

STABILITY AND CHANGE IN THE BIRD COMMUNITIES OF THE CHANNEL ISLANDS

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ABSTRACT

Avifaunal datasets from the California Islands played a prominent role in the development of the equilibrium theory of island biogeography. I have re-analyzed these data using a functional spatial approach and separating short-term ecological from long-term evolutionary processes and dynamics. I distinguish between insular and continental taxa found on islands and define the concept of biotic space as a crucial functional element of persistence. Insular taxa are restricted to a particular island or archipelago. They have evolved and adapted within an island's environment. Continental island populations are connected to a larger mainland complex of populations; individual satellite or island populations may be quite unstable and non-viable over longer time scales. The continental taxa of the Channel Islands have experienced frequent turnover within and between taxa. By contrast, the insular taxa have been stable and have persisted with few exceptions. These findings contradict basic assumptions of the theory of island biogeography. The application of the concept of functional insularity to the problem of conserving mainland remnants and fragments shows that these isolate habitats and their biotic communities face survival problems that differ substantially from those of true oceanic islands and their insular biota.

Keywords: Island biogeography; extinction; turnover rates; functional areography; insular species; Channel Islands, California.

INTRODUCTION

The avifauna of the eight Channel Islands of southern California has played a significant role in contemporary ecology and conservation biology. Diamond's analysis of long-term changes in the bird communities of each of the Channel Islands (Diamond 1969) contributed crucial evidence supporting the concept of island biotas maintaining dynamic equilibrium numbers of species depending on island size and isolation. This was a fundamental requisite for the development of the *theory of island biogeography* (MacArthur and Wilson 1967; Simberloff 1974). Diamond's paper also sparked a controversy on the proximate and ultimate causes of the observed avian turnover rates (Lynch and Johnson 1974; Jones and Diamond 1976; Diamond and Jones 1980). Did the data accurately portray actual turnover and were

such turnovers between species a consequence of natural or anthropogenic factors?

In hindsight and in the presence of new conceptual developments, this heated debate has lost relevance. Chaos theory and widespread evidence for the existence of non-equilibrium ecological communities (Lack 1976; Gilbert 1980; Williamson 1981; Case and Cody 1983; Wiens 1989; Pimm 1991; Simberloff 1994; Thornton 1996; Brown and Lomolino 1998) have shifted the focus of biogeographers and conservation biologists to a closer examination of the general processes underlying biotic change. The simplistic and mechanistic approach of the MacArthur-Wilson school has given way to a more differentiated and multi-factor approach to the different taxonomic, trophic, ecological, and functional elements of island life (Minelli 1990; Solem 1990; Rosenzweig 1995; Tilman and Kareiva 1997). Viewed from this context, a re-examination of the avifauna of the Channel Islands may offer valuable insights for a better understanding of spatio-temporal dynamics on islands and continents.

In this paper I attempt to accomplish three objectives:

- 1) A *functional areographic analysis* of the Channel Islands avifauna will divide the avifauna into different spatial sets and subsets. This will facilitate a discussion on the causes of turnover, colonization and extinction in this archipelago.
- 2) A *separation of scales and processes* in the temporal dynamics of avifaunas will lead to the distinction between seasonal or annual dynamics of the various bird taxa on an island and long-term adaptation and selection processes leading to evolutionary divergence, speciation, and persistence.
- 3) The *results* of this analysis will then be used to evaluate contemporary concepts of survival and extinction in isolated and connected communities.

AREOGRAPHIC CONCEPTS

Areography concerns itself with the structure of biotic distribution areas (Rapoport 1982). In the following, I have expanded this subfield by the addition of a functional

component. Each taxon occupies a distinct *biotic space* composed of its geographic dispersion, the resources contained therein that are required for survival, and the functional interactions between different elements of the taxon (individuals, families, subpopulations, etc.) that their spacing behaviors permit. Of great importance for the conservation management of populations and species is a fundamental dichotomy between taxa occupying *insular* and *continental* spaces.

An *insular* taxon is confined to a geographic island; isolated from other lands it functions and thrives in its island environment. The latter meets all its needs and enables its long-term viable persistence. In many cases, an island's isolation and protection from continental factors (like mammal predators and protection from continental factors (like mammal predators) has resulted in unique adaptations to the island environment (example: flightlessness in many island bird species). Insular taxa (Figure 1A) exist only because of the very existence and physical and biotic landscape of islands; often, they can only function and remain viable as long as the island maintains its isolation from the continental source region of other biota. Many but not all insular taxa are island endemics such as the dodo of Mauritius, the Darwin finches of the Galapagos Islands, or the landbirds of the Revillagigedo Islands (Walter 1998). The terrestrial animals of remote oceanic islands are generally completely insular.

A *continental* taxon occupies a geographic area on a mainland (Figure 1A). Its biotic space differs from that characteristic for insular biota because its distribution area is not defined by an island's perimeter and saltwater barrier. A large variety of continental factors (predators, competitors, diseases, parasites) will interact with such a taxon. Continental taxa may expand or contract, fragment or connect part of their distribution area over time. Their very persistence can be explained by the opportunities for survival in a complex continental setting and functional spatial response to the many adverse limiting factors of continental environments. Habitat fragments on continents do not qualify as islands *sensu strictu* because they cannot harbor insular species; they are *isolates* and contain isolate populations of continental origin.

A third set of species can be called *global* in terms of the functional relevance of space. These species breed on islands and/or continents; it does not matter to them whether they are isolated by saltwater barriers or not because their spacing behavior and area structure does not recognize such a barrier.

Many continental species occur also on islands but their persistence on the latter is often dependent on recruitment from and links to continental populations of the same species. Source-sink systems and metapopulation dynamics may support island components of these species. Most continental islands are occupied by such populations (Figure 1B). Some populations, however, thrive on continental or landbridge islands and become spatially and numerically independent from their conspecific mainland population

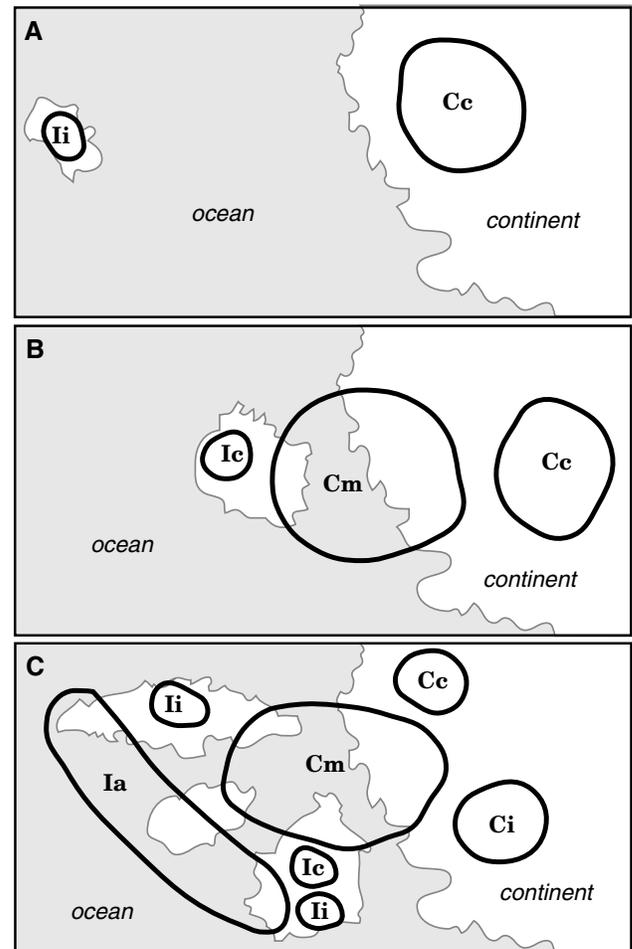


Figure 1. A simplified model of biotic space on islands and continents. A. Oceanic island and continent. B. Continental island and continent. C. Channel Islands and mainland coast of California. The spatial subsets are: Cc = continent-confined, Ci = functional continental, of island origin (rare), Cm = continental, mainland-dependent; Ii = functional insular endemic on single island, Ia = functional insular endemic within archipelago, Ic = functional insular, of continental origin.

areas. Very rarely do endemic island taxa colonize part of a continent and become functionally continental.

A simple functional classification of biotic space (with examples from the Channel Islands) has three sets and six subsets:

1. Insular(I)

Ii - island endemic, on one island only (island scrub jay, *Aphelocoma insularis*)

Ia - archipelago endemic, only on a particular archipelago or island group (horned lark, *Eremophila alpestris insularis*)

Ic - continental origin but independent from continental area (chipping sparrow, *Spizella passerina*)

2. Continental(C)

Cc - on mainland only, not on island(s) (wrentit, *Chamaea fasciata*)

Cm - Occupies island(s) but dependent on mainland area for island existence (American kestrel, *Falco sparverius*)

Ci - island origin but independent from island area (orange-crowned warbler, *Vermivora celata sordida*, Allen's hummingbird, *Selasphorus sasin sedentarius*; both breed in coastal mainland habitats of southern California)

3. Global(G)

No Channel Islands landbird taxon falls into this category.

DATA SOURCES AND METHODOLOGY

The paper concerns itself only with the landbirds of the eight Channel Islands lying off the coast of Santa Barbara and Los Angeles. Aquatic, seabirds, and other birds acquiring most or all of their energy sources at sea or below the high tide zone are not considered to be landbirds. Table 1 in Diamond and Jones (1980) is the principal data source for this paper. Bald eagle, osprey, peregrine falcon, American oystercatcher, and black oystercatcher were deleted from the list of landbirds due to their principal foraging of marine creatures. This leaves a total of 51 landbird species breeding at least once on one or more of the eight islands. In addition, Table 1 in Johnson's (1972) valuable paper provided the essential reference on endemic island taxa. These lists were complemented by further analysis and field observations found in Howell (1917), Miller (1951), Townsend (1968), Hunt and Hunt (1974), Jones and Diamond (1976), and Power (1980). Recent insights on the role of humans and their livestock in the modification of the vegetation of Santa Cruz Island were summarized by Junak et al. (1995).

The author has studied the landscapes and abundant bird populations on two of the islands: he spent several days on Santa Cruz Island approximately every two years since 1972. He has camped on Santa Catalina twice for a week-long stay in 1987 and 1997. He is currently engaged in bird surveys of all Channel Islands.

Bird species will be listed as *regular* breeders (symbol: X) if there is no record or a low probability of their disappearance in historic time. Birds colonizing an island for the first time during the past 50 years of observation and persisting there are listed separately as *new regular* breeders (N). *Occasional* breeders are classified as such (O), vanished island populations of taxa still existing elsewhere are listed as *disappeared* (D), and vanished populations of an endemic island taxon are classified as *extinct* (E).

Based on general guidelines from basic conservation biology and more recent evidence from persisting small and isolated bird populations (Walter 1990 and unpublished) a viable island population for short-term persistence should have at least 20 (large birds) to 50 (small birds) breeding pairs. Such a population is considered resistant to short-term extinction, relies solely on island resources in its realized

ecological niche, and therefore occupies an insular biotic space.

RESULTS

Endemic Taxa

Thirteen species have 57 island populations on the eight Channel Islands (Table 1) belonging to seventeen endemic subspecies and one endemic species (island scrub jay). Eight of these taxa are confined to a single island. All of these populations show morphological distinctions that set them apart from continental conspecific or congeneric relatives on the mainland. A few show clear behavioral differences in song, phenology, and foraging behavior; the others are likely to possess them as well but comparative studies have not been carried out for most taxa. These are the insular taxa (I) with the subsets Ii (8 taxa) and Ia (49 populations of 11 taxa).

Forty-six of 57 populations (81%) are considered regular breeders on their respective islands. Only two verified colonizations of formerly unoccupied islands have occurred resulting in viable populations of Allen's hummingbird on San Miguel and of the orange-crowned warbler on San Nicolas. The five disappeared and extinct taxa (8.8%) vanished from two islands for rather unnatural reasons: 1) on *Santa Barbara Island* the island vegetation was heavily overgrazed by rabbits and consumed by a human-caused wildfire (Hunt and Hunt 1974), and 2) on *San Clemente Island* overgrazing by goats and introduced predators (cats) severely degraded the integrity of the island's ecosystems. Only two taxa have gone extinct in the traditional sense of this term: they will not come back. This is the Santa Barbara Island subspecies of the song sparrow, *Melospiza melodia graminea*, and the San Clemente Island subspecies of the Bewick's wren, *Thryomanes bewickii leucophrys*. Only four islands have been listed as occasionally harboring breeding populations of the endemic loggerhead shrike and rufous-crowned sparrow (Table 1).

Rather unusual in island biogeography is the fact that two of the island subspecies have established viable 'beachheads' on the mainland coast near the islands. Allen's hummingbird is currently expanding its population size and overall density in the Los Angeles area (Walter, unpublished data). Less is known of the population size of the island taxon of the orange-crowned warbler in southern California's coastal habitats. Both taxa occupy continental biotic space Ci (see Figure 1C).

Non-Endemic Taxa

Among the 38 non-endemic breeding landbirds (Table 2) at least 136 breeding populations have been documented (Diamond and Jones 1980, Jones and Diamond 1976) for the Channel Islands. Only 81 (60%) are considered regular breeders; 18 new island colonizations (13%) have been documented. Some 34 populations are listed as occasional breeders. All of these populations are continental in origin. Only

Table 1. Endemic landbird taxa of the Channel Islands.

Taxon	Islands Occupied by Taxon								Total Islands
	MIG	ROS	CRU	ANA	BAR	CAT	NIC	CLE	
Horned Lark	X	X	X	X	X	X	X	X	8
Orange-crowned Warbler	X	X	X	X	X	X	N	X	8
Allen's Hummingbird	N	X	X	X	~	X	~	X	6
Loggerhead Shrike A	O	X	X	O	O	X	~	~	6
Western Flycatcher	~	X	X	X	~	X	~	X	5
House Finch	~	~	~	~	D	X	X	X	4
Bewick's Wren A	~	X	X	X	~	~	~	~	3
Spotted Towhee	~	X	~	~	~	X	~	D	3
Song Sparrow A	~	X	X	X	~	~	~	D	4
Rufous-crowned Sparrow	~	~	X	O	~	~	~	~	2
Loggerhead Shrike B	~	~	~	~	~	~	~	X	1
Bewick's Wren B	~	~	~	~	~	X	~	~	1
Bewick's Wren C	~	~	~	~	~	~	~	E	1
Song Sparrow B	X	~	~	~	~	~	~	~	1
Song Sparrow C	~	~	~	~	E	~	~	~	1
Sage Sparrow	~	~	~	~	~	~	~	X	1
California Quail	~	~	~	~	~	X	~	~	1
Island Scrub Jay	~	~	X	~	~	~	~	~	1
Subtotals									
Regular Breeders	3	8	9	6	2	9	2	7	46
Occasional Breeders	1	~	0	2	1	~	~	~	4
Disappeared	~	~	~	~	1	~	~	2	3
Extinct	~	~	~	~	1	~	~	1	2
New Colonization	1	~	~	~	~	~	1	~	2
Grand Total	5	8	9	8	5	9	3	10	57

X = regular, O = occasional, N = new regular, D = former, and E = extinct breeding population.

three of 136 breeding populations have apparently vanished: the house sparrow (*Passer domesticus*) from Santa Rosa (after an earlier successful colonization), the raven (*Corvus corax*) from San Miguel, and the bushtit (*Psaltriparus minimus*) from Santa Catalina.

Insular Space versus Continental Space

Many of the non-endemic island populations are quite large and meet the criteria for viable island populations (31 regular and 7 recent colonists, or 23%). They persist without any apparent support from the mainland source populations at present and occupy therefore the insular continental biotic space (Ic). When we add all populations occupying an insular biotic space (subsets Ii, Ia, and Ic) we have 53 endemic and 38 non-endemic populations. Among these, there have only been five disappearances and extinctions. Thus, 86 (95%) viable bird populations, each with more than 20 breeding pairs per island, have persisted over historic time.

A total of 61 old and new regular breeders as well as the 34 occasional breeders are classified as mainland-dependent taxa (Cm biotic space); these 95 populations (70% of all non-endemic populations) consist of one to fewer than

20 breeding pairs per island. These are by definition the less abundant, rare and irregular breeders of the Channel Islands.

DISCUSSION

Areography

The Channel Islands and the adjacent mainland coast contain all of the insular and continental subsets of functional biotic space (Figure 1C). This archipelago was not connected to the mainland during the last ice ages; although lying close to the Santa Barbara coastline, the islands remained isolated and preserved the insular spaces of many endemic taxa. The narrow distance to the islands enabled many birds, however, to cross the water barrier and to attempt colonization. Today, the islands contain an avifauna that is a composite of insular and continental areographic elements.

Persistence of Insular Endemics

The insular endemics (Table 1) have persisted everywhere except where massive human-caused interference has eliminated the resource base and/or the island was overrun

Table 2. Non-endemic breeding landbird species.

Island	Breeding Status				
	Regular	New Regular	Occasional	Disappeared	Total No. Species
San Miguel	5 (2)	2 (0)	3	1	11
Santa Rosa	13 (6)	2 (0)	2	1	18
Santa Cruz	21 (11)	4 (3)	4	~	29
Anacapa	6 (0)	2 (0)	6	~	14
Santa Barbara	4 (0)	1 (0)	5	~	10
Santa Catalina	19 (8)	3 (2)	4	1	27
San Nicolas	4 (2)	2 (2)	6	~	12
San Clemente	9 (2)	2 (0)	4	~	15
Total No. of Populations	81 (31)	18 (7)	34	3	136 (38)

() = Estimated number of viable island populations [insular, of continental origin (Ic)]

Sources: Diamond and Jones (1980), Johnson (1972), Power (1980)

with introduced house cats. These insular populations (Ii and Ia) have therefore demonstrated a remarkable stability and resiliency over historic time as well as prehistoric time. They are as stable as the endemic landbirds of the Revillagigedo Islands in the Mexican Pacific (Walter 1998). It is highly probable that all the prehistoric endemic island populations would be more abundant today were it not for the potent transformation and degradation of the Channel Islands during the past 200 years (Junak et al. 1995). One element favoring the survival of these endemics is the often less specialized nature of island taxa compared to continental relatives. This adaptation to island life may help these taxa to cope with many anthropogenic modifications; nothing, of course, can be done in situ if scrub and woodland birds are faced with a bare island and hundreds of hungry cats as has been the case of S. Clemente Island and its extinct and vanished bird taxa (Table 1).

MacArthur-Wilson biogeography cannot account for the stability of this endemic avifauna but Lack's alternate theory of the 'ecological poverty' of island faunas (Lack 1976; Walter 1998) predicts a high level of stability for island landbirds in undisturbed landscapes.

The insular continental populations (Ic) are also unlikely candidates for disappearance from one or more islands because they are buffered by large numbers of breeding pairs (often hundreds of pairs); several of the recent immigrant taxa have become highly successful colonists and possess functional insularity. These are net additions to the avifauna of the islands that are the result of diffuse factors operating on the islands as well as on the continent. It may sound elementary but it has to be stated that common or abundant island birds normally do not vanish or suffer 'local extinction' unless there is anthropogenic destruction of habitats and predation or outright persecution.

Instability of Continental Taxa

The subset of mainland-dependent taxa (Cm) is responsible for most of the reported turnovers (Jones and Diamond 1976). This subset has also been the subject of many works dealing with island biogeography (see Pimm 1991). Four systems of spatial dynamics may be responsible for the persistence of these types of permanent or temporary mainland and island distributions:

1. Source-sink systems where an island population has low ecological fitness and regularly receives extra progeny from a continental source population (Ritchie 1997).
2. Primary-secondary habitat selection favors the continental habitat but many birds will choose the secondary habitat in some years due to overcrowding or unfavorable physical conditions in the primary area. This spatial dispersion system has been documented in German populations of the pied flycatcher (*Ficedula hypoleuca*) by Berndt and Winkel (1974).
3. Metapopulation dynamics with one or more islands as breeding patches in a largely continental system of loosely connected satellite areas. One or more of the patch populations may disappear at one time and be recolonized again from other patches in the future. Song sparrow populations in the San Juan Islands of British Columbia fit this spatial system (Smith et al. 1996).
4. Satellite populations on an island that are simply an isolate of a large continental distribution area.

The saltwater barrier separates the two populations but the island area is just as good or bad as the mainland area. The only difference is the much smaller population size on the island.

We do not know at present to which of the above spatial systems the non-viable and occasional breeders of the Channel Islands belong. But the possibilities for causing repeated presence-absence patterns are enormous: (a) Favorable breeding conditions on the mainland may flood the islands with year-old breeders during the next breeding season; (b) cold winter and spring seasons may thin the continental breeding population and drain the island population; (c) the same bird may breed on mainland and island in alternate years; (d) a single pair breeding on an island may just be a random event, a statistical outlier, or the beginning of a colonization trend. All these scenarios deal with ecological time scales and the spatio-temporal dynamics of bird populations. They tell us much about the aut- and demecology of birds, of their islands, and even more about their continental ranges but very little about island biogeography, because the driving forces regulating long-term island occupancy, evolution, and diversity overlap only slightly with these short-term population dynamics of mainland-dependent taxa.

Relevance for Conservation Management

The landbird data from the Channel Islands show that the usually scant breeding populations of the mainland-dependent subset (Cm) are responsible for most of the observed turnovers (species loss and species gain), not the more typical and more abundant island dwellers that have become functionally insular. The latter are buffered by their numbers and by island adaptation. We should perhaps disregard all non-viable populations and include only large insular taxa in our discussions of island ecology and biogeography. This might provide a more accurate representation of resource-adapted island diversity.

The landbirds of the Channel Islands cannot be used as an island model for the study and management of continental habitat isolates such as fragments of forest, prairie or chaparral.

First, fragments are not islands at all. They are connected in many ways to the surrounding terrestrial matrix or 'Umfeld' (a German term for spatial environment) that is rich in predators, competitors, parasites, etc. which can and will invade and impact the fragment sooner or later. Basically, a continental fragment lacks the protective isolation that is characteristic of all true islands (Laurance 1991:85-86).

Second, the biotic taxa found in continental fragments have evolved and persisted in continental biotic space containing extensive and contiguous habitats with the required resources over hundreds and thousands of square kilometers. Many large carnivores and herbivores need this kind of functional space over their evolutionary life span to avoid extinction due to global and regional climate and biotic change. Being trapped in a human-caused habitat fragment

would mean the loss of their ability to use their large functional space for purposes of persisting in the optimal portions of the range. By contrast, the insular species of islands need isolation and thrive in restricted areas because they have been selected for this functional space over evolutionary time periods (Walter 1998).

Third, the insular taxa of the Channel Islands have proved to be remarkably resistant to disappearance and extinction. These islands have suffered from overgrazing, erosion, invasions by alien weeds and predators, human disturbance, and other common extinction factors. Yet, most insular taxa have tolerated this disturbance and destruction.

It is doubtful that similar impacts would be tolerated by continental biota in restricted continental fragments; more likely is that they would attempt to evade these extinction factors by leaving the fragment. A likely explanation for the high persistence of the endemic avifauna of the Channel Islands may be found in the natural rigor of the physical and biotic environment of this southern Californian archipelago. At the end of the extremely long and dry summer months even the undisturbed habitats appear ecologically stressed. This natural phenomenon may predispose the insular endemics of this archipelago to possess an ecological valency that tolerates some environmental disturbance. Similarly, the long-term presence of fox and skunk as well as of Amerindian encampments on the major islands may have resulted in less predator-naïve island birds than we expect to find on remote oceanic islands.

Finally, considerable attention should be given to all insular endemics; they have nowhere else to go and need the functional space of the Channel Islands. Hopefully, the environmental abuse of the past 200 years has abated forever. Of particular urgency is the plight of the endangered landbirds of San Clemente and San Nicolas Island. With regard to the likely fate of continental biota trapped in remnant habitats, this discussion of island birds has shown how precarious and dangerous life in a continental fragment must be compared to the relative security that functional insularity provides for many island dwellers.

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APPENDIX

List of scientific names of endemic landbird taxa of the Channel Islands (see Table 1)

- California Quail (*Lophortyx californica catalinensis*)
Allen's Hummingbird (*Selasphorus sasin sedentarius*)
Western Flycatcher (*Empidonax difficilis insulicola*)
Horned Lark (*Eremophila alpestris insularis*)
Island Scrub Jay (*Aphelocoma insularis*)
Bewick's Wren (*Thryomanes bewickii*)
 Subspecies A (*T. b. nesophilus*)
 Subspecies B (*T. b. catalinae*)
 Subspecies C (*T. b. leucophrys*)
Loggerhead Shrike (*Lanius ludovicianus*)
 Subspecies A (*L. l. anthonyi*)
 Subspecies B (*L. l. mearnsi*)
Orange-crowned Warbler (*Vermivora celata sordida*)
House Finch (*Carpodacus mexicanus clementis*)
Spotted Towhee (*Pipilo maculatus clementae*)
Rufous-crowned Sparrow (*Aimophila ruficeps obscura*)
Sage Sparrow (*Amphispiza belli clementae*)
Song Sparrow (*Melospiza melodia*)
 Subspecies A (*M. m. clementae*)
 Subspecies B (*M. m. micronyx*)
 Subspecies C (*M. m. graminea*)