THIRTY YEARS OF RESEARCH ON CALIFORNIA'S CHANNEL ISLANDS: AN OVERVIEW AND SUGGESTIONS FOR THE NEXT 30 YEARS

Robert C. Klinger[1, 3] and Dirk Van Vuren[2]

[1]The Nature Conservancy, 213 Stearns Wharf, Santa Barbara, California 93101
(805) 962-9111, E-mail: rckscip@aol.com
[2]Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, 95616
(530) 752-4181, E-mail: dhvanvuren@ucdavis.edu
[3] Current Address: Section of Evolution and Ecology, University of California, Davis, CA 95616
(530) 752-1092, E-mail: rcklinger@ucdavis.edu

ABSTRACT

In the 32 years since the publication of the first symposium on the biology of the California Islands, there have been distinct stages that have emphasized different aspects of the biology and management of the islands. Using papers published in the proceedings, we describe these different stages in relation to broader contemporary themes in ecology, evolution, and conservation, and comment on how these themes may have shaped island research agendas. We compare and contrast earlier research on the islands to what is currently underway, then make suggestions on how greater coordination and integration of academic and management studies can lead to a broader understanding of California Island ecosystems, and unify conceptual themes for research and management across the eight islands.

Keywords: Anthropology, archaeology, biogeography, botany, California Islands, Channel Islands, conservation, ecology, evolution, geology, islands, research, zoology.

INTRODUCTION

The four symposia on the California Islands (Philbrick 1967; Power 1980b; Hochberg 1993; Halvorson and Maender 1994) represent an impressive collection of scientific information that spans a period of rapid and significant evolution of thought in the physical and biological sciences. In the more than 30 years since the first symposium on the California Islands was held, major conceptual and technological advances in the physical and biological sciences have occurred at a startling rate. In his introduction to the second symposium, Power (1980a) noted that in the 13 years since the first symposium there had been major changes in scientific concepts and techniques. These included the way scientists perceived the dynamic nature of biological and geological systems, the ways which taxonomic relationships could be tested and represented, and how computers were starting to be used to help analyze large and unwieldy data sets. Since Power's observations, not only have we seen these concepts and techniques increase in sophistication but also new ones have continued to be developed. For example, relatively simple concepts of ecological succession have been largely superseded by more complex patch dynamic/disturbance driven mechanisms of community change (Pickett and White 1985), concepts of the dynamic equilibrium of island biogeography are now nested within the framework of metapopulations (Hanski and Gilpin 1997), the taxonomy and systematics of many groups of organisms are being revised based on analyses done at the genetic level (e.g., Burns 1998; Steppan 1998), and the cyclical nature of some populations is seen as a special case of more complex spatial and temporal patterns of population change (Korprimaki and Krebs 1996; Rohner and Krebs 1998).

Just as scientific techniques and concepts have evolved, so have ownership status, land use activities and management priorities on the islands. The National Park Service designated the Northern Channel Islands as a National Park, assumed management of San Miguel Island from the U.S. Navy, and bought Santa Rosa Island and part of Santa Cruz Island. The Nature Conservancy acquired ownership of the western 90% of Santa Cruz Island, and land use on Santa Catalina Island shifted away from ranching and hunting to ecological preservation and restoration. The U.S. Navy started an active natural resource management program on San Nicolas and San Clemente islands. And, as the human population of southern California has expanded, so have direct and indirect impacts to the islands associated with this growth. One result of these changes is that the physical and biological systems on the islands are also changing, and this has resulted in an increasing amount of research on a wider variety of topics.

In this paper we take an overview of the last 30 years of research on the California Islands. Our primary goal is to identify patterns in how research on the islands has evolved and characterize the dynamic nature of this intellectual evolution. By relating these changes to contemporary developments in scientific concepts, we can begin to identify significant gaps in our knowledge of particular processes or groups of organisms, and hopefully create a foundation for guiding research into the next 30 years.

METHODS

We based our analysis on a summary of the contents of the four previously published symposia (Philbrick 1967; Power 1980b; Hochberg 1993; Halvorson and Maender 1994). We limited the scope of our analysis to papers published in the four symposia because they are the only body of work that collectively represents the dynamic nature of research on the islands. Papers published in refereed journals or in special proceedings on specific topics (e.g. entomology, Menke and Miller 1985) are most likely not representative of the scope of research being conducted on the islands.

We tallied the number of papers and authors from the proceedings of each symposium. The affiliations of all coauthors on a paper were classified as Academic, Museum (including botanic gardens), Government, and Private (nonpublic trust organizations such as The Nature Conservancy or Catalina Island Conservancy, consulting businesses, etc.). Multiple publications by authors were treated independently.

We used all papers published in the first four symposia to define two sets of categories. The first was a set of seven general subject groupings, each defining a particular area of natural or cultural science that we felt best described the content of the paper. These categories included Anthropology (research focused on cultural systems predating European settlement of the islands), Botany (research focused on terrestrial and marine plants), Conservation (research focused on the preservation of natural resources), Ecosystem Processes (research focused on the relationship between physical and biological systems, and involving organisms spanning different phylogenetic kingdoms), Geology (research focused on earth structure/history), History (research focused on recent cultural systems), and Zoology (research focused on terrestrial and marine animals).

Next, we categorized papers into 11 groups based on the concept that we felt best described the content of the paper. These included Anthropology (same definition as above), Community Ecology (studies on patterns in the interrelationships of multiple species and the processes driving these patterns), Comparative/Descriptive Ecology (natural history observations or patterns for multiple species, but not analyzing the interrelationships among the species or the processes driving the patterns), Conservation Biology (studies focused on the preservation of natural systems, communities, and species), Ecosystem Processes (same definition as above), History (same definition as above), Island Biogeography (studies focused on factors determining species distribution, abundance, and persistence on the islands, and usually relative to the mainland), Paleontology (studies focused on the geologic record of organisms on the islands), Physical Geology (studies focused on geological processes, structure, and history of the islands), Population Biology/ Ecology (studies focused on the ecology of individual species), and Systematics/Evolution (classification and evolution of organisms).

The classification scheme we used for the papers is admittedly subjective, but we feel it captures the most significant areas of research in the islands over the last four decades. Some of the categories we used to classify the papers overlap to a degree (for example, Comparative/Descriptive Ecology and Population Biology/Ecology), and we recognize that legitimate justification could be made for inclusion of some papers into more than one category. However, we did not encounter this situation very frequently.

RESULTS

The number of papers increased 153% from the first to the second symposia, but increased only 9% from the second to the third and 6% from the third to the fourth (Table 1). The number of authors increased 175% from the first to the second symposia, 18% from the second to the third, and 17% from the third to the fourth. Authorship was dominated by academics in the first two symposia (almost 90%) but decreased in the third and fourth (55% and 52% respectively). The percentage of authors affiliated with government organizations increased steadily with each symposium, while the percentage of authors affiliated with museums fluctuated from 7 to 17% (Figure 1). Authors from private organizations did not appear on any papers in the first two symposia, but comprised 14 to 17% in the last two symposia.

In terms of general subject categories, botany and zoology dominated the first and second symposia (76% and 71% respectively), but decreased 25 to 50% in the third and fourth symposia, although they still made up a higher proportion of papers than other categories (Table 1). Zoology papers dominated the second and third symposia. The percentage of papers on anthropology doubled in the last two symposia compared with the first two symposia, while the percentage of papers on geology remained relatively constant, except for a drop in the second symposium. The percentage of papers addressing conservation issues increased three to five fold in the fourth symposium compared with the first three symposia. History as a subject first appeared in the third symposium, and the percentage of papers in this

Table 1. The number of papers in seven subject categories published in the proceedings of the four California Islands symposia, 1967-1994.

Subject	Symposium				
Category	1st	2nd	3rd	4th	Total
Anthropology	1	2	5	5	13
Botany	7	7	6	7	27
Conservation	0	2	3	11	16
Ecosystems	0	5	2	4	11
Geology	3	3	7	7	20
History	0	0	3	5	8
Zoology	6	24	21	11	62
Total	17	43	47	50	157

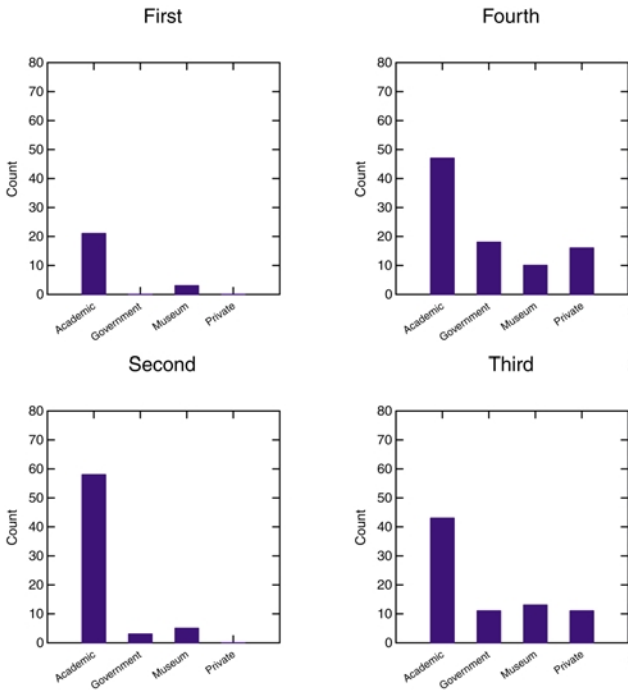

Figure 1. The organizational affiliation of authors of papers published in the proceedings of the four California Islands symposia, 1976-1994.

category almost doubled from the third to the fourth symposia. A relatively low percentage of papers dealing with ecosystem processes appeared in the last three symposia.

Studies on marine organisms and invertebrates have shown an overall increase. Of the seven botany papers in the first symposium, two looked at components of the marine environment. Two of the six papers on zoology in the first symposium focused on marine animals, while 14 papers in the second symposium were related to marine organisms; proportionally this is about the same as in the first (about 25%). Only one botany paper dealing with marine organisms appeared in the third symposia, but in the fourth symposium three papers addressed marine plants directly and another three had aspects of marine plants incorporated in them. Sixteen papers in the third symposium were focused on marine animals, while only seven did in the fourth symposium.

There were very clear shifts between the four symposia in the 11 groups we used to describe the conceptual content of the paper (Table 2). In the first two symposia, island biogeography, evolution, and descriptive ecology made up about half of all of the papers presented. However, by the third and fourth symposia, island biogeography and evolution comprised less than 6% of the papers. About 20% of the papers in the third symposium were in the descriptive ecology category, but these fell to about 7% in the fourth symposium. The proportion of papers dealing with paleontology, ecosystem processes, and community ecology fluctuated widely among the four symposia, and in no discernible pattern. No papers on conservation biology appeared in

Table 2. The number of papers in eleven conceptual categories published in the proceedings of the four California Islands Symposia, 1967 - 1994.

Subject Category	Symposium 1st	2nd	3rd	4th	Total
Anthropology	1	2	5	5	13
Community Ecology	2	0	6	3	11
Conservation Biology	0	0	3	11	14
Descriptive Ecology	4	8	9	4	25
Ecosystems	0	6	1	6	13
Evolution	3	8	2	1	14
Geology	4	2	5	7	18
History	0	0	3	5	8
Island Biogeography	2	7	1	1	11
Paleontology	0	4	2	1	7
Population Biology	1	5	10	7	23
Total	17	43	47	50	157

the first two symposia, but increased dramatically between the third and fourth ones. The proportion of papers on population biology increased two to four fold during the first three symposia, then declined about 50% from the third to the fourth symposia. With the exception of the second symposium, the proportion of papers on geology ranged from 10 to 23%. Although the proportion of papers on anthropology and history has never exceed 10% in any one symposium, the proportion has doubled in the third and fourth symposia when compared with the first two.

DISCUSSION

The symposia on the California Islands represent one of the more long-term and comprehensive collections of information on any area of the world. What makes this body of knowledge all the more impressive is that there has been no one single theme, process, or organism that has served to unify the tremendous variety of work being done on the islands. Also, there has been no formal group of people whose primary responsibility was seeing that the data were coordinated and presented professionally on a regular basis. Instead, it has been the nature of the islands themselves, and the multitude of issues associated with them, that has attracted so many scientists for so many years to devote themselves to bring about an understanding of the system, and consequently a better understanding of nature in general. Consequently, it has been the efforts of numerous dedicated people from many different organizations who have managed to find funding, and the time, to organize a forum and publish the results for most of the ongoing work in the islands.

The major patterns we observed among the four California Islands symposia reflect the evolution of scientific concepts, changes in ownership and management of the islands, and recognition of the influence of human use on the

island's natural systems. The shifts that can be seen in the relative importance of different disciplines, concepts, and organizational affiliation of the authors all demonstrate these changes.

The clearest example of a dramatic shift in scientific thinking is away from the "islands as natural laboratories" philosophy which dominated the period from the 1960s through the early 1980s. Island biology has evolved beyond simply describing natural patterns and processes to increased interest in preserving island resources. Over the last 10 to 15 years conservation biology has emerged as an identifiable discipline, and as a result the "natural laboratory" philosophy has been modified and transformed into focusing on conserving the unique species and natural communities on the islands.

In the first two symposia, the dominant themes were evolution and island biogeography. This reflected the general interest in the type of adaptations characteristic of island populations (Carlquist 1974), and how these adaptations evolved. Similarly, the concept of island biogeography was one of the major ecological and evolutionary paradigms of the 1960s and 1970s (MacArthur and Wilson 1967). Of major importance in this shift in philosophy is that the theory of island biogeography has declined in importance as a freestanding paradigm (Hanski and Gilpin 1997). Although it served as the foundation for an increase in the theory and practice of conservation (Simberloff 1988; Shafer 1990), the underlying concepts of classical island biogeography have been absorbed and modified by other ideas and concepts in ecology and conservation biology. From a theoretical standpoint it is now generally considered as a variation of metapopulation dynamics within the context of fragmented habitats and populations (Harrison 1994; Hanski and Simberloff 1997). From a practical standpoint there has been an increased recognition that dispersal among many isolated populations at the landscape level is probably more important in the persistence of most species than classical immigration-extinction processes (Wiens 1997). Although there is still substantial interest in evolutionary adaptations of island populations, the functional context in which the species exist has taken on great importance, as has the importance of their conservation (Vitousek et al 1995).

Of note is the increase in the diversity of topics over the last 30 years. This has been especially true for studies on the marine environment, invertebrates, and the history of human cultures on the islands. Studies on marine organisms and systems increased in both scope and complexity, and by the fourth symposium an entire section was devoted to studies on the marine environment. Similarly, a very large component of the third symposium focused on invertebrates, a group of organisms that had not been well represented in the previous two symposia.

The first two symposia had a very small proportion of papers dealing directly with the patterns, trends, and impacts of human use on the islands. While the emphasis of the third and fourth symposia still remained natural science, the proportion of papers dealing with human culture has substantially increased. An excellent example of the importance of maintaining this interdisciplinary approach is Glassow's (1993) paper on archaeological evidence of long-term climate change on the northern islands.

The importance of ownership and land management on the types and emphasis of scientific research on the islands should not be underestimated. To varying degrees, the National Park Service, The Nature Conservancy, the Catalina Island Conservancy, the National Oceanic and Atmospheric Administration, and the U.S. Navy all have the protection and restoration of the biological diversity of the lands and waters of the islands they own as a management goal. In addition, various county, state and federal agencies have regulatory authority and responsibility on the islands. As ownership and land management on the islands changed over the last 30 years, so did the nature of some of the research. It is likely that the increase in the proportion of non-academic authors and increased emphasis on topics related to resource conservation are directly related to these ownership and land management changes.

A dominant theme of the early symposia was descriptive ecology. The collection of basic life history observations is a typical first step in the scientific process. This was probably facilitated by increased accessibility to the islands as a result of the changes in ownership and land use practices, as well as establishment of field stations for scientific research on Santa Cruz and Santa Catalina islands. However, in the fourth symposium papers dealing with descriptive ecology dropped by 65% from the previous three meetings. It would be unfortunate to see this trend continue because our knowledge of the basic life history of the majority of species on the islands needs further work, especially for many of the rare and/or endemic species.

Knowledge of the life history patterns of the plant and animal species on the islands is important from both scientific and management perspectives. For example, without these data scientists will not be able to compare the life history strategies of endemic and non-endemic species, or analyze how adaptations of island species evolved relative to conspecifics on the mainland. Two recent examples point out the importance for resource management of having basic life history information. Since the last symposium, over a dozen endemic plants on the northern Channel Islands have been listed as threatened or endangered by the U.S. Fish and Wildlife Service, and island foxes (*Urocyon littoralis*) on San Miguel and possibly Santa Cruz islands have undergone severe population declines (Coonan et al. 1998). The conservation of these species will depend directly on an understanding of their basic life history (e.g., reproductive biology, recruitment and mortality patterns, age structure, distribution, habitat requirements, diet).

We found it interesting that of the four symposia only the first had a stated focus (Philbrick 1967). Understanding how the subjects of research on the islands have changed over the last 30 years not only enables us to evaluate what has been done, but to also identify what hasn't been done. This in turn can lead to the development of a framework

that could help to integrate and coordinate research among the islands over the course of the next 30 years. Not only would this be an effective step in the process of synthesizing a cohesive understanding of different ecological and evolutionary processes across the islands, but it would give resource managers an extensive database for developing, monitoring, and evaluating management programs. As an initial step in developing a research framework for the islands, we propose four general suggestions that we feel would be useful for optimizing the use of scientific expertise and resources.

Our first suggestion is, whenever possible, to set research and management projects in an appropriate theoretical framework. For example, despite an overall increase in the diversity of topics and the number of papers and authors, many important concepts in the fields of ecology, evolution, and conservation biology have been neglected in publications in the symposia. Some concepts that have direct importance to the islands include metapopulations, disturbance and patch dynamics, community assembly processes, the biology of small populations (Viable Population Theory), and landscape ecology. Studies focused around these concepts would give a theoretical foundation and empirical unity to a large array of potential research projects among the islands. For example, because of the many rare species on the islands, it would be worthwhile to identify which ones (if any) demonstrate metapopulation dynamics, or determine which ones are at risk from different deterministic or stochastic processes (e.g., habitat alteration, demographic stochasticity, etc.). Similarly, with the ongoing removal of feral animals and livestock, studies that focused on how species within the communities reassemble themselves against a backdrop of deterministic successional processes and stochastic disturbance events would have importance from both academic and practical perspectives.

Our second suggestion is that genetic, demographic, and evolutionary studies of rare populations be linked across all of the islands. The demographic trends should be collected over long time periods (>10 years) and associated closely with levels of genetic diversity and environmental variability (e.g., weather, habitat changes). Some aspects of this have been underway for several years (R. Klinger, unpubl. data; D. Wilken and K. McEachern, pers. comm.), but there is a need to initiate studies in a coordinated program across more islands. Ongoing and residual impacts from the degradation and loss of habitat from overgrazing by feral and domestic livestock will continue to occur on the islands for many years. Identifying which species are most at risk from particular impacts will be a tremendous tool for protecting or restoring these species, as well as contributing to a greater understanding of the biology of rare species.

Third, we recommend the continuation of basic life history studies of both plant and animal species. Basic data to collect would include distribution, habitat occurrence, relative abundance among habitat types, and reproductive patterns. Because it is unrealistic to expect to obtain detailed information on many species in a meaningful period of time, we advocate a prioritization procedure based on species diversity within taxa, ecological importance, and management significance. For instance, there are relatively few species of herptiles and terrestrial mammals, so these species would be relatively high in priority. Among these species, the island spotted skunk (*Spilogale putorius littoralis*) is one of only two mammalian terrestrial predators on the islands, it only occurs on two islands, and it is thought to be low in abundance (Crooks and Van Vuren 1994). Based on the above criteria, spotted skunks would be a high priority species. Some alien plants such as fennel (*Foeniculum vulgare*), horehound *(Marrubium vulgare*), and milk thistle (*Silybum marianum*) would also be high priority because of their management significance.

Our final suggestion is that ecosystem studies based on resource monitoring programs be used as ways of integrating community and single species studies at multiple scales. Dramatic changes in the island's plant and animal communities can be expected to occur as different land management programs are phased out and others implemented. Relating these changes to biotic and abiotic variables at multiple scales will not only increase our understanding of how different ecological processes operate at different scales, but will provide resource managers with the basic data needed to prioritize, design and evaluate management programs in a specific ecological context (Klinger 1998). The most comprehensive monitoring program in the islands is that of Channel Islands National Park (Davis et al. 1994), and we recommend that many of the protocols they have developed be adopted on all of the islands.

Of importance in this discussion is a mechanism for implementing these suggestions. Of obvious importance are funding and personnel, but less obvious is how to structure and coordinate these programs among so many different organizations. Although proposing a detailed structure that deals with these issues is beyond the scope of this paper, we do offer some initial suggestions.

Probably the most important step is to expand the scope of activities of the Channel Islands Research Coordinating Committee (CIRCC). This group was originally set up as a steering committee for meetings, and as a way of disseminating information among the various agencies and organizations conducting research on the islands. Representatives from most of the organizations and agencies participate in CIRCC, and the more or less annual updates on respective research and management activities have been effective. However, CIRCC has never developed a process to truly coordinate research among the agencies. We propose that CIRCC hold a series of meetings to identify key ecological issues and questions common to all the islands, develop protocols for addressing the issues in an integrated program, and jointly present these recommendations to each organization and agency.

Funding is always a difficulty, but several groups exist that could possibly be useful in securing both private and public funding for research and management programs. The Friends of the Channel Islands (Park Service), Friends of

Santa Cruz Island (The Nature Conservancy), and the Santa Cruz Island Foundation have all been set up to support various research and management activities on the islands. Coordinating these groups with fund raising activities of various local organizations such as the University of California, Santa Barbara Museum of Natural History, and Santa Barbara Botanic Garden could provide valuable leverage in securing funds for coordinated, multi-island projects.

Over the last 30 years, a large amount of research has been done on the islands, which is a credit to the many scientists, students, and managers who have conducted the work. But research questions and resource management issues have become increasingly complex, expensive and varied. Just as the emphasis on different concepts and subjects has shifted over the years in the California Islands, so must the way we approach studying and managing the islands. We believe the time is right to introduce a programmatic approach to some of the ecological and conservation issues that are common to all of the islands. While not discouraging independent research, we think that focusing resources and effort in a coordinated, multi-island approach will deepen our understanding of certain ecological and evolutionary patterns and processes. In turn, we believe using this approach will build on the solid foundation of research done over the last four decades, and lead to more effective management of the natural and cultural resources of the islands.

LITERATURE CITED

Burns, K. J. 1998. Molecular phylogenetics of the genus *Piranga*: implications for biogeography and the evolution of morphology and behavior. Auk 115:621-634.

Carlquist, S. 1974. Island biology. Columbia University Press, New York, NY.

Coonan, T. J., G. Austin, and C. Schwemm. 1998. Status and trend of island fox, San Miguel Island, Channel Islands National Park. Channel Islands National Park Tech. Rep. 98-01. 27 pp.

Crooks, K. R. and D. Van Vuren. 1994. Conservation of the island spotted skunk and island fox in a recovering island ecosystem. Pages 379-386 *in* Halvorson, W. L. and G.J. Maender (eds.), The Fourth California Islands Symposium: Update on the Status of Resources. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Davis, G. E., K. R. Faulkner, and W.L . Halvorson. 1994. Ecological monitoring in Channel Islands National Park, California. Pages 465-484 *in* Halvorson, W. L. and G. J. Maender (eds.), The Fourth California Islands Symposium: Update on the Status of Resources. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Glassow, M. A. 1993. The occurrence of red abalone shells in Northern Channel Island archaeological middens: implications for climatic reconstruction. Pages 567-578 *in* Hochberg, F. G. (ed.) The Third California Islands Symposium: Recent Advances in Research on the California Islands. Santa Barbara Museum of Natural History, Santa Barbara, CA.

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

Hanski, I. A. and M. E. Gilpin (eds.). 1997. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego, CA.

Hanski, I. A. , and D. Simberloff. 1997. Pages 5-26 *in* Hanski, I. A. and M. E. Gilpin (eds.), Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego, CA.

Harrison, S. 1994. Metapopulations and conservation. Pages 111-128 *in* Edwards, P.J., N.R. Webb and R.M. May (eds.), Large-Scale Ecology and Biology. Blackwell, Oxford.

Hochberg, F. G. (ed.), 1993. The Third California Islands Symposium: Recent Advances in Research on the California Islands. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Klinger, R. C. 1998. Santa Cruz Island monitoring program. Volume 1: Vegetation communities 1991-95 report. The Nature Conservancy, Santa Barbara, CA. 59 pp.

Koprimaki, E., and C. J. Krebs. 1996. Predation and population cycles in small mammals. Bioscience 46:754-764.

MacArthur, R. H. and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Menke, A. and D. Miller. 1985. Entomology of the California Channel Islands. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Philbrick, R. N. (ed.), 1967. Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Botanic Garden, Santa Barbara, CA.

Pickett, S. T. A. and P. S. White (eds.). 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, NY.

Power, D. M. 1980a. Preface *to* The California Islands: Proceedings of a Multidisciplinary Symposium. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Power, D. M. (ed.), 1980b. The California Islands: Proceedings of a Multidisciplinary Symposium. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Rohner, C. and C. J. Krebs. 1998. Response of great horned owls to experimental “hot spots” of snowshoe hare density. Auk 115:694-705.

Shafer, C. L. 1990. Nature Reserves: Island Theory and Conservation Practice. Smithsonian Institution Press, Washington, DC.

Simberloff, D. 1988. The contribution of population and community ecology to conservation science. Annual Review of Ecology and Systematics 19:473-511.

Steppan, S. J. 1998. Phylogenetic relationships and species limits within *Phyllotis* (Rodentia: Sigmodontidae): concordance between mtDNA sequence and morphology. J. Mammal. 79:573-593.

Vitousek, P. M., L. L. Loope, and H. Adsersen (eds.), 1995. Islands: Biological Diversity and Ecosystem Function. Springer-Verlag, Berlin.

Wiens, J. A. 1997. Metapopulation dynamics and landscape ecology. Pages 43-68 *in* Hanski, I. A. and M. E. Gilpin (eds.), Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego, CA.

SOURCES OF UNPUBLISHED MATERIALS

McEachern, Kathryn. Biological Resources Division, U.S. Geological Survey. Channel Islands National Park, 1901 Spinnaker Drive, Ventura, California, 93001. Personal Communication 1996.

Wilken, Dieter. Santa Barbara Botanic Garden. 1212 Mission Canyon Road, Santa Barbara, California, 93105. Personal Communication 1996.