The Fourth California Islands Symposium: Update on the Status of Resources
Edited by W. L. Halvorson and G. J. Maender. 1994. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Biogeography of Lepidoptera on the California Channel Islands

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Abstract. The biota of the California Channel Islands was altered appreciably by feral ruminants and nonnative, weedy plants prior to any Lepidoptera collections. There are only a few records before 1900, and nearly all the inventory has taken place since 1927, a century after introduction of goats and sheep. Most of the data originate from 1966–1991. About 750 species of Lepidoptera are recorded on the islands, about 550 of them on Santa Cruz Island and 370 on Santa Catalina Island. It is likely that the species of the better surveyed islands (Anacapa, Santa Cruz, Santa Catalina) are no more than 70–75% known, those of San Miguel and Santa Rosa less than 50% known. Species numbers per island of butterflies and of Lepidoptera as a whole show correlations to island area but are more strongly predicted by numbers of vascular plants. The area/species relationships reflect habitat diversity and not an equilibrium, with Lepidoptera undersaturated compared to possible diversity had there been no perturbation of the flora. Species or subspecies representing 26 species are recognized as endemic to the islands, about 3.3% of the fauna. These are primarily vicariant derivatives of mainland species; a few are relicts associated with endemic plants that had mainland distributions in the past. There are no examples recognized as vicariance speciation among islands. In addition to endemics, there are 5 geographical components that contribute to the Lepidoptera fauna: (1) widespread mainland species; (2) California Province endemics; (3) coastal strand elements; (4) desert affinities, species occurring mainly in interior southern California and Baja California that are represented primarily on the southern islands; and (5) northern species, relicts of past pluvial times that range on the mainland from San Luis Obispo to Marin County northward, represented mainly on the northern islands.

Keywords: moths; butterflies; species/area and insect/plant numbers relationships; endemism; relicts; vicariance.

Introduction

The 8 continental shelf islands situated in the southern California Bight (Fig. 1) support a diverse fauna of phytophagous insects, despite a history of severe impact by domesticated and feral mammals. There were only a few records of Lepidoptera (moths and butterflies) prior to the late 1920s, about a century after the introduction of goats and sheep to the islands (Coblentz 1980), and the vast majority of collections have originated since 1966. I presented an analysis of the Lepidoptera based on collections through mid-1981 (Powell 1985), which was obviously preliminary because there had been inadequate sampling of the island moths, because collections were not thoroughly studied, and because the lepidopterous fauna of the mainland was not well documented in most families. While all of these disclaimers remain true, in the subsequent decade there have been additional collections from nearly all of the islands, and further taxonomic study of existing specimens, increasing our knowledge of the island faunas appreciably. Moreover, I have coordinated a comprehensive inventory at a coastal locality in Monterey County that provides a much better understanding of relationships of coastal mainland and island species, and a documented idea of the effort required to census a lepidopterous fauna in this region.

Geological history and origins of the fauna

The California Channel Islands are continental in origin, but their geologic history is complex and not completely documented. The Neogene history of the California borderland provinces has been reviewed by Crouch (1979), Vedder and Howell (1980), Luyendyk et al. (1980), Hornafius et al. (1986), and Luyendyk (1991), providing a scenario that contradicts earlier proposals of a late Pleistocene land bridge for the northern islands. Instead, any mainland connections for lands now represented by the larger islands were likely independent for the northern group, Santa Catalina, and San Clemente and not later than early Miocene. By mid Miocene (ca. 12–16 MyrBP), peak volcanic activity and the formation of dis-

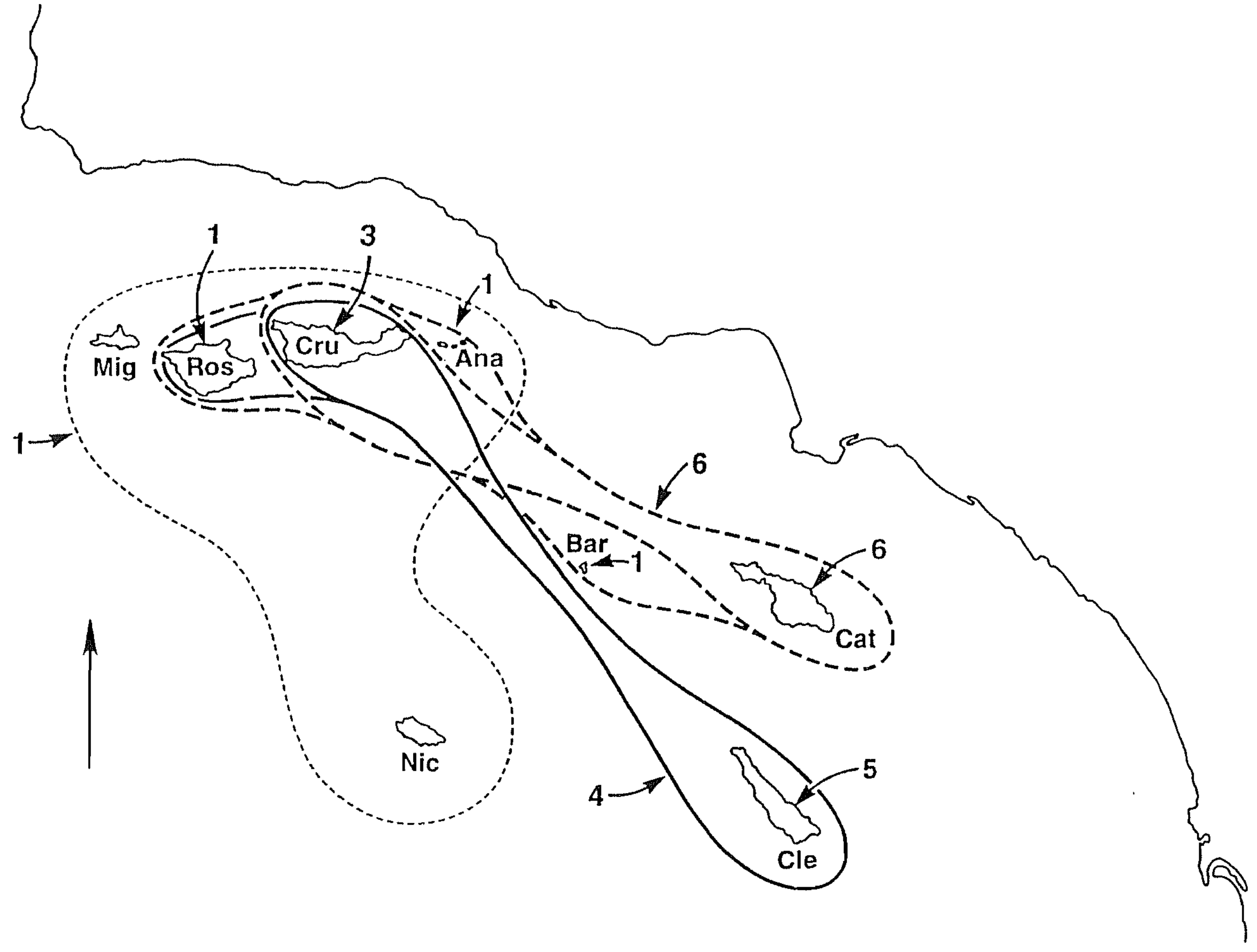

Figure 1. Map of the California Channel Islands and adjacent mainland shoreline, depicting distribution patterns of the insular endemic Lepidoptera. Numbers refer to taxa (species and subspecies) restricted to single islands or occurring on multiple islands enclosed by the curvilinear figures. Abbreviations: **Mig** = San Miguel, **Ros** = Santa Rosa, **Cru** = Santa Cruz, **Ana** = Anacapa, **Bar** = Santa Barbara, **Cat** = Santa Catalina, **Cle** = San Clemente, **Nic** = San Nicolas.

crete basins and ridges were occurring, producing the deep channels that separate the islands from the mainland and the southern islands from one another and from the northern group.

Moreover, the positions of the islands were altered both by fault displacements and by clockwise rotation of coastal blocks during early to late Miocene, inferred from modern paleomagnetic data (Hornafius et al. 1986; Luyendyk 1991). This evidently occurred independently in the Western Transverse, San Nicolas, and Catalina blocks, each bounded by sinistral faults, affecting the relative positions of the present-day islands. Slippage along the Santa Cruz and Santa Rosa island faults moved the southern and northern portions of both islands into their present juxtapositions. An estimated 260-km displacement along the San Clemente fault brought the outer borderland with the present day San Clemente Island northward in relation to the Catalina block, which simultaneously rotated clockwise. Hence, the lands now represented by Santa Catalina and San Clemente islands were more distantly separated prior to early Miocene than now (Hornafius et al. 1986). When and where either may have been connected to the mainland remains uncertain.

During the Pleistocene, fluctuating eustatic sea levels exposed and submerged the islands to greater extremes than the present. At maximum extent of the sea during the last 500,000 yr, only the higher parts of Santa Rosa, Santa Cruz, Santa Catalina, and San Clemente islands were above sea level (Johnson 1978). Santa Barbara and San Nicolas islands were inundated and therefore have received their flora and insect faunas via overseas immigration since late Pleistocene. Anacapa island and probably San Miguel were submerged but subsequently have been connected to the larger northern

islands during periods of sea-lowering, 17,000–18,000 yr ago. At maximum Wisconsin glaciation, the northern islands were joined into a single large island that extended eastward, possibly to within 6–10 km of the expanded mainland shoreline at maximum extent (Vedder and Howell 1980). This event would have opened a wide gate for immigrating Lepidoptera.

Thus the phytophagous insect fauna probably is of various origins:

1. species inhabiting the lands when they were connected to the mainland, 20–30 MyrBP. Examples include the leaf miner fauna of trees and shrubs, at least on the northern islands. Oversea immigration presumably would have resulted in a sporadic representation of the mainland fauna, rather than its nearly intact membership (Powell and Wagner 1993). Fossil mines recognizable as modern genera of Lepidoptera are known in Miocene equivalents of modern oaks (Opler 1973).
2. species that immigrated via oversea flight or flotsam at any time during the late Miocene to recent, but especially during times of Pleistocene sea lowering when water gaps were narrow (e.g., most of the fauna of Santa Barbara and San Nicolas islands).
3. species introduced or encouraged by human activities, particularly those that feed on introduced plants (Powell 1981a, 1985), beginning several centuries ago with prehispanic natives.

Vegetation changes and the impact of feral animals

Most plant communities were altered appreciably by introduced animals and plants prior to records of Lepidoptera. Goats probably were released by traders in the early 1800s as a source of milk and food and as a means of avoiding duty payments (Coblentz 1980). There was extensive grazing of domesticated sheep by the 1850s (Curtis 1864 cited by Johnson 1980; Minnich 1980). Vegetation on Santa Cruz was said to be ravaged by 1875 (Rothrock in Wheeler 1876, cited by Minnich 1980), and photographs show obvious evidence of vegetation stripping on Santa Catalina in the 1880s (Minnich 1980). On smaller San Miguel and San Nicolas islands, sheep were maintained in excess of capacity during periods of drought in the 1860s. The animals were forced to strip the foliage and bark and dig for roots, and all the trees and shrubs of those islands were said to be killed (Johnson 1980). All the islands have suffered from domestic and feral mammals, including ruminants, pigs, even buffalo and other game animals on Santa Catalina, and rabbits on Anacapa and Santa Barbara islands.

The impact of introduced weedy plants in such perturbed habitats is far greater than numbers of species indicate; the vegetation of the islands is dominated by nonnative species (Halvorson 1992). In the seasonal drought climate of coastal California, native plants cannot compete with introduced annual grasses, anise, and other weeds, and land may remain weedy for decades after release from grazing. The floras had been profoundly altered by the time the first botanical explorations occurred in the late 1800s. For example, Raven (1963) described the historical changes on San Clemente: by 1840, this island was densely populated with goats (Farnham 1947). It has been owned continuously by the U.S. Government, but it was leased to a sheep company from 1877 to 1934. Botanists did not visit until 1885, and it was 1903 before the whole island had been explored botanically. By that time, many species, endemics among them, survived only on steep canyon walls inaccessible to grazing animals. These conditions continued for decades via feral goats; by 1972, when I first visited the island, the terrain resembled a moonscape. Mature native trees survived in steep canyons, but without understory or leaf litter. Except in the sand dunes, native herbs were reduced to isolated specimens on vertical canyon walls or in large cactus patches.

Ruminants were excluded from the south part of Santa Catalina Island in the early 1900s and the area gradually has returned to a chaparral community. Removal efforts have greatly reduced goats from the western part of the island in recent years (Laughrin et al., this volume). During the 1940s and 1950s, grazing animals were removed from San Miguel and San Nicolas islands by the U.S. Navy, which began eradication of the goats on San Clemente in the late 1970s. Protests by animal rights activists, who evidently felt the goat to be more important than native, island endemic plants, delayed the process, but goat and feral pig removal was completed by 1991 (Keegan et al., this volume). Feral sheep were excluded by fencing some parts of Santa Cruz Island, beginning in 1950, and removal from all but the east end was achieved by The Nature Conservancy by 1989 (Schuyler 1993). Cattle also have been removed except for a few head kept at the ranch headquarters. Rabbits have been exterminated from Anacapa and Santa Barbara islands in recent years.

Inventory approaches

Three main approaches were taken: (1) daytime searches for butterflies and diurnal moths, (2) nocturnal sampling by ultraviolet or mercury vapor lights, and (3) rearing collections of larvae. Most Lepidoptera larvae cannot be determined to species without associated adults, although larval mines and galls often are identifiable and the most easily discovered stage. Ideally, census would involve Lepidoptera specialists living at the locality for several years. This would enable sampling comprehensively through all seasons and through fluctuations in year-to-year abundance, and it would identify vagrant and migrant species that are not resident. Except for Santa Catalina, there have been no resident lepidopterists on the islands, and visits have been sporadic in seasonal timing and in habitat coverage and inventory approaches (Powell 1985). Sampling at lights was limited to 1 or a few sites on each island, and larval collections generally have been neglected.

Taxonomy

We have attempted to confirm identifications of all older literature records by reexamination of specimens. This study would not have been possible without the assistance of numerous taxonomists (see acknowledgments). Nomenclature has been updated to conform with Hodges et al. (1983) or more recent publications. Meadows (1939) listed Sphingidae and Arctiidae of Santa Catalina and prepared an unpublished list of some other macro moths, but there has been no comprehensive moth list published for the Channel Islands. Scattered descriptions in taxonomic works and other records in the literature have been reviewed by Miller and Menke (1981), Miller (1985b), and Powell (1985). Scott Miller and I developed a database of all species and their individual island occurrence. We expect to distribute hard copies in 1994.

There are, however, many species for which identifications are provisional or unknown. Species of several genera of Tineidae and Gracillariidae, all the Blastobasidae and most Coleophoridae, and several genera of Gelechiidae are insufficiently studied on the mainland to know if the island species are described and/or in some examples whether those of 2 islands are the same. They are included in counts of individual island species but are omitted from inter-island relationship calculations. As a result, the total number of species on the islands is unresolved.

Data retrieval

The butterfly records have been summarized (Miller 1985a). Collection records for all species are accumulated in 2 sources: (1) island-by-island files (partly in databases) at the Essig Museum of Entomology, University of California, Berkeley; and (2) 2 databases at the Bishop Museum, Honolulu. The latter incorporate all literature records we have seen (Miller and Menke 1981; Miller 1985b; and subsequent publications through 1993) and specimen collection records from LACM, SBMNH, and USNM, but lack CAS, EME, PMY and some USNM data and contain less than half of the species-island records. The files at Berkeley are based entirely on specimens examined, primarily from CAS, EME, LACM, SBMNH, SDNHM, USNM, and microlepidoptera at PMY (abbreviations in acknowledgments).

The largest numbers of specimens are deposited in EME, LACM, and PMY; less extensive collections are in CAS, SBMNH, SDNHM, and USNM. Data from the macro moths at Yale and from any Lepidoptera in CDFA, UCD, and UCR, which have had entomological survey trips to the islands that did not include lepidopterists, have not been captured.

Composition of the Lepidoptera Fauna

Faunistic numbers

There are 726–760 species of Lepidoptera recorded on the Channel Islands, ranging from 50 known on San Miguel to 543+ on Santa Cruz (Table 1). Of the total, 605+ have been recorded on the northern islands (ca 80–83%); about 44% are widespread, occurring on at least one of both the northern and southern islands, while 38% are restricted to the northern group, and 18% to the southern islands.

Resident species judged to be introduced by human activities and/or dependent upon introduced plants, together with suspected vagrants make up about 10% of the fauna but vary from 9–31% on individual islands (Table 2). The proportion is highest on Santa Barbara and San Nicolas (29–31%) because they are remote, and their fauna consists entirely of over water colonists, richer in polyphagous, homodynamic, strong flying dispersers, analogous to the Lepidoptera of Bermuda (Ferguson 1991). On the 2 islands with the richest communities of native plants, Santa Cruz and Santa Catalina, the percent is higher on Catalina because it has a large urban settlement, more ornamental plants, and more traffic from the mainland. The pattern corresponds to the proportions of introduced plant species: 37% on San Nicolas, 29% on Santa Barbara, 30% on Santa Catalina, and 18–24% on the other islands (Table 2) (Wallace 1985; Halverson 1992). The introduction of weeds has paved the way for establishment and has favored the abundance of vagile, "weedy" insects on all the islands.

How well have the Lepidoptera been censused?

We have summarized the history of entomological investigations on the Channel Islands (Miller and Menke 1981) and of Lepidoptera collections through 1981 (Powell 1985). During the past 12 yr there have been productive field surveys on all islands except San Nicolas (acknowledgments). These efforts increased the numbers of known species by 3–28% on the larger islands, 33 to 100+% on the smaller islands.

During 1982–1993, we carried out an extensive inventory of Lepidoptera on the coastal mainland at the University of California Big Creek Reserve, Monterey County, approximately 270 km northwest of the northern island group. The reserve encompasses 16 km², extending from 0 to 900 m elevation, and includes coastal sage scrub, riparian, redwoods, mixed hardwoods, chamise chaparral, and live oak-madrone-ponderosa pine woodlands. Thus it is less than half the area of San Miguel but much larger than Anacapa and Santa Barbara islands, and it includes a greater elevational range than the largest islands. The floral richness is comparable to San Clemente and Santa Rosa. We sampled on 180 dates in all months, made more than 260 ultraviolet light samples, and processed 1,350 larval collections and their rearing (> 90% complete, with fewer than 3% new species of each 3-date sample during the past year, Fig. 2). This is a much more comprehensive sampling effort than has been made at any one of the islands. For example, Santa Cruz, which is 15 times the size of Big Creek Reserve, has been censused for Lepidoptera on about 120–140 dates, with about 100 UV-light samples and fewer than 200 larval collections. The results at Big Creek provide us with a realistic idea of the amount of effort required to achieve a species accumulation curve that approaches an asymptote (Fig. 2).

Table 1. Numbers of species recorded for each superfamily of Lepidoptera on the eight California Channel Islands. See Fig. 1 for island abbreviations.

Superfamily	Mig	Ros	Cru	Ana	Bar	Cat	Nic	Cle	Total
Eriocranioidea			3						3
Nepticuloidea			21			9		4	21
Incurvarioidea		1	11			1			11
Tineoidea	1	5	54	5	4	23	7	10+	65–72
Gelechioidea	5	7	85+	20	13	47+	9	30	127–142
Copromorphoidea			1			1			2
Yponomeutoidea	1	1	9	1	1	4	1	4	11
Sesioidea		1	3	1	1	4		2	5
Cossoidea			2			1			2
Tortricoidea	4	8	46	14	5	37	6	13	63–65
Pyraloidea	5	13	72	19	13	50	12	21	90–92
Pterophoroidea	4	6	12	7	3	13+	4	9	20–22
Geometroidea	5	20	67	17	6	50	6	16	86–88
Bombycoidea			2			1			2
Sphingoidea	1	2	5	2	1	5	1	1	6
Noctuoidea	16	44	114	35	27	97	35	43	168–172
Hesperioidea	2	3	5	2	1	4	1	1	7
Papilionoidea	6	17	30	13	7	25	9	12	37
Totals	50	125	543+	135+	82	372+	91	166+	726–760

Three comparisons of the inventories of the islands and Big Creek can be made: (1) sampling effort (number of dates); (2) taxonomic proportions of the recorded fauna; and (3) numbers of Lepidoptera species related to floral richness.

Sampling effort

In collection dates, Santa Catalina has been the most often sampled, with resident collectors, D. Meadows in 1927–1934 and S. Bennett in 1980–1982. However, nearly all nocturnal collections, including those of visitors, have been at Avalon, Middle Ranch, or Toyon Bay, and

Table 2. Geographic features, numbers, and proportions of nonnative and native species of vascular plants and Lepidoptera of the California Channel Islands. See Fig. 1 for island abbreviations.

	Mig	Ros	Cru	Ana	Bar	Cat	Nic	Cle
Area (km2)	37	217	249	2.9	2.6	194	58	145
Max elev (m)	254	485	744	284	194	644	277	601
n plants	221	450	604	204	101	592	180	342
% nonnative	23	18	23	20	29	30	37	24
n butterfly	8	20	35	15	8	29	10	13
n Lepidoptera	50	125	543	135	82	372	91	166
% vagrant and nonnative Lepidoptera	20	15	9	19	29	16	31	19
Lepidoptera spp/ native plant sp	0.29	0.38	1.14	0.81	1.39	0.89	0.80	0.64

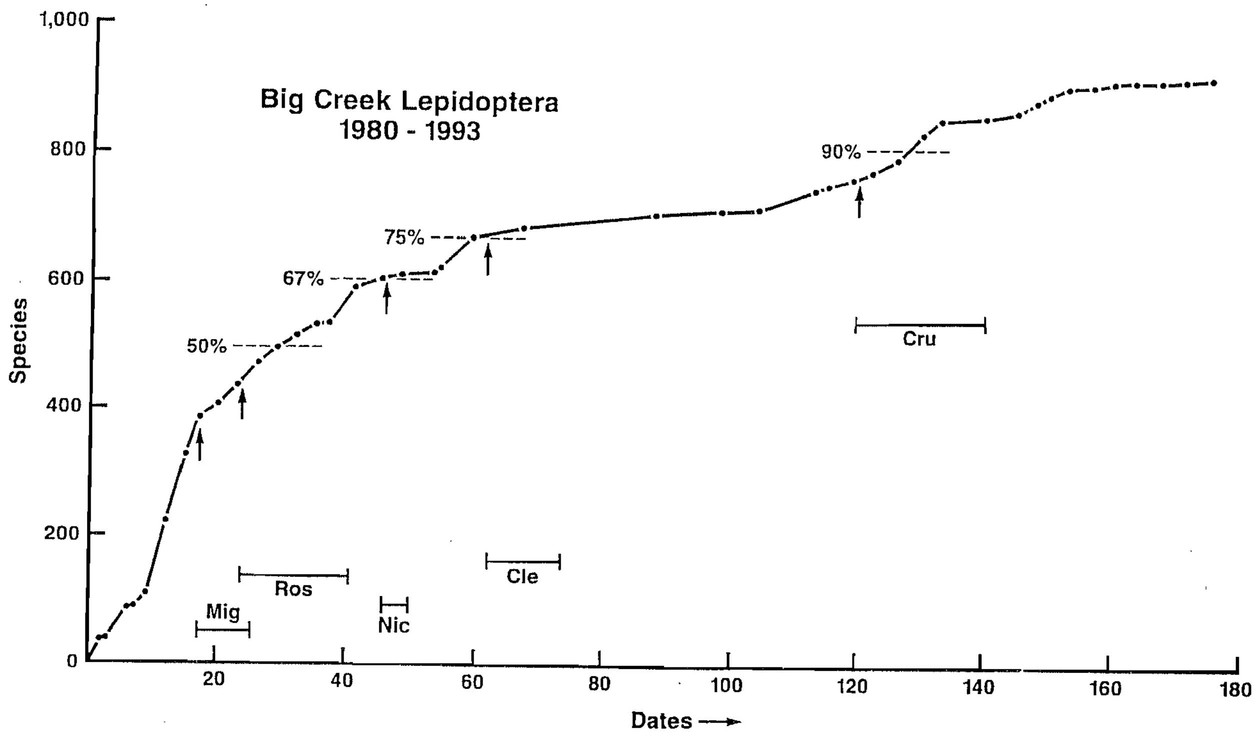

Figure 2. Species accumulation curve compiled during inventory of Lepidoptera at Big Creek Reserve, Monterey Co., CA, with percent accumulation to 900 species (believed to be > 90% of the total fauna). Horizontal bars depict estimated numbers of sampling dates and their respective levels of recorded species for selected Channel Islands (abbreviations, see Fig. 1): minimum dates (larger collections) to maximum dates (including incidental collections of 5 or fewer species).

larval collections have not been emphasized. Santa Cruz has had the most comprehensive emphasis in sampling, but nocturnal collections are primarily from the U.C. Biological Station, with a few at 4 other sites, a sketchy census considering the size and diversity of habitats of Santa Cruz. Because they are so small (2.6, 2.9 km^2), Santa Barbara and Anacapa have had the most sampling per unit area, and their Lepidoptera may be the most completely known despite lack of emphasis on larvae.

Projections based on the rate of species accumulation at Big Creek and the numbers of sampling dates (Fig. 2) suggest that San Miguel and Santa Rosa are less than 50%

sampled, San Nicolas 67%, San Clemente 75%, and Santa Cruz about 85% recorded. This may be a realistic estimate for the smaller islands, but the diversity of habitats on the larger islands dictate the need for greater sampling effort than at Big Creek.

Taxonomic composition

To compare the composition of the fauna with that of the mainland and to project expected total species numbers, we can use 4 taxonomic "guilds." While none comprises a monophyletic taxon, each forms a distinguishable biological group:

1. Microlepidoptera: a paraphyletic assemblage of primitive moths and the more ancestral Ditrysians (upper 10 superfamilies in Table 1). Larvae of Microlepidoptera are nearly all endophagous (leaf miners, stem and root borers, gall inducers) or concealed feeders that make shelters of silk, such as leaf rolls; the vast majority are host plant specialists; about 10% are detritivores. They are tiny to small (FW length mostly 2–12 mm) and often maintain populations in small host plant patches; about 16% are diurnal moths.
2. Pyraloidea + Pterophoroidea; small to moderate-sized moths (FW mostly 8–18 mm), mostly endophagous or concealed feeders, including both specialists and generalists, some of which feed in fungi, dry flowers or seeds, cacti, succulents, or are scavengers in organic refuse. Almost all are nocturnal.
3. macro moths (Geometroidea + Bombycoidea + Sphingoidea + Noctuoidea); moderate sized to large (FW mostly 12–45 mm) and almost all larvae feed exposed, although many at night, retreating to shelter by day; some are specialists, but many are relative generalists in host plant selection. Roughly 95% are nocturnal.
4. butterflies (Hesperioidea + Papilionoidea); moderate sized to large (FW mostly 12–45 mm); larvae usually are specialists and feed exposed, remaining so by day, protected by crypsis. Butterflies are diurnal and use visual cues in the mating systems, with pheromones in close-range courtship, and hence many need larger home ranges than most moths, which use pheromone attraction, usually emitted by stationary females.

There is no comprehensive list of Lepidoptera of California, nor any of its 58 counties. There are partial lists for numerous localities, but only the inventory at the Big Creek Reserve, Monterey County, described above, is considered to be thorough. Table 3 summarizes occurrence of the major guilds by island and at Big Creek. Obviously the representation of microlepidoptera is low and of butterflies high for most of the islands, indicating skewed emphasis in inventory.

The proportions of the known fauna represented by micro-, macro-moth, and butterfly superfamilies indicate that the 4 islands where our Berkeley group has surveyed are more comprehensively documented (Tables 1 and 3).

Table 3. "Guild" composition of the Lepidoptera fauna of the California Channel Islands and Big Creek Reserve, Monterey Co., California, expressed as percent of total species (given in parentheses). See Fig. 1 for island abbreviations.

Locality	(Total)	Microlep	Pyral-Pter	Macromoth	Butterfly
Big Cr	(901)	41	11	41	6.7
Mig	(50)	22	18	44	16
Ros	(125)	18	15	53	16
Cru	(543)	43	15	35	6.5
Ana	(135)	30	19	40	11
Bar	(82)	29	20	41	10
Cat	(372)	34	17	41	7.8
Nic	(91)	25	18	51	11
Cle	(166)	38	18	36	7.8

We emphasized microlepidoptera and larval collections, in surveys of Santa Cruz, Santa Catalina, San Clemente, and San Nicolas on 6, 4, 4, and 1 visits of 30, 9, 14, and 3 days respectively, with groups of 2–6 persons. As a result, microlepidoptera are better known on these islands; for example, there are 235+ microlepidoptera recorded for Santa Cruz (43% of the known fauna) and 127 for Santa Catalina (34%), but only 22 (18%) on the second largest island, Santa Rosa (Table 1). The relative proportions of these guilds show San Miguel and Santa Rosa to be the least censused and the 3 other large islands, Santa Cruz, Santa Catalina, and San Clemente to be the most comprehensively surveyed (Table 3).

Lepidoptera/floral richness

The numbers of Lepidoptera per native plant species (Table 2), also indicate that San Miguel and Santa Rosa islands are poorly known relative to the other 6 islands. Numbers of native plants per unit area decrease approximately logarithmically with increasing area among local floras in California. This relationship exists among the Channel Islands, with numbers fewer than expected on Santa Barbara and San Nicolas, greater than expected on Anacapa (data from Wallace 1985). Data are insufficient to confirm if the same is true of phytophagous insects, so it is unknown whether we should expect the number of Lepidoptera per plant to be comparable between localities of different sizes. There are about 3.1 Lepidoptera/plant species at Big Creek (2.6/native plant). If we assume that phytophagous insects are more depauperate than insular plants because there are many examples of mainland Lepidoptera that seem to be lacking from their host plants on the islands (Powell and Wagner 1993), we might project a ratio of 2.0 species per plant on the islands. Santa Cruz and Santa Barbara, with 1.14 and 1.39 species per plant, have about 60–70% of expected species, while other islands have only about 35–45%, and San Miguel and Santa Rosa 15–20%.

Projected fauna based on butterfly census

Previous projections of the Lepidoptera faunas of San Clemente, Santa Catalina, and Santa Cruz (Powell 1985) were based on the relative proportions of butterfly species recorded and an assumption that all Lepidoptera are similarly depauperate. We now realize those estimates were overly optimistic because the representation of the major guilds in the islands' faunas is disharmonious in contrast to those of the mainland. Leaf miners and other small microlepidoptera are better represented than larger Lepidoptera (Powell and Wagner 1993). The leaf-miner complex is 80–90% intact on host plants that occur on Santa Cruz, and about 70% of the coastal mainland species are known on Santa Cruz, while resident butterflies and larger moths are only about 50% as species rich as a comparable area of the mainland (Miller 1985a, Powell and Wagner 1993).

Based on our analysis (Powell and Wagner 1993), the fauna of Santa Cruz is expected to contain about 48% microlepidoptera, 12% pyraloid-pterophoroids, 35% macro moths, and 5% butterflies. If the butterflies are all recorded, a total of 700 species projected, of which 77% are recorded. Santa Catalina likely has a similar composition, with 580 species projected (64% known). San Clemente may have had comparable faunal makeup but is severely perturbed; if the 11 butterfly species that are believed to be resident comprise the whole fauna, 220 species of Lepidoptera are projected (75% known). Anacapa and San Miguel should be richer than Santa Barbara and San Nicolas, having been connected to Santa Cruz subsequent to submergence. With 14 butterfly species recorded, Anacapa projects to 280 species, and only 48% recorded, which seems possible considering its flora (Table 2). However, more vagile species such as larger butterflies may be overrepresented owing to the islets' proximity to Santa Cruz and the mainland. Santa Barbara and San Nicolas, having been submerged during the Pleistocene, evidently have larger, vagile species more prevalent. The census of Santa Rosa and San Miguel are insufficient to permit projections, but even if the butterflies have been completely inventoried, they may be only 30% recorded.

Santa Cruz possesses about 73% of the species known from the Channel Islands. If that proportion is reduced minimally with further survey and the above projection is reliable, a conservative estimate of about 1,000 species of Lepidoptera is projected for the islands.

Area/Species Relationships

Larger islands tend to have higher elevations and greater topographic relief than smaller ones and therefore more habitats and plant species. As a result, we expect animals, particularly phytophagous insects, to be more diverse on larger islands. For butterflies and the remarkably similar numbers of species in Orthoptera, there is a correlation in area-species relationships (Weissman and Rentz 1976; Powell 1985) (Table 2 and Fig. 3). The correlation coefficient and slope are lower for butterflies (r = 0.61, z = 0.183) than for grasshoppers and relatives (r = 0.74, z = 0.284) but not significantly. Numbers are low for San Miguel, possibly due to its remoteness, and high for Anacapa, as noted. The numbers of butterfly species in Table 4 exclude island records believed to be non-breeding, transient species, but those of unknown status are included, several of which may be older records of vagrants or extinct on particular islands now (Powell 1985).

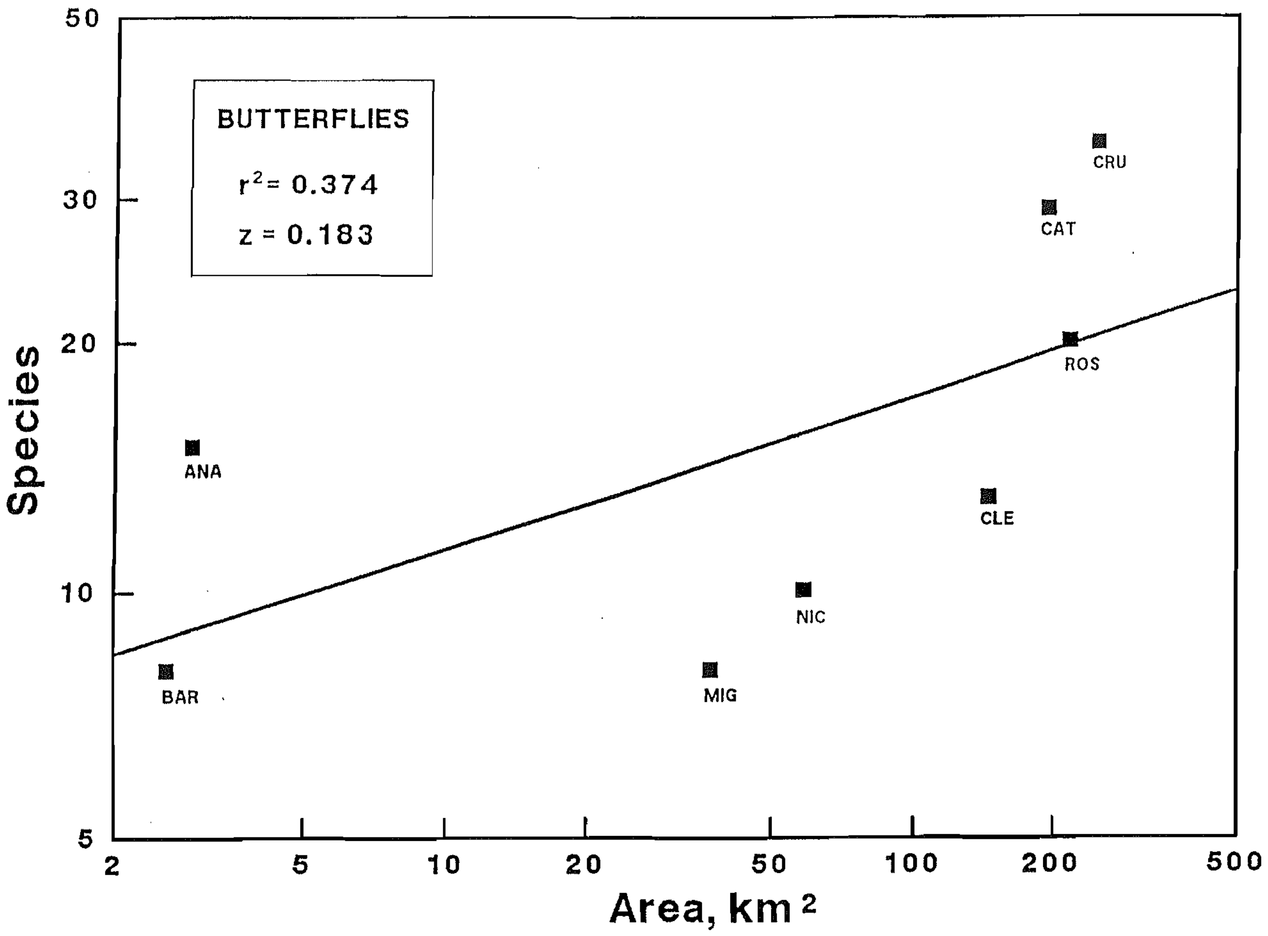

Figure 3. Log-log correlation between number of butterfly species and island area on the California Channel Islands (abbreviations, see Fig. 1).

For moths and Lepidoptera as a whole, there are too few records of microlepidoptera for San Miguel and Santa Rosa to allow meaningful comparison with the other islands (Tables 1 and 3). The log-log linear regression for all species on the other 6 islands shows a better correlation and steeper slope (r = 0.715, z = 0.260) than do butterfly data alone (Fig. 4). These values are lower than those calculated for native vascular plants of the Channel Islands (r = 0.89, z = 0.38) (Raven 1967). For this assessment, I included species thought to be vagrants because decisions must be subjective, and their numbers are negligible relative to island totals. Native species that depend upon introduced plants and nonnative species that have been introduced from other parts of the world and feed on weedy or native plants are included (Powell 1985, examples).

Maximum elevation and numbers of vascular plant species are correlated with area and are principal predictors of species richness in birds of the Channel Islands (Power 1976). Elevations of the 8 Channel Islands explain species numbers of Orthoptera better than area (Weissman and Rentz 1976). For Lepidoptera, the same is true for both plant numbers and elevation (Figs. 5, 6). I used numbers of plants given by Wallace (1985), including nonnatives because many Lepidoptera feed on them. I compared species numbers to maximum elevations, converted to metric from maps published by Menke (1985), which are based on USGS topographic sheets. Elevations given by Wallace, Weissman and Rentz (cited by Power), and by Menke differ among the islands inconsistently and in some cases 10–12%.

If the Channel Islands were of the same age, topographically and ecologically uniform, equidistant from the mainland, undisturbed by nonnative plants and animals, and thoroughly censused, the numbers of species per island might be at equilibrium between extinction and colonization (Munroe 1953; MacArthur and Wilson 1963). Of course the islands share none of these qualities; the area/species relationships reflect habitat diversity and not a dynamic equilibrium between extinction and colonization. Rather, I believe the islands are undersaturated because there was suppression of the original numbers by

Table 4. Described and undescribed Lepidoptera that are considered to be endemic to the California Channel Islands. See Fig. 1 for island abbreviations.

Nepticuloidea
    Stigmella n. sp. (*Lyonothamnus*) Davis (Cru, Cle)

Tineoidea
    Acrocercops insulariella Opler, 1971 (Cru)

Gelechioidea
    Agonopterix toega Hodges, 1974 (Cle)
    Holcocera phenacocci Braun, 1927 (Cat)
    Chionodes n. sp. Hodges ms (Cru, Ana, Bar, Cat)
    Coleotechnites n. sp. (*Lyonothamnus*) Powell (Cru, Cle)
    Ephysteris n. sp. Povolny ms (Cru)
    Scrobipalpula n. sp. nr. *chiquitella* Povolny ms (Cle)
    Scrobipalpula n. sp. (*Lycium*) Povolny ms (Cle)
    Vladimiria? n. sp. Povolny ms (Cru, Cle)

Yponomeutoidea
    Ypsolopha lyonothamnae (Powell), 1967 (Cru, Cle)

Tortricoidea
    Argyrotaenia franciscana insulana Powell, 1964 (Mig, Ros, Cru, Ana, Nic)
    Argyrotaenia isolatissima Powell, 1964 (Bar)

Pyraloidea
    Evergestis angustalis catalinae Munroe, 1973 (Cat)
    Sosipatra proximanthophila Neunzig, 1990 (Cru, Cat)
    Vitula insula Neunzig, 1990 (Cru, Cat)

Geometroidea
    Pero catalina Poole, 1987 (Cat)
    Pero n. sp. nr. *gigantea* Grossbeck, Poole (Cle)
    Pterotaea crinigera Rindge, 1970 (Cle)

Noctuoidea
    Arachnis picta insularis Clarke, 1940 (Ana)
    Arachnis picta meadowsi Comstock, 1942 (Cat)
    Lophocampa indistincta (Barnes & McDunnough), 1910 (Ros?, Cru, Ana, Cat)
    Feralia meadowsi Buckett, 1968 (Cru?, Cat)
    Zosteropoda clementei Meadows, 1942 (Ros, Cru, Cle)

Hesperioidea
    Ochlodes sylvanoides santacruza Scott, 1981 (Cru)

Papilionoidea
    Anthocharis cethura catalina Meadows, 1937 (Cat)
    Strymon avalona (Wright), 1905 (Cat)
    Euphydryas editha insularis Emmel & Emmel, 1975 (Ros)

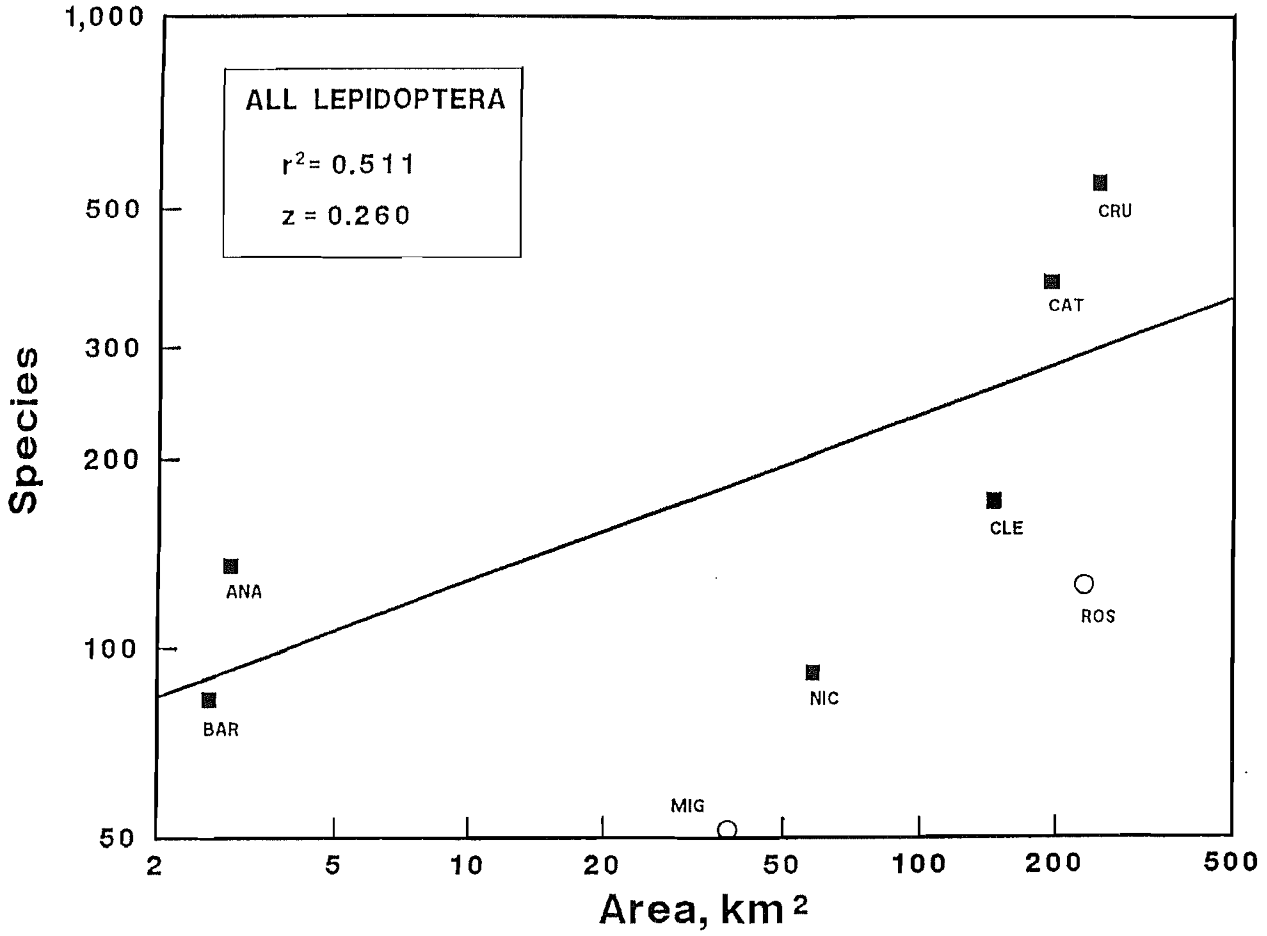

Figure 4. Log-log correlation between number of all recorded Lepidoptera and island area for 6 California Channel Islands (abbreviations, see Fig. 1). Data for San Miguel and Santa Rosa are indicated for reference purpose (circles) but are omitted from the regression because Lepidoptera sampling is insufficient for comparison.

restriction of the islands during Pleistocene submergence and by vegetational stripping by ruminants and weed invasion during the past 150 yr. Despite presence of their larval host plants, many species of the adjacent mainland are missing, and their absence cannot be accounted for by competitive exclusion of ecological homologues (Powell 1981a, 1985, examples).

Endemism

There have been at least 25 species or subspecies of Lepidoptera described from type localities on the Channel Islands, including several that are now considered to be synonyms or are known on the mainland (Powell 1985 review; Poole 1987; Neunzig 1990; Landry 1991). Several undescribed species are believed to be endemic, yielding a total of 28 endemic taxa, members of 26 species, about 3.3% of the fauna (Table 4). Among these, 21 are treated as distinct from any mainland species, although the mainland relatives of several have not been adequately studied. The endemics represent 10 superfamilies; apparent concentration in Gelechioidea probably is a measure of the preliminary state of knowledge of the mainland fauna. There are numerous additional undescribed species, primarily in Tineoidea and Gelechioidea, but the California fauna is too poorly known to identify mainland populations in these taxa.

Endemic taxa appear to be of 2 basic kinds: those that evolved by adaptation under island conditions, and relicts that were more widespread and now are restricted to the islands because of changing conditions on the mainland. Most are closely related to mainland sister groups. There is no direct evidence as to whether they were isolated originally by vicariant separation during geologic events or whether they reached individual islands by dispersal. Differentiated endemics on separate islands are recognized in *Arachnis picta* Packard and the *Argyrotaenia franciscana* (Walsingham) complex, but there are no sympatric sister taxa as are known in flightless crickets (*Cnemotettix*) (Weissman and Rentz 1976).

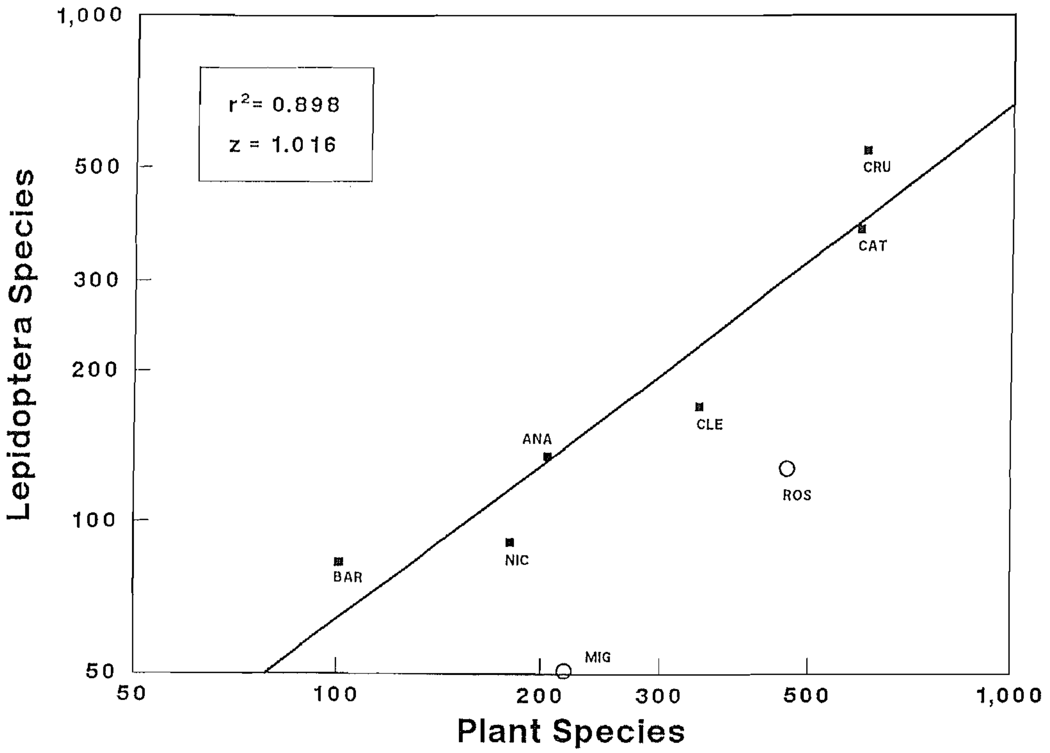

Figure 5. Log-log correlation between numbers of vascular plants and Lepidoptera on 6 California Channel Islands (abbreviations, see Fig. 1). Data for San Miguel and Santa Rosa are indicated for reference purpose (circles) but are omitted from the regression because Lepidoptera sampling is insufficient for comparison.

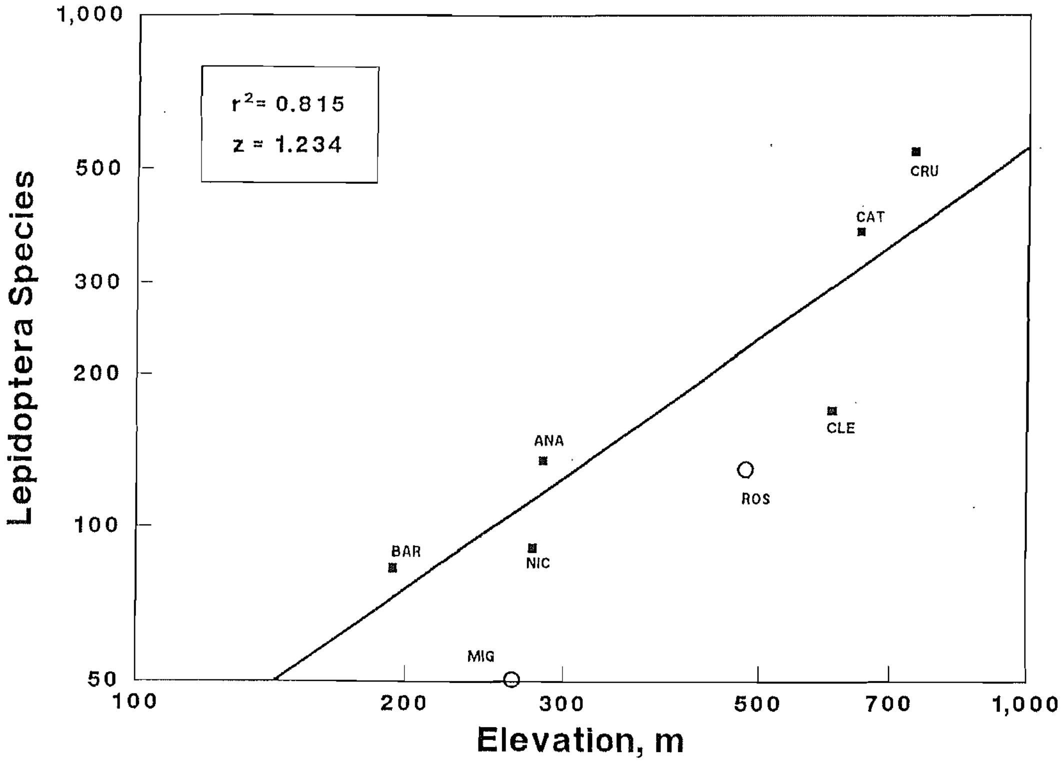

Figure 6. Log-log correlation between number of Lepidoptera and maximum elevation of 6 California Channel Islands (abbreviations, see Fig. 1). Data for San Miguel and Santa Rosa are indicated for reference purpose (circles), but are omitted from the regression because Lepidoptera sampling is insufficient for comparison.

Presumed relicts include 3 species whose larvae feed on the endemic tree, *Lyonothamnus* (Rosaceae): an undescribed nepticulid, *Coleotechnites* n. sp., and *Ypsolopha* (*Trachoma*) *lyonothamnae*. There are fossil equivalents of *Lyonothamnus floribundus* in widespread mainland floras of the Miocene (Raven and Axelrod 1978). One of 2 Rosaceae-feeding species of the *Trachoma* group on the mainland is presumed to be the sister of *Y. lyonothamnae* (Powell 1967). *Coleotechnites* n. sp. also feeds on other Rosaceae on San Clemente, *Prunus lyonii*, a plant represented by a similar evergreen cherry in Miocene floras of the mainland, and on *Heteromeles arbutifolia*. A sister *Coleotechnites* in the San Francisco Bay area feeds on *H. arbutifolia*.

The endemic Lepidoptera display interesting geographical patterns (Fig. 1). Most (60%) are restricted to 1 island, and all but San Miguel and San Nicolas have at least 1 endemic, with 6 on Santa Catalina and 5 on San Clemente, but none occurs on both of the large southern islands, reflecting their long history of isolation and more distant separation prior to mid-Miocene. Six occur on both Santa Cruz and Santa Catalina but not San Clemente (2 of them also on Anacapa and/or Santa Barbara), while conversely, 4, including the 3 *Lyonothamnus* associates, are known from Santa Cruz and San Clemente but not Santa Catalina. The latter guild perhaps have been overlooked on Santa Catalina, but Miocene fossils allied to the typical subspecies of *L. floribundus* on Santa Catalina are coastal, west of the San Andreas fault, while those of the Santa Cruz-San Clemente subspecies, *L. f. aspleniifolius*, occur to the north in the interior (Raven and Axelrod 1978).

Endemic differentiation also occurs at more subtle levels in many moths, such as in proportions of polymorphic phases in Arctiidae, size of individuals, larger or smaller, food plant preference, and seasonal phenology (Powell 1985, examples).

Faunal Relationships

Geographical distribution patterns of Lepidoptera of the California Channel Islands may be categorized into 5 types, in addition to insular endemism:

1. *Widespread.* Most Channel Island insects occur widely on the mainland, in California ranging from the southern California coastal area or the Peninsular Ranges to northern California and beyond. As noted, 44% of the species occur on 1 or more of both the southern and northern islands, but many others that are known only from 1 island, particularly Santa Cruz or Santa Catalina, are widespread on the mainland. An estimated 70–75% of the total fauna are widespread, including 10% that are nonnative, weedy, and/or vagrant species.
2. *Californian Province.* This region harbors many unique communities of plants and animals rich in endemic taxa (Miller 1951; Stebbins and Major 1965). It has been defined as the cismontane portion of southern California, including the Peninsular Ranges, and adjacent Baja California, extending northward to the Santa Lucia Mountains and Monterey area or the Hamilton Range in the San Francisco Bay area (Miller 1951; Powell and Hogue 1979). Many of its Lepidoptera occur on the Channel Islands, including the 21 endemic species; I estimate that about 10% of the island fauna consists of species limited to this region. The tortricid, *Argyrotaenia niscana* (Kearfott), a specialist feeder on chamise (*Adenostoma fasciculatum*) (Rosaceae) is typical (Powell 1985, examples).
3. *Coastal Strand.* A small element of the insular fauna (ca 2%) consists of beach dune and coastal strand insects (Powell 1981b). Although this component consists partly of Californian Province species, others are more widely distributed along the Pacific Coast and even Gulf and East coasts. Species of microlepidoptera that feed on *Ambrosia chamissonis* exemplify the group, which has exceptional ability to immigrate and colonize, such as on isolated, small beaches. For example, only 14% of the species on San Nicolas, the most remote island, are oligophagous plant feeders, all of them on beach and coastal strand plants (Powell 1985).
4. *Desert.* As is true of the flora (Raven and Axelrod 1978), an appreciable number of Lepidoptera on the Channel Islands have affinities to the arid south or east, usually interior mainland communities. They often occur disjunctly away from the adjacent coast, examples include *Lithariapteryx jubarella* Comstock, on Santa Cruz (Powell 1991); *Noctueliopsis grandis* Munroe, a San Clemente crambid known on the mainland only from north-central Baja California, and the endemic geometrid, *Pterotaea crinigera* on San Clemente and its low desert sister species, *P. crickmeri* (Sperry) (Rindge 1970). Such species may be very widespread in the arid Southwest, e.g., the scythrid, *Arotrura longissima* Landry (1991), which occurs on all 4 southern islands and ranges to western Texas and the Tres Marias Islands off the coast of Nayarit, Mexico. About 6–8% of the insular fauna shows this affinity, particularly in the southern islands (14% on San Clemente). Presumably these represent relicts of past arid climates, from mid-Pliocene, which was the driest part of the Tertiary in the region, into the Xerothermic period, 4–8,000 yr ago (Raven and Axelrod 1978).
5. *Northern.* Raven (1967) estimated that at least 10% of the vascular plants of the Channel Islands have mainland distributions not adjacent to the islands, and the

great majority of those are northern species. Based on macro moths and selected taxa of pyraloids and microlepidoptera, I estimated that about 14% of the fauna of the northern island group and 6% of the southern show this northern affinity (Powell 1985). For instance, 5 species of Incurvarioidea that occur on Santa Cruz are abundant in the central Coast Ranges and Sierra Nevada foothills but are absent or persist only in a few locally favorable sites in southern California, presumably relicts of past pluvial times (Powell 1985). This relationship is reflected in the higher proportion of shared species between Big Creek, Monterey Co., and Santa Cruz (29%) than between Big Creek and Santa Catalina (20%) (Table 5).

Inter-island similarity

Pair-wise comparisons of the species roster between islands shows low percent similarity when shared species are compared to total species (Table 5), because so many species are known only from Santa Cruz or Santa Catalina. Comparison of shared species to the smaller fauna in each pair shows 77–79% resemblance between Santa Cruz and the adjacent islands that were joined during glacial times. By contrast, among the other larger islands, Santa Catalina and San Clemente share about the same proportion of their fauna with Santa Cruz, 66% and 69% respectively, as San Clemente does with Santa Catalina (67%).

Santa Catalina and San Clemente are situated only 35 km apart and are more similar in size than either is to Santa Cruz. However, they share only 27% of their total species inventory, and this is attributable to several factors. Geological evidence reviewed above indicates much more distant origins for these 2 islands than today's geography indicates. Separate origins are suggested by marked differences in the flora (Raven 1963), in patterns of endemism in Lepidoptera (Fig. 1), and by the different relationships to Miocene fossil floras of the mainland, such as the *Lyonothamnus* example noted above. San Clemente is more arid, and this is reflected in the vegetation. Santa Catalina has 45% coastal sage scrub and 1.3% oak woodland (Minnich 1980). It is a much richer flora (1.6X the number of species, Wallace 1985), with a long roster of species and genera that are lacking from San Clemente (Raven 1963). Included are many perennials used by Lepidoptera as larval hosts, such as *Populus, Salix, Cercocarpus, Holodiscus, Rosa, Rubus, Arctostaphylos, Brickellia, Solidago*, and species of many other genera that provide the framework of the Santa Catalina Lepidoptera community. Irrespective of similarity in size, San Clemente could not support the diversity and richness in phytophagous insects that its neighbor does. Finally, San Clemente had a more severe impact from ruminants, particularly goats, which fragmented many of the extant plants into tiny patches.

Butterflies show much higher percent congruence between islands than do the moths. This may be in part an artifact of sampling, with the butterfly census more complete on all islands. However, the insular butterflies tend to be species that are wide ranging as adults (i.e., *Papilio*, pierids, *Junonia, Vanessa*, and weedy Hesperiidae make up about 40% of the species), most are homodynamic (55%), and polyphagous and/or feed on weedy plants (58%) (Powell 1985). Taxa that are more niche-specific, often with univoltine species (e.g., *Speyeria*, melitaeine Nymphalidae, Lycaenidae) are rare on the islands. Homodynamic, polyphagous, and weedy species are proportionately less numerous among moths, especially Geometridae and microlepidoptera.

Table 5. Pairwise similarity in Lepidoptera species between Big Creek, Santa Cruz, Santa Catalina, and San Clemente islands, and between Santa Cruz and adjacent islands, expressed as total shared species (upper right matrix), percent shared of total fauna (left of slash), and percent of species shared in the smaller fauna of each pair (*italics*). See Fig. 1 for island abbreviations.

	BigCr	Ros	Cru	Ana	Cat	Cle
BigCr		—	320	—	215	87
Ros	—		96	—	—	—
Cru	29/*60*	17/*77*		106	247	115
Ana	—	—	19/*79*		—	—
Cat	20/*58*	—	37/*66*	—		112
Cle	9/*52*	—	19/*69*	—	27/*67*	

Acknowledgments. In addition to the collectors and taxonomists cited elsewhere (Powell 1985, Powell and Wagner 1993), I acknowledge the following for inventory efforts during recent years: S. Bennett (Santa Catalina 1981–1982), C. Drost (Anacapa, Santa Barbara 1985–1988), J. De Benedictis (San Clemente 1987), P. Super (San Miguel 1990). This study has been made possible by the assistance of taxonomists; I again thank those previously credited, as well as Y.-F. Hsu (Heliodinidae), J.-F. Landry (Coleophoridae, Scythrididae), D. Lafontaine and R. Robertson (Noctuidae), H. Neunzig (Pyralidae), D. Povolny (Gelechiidae). The species numbers regression calculations and figures were prepared by J. De Benedictis. Cooperation by authorities of the following institutions enabled use of collections in their care: California Academy of Sciences (CAS); Essig Museum of Entomology, U. Calif. Berkeley (EME); Los Angeles County Museum of Natural History (LACM); Peabody Museum, Yale University (PMY); Santa Barbara Museum of Natural History (SBMNH); San Diego Natural History Museum (SDNHM); National Museum of Natural History (USNM). Helpful comments on the manuscript were provided by Paul DaSilva and two anonymous reviewers.

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The Fourth California Islands Symposium: Update on the Status of Resources
Edited by W. L. Halvorson and G. J. Maender. 1994. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Ecological Monitoring in Channel Islands National Park, California

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Abstract. Natural resource managers need to understand the natural functioning of and threats to ecosystems under their management. They need a long-term monitoring program to gather information on ecosystem health, establish empirical limits of variation, diagnose abnormal conditions, and identify potential agents of change. The approach used to design such a program at Channel Islands National Park, California, may be applied to other ecosystems worldwide. The design of the monitoring program began with a conceptual model of the park ecosystem. Indicator species from each ecosystem component were selected using a Delphi approach. Scientists identified parameters of population dynamics to measure, such as abundance, distribution, age structure, reproductive effort, and growth rate. Short-term design studies were conducted to develop monitoring protocols for pinnipeds, seabirds, rocky intertidal communities, kelp forest communities, terrestrial vertebrates, land birds, terrestrial vegetation, fishery harvest, visitors, weather, sand beach and coastal lagoon, and terrestrial invertebrates (indicated in priority order set by park staff). Monitoring information provides park and natural resource managers with useful products for planning, program evaluation, and critical issue identification. It also provides the scientific community with an ecosystem-wide framework of population information.

Keywords: Channel Islands National Park; natural resources monitoring; pinnipeds; seabirds; rocky intertidal; kelp forest; terrestrial vertebrates; land birds; terrestrial vegetation; fishery harvest; visitors; weather; sand beach; coastal lagoon; terrestrial invertebrates.

Introduction

How healthy are ecosystems in Channel Islands National Park? Without management intervention, are they capable of coping with altered water supplies, human consumption of "renewable" resources, accelerated invasions of nonnative species, physical impacts of visitors, and air pollution? How do we determine when to intervene in natural resource issues, and how far should we go in our remedial actions? Land managers need answers to questions like these to protect threatened ecosystems worldwide.

Ecosystems are changing in ways never before seen. Lack of historical and contemporary data makes it difficult to clearly define the nature and extent of these changes (Orians 1986). Unless we begin to gather empirical data on the health of ecosystems now, the changes may become irreversible and fatal. Alternately we may unnecessarily impose constraints on human endeavors out of fear of the unknown. Politically, this kind of uncertainty tends to freeze action for fear of over-reacting or changing systems perceived as naturally static (Wurman 1990). Uncertainty about ecosystem dynamics ranges from concerns for global climate change to visitor disturbance of wildlife and trail erosion.

In this paper we present a conceptual approach to designing ecological monitoring programs to address these kinds of issues. We also describe a specific application of this concept to Channel Islands National Park and International Biosphere Reserve, California, to serve as a model for the U.S. National Park System and other protected natural areas.

Design of a Monitoring Program

An appropriately designed natural resources monitoring program can reduce uncertainty and address critical questions about system dynamics. What to monitor, and the appropriate level of accuracy, varies from area to area, but the basic reasons for monitoring are universal. They are to: