on the mainland and on the island. However, we doubt that more than a 10-20% increase will occur in any total or that the percent relationships will be altered significantly. Certainly there is no evidence to suggest that pyralids and tortricids have been sampled differentially; the discrepancy between their insular and mainland representation evidently is real.

In order to avoid the problem of unsampled or differentially sampled host plant species, we compared butterflies and leaf miners that feed on well surveyed host plants known to be used by three or more species of the insects (Table 5). In this instance, one 'host plant' is a species (*e.g.*, *Cercocarpus betuloides*), a species pair (*e.g*, *Quercus agrifolia/wislizenii*), a genus (*e.g.*, *Ceanothus*) or for Hesperiidae and Satyridae, the family Poaceae.

There are 12 of these hosts supporting 53 species of butterflies on the mainland; 23 (43%) of these occur on SCrI, a proportion close to that of the island butterfly fauna as a whole. By contrast, 7 multiply-used plants are hosts to 49 mainland leaf miners, more than 90% of which are present on the island (Table 5).

We also looked at plant genera that are shared by species of butterflies and leaf miners. There are three of these, *Salix* (Salicaceae), *Quercus* (Fagaceae) and *Ceanothus* (Rhamnaceae). Combined, they serve as hosts to 17 mainland species of butterflies, but only 6 on SCrI, again a percent similar to the fauna as a whole. The same genera are home to 38 species of leaf miners in central coastal California, 33 (86.8%) of which live on the island (Table 6).

Discussion

The data indicate that among phytophagous Lepidoptera, butterfly and moth families characterized by larger individuals with externally feeding larvae are more depauperate on Santa Cruz Island compared to their mainland counterparts, than are leaf-mining families.

The presence/absence of host plants fails to explain the depressed richness of butterfly species, but it is particularly useful as a predictor of leaf miner richness. We know of very few coastal mainland elements that are missing from island plants. The leaf miner faunas of *Rhamnus crocea* and *Prunus ilicifolia/lyonii* are intact (6 spp.) and *Quercus agrifolia*, which has the greatest species richness of any plant in California (Opler 1974), is nearly completely represented, with 15 of 17 species on SCrI. The two missing members of this guild are characteristically low density species which may have been overlooked.

A primary factor that determines the survival of species is effective population size, which is correlated with size of individuals and home range. The Lepidoptera on SCrI treated here range in forewing length from 2 mm (*Coptodisca arbutiella* Busck) to 55 mm (*Papilio eurymedon* Lucas). Probably there is a substantial discrepancy in the areas required by their effective populations, large butterflies using several ha and minute leafminers one or a few trees. Larger species presumably need more area of habitat for dispersal, mate location, location of suitable nectar sources, *etc.*, than do tiny moths. The mere presence of the larval food plant is not the only, nor always the most critical requisite. Large colonies of leaf miners can exist on a single tree, and populations consisting of hundreds or thousands of individuals can subsist in relatively small patches of habitat (*e.g.*, less than 0.1 ha), where butterflies and other large, vagile species may not maintain persistent populations. An example is the presence on SCrI of the leaf miner, *Phyllonorycter fellinelle* Heinrich (Gracillariidae), which lives on a few sycamore trees that were planted along the creek in Cañada del Puerto in the 1930's.

The larval biology is in part correlated with size of individuals and insular richness. Internal feeders tend to be smaller and are better represented. Butterflies, Arctiidae, and Geometridae are external feeders, while phycitine Pyralidae, which are relatively well represented, considering their size, are 90% internal feeders in the SCrI fauna. Tortricidae are either external feeders concealed in shelters (55% on the island) or internal borers and are comparatively depauperate. Among leaf miners, some tineoid genera are external feeders in the late instars, either concealed in a leaf fold (*Caloptilia*) or exposed (*Bucculatrix*); by contrast, members of the primitive families treated here live within the leaf throughout larval growth and are better represented than the other taxa (Table 4).

Historical Factors: Sources of impoverishment include absence at the time of original separation from the mainland, subsequent extinction and failure to colonize.

Genus level associations of leaf miners and their host plants are known in Miocene fossil equivalents of modern Nearctic oaks (Opler 1973); hence, associations of leaf miners in many California trees and shrubs may be more ancient than is true in more derived Lepidoptera, many of which may have arrived on the coastal mainland during climatic and floristic changes in more recent times.

Restriction of the island size during the Pleistocene (Johnson 1978) presumably would have been more critical to survival of species that need more area than do those with smaller requisites. Extinction of some species also may have resulted from destruction of natural habitats by human influence, particularly the effects of feral vertebrates and spread of introduced weeds, which have altered the extent of native plants on the island as well as on the mainland (*e.g.*, grass-feeding species during extraordinary overgrazing in periods of drought). Such perturbance results in reduced populations of potential immigrant sources on the mainland and in smaller available host plant patches on the island, which lowers chances of colonization and persistence of colonists, problems that are more pronounced for larger Lepidoptera.

Dispersal is not well documented in Lepidoptera, but mark-release-recapture studies indicate that many butterflies are sedentary, particularly Lycaenidae (see Arnold 1983; Keller *et al.* 1966), which account for the largest number (18) of absentee species among the SCrI butterflies. Hence, low rate of dispersal may prevent immigration to a greater extent than might be expected in larger, seemingly vagile species, even though examples of long-distance dispersal over bodies of water are known for many butterflies and larger moths (Fox 1973; Tomlinson 1973), microlepidoptera (Shaw & Hurst 1969) and even leaf mining moths (Smithers 1977).

Hence, several factors are likely to play a role in the faunal disharmony that we have identified. These include: 1) historical components of the island biota; 2) differential dispersal rates from the mainland species pool; 3) abilities to establish new colonies and, perhaps most importantly, 4) survival once established on isolated host plant populations.

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Changes in Urchin and Kelp Densities at Anacapa Island, California

Richard F. Ambrose[1], John M. Engle[2], James A. Coyer[3] and Bobette V. Nelson[1]
[1] Marine Science Institute, University of California, Santa Barbara, CA 93106
[2] Department of Biological Sciences, University of California, Santa Barbara, CA 93106
[3] University of California, Los Angeles/Hopkins Marine Station, Pacific Grove, CA 93950

Abstract – The densities of three species of sea urchins and the giant kelp *(Macrocystis pyrifera)* were monitored at a site near Anacapa Island, California. Although the study site had previously supported a dense kelp bed, from 1981-1983 it was dominated by urchins and coralline algae, and *Macrocystis* was restricted to a narrow band in shallow water. After limited recruitment in 1984, *Macrocystis* recruited heavily throughout the study site in 1985, resulting in an extensive kelp bed; the recruitment event was not accompanied by a sharp decline in urchin densities. However, high existing urchin densities, accompanied by unusually heavy urchin recruitment in 1985, resulted in the gradual decline of the kelp bed. By 1987, the kelp bed was again restricted to a narrow band in shallow water.

Introduction

Sea urchins can dramatically influence the structure of temperate marine communities. In some areas, overgrazing by sea urchins results in the removal of all macroscopic algae (Lawrence 1975; Breen & Mann 1976a; Hagen 1983; Himmelman *et al.* 1983; Kitching & Thain 1983). The resulting "sea urchin barrens", more appropriately termed a "crust-dominated community", can persist for years, and is dominated by urchins and encrusting coralline algae that are resistant to grazing (Mann 1977; Wharton & Mann 1981; Hagen 1983; Breitburg 1984). Crust-dominated communities are found throughout the world, including Alaska (Estes & Palmisano 1974; Simenstad *et al.* 1978; Duggins 1980), western Canada (Foreman 1977), eastern Canada (Mann & Breen 1972; Breen & Mann 1976a; Lang & Mann 1976), New Zealand (Ayling 1981; Schiel 1982), Ireland (Kitching & Thain 1983), Japan (Ohmi 1951; Noro *et al.* 1983) and Norway (Hagen 1983).

Crust-dominated communities are generally considered to be caused by increases in the intensity of urchin grazing. Two mechanisms have been proposed to explain the increased grazing. First, increases in urchin densities may result from decreased predation on urchins (Leighton *et al.* 1966; Estes & Palmisano 1974; Dayton 1975; Breen & Mann 1976b; Mann 1977; Breen 1980; Tegner 1980; Tegner & Dayton 1980; Wharton & Mann 1981; Pringle *et al.* 1982; Hagen 1983) or changing oceanographic conditions that favor urchin recruitment (Foreman 1977; Hagen 1983). Second, increased grazing may be due to changes in urchin behavior, the most important factor being the availability of drift algae. When drift abundance decreases, urchins forage more widely from protective crevices (Mattison *et al.* 1977; Dean *et al.* 1984; Harrold & Reed 1985) and graze more intensely on attached plants.

Kelp beds in southern California are very dynamic, as density can fluctuate considerably over time due to both oceanographic and biological factors (Dayton *et al.* 1984). In many cases, grazing by urchins appears to have caused the disappearance of kelp beds in southern California (Leighton *et al.* 1966; North & Pearse 1970; Dayton *et al.* 1984; Ebeling *et al.* 1985). Harrold & Reed (1985) have developed a model of the dynamics of kelp and crust-dominated communities based on a study at San Nicolas Island in the California Channel Islands. With unfavorable hydrographic conditions (such as severe storms, low nutrients, or warm temperatures), low algal