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Reproductive insularity in a migratory sparrow: A field study of Lincoln's sparrow populations in Southern California

Cin Greyhaven

REPRODUCTIVE INSULARITY IN A MIGRATORY SPARROW: A FIELD STUDY OF LINCOLN'S SPARROW POPULATIONS IN SOUTHERN CALIFORNIA

A Thesis

Presented to the

Faculty of

California State University,

San Bernardino

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Biology

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by

Cin Greyraven

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ABSTRACT

Over a four-year period, Lincoln's Sparrows (Melospiza lincolnii) were captured, marked, measured, and released for observation within their subalpine breeding meadows in the San Bernardino and San Jacinto mountain ranges of southern California, generating preliminary evidence of reproductive insularity in these migratory populations.

Migrational return of adults averaged 50% annually. Over 85% of these birds settled on previously-held or nearby territories. Maximum observed dispersal was two kilometers. Dispersers moved from smaller to larger habitat patches, and slight gender biases in territoriality were seen.

Nesting success appeared high, and double-brooding was confirmed. However, only 1% of Lincoln's Sparrows banded as immature birds returned as adults. All were male and established territories near their natal sites. Non-returning individuals may have dispersed or may have died.

Morphometric analysis of five measured characters among four geographic subgroups yielded statistically-significant differences in means only in tarsal lengths. Similar tarsal length variations were noted by Miller and McCabe in 1935 and may be being maintained in these populations through inbreeding sustained by strong philopatric tendencies.

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Many people (named and unnamed) aided me along the long road leading to completion of this research project. I hope that the information gained during this study will contribute to the understanding and preservation of the wild lands and species we cherish.

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Barbara A. Carlson - who opened all the doors that made the realization of my dreams possible.

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INTRODUCTION

An understanding of the principles influencing habitat island ecological and evolutionary dynamics is becoming more important with every passing day. The world's wild lands are being consumed at a frightening pace by accelerating human population pressures. Remaining natural areas are increasingly fragmented and isolated from each other. An exhaustive understanding of the dynamics of biogeographical islands will be required if we are going to have any hope of preserving species diversity in extant floras and faunas.

In the western United States, "islands" of cool, mesic habitat exist wherever mountain ranges rise high enough above the surrounding arid desert lowlands (Brown 1971, MacArthur 1972). The high-elevation mountain biota of these ranges may represent remnants of formerly-continuous Pleistocene forest populations or may have resulted from colonization by long-distance dispersers from boreal North America (Johnson 1975). In either case, these altitudinal islands can provide valuable "outdoor laboratories" for investigations into population dynamics and evolutionary processes.

Small, disjunct populations restricted to these mountaintops are expected to be very vulnerable to cycles of local extinction and refounding (MacArthur 1972). However, documentation of cycles of local extinction and refounding in montane bird species is scant or equivocal (King and Mewaldt 1987). One recent report (Hendricks and Pidgeon 1990) describes the colonization of an alpine willow habitat in Wyoming by Savannah Sparrows and the concurrent extinction of the Lincoln's Sparrow population there. Lincoln's Sparrows are obligates of montane riparian zones during their breeding season, and thus are restricted not only to altitudinal islands but also to scattered habitat patches within each montane island. This makes the species an ideal subject for investigations into the dynamics of fragmented populations.

In 1935, Alden H. Miller and T. T. McCabe of the Museum of Vertebrate Zoology, Berkeley, California, reported finding morphological variations between Lincoln's Sparrow museum specimens collected in the San Jacinto mountains and specimens collected in the adjacent San Bernardino mountains. These two southern California mountain ranges mark one of the southernmost latitudinal limits of the species breeding range and are very similar environmentally. Miller and McCabe (1935) speculated that the "local differentiation" and "population homogeneity" observed in the two montane sparrow populations probably arose from founder effects common to isolated, inbreeding populations. Birds present a special case in the study of dispersal, because avian species enjoy an unrivalled capacity for dispersal via flight. Yet, in spite of their capacity for mobility, many avian species do not disperse randomly but are instead strongly attached to home territories (Greenwood and Harvey 1982). Territoriality and dispersal have long been recognized as critical determinants of gene flow, evolutionary change, and population size and structure (Wright 1946, Howard 1948). Important consequences for gene flow and population structure arise from variations in dispersal distance, proportion of the population demonstrating philopatry, and age or sex biases in dispersal behavior (Greenwood 1980). Widespread dispersal disrupts local adaptations, while gene flow restriction may promote inbreeding and genetic differentiation of neighboring groups (Wright 1946).

This study tested the hypothesis that migratory montane Lincoln's Sparrows exist in insular, reproductively-isolated populations by (1) directly observing population dispersal patterns, (2) examining patterns of morphological variation in selected Lincoln's Sparrow populations breeding in Southern California, and (3) collecting data on demographic, behavioral, and physiological aspects of the summer biology of montane Lincoln's Sparrows (Figure 1).

Figure 1.--Color banded adult Lincoln's Sparrow (male, captured in the Bluff Mesa area of the San Bernardino mountains, California).

RESEARCH SUBJECT

SPECIES DESCRIPTION.

Lincoln's Sparrow (Figure 1), like other sparrows of the subfamily Emberizinae (Aves, Passeriformes, Emberizidae), is a small (17 gram), brownish, streaked bird associated with grassy habitats (Farrand 1983).

Taxonomic background. The taxonomic classifications of avian species have long been the subject of considerable debate. As a consequence of this debate, the Lincoln's Sparrow has accumulated a string of generic aliases. John James Audubon published the first description of Lincoln's Sparrow in 1834, naming it *Fringilla lincolnii* in honor of Thomas Lincoln, a companion on Audubon's 1833 Labrador field trip (Miller and McCabe 1935). The generic designation was changed to *Melospiza* in acknowledgement of the species perceived similarity to the Song Sparrow (*M. melodia*) and Swamp Sparrow (*M. georgiana*). To promote larger generic groups, Linsdale (1928) proposed merging *Melospiza* into *Passerella*, and Paynter (1964) suggested merging both genera into *Zonotrichia*. Some authors have used these alternate designations in their publications. The American Ornithologists' Union (1983) still designates *Melospiza lincolnii* as the official name for Lincoln's Sparrow, and Zink (1982) recommends maintenance of the genus Melospiza based on his analysis of its genetic and morphological affinities.

Previous research. Despite all the arguments over its name, the species has not been closely studied. Much of the available literature that mentions Lincoln's Sparrows does so in the context of research on other species, e.g., song mimicry in White-crowned Sparrows (Borror 1961, Baptista et al. 1981, Baptista and Morton 1988). Some work has been published on diet (Raley and Anderson 1990) and identification criteria for banders (Rimmer 1986, Yunick 1990). Most other mentions are distributional notes (Grinnell and Miller 1944) and general life history observations (Speirs and Speirs 1968, Austin 1968). No long-term investigations of montane breeding populations have been published.

SPECIES DISTRIBUTION.

Range. Lincoln's Sparrows are intracontinental migrants that summer (and breed) in the cool bogs and meadows of the North American boreal zone and winter in warmer lowlands as far south as Central America (Figure 2). Three subspecies or geographic races have been recognized.

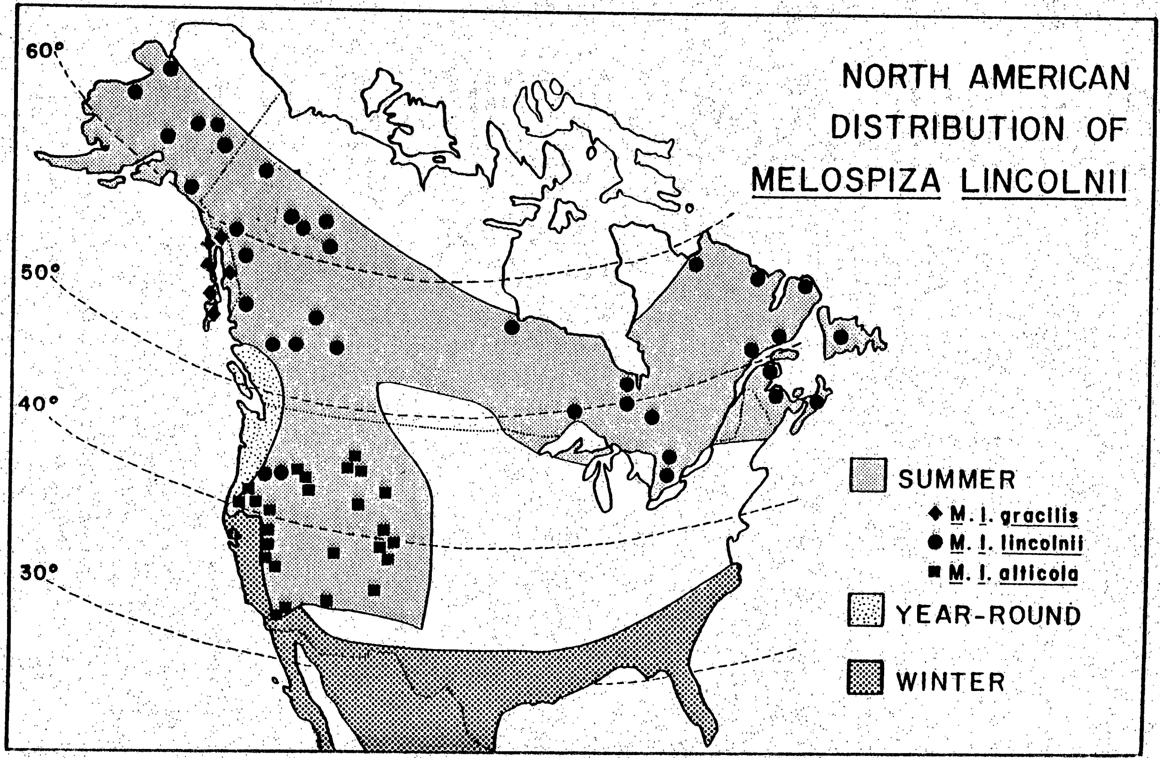

Figure 2.--North American distribution of Lincoln's Sparrows, showing the breeding ranges of the three geographic races. Redrawn and modified from Miller and McCabe (1935).

Audubon described the northern race, Melospiza lincolnii lincolnii, which breeds transcontinentally from the east coast of New England and Canada to Alaska (Howard and Moore 1980). A second geographic race, M. l. gracilis, was identified in the southern Alaskan archipelago and along the western Canadian coast by Kittlitz in 1858 (Howard and Moore 1980). After examining 1078 Lincoln's Sparrow museum specimens from across North America, Miller and McCabe (1935) confirmed the validity of these racial subdivisions and additionally identified a third race, M. l. alticola, breeding in the higher mountains of the western United States.

Morphological differences between the races are not absolute but are a matter of shifts in the prominence of characteristics such as head-stripe patterns, back color, and overall size (Miller and McCabe 1935). Individuals of all three races have been reported as winter visitors and migrants in the lowlands of Southern California (Grinnell and Miller 1944). The montane race is the subject of the present study.

Breeding habitat specificity. The Lincoln's Sparrow is noted for its strict adherence to a sharply-circumscribed breeding habitat of boggy meadows (Miller 1942). In the western United States, breeding habitat suitable for Lincoln's Sparrows occurs only in the higher elevation mountain ranges. Typically, species-appropriate meadows are small and scattered, separated by regions of unsuitable habitat both within and between mountain ranges.

SPECIES BEHAVIOR.

General. Lincoln's Sparrows are usually glimpsed in low, furtive flight between wet thickets where they forage solitarily for seeds, insects, and small amounts of young foliage, berries, and buds (Grinnell and Miller 1944).

Breeding biology. In the spring, Lincoln's Sparrows depart from lowland wintering grounds and seek out suitable breeding habitat. Sex hormones flow, gonads increase in size, males claim territories with song and aggressive behavior, pair bonds are established or reaffirmed, and mating occurs (Gill 1990, p.224). Montane Lincoln's Sparrows have been identified on breeding habitat as early as mid-April (Garrett and Dunn 1981), but egg-laying does not commence until late May or early June.

The female Lincoln's Sparrow lays three to six eggs, which she incubates for two weeks in a dry grass, open-cup ground nest. Nests are placed on mounds within or at the edges of wet areas and are well-hidden in herbaceous vegetation (Harrison 1978). Both parents attend the altricial young, which open their eyes at five to six days of age and leave the nest at ten to twelve days of age (Harrison 1978).

Territoriality weakens after the last chicks have fledged. Adults undergo a complete feather molt and juveniles undergo a partial molt of body feathers in preparation for September to October migration to wintering grounds (Pyle et al. 1987).

STUDY AREA

AREA DESCRIPTION.

Mountain range physiography and climate. The San Gabriel, San Bernardino, and San Jacinto ranges of southern California are steep fault-block mountains of granitic and metamorphic rock rising approximately two vertical miles above hot interior deserts to the north and east and mediterranean coastal lowlands to the south and west (Arno 1984). Cold, snowy winters and cool, dry summers create a climate similar to that of the Sierra Nevada. Many outliers of the Sierra Nevadan floristic province are found within the southern California mountain ranges (Arno 1984).

Site description. Research was conducted in wet subalpine meadows (Figure 3) being utilized by Lincoln's Sparrows as breeding habitat. These meadows characterized by lush herbaceous growth and low willow clumps, bordered by mixed coniferous forest and mountain chaparral (see Table 1 for vegetative species list). The State of California Department of Fish and Game Natural Diversity Data Base (Holland 1986) lists this type of herbaceous community as "montane wet meadow" (element code 45110), occurring from 5,000 to 9,000 feet above sea level in the southern mountain ranges of California.

Figure 3.--Characteristic Lincoln's Sparrow breeding habitat. Extremes are represented by: A) a large, open meadow (Round Valley, San Jacinto State Park), and B) a shrubby willow-infested meadow (Fish Meadows, San Gorgonio Wilderness Area).

Table 1.--Characteristic vegetation of wet montane meadows of Southern California[a].

Genus/species name	Common name
Meadow vegetation:	
Achillea lanulosa	Yarrow
Agastache urticifolia	Giant Hyssop
Aquilegia formosa	Columbine
Aster alpigenus	Aster
Castilleja miniata	Paintbrush
Carex spp.	Sedges
Dodecatheon alpinum	Shooting Star
Eleocharis spp.	Spike Rush
Equisetum arvense	Horsetail
Geranium richardsonii	Cranesbill
Habenaria dilatata	Rein Orchid
Heracleum lanatum	Cow Parsnip
Juncus spp.	Rushes
Lilium parryi	Lemon Lily
Lupinus polyphyllus	Lupine
Mimulus primuloides	Monkey Flower
Pteridium aquilinum	Bracken Fern
Ribes nevadense	Currant
Rosa californica	Wild Rose
Salix spp.	Willow
Thalictrum fendleri	Meadow Rue
Veratrum californicum	Corn Lily
Surrounding forest and chaparral vegetation:	
Abies concolor	White Fir
Arctostaphylos spp.	Manzanita
Calocedrus decurrens	Incense Cedar
Ceanothus spp.	Snowbrush
Chrysolepis sempervirens	Chinquapin
Pinus contorta murrayana	Lodgepole Pine
Pinus jeffreyi	Jeffrey Pine
Pinus ponderosa	Ponderosa Pine

[a]Sources: Jaeger and Smith 1966, Munz 1974, and Holland 1986.

These meadows may be late hydroseres or may be maintained by streams that flow through them (Holland 1986). Meadow vegetation is dormant in winter, with the growing period beginning in late spring or early summer and ending in fall or early winter, depending on altitude and snow presence. Meadow soils are saturated and remain wet throughout the year, although some seasonal drying may occur and dry meadow vegetation may exist in a ring around a wet center (Holland 1986).

Ownership and access. Much of the Lincoln's Sparrow breeding habitat in the San Bernardino and San Jacinto mountain ranges is located on public land managed by the U.S. Forest Service or the California State Parks Department. Some meadows are within roadless wilderness areas where permit systems regulate access. Other meadows occur on private property enclaves within the National Forest. Meadows are popular as campsite, picnic, and pasture areas; as a result, many are adjacent to paved or dirt roads or accessible by well-maintained foot trails.

SITE SELECTION.

The San Bernardino and San Jacinto ranges have been known to support small but locally abundant Lincoln's Sparrow populations since at least the beginning of this century (Grinnell 1908, Grinnell and Swarth 1913, Grinnell and Miller 1944, Garrett and Dunn 1981, Kratter 1988). Because the known population of Lincoln's Sparrows in the

San Gabriel mountains consisted of only two pairs at Big Pine (Garrett and Dunn 1981, Kratter 1988), I excluded the San Gabriel mountains from this study.

Known Lincoln's Sparrow breeding sites (from above references) and additional areas offering potentially-appropriate habitat for Lincoln's Sparrows in the San Bernardino and San Jacinto mountain ranges were explored. Sites chosen for sampling (Figures 4 and 5; Table 2) were selected after weighing potential research value against time, manpower, and access constraints. An archipelago of meadows in the Bluff Mesa region of the San Bernardino mountains (Figure 6) was chosen as a focal area for extended observation of breeding behavior.

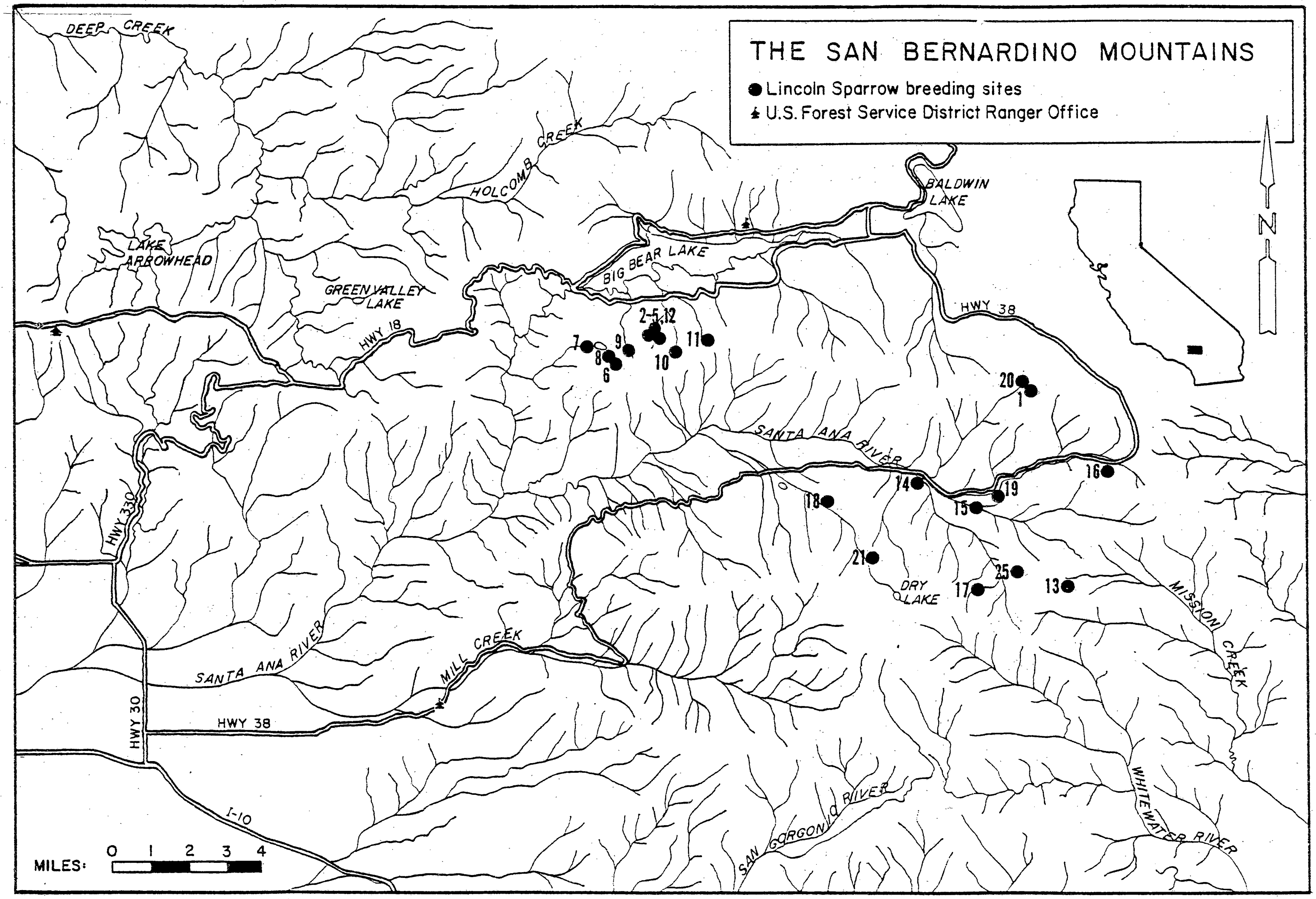

Figure 4.--Lincoln's Sparrow study sites in the San Bernardino Mountains.

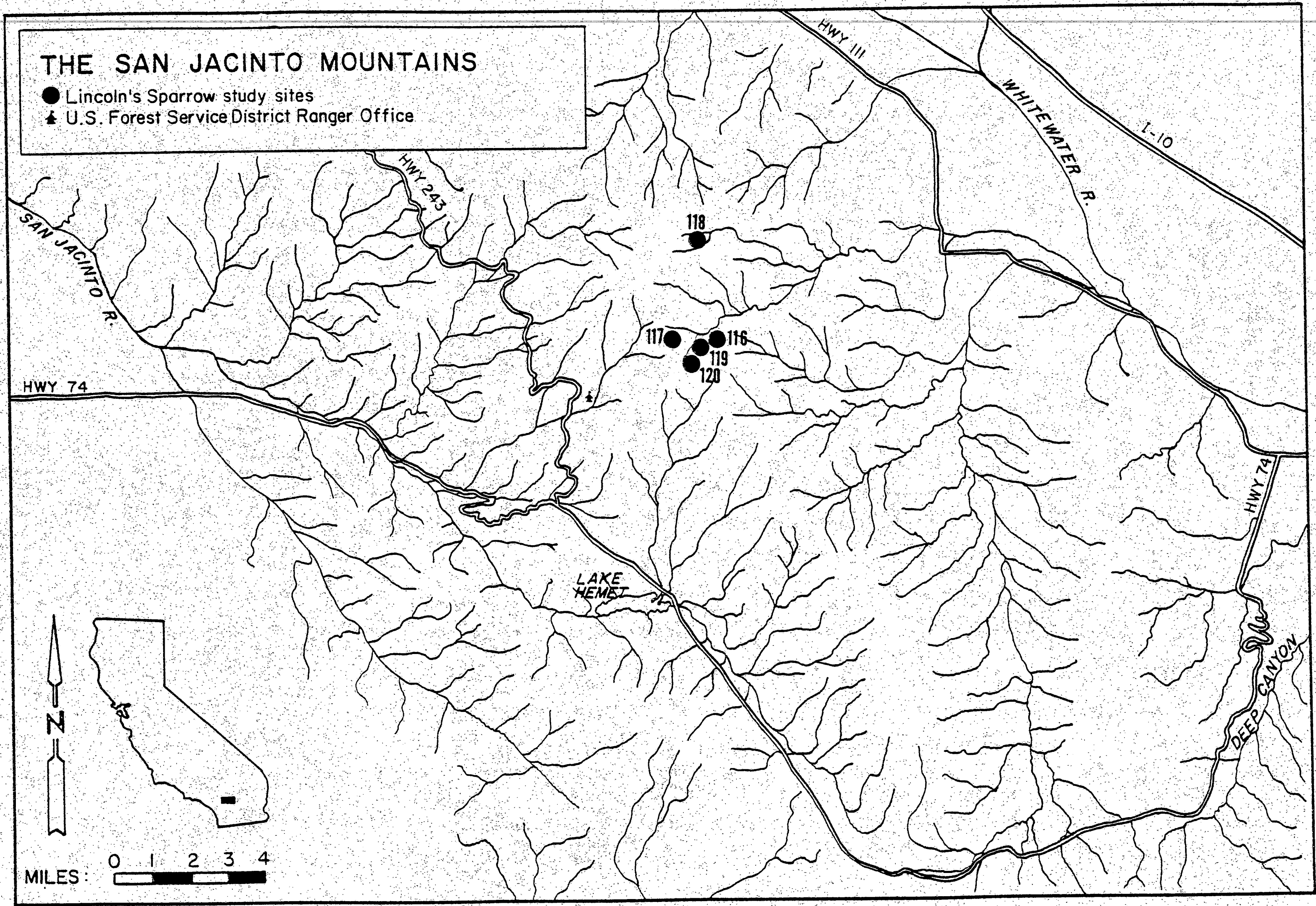

Figure 5.--Lincoln's Sparrow study sites in the San Jacinto Mountains.

Table 2.--Lincoln's Sparrow study sites in the mountain ranges of southern California.

Site Code	Meadow name	Elevation in meters (feet)	Approximate UTM[a] coordinates
SAN BERNARDINO MOUNTAIN RANGE			
BLUFF MESA REGION			
02	Metcalf Meadow (Lower)[b]	2,225 (7,300)	3,786,800 m N, 505,600 m E
03	Metcalf Meadow (Middle)[b]	2,243 (7,360)	3,786,700 m N, 505,800 m E
04	Metcalf Meadow (Upper)[b]	2,249 (7,380)	3,786,500 m N, 506,000 m E
12	Metcalf Spring	2,243 (7,360)	3,786,500 m N, 505,500 m E
05	Boulder Camp Meadow[b,c]	2,268 (7,440)	3,786,500 m N, 505,300 m E
09	North Creek Verge[c]	2,290 (7,520)	3,786,500 m N, 504,200 m E
06	Far East Meadow[b,c]	2,329 (7,640)	3,786,100 m N, 504,000 m E
08	Bluff Lake Meadow East[b]	2,316 (7,600)	3,786,200 m N, 503,600 m E
07	Champion Meadow[c]	2,310 (7,580)	3,786,300 m N, 502,500 m E
11	Deer Camp Meadow[c]	2,304 (7,560)	3,786,500 m N, 507,700 m E
SANTA ANA RIVER VALLEY			
01	Wildhorse Spring[b]	2,658 (8,720)	3,784,400 m N, 521,400 m E
20	Wildhorse Meadows	2,646 (8,680)	3,783,800 m N, 520,300 m E
14	College Camp Verge[c]	1,960 (6,430)	3,780,600 m N, 517,200 m E
19	Seca 7000 Verge[c]	2,134 (7,000)	3,780,500 m N, 520,300 m E
16	Little Cienega Seca	2,362 (7,750)	3,781,300 m N, 524,600 m E
15	Big Meadows	2,060 (6,760)	3,779,800 m N, 519,400 m E
13	Mission Creek Spring	2,377 (7,800)	3,776,000 m N, 522,800 m E
25	FC Trailhead Meadow[c]	2,414 (7,920)	3,776,300 m N, 520,700 m E
17	Upper Fish Creek Meadow	2,450 (8,040)	3,775,800 m N, 520,300 m E
18	Horse Meadow	2,268 (7,440)	3,778,900 m N, 513,000 m E
SAN JACINTO MOUNTAIN RANGE			
TAHQUITZ FLATS			
117	Skunk Cabbage Meadow	2,423 (7,950)	3,737,000 m N, 531,000 m E
119	Tahquitz Valley	2,426 (7,960)	3,736,300 m N, 531,000 m E
120	Little Tahquitz Meadow	2,438 (8,000)	3,736,800 m N, 531,200 m E
116	Reed's Meadow	2,390 (7,840)	3,736,600 m N, 531,700 m E
SAN JACINTO PLATEAU			
118	Round Valley	2,652 (8,700)	3,740,300 m N, 531,500 m E

[a]Universal Transverse Mercator.

[b]Site was included in Barbara A. Carlson's avian population research.

[c]Name was assigned by researcher; no existing designation was found on maps.

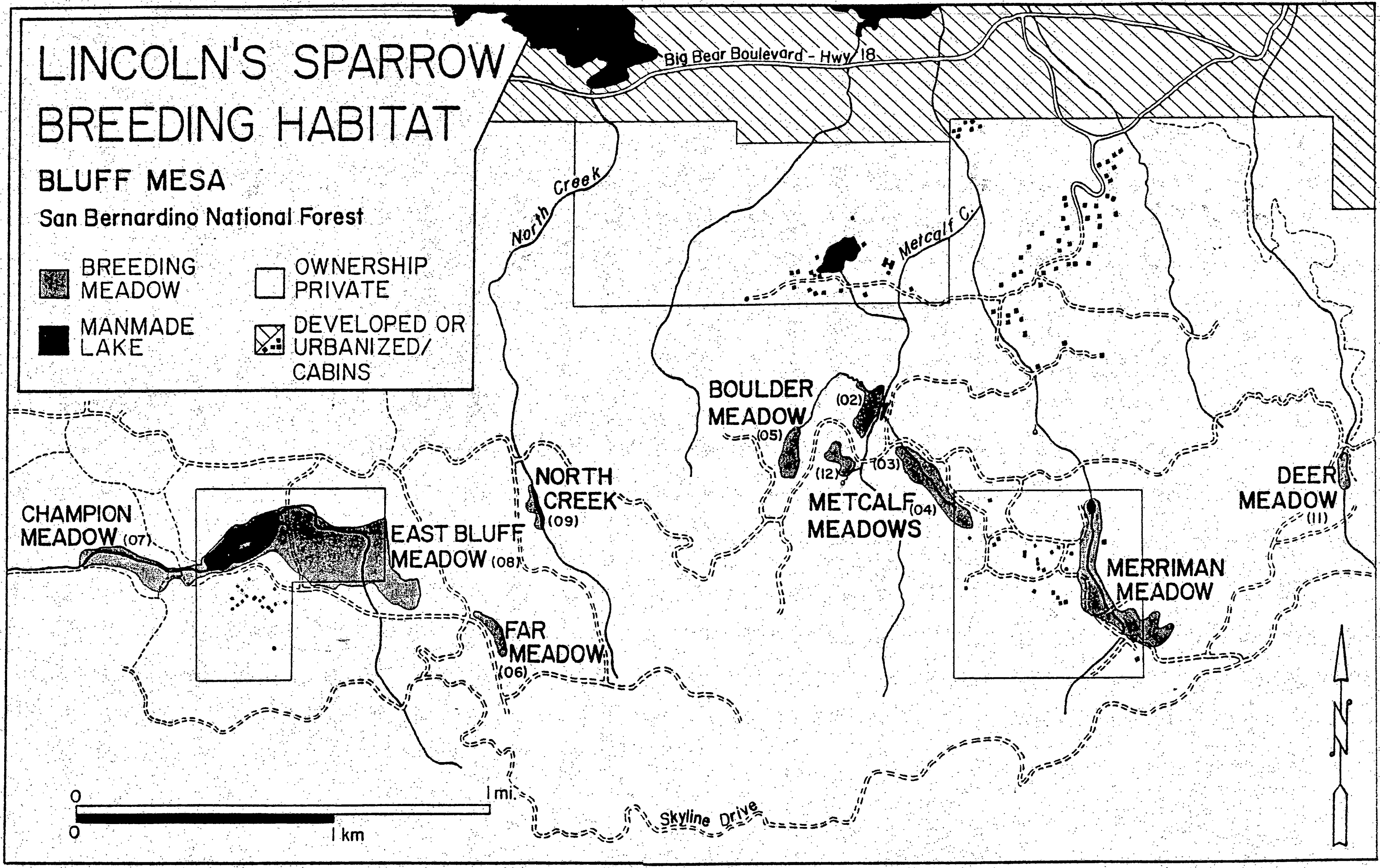

Figure 6.--The meadow "archipelago" in the Bluff Mesa region of the San Bernardino mountains of southern California that served as a focal area for observation of Lincoln's Sparrows.

MATERIALS AND METHODS

PERMITS REQUIRED.

Government permits. Before sampling bird populations, a Federal Bird Marking and Salvage Permit is required. These permits are issued by the U.S. Department of Interior Fish and Wildlife Service (USFWS), Office of Migratory Bird Management, Laurel, Maryland 20708. Applicants must explain their research intent, and--if lacking ornithological expertise--work under the supervision of an experienced researcher. Master bander Barbara A. Carlson, manager of the University of California at Riverside Motte Rimrock Reserve, sponsored my subpermit (#22251-A; Appendix A), which included a auxiliary-marking authorization for color banding of Lincoln's Sparrows.

CSUSB campus permits. The research protocol for this project was approved by the Animal Care Committee of the California State University at San Bernardino in accordance with federal regulations requiring annual reviews of all research involving animals at the University.

PHILOSOPHICAL APPROACH.

The Animal Behavior Society (1986) states that an important tenet of field research is that "investigators should always weigh any potential gain in knowledge against the adverse consequences of disruption." The U.S. Fish and Wildlife Service (1977) cautions bird banders "to bear in mind that the welfare of the bird is of the utmost importance." In concordance with these ideals, all research activities were planned and carried out with the intention of minimizing possible negative impacts upon the study species, its habitat, or associated organisms.

CAPTURE OF SUBJECTS.

Mist net trapping equipment and procedures. Adult and fledged juvenile birds were captured in mist nets (nine- or twelve-meter length, four-tiered, two meter high, 1.5 inch mesh of 70 denier two-ply nylon thread, purchased from the Eastern Bird Banding Association). Each mist net was stretched between two hollow poles inserted over anchoring rods hammered into the ground. When a small bird flew into the net, its momentum dropped it into a pocket of loose net below a horizontal tier line where it became harmlessly trapped. No trapping was conducted when wind, rain, or high temperatures might have endangered trapped birds.

Two approaches to trapping Lincoln's Sparrows with mist nets were employed during this study.

1. Targeted deployment. After observation of the movement patterns of an individual or pair of Lincoln's Sparrows (any time from dawn to dusk), a single mist net would be placed so as to intercept an anticipated line of flight. Optionally, a pocket-sized, battery-operated

cassette tape player was placed in the grass near the middle of the net and set to play a loop recording (Gunn and Kellogg 1975) of male Lincoln's Sparrow songs.

If the playback successfully lured a subject into the net, the tape player was shut off and the trapped bird was removed from the net. The net was taken down after data collection was complete, usually within thirty minutes of setup.

If the tape-recorded "intruder" did not provoke a territorial response within five to ten minutes, the playback was terminated. In such cases, the net might be left in place during further observation or might be relocated to a new position immediately. This low-profile approach required only a single researcher and minimal capture equipment and was employed at all study sites.

2. Intensive deployment. A cooperative association with Barbara A. Carlson permitted an intensive sampling of several meadows in the San Bernardino mountains (refer to Table 2). Using a standardized procedure to survey avian diversity in montane meadows, M. Carlson's team of three to six volunteer field assistants placed ten to thirteen mist nets in specific meadow locations. Nets were usually located among meadow willow thickets, which decreased net visibility and increased likelihood of bird traffic. Nets were opened at dawn and monitored at intervals of thirty minutes or less for six hours.

Hand capture. Lincoln's Sparrows were captured by hand as nestlings or non-flying fledglings. Nestlings were ideally banded on day six or seven following hatching, when their legs were large enough to retain adult-sized bands but before nest disturbance was likely to precipitate premature fledging. Unlike captured adults or older, mobile juveniles, these young captives had known birth sites, parents, siblings, and hatch dates (within a few days). Nests and newly-fledged juveniles were located in three ways.

1. Visual observation of adults. While nest building or provisioning hungry young, adults were secretive but somewhat repetitive in their behavior. Careful observation of adult movements provided clues to nest or fledgling location.

2. Aural clues. The repetitive vocalizations of older nestlings and recently-fledged young were sometimes useful in tracking chick location.

3. Meadow traverse. Deliberate transects back and forth across a meadow could cause pre-flight young to break from cover or could flush an incubating/brooding female from a nest. Serendipitous nest discovery also occurred.

General handling procedures. Captured birds were processed as quickly and carefully as possible to minimize stress. Field workers received instruction in proper retrieval of birds from nets and safe handling procedures.

Beginning banders were closely supervised by experienced field workers until competency was assured.

1. Mist-netted birds. After extrication from the net (a process that usually takes less than one minute, but sometimes as much as fifteen minutes), captured birds were placed in individual 25 x 25 cm cloth or mesh holding bags for transport to the closest dry spot (during targeted trapping) or to the team banding station at the meadow's margin (during intensive net deployment).

All birds were released once data collection was complete, usually within fifteen to thirty minutes after initial capture. Lincoln's Sparrows that had been transported outside of their estimated territorial boundaries were returned prior to release. Individuals captured a second time in a single day were either released immediately after extrication from the mist net or held for an abbreviated data collection procedure.

2. Special procedures for nestlings. Hand-captured nestlings from a single nest were placed together in a single holding bag and transported approximately ten to twenty meters away from the nest for banding and data collection. This distance represented a compromise between the need to minimize researcher presence at the nest site (which is associated with increased risk of attracting predators to the nest) and the need to band, measure, and return the chicks to the nest without permitting the

parents the opportunity to visit the empty nest (which is associated with increased risk of parental desertion).

CONFIRMATION OF SPECIES IDENTITY.

Lincoln's Sparrows. Assurance of proper species classification relied on a combination of size and plumage traits that distinguish Lincoln's Sparrows from other sparrow species in the study area (Petersen 1983). The most obvious field mark of a Lincoln's Sparrow is a distinct buffy breast band. Classification of adults to species is not difficult, but many young sparrows--including locally sympatric Song Sparrows--share similar juvenal plumages. Species classifications of juvenile birds were made after carefully reviewing criteria available in published guidelines (U.S. Fish and Wildlife Service 1977, Rimmer 1986, Pyle et al. 1987, Yunick 1990).

Non-target species. Other captured bird species were identified using available U.S. Fish and Wildlife Service dichotomous keys (1977) and illustrated field guides to ensure accurate conclusions.

MARKING.

USFWS leg bands. Following species classification, each captured Lincoln's Sparrow was fitted with a uniquely-numbered "Size 1" aluminum leg band provided by the U.S. Fish and Wildlife Service (USFWS). The USFWS bands are federally-registered, which allows identification of banded birds no matter where, when, or by whom the birds are recaptured. In 1988, all small bird species caught during the course of my research were banded with appropriately-sized USFWS bands. In 1989 and 1990, I released non-target species without banding.

The USFWS leg bands come pre-formed as closed cylindrical "bracelets" strung in numerical sequence on a wire. Specially-designed banding pliers (Roger N. MacDonald, 850 Main St., Lynnfield, Massachusetts 01940) were used to partially open the aluminum band. The pliers then gripped the band so that it could be slipped over the bird's tarsometatarsus and safely returned to a cylindrical shape. All banding equipment is shown in Figure 7.

<u>Color bands</u>. In addition to the numbered aluminum USFWS leg band, each Lincoln's Sparrow was marked with a unique combination of three colored-plastic leg bands (L & M Bird Leg Bands, 4164 Pershing Ave., San Bernardino, California 92407). These colored leg bands permit identification of individual birds in the field without the necessity of recapture. Adults and independent juveniles were banded with one color band above the aluminum USFWS band on the right leg and two color bands on the left leg. To distinguish individuals banded as nestlings or flightless fledglings, the USFWS band was placed in the bottom position on the left leg.

In 1988, the colors used were RED, LIGHT BLUE, GREEN, YELLOW, and PINK, and an attempt was made to code birds by

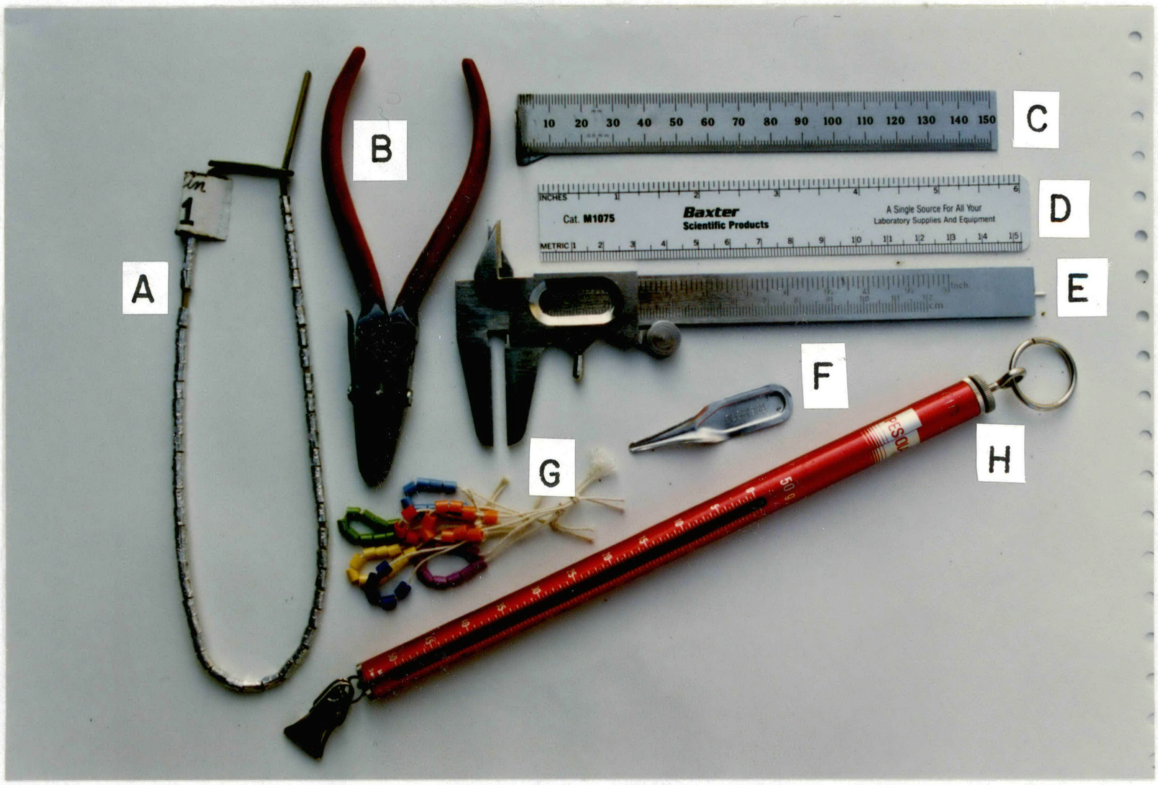

Figure 7.--Equipment used in banding and measuring Lincoln's Sparrows. A) U.S. Fish and Wildlife Service numbered aluminum leg bands, B) banding pliers, C) metric wing ruler, D) plastic metric ruler, E) vernier calipers, F) plastic leg band applicator, G) assorted colored-plastic leg bands, and H) metric spring scale.

using the color of the band above the USFWS band to indicate initial capture area. This plan not only restricted the available color band combinations but also potentially added a non-random factor to the study.

In 1989, color band combinations were chosen at random. VIOLET was added to the previous year's color selections. The use of PINK was discontinued due to color fade problems (see Results section). In 1990, NAVY BLUE and ORANGE were added to the color selections.

DATA COLLECTION.

Sex and age classification. Lincoln's Sparrows are a mostly monomorphic species. Males are (on average) larger than females, but there is considerable overlap in this size dimorphism. The sexual identity of juvenile and non-breeding adult Lincoln's Sparrows can be confirmed only through surgical methods such as laparotomy. Laparotomy does not appear to affect survival or disrupt breeding activity (American Ornithologists' Union 1988), but I lacked training in the technique and relied entirely on external characteristics for classification. During breeding season, the following characteristics allow identification of sex and confirmation of age in captured adult Lincoln's Sparrows:

1. Cloacal protuberance. A characteristic of breeding male passerines is a cloacal protuberance: a swelling and protrusion of the posterior wall of the male

proctodeum that contains vasa deferentia. This protuberance reaches its maximum size at the peak of the breeding season and then subsides until the male cloaca is indistinguishable from that of females (Pettingill 1970). Each cloacal protuberance was assigned a numerical rating (Table 3) as an indicator of breeding condition. A strong cloacal protuberance was considered confirmation of male sexual identity. Females may sometimes exhibit minor (stage 1) cloacal swelling but would generally have brood patches at the same time (Pyle et al. 1987). Because most wild North American birds do not breed until approximately one year of age (Pettingill 1970), the presence of a cloacal protuberance also confirms a bird's age as after-hatch-year.

2. Brood patch. A brood or incubation patch is a feather-free area of thickened, vascularized skin on the ventral surface of a bird's body that facilitates transfer of body heat to eggs (Pettingill 1970). The stage of brood patch development provides insight into the breeding condition of captured individuals, and numeric codes were assigned to the most distinct stages for data collection purposes (Table 4). In most passerines, only females develop brood patches, presumably because they do all or most of the incubation, especially at night when heat transfer is most critical (Pettingill 1970). Brood patch presence is considered a reliable confirmation of female

Table 3.--Stages of cloacal protuberance (used to identify the sex and breeding condition of adult male Lincoln's Sparrows).

Numeric Code	Description		Approx. Timing
0	Slight protuberance of females and non-breeding males		Year-round
1	Partial breeding males		Early spring or post-breeding
2	Full breeding males		Onset of egg-laying (in females)
3	Wow!; a continuation of full breeding males		Same as above

Sources: Carlson 1989, modified from Pyle et al. 1987.

Table 4.--Stages of brood patch development (used to identify the sex and breeding condition of adult female Lincoln's Sparrows).

Numeric Code	Description	Approx. Timing
0	No brood patch	Pre-reproductive
1	Defeatherization: feathers lost from ventral apterium	3-6 days before first eggs laid
2	Vascularization: blood vessels in dermis increase in size and number, becoming easily visible	Egg laying
3	Edema: skin thickens, is visibly fluid-filled and heavily vascularized	Incubation
4	Recovery: vascularization subsides, skin is wrinkled, grayish, scaly	Hatchlings become homothermic

Sources: Carlson 1989, based on Pyle et al. 1987 and Bailey 1952.

sexual identity and also confirms after-hatch-year status. Hatch-year birds in juvenal plumage also lack feathers on the abdomen, but an experienced researcher can distinguish these juvenal bare patches from true brood patches.

3. Skull pneumatization. Incomplete pneumatization in the cranium of passerine birds is considered evidence that these individuals are in their hatch year. In newly-hatched passerines, the cranium initially consists of a single layer of bone; as time passes, a second layer develops underneath and is joined to the first by many small columns of bone (Pyle et al. 1987). This process may take from four to twelve months (Pyle et al. 1987), possibly depending on dietary calcium levels (Hamel and Wagner 1990). Numeric codes were assigned to describe approximate stages of skull development (Table 5).

Skull pneumatization can be observed through the skin of most passerine birds. Use of a hand lens or other magnifying device is recommended by Ralph (1988) but is not usually necessary. Poor lighting, subdermal hemorrhages, or heavy head molt can make "skulling" difficult or impossible.

4. Plumage. Some plumage characteristics of Lincoln's Sparrows are useful in assigning age. First, compared to adult plumage, juvenal plumage is more brownish and streaked, with a loose texture to the body feathers. Second, all North American passerines undergo a postnuptial

Table 5.--Stages of skull pneumatization (used to confirm hatch-year status in Lincoln's Sparrows).

Numeric Code	Description
1	Beginning pneumatization near base of cranium
2	Early pneumatization, along either periphery or median line
3	Moderate pneumatization, with large central windows
4	Advanced pneumatization, with small windows
5	Complete pneumatization

Source: Carlson 1989, based on Pyle et al. 1987.

(prebasic) feather molt following breeding season. In many species, prebasic molt differs in extent or timing between hatch-year and adult birds. In Lincoln's Sparrows, adults replace all feathers during prebasic molt, while hatch-year birds get new body feathers but not new flight feathers (primaries, secondaries, and rectrices) (Pyle et al. 1987).

Morphological measurements. In order to obtain the highest possible level of methodological consistency and accuracy, I took all morphological measurements myself and used the same equipment for measurement throughout the entire study (Figure 7). Measurements of wing length, deck length, bill length, bill width, and tarsal length were collected from each captured adult and fledged juvenile Lincoln's Sparrow. Nestlings were not measured, except where specially noted, in order to minimize handling.

1. Wing length. The unflattened wing length or wing chord of the right wing was measured to the nearest millimeter (mm) using a stainless steel metric ruler equipped with a perpendicular stop at zero (Chris N. Rose, 98 Lopez Rd., Cedar Grove, NJ 07009). With the wing in its resting position, a measurement was taken from the wing bend (carpal joint) to the tip of the longest primary feather. Because feather wear can reduce feather length and affect statistical analysis of data, numeric ratings of primary feather condition were recorded for each bird (Table 6).

Table 6.--Stages of primary feather wear (used to evaluate feather condition in Lincoln's Sparrows).

Numeric Code	Description
0	Feather edges perfect, as indicated by a light-colored edge. Seen on fledglings or newly-molted birds.
1	Light-colored edge worn away from tips, but feathers still in excellent condition with no fraying or nicks.
2	Light wear, consisting of perhaps a few small nicks and very minimal fraying of feather edges.
3	Moderate wear, with feather edges showing definite fraying, with obvious nicks and chips from edges.
4	Heavy wear; feathers are very worn and frayed, tips often worn off down to fade line.
5	Excessive wear, with feather shafts exposed beyond vane and most tips completely worn or broken off.

Source: Carlson 1989, following Ralph 1988.

3. Deck length. The tail length of each sparrow was measured to the nearest millimeter using a thin plastic metric ruler trimmed so that the end of the ruler coincided exactly with the zero mark. The ruler was inserted below the two central tail feathers (also known as the "decks") until the zero end of the ruler was pushed firmly against the point of feather insertion. The measurement was read from the tip of the right deck. In cases where the left deck was noticeably longer than the right, a note of the asymmetry made and that deck was also measured. A numeric rating of deck condition was assigned in order to evaluate potential for reduced measurements due to feather wear or molt (Table 7). Any discrepancies between deck wear and tail feather wear as a whole were described in notes.

4. Bill length. Bill length (from the anterior end of the nostril to the tip of the bill) was measured with vernier calipers to the nearest 0.1 mm.

5. Bill width. Bill width (at the anterior point of the nostril) was measured to the nearest 0.1 mm, using vernier calipers. This measurement was not included in the standard morphological data collection series until 1989.

6. Tarsal length. The tarsometatarsus (hereinafter referred to as the tarsus, for brevity's sake) was measured from the intertarsal joint to the distal end of the last leg scale to the nearest 0.1 mm with vernier calipers.

Table 7.--Stages of deck feather wear (used to evaluate feather condition in Lincoln's Sparrows).

Numeric Code	Description
0	Decks missing
1	Decks in sheath (growing)
2	Decks appear fully grown but brand new; a fine light edging exists on feather tips
3	Slight wear, with some small nicks and light fraying
4	Very heavy fraying and nicking of edges; feathers probably no longer at full length
5	Extreme wear, with exposed and/or broken shafts

Source: Carlson 1989.

Pyle et al. (1987) state that the tarsal length "is a relatively difficult measurement to perform on live birds" without explaining why. I found the measurement difficult at first due to an inability to consistently identify the starting and ending points of the tarsal segment. After a frustrating 1988 field season, I standardized my tarsal measurement technique through consultations with project advisor Barbara A. Carlson, master bander C. J. Ralph at the 1988 Western Bird Banding Conference in Arcata, California, and curator Gene Cardiff of the San Bernardino County Museum who graciously permitted me to practice my measurement on Lincoln's Sparrow museum specimens.

Dynamic physical and physiological data. Selected physical and physiological conditions of captured birds were measured or described using categorical numerical classifications to record behavioral characteristics and physiological conditions pertinent to the breeding biology of Lincoln's Sparrows.

1. Wingtip fade. Prolonged exposure to sunlight breaks down feather pigments. The extent of this exposure can be evaluated on the primaries where feather overlap creates distinct fade lines. Feather fade can provide indirect clues to the amount of time the bird has spent foraging in exposed areas versus beneath vegetative canopies. Feather fade can also provide clues to the length of time an individual has had its flight feathers,

assisting with age classification. The degree of fade was rated on a numeric scale (Table 8).

2. Weight. Weight was determined to the nearest tenth of a gram (g) using a 50 g Pesola spring scale tared for and briefly clipped to a lightweight plastic bag which restrained and supported the bird during the brief (less than 30 seconds) weighing process. Nestlings were also weighed during handling.

3. Subcutaneous fat deposits. Fat accumulation, particularly in the interclavicular region (furcula), is easily visible through the skin as whitish or yellowish patches contrasting against reddish muscular background. Various stages of fat accumulation were rated on a numeric scale (Table 9). This is a widely-used field method of estimating total body fat in birds. New technology for nondestructive fat scoring is being investigated (Castro et al. 1990), but observational scoring has been shown to be quite reliable for intraspecies comparisons carried out by a single researcher (Krementz and Pendleton 1990). The fat deposits exhibited by nestlings were recorded.

3. Body feather molt. A numeric scale was used to rate the extent of body molt (Table 10). As time and field conditions allowed, additional notes were made describing patterns of body, wing, and tail feather molt.

Table 8.--Stages of wing tip fade (used to evaluate fade patterns of primary flight feathers of Lincoln's Sparrows)

Numeric Code	Description
0	No fade line evident
1	Light fade line, visible only in good light
2	Moderate fade line
3	Heavy fade line, easily discernible in all light

Source: Carlson 1989.

Table 9.--Stages of subcutaneous fat accumulation (used to assess extent of subdermal fat deposits in Lincoln's Sparrows)

Numeric Code	Description
0	No visible fat
1	Trace of fat in furcula
2	Thin layer of fat in furcula
3	Furcula partially filled with fat
4	Furcula completely filled with fat
5	Fat slightly mounded above furcula
6	Fat distending considerably above furcula
7	Fat pad of furcula and abdomen merge

Source: Carlson 1989, see also Helms and Drury 1960.

Table 10.--Stages of body feather molt (used to describe extent of body molt in Lincoln's Sparrows)

Numeric Code	Description
0	No molt evident
T	Only a few sheaths visible or molt is occurring non-symmetrically
1	Up to 1/3 of body in molt
2	Up to 2/3 of body in molt
3	Over 2/3 of body in molt

Source: Carlson 1989

4. Injury, disease, and mortality. Any parasites, wounds, or indications of disease observed during handling were described in field notes. After handling a bird with a possibly communicable disease, holding bags and weighing bags were discarded immediately. Otherwise, holding and weighing bags were generally washed or replaced weekly.

Any Lincoln's Sparrow that died as an immediate result of capture or handling was treated as a living specimen as far as the collection of capture data was concerned. Following data collection, the dead bird was labeled as a salvage specimen and placed in a plastic bag for freezing and eventual preparation as a study skin or museum mount in the ornithological collection of the University of California at Riverside.

FIELD OBSERVATIONS.

Observational equipment. Most field observations were done with binoculars (J.C. Penney 7x50). A spotting scope (Clover 20x-50x60 m/m zoom) provided excellent magnification but was used only a few times because the frequent, rapid movements of Lincoln's Sparrows made it difficult to keep subjects focused and in the field of view. Photographs of selected breeding sites and study subjects were taken with a Pentax K-1000 camera with a 28-70 mm zoom lens.

Observational objectives. In addition to observations leading to capture attempts, field observations of

Lincoln's Sparrows were undertaken to confirm survival of banded birds, provide estimates of territorial boundaries, identify pair-bonds and parent-offspring relationships, and generally investigate ecological and behavioral dynamics.

RECORD KEEPING.

Field notes. A field notebook was maintained to record general field conditions such as time, temperature, weather, and identity of field companions (if any) for each day spent in the field. These notes also included observational details regarding condition of vegetation, evidence of other wildlife, sightings of color-banded Lincoln's Sparrows, interesting behaviors, nest visits, and so on.

Trapping journal. Whenever mist nets were set up, a record was kept of exact net location, time period in place, and trapping success.

Banding data sheets. A gridded record sheet was used to organize capture data in sequence by USFWS band number. These record sheets documented color-band combinations assigned, time and date of capture, capture site codes for mountain range, meadow, and placement within the meadow, and the data collected for each individual.

Color-band control. A list of all possible color-band combinations was maintained to eliminate duplication of color combinations. When a color-combination was assigned, a notation of the associated USFWS number, date, and approximate banding site was made on the control sheet.

Site diagrams. Sketch maps of each banding site were used to illustrate mist net deployment, territorial boundaries, and nest sites. Elevations were estimated from 7.5-minute or 15-minute series U.S. Geological Survey topographic maps.

Individual life history record sheets. Information from banding and observation was consolidated into life history records that documented year-to-year patterns of capture, pair-bonds, breeding success, and other data for each individual Lincoln's Sparrow.

U.S. Fish and Wildlife Service reports. At the end of each research season, a report of the USFWS band number, species, age, sex, date of banding, and 10-minute latitude/longitude block of capture for each banded bird was submitted to the USFWS Banding Laboratory in Maryland.

DATA ANALYSIS.

Data processing equipment. Field data were organized and processed for statistical analysis using the SUPERCALC 4 spreadsheet program on an IBM-compatible microprocessor.

Defining the morphological data base. The final data base included first-time measurements of all Lincoln's Sparrows banded in 1988 and 1989, plus the first-time measurements of recaptured birds banded (but not measured by me) in 1987, plus first adult recapture measurements of birds banded as juveniles. Deck measurements with a rating of "0" (missing) or "1" (growing) and measurements of wing chord and deck length associated with wear ratings of "5" (refer to Tables 7 and 8) were dropped from the data set because of the extreme likelihood that the measurements were truncated. A more conservative approach would have also dropped measurements associated with wing or deck ratings of "4". I chose to retain these measurements in order to avoid further reduction in the size of the data base, after confirming that their inclusion did not appear to distort distributional curves.

Data manipulations. Because of size dimorphism between male and female Lincoln's Sparrows (Pyle et al. 1987), the data set was subdivided by sex. The adult data sets were then sorted by capture site into four general geographic regions: 1) Bluff Mesa and 2) Santa Ana River drainage in the San Bernardino mountains and 3) Round Valley and 4) Tahquitz Flats in the San Jacinto mountains (refer to Figures 4 and 5, Table 2). Juveniles and adults of unknown sexual identity were placed in separate categories.

The juvenile data set was subdivided into four developmental stages rather than geographic groupings: 1) nestlings, 2) pre-flight-capable fledglings, 3) flight-capable but parentally-dependent fledglings, and 4) independent juveniles. The category of adults of unknown sexual identity contained only three individuals and was not included in statistical processing.

Recapture and observational data. Data collected from repeat captures and resightings of previously-banded individuals from 1987 through 1990 were used in the analysis of within-year and between-year site fidelity patterns and in quality-control checks of measurement accuracy. Qualitative physical and physiological data were not statistically analyzed in this study but provided important referents to individual physiological condition.

Statistical analysis. After data sorting was complete, basic descriptive statistics (mean, range, sample standard deviation, standard error, and coefficient of variation) for each of the five measured morphological features were calculated for each data base and its subsets. F-test and Student's T-test were used to evaluate the significance of variation between means.

RESULTS

OVERVIEW.

From 1987 to 1990, a total of 259 Lincoln's Sparrows were live-trapped, banded, measured, and released for observation on their breeding grounds in the San Bernardino and San Jacinto mountains of Southern California. Recapture, mensural, and observational data collected during 724 field hours were analyzed to determine patterns of site fidelity, morphological variation, and breeding biology (Tables 11 through 24).

CAPTURE DATA.

Population demography. Approximately half (136) of the 259 Lincoln's Sparrows were identified as after-hatch-year (AHY) birds at first capture (Table 11). The age of these birds was unknown except that they were in at least their second calendar year. The sex of about 1% of the adult population was indeterminable. Among the adults of identifiable sex, 80 were male and 51 were female. Males consistently outnumbered females by at least a 3:2 ratio in each year of the study and in both newly-captured and previously-banded adult Lincoln's Sparrow sample sets.

Of the 123 hatch-year (HY) Lincoln's Sparrows captured, 48 were banded as nestlings, 4 as pre-flight-capable fledglings, and 10 as flight-capable but

Table 11.--Number of Lincoln's Sparrows captured or visually identified in the San Bernardino and San Jacinto mountain ranges of southern California, 1987-1990, by age and sex classes.

	Adults						Hatch-year					
	Male		Female		Unknown		Juvenile		Locals		Total	
	(c)	(o)	(c)	(o)	(c)	(o)	(c)	(o)	(c)	(o)	(c)	(o)
1987												
Newly-banded	6	...	3	...	2	...	9	...	...	...	20	...
1988												
Newly-banded	34	...	27	...	2	...	9	...	20	...	92	...
Recoveries												
banded in '87	3	...	1	...	1[a]	...	...	...	...	...	5	...
1989												
Newly-banded	33	...	17	...	1	...	29	...	42	...	122	...
Recoveries												
banded in '87	2	...	...	...	...	...	...	...	...	...	2	...
banded in '88	13	3	11	4	...	...	1[a]	...	2[a]	...	27	7
1990												
Newly-banded	7	...	4	...	...	...	14	...	0	...	25	...
Recoveries												
banded in '87	1	...	...	...	...	...	...	...	...	...	1	...
banded in '88	1	4	2	4	...	...	...	...	1[a]	1[a]	4	9
banded in '89	3	1	1	1	...	...	...	...	...	...	4	2
Total number of individuals banded	80		51		5		61		62		259	

[a]Identified as AHY-M at time of recapture.

dependent fledglings (these three categories are jointly referred to as "locals" in Table 11). The remaining 61 hatch-year birds were banded as apparently independent juveniles. Hatch-year Lincoln's Sparrows were not sexed, but a bimodal curve in the juvenile Lincoln's Sparrow histogram for wing chord (Figure 8) suggests that males may outnumber females in the captured juvenile population.

Unbanded birds. Unbanded adult Lincoln's Sparrows (of unknown origin, unknown age) were observed or captured in each year of the study, in all meadows--including the most heavily sampled sites (Table 12). The ratio of unbanded to banded adults in the population decreased with each year of the study but unbanded adults continued to account for a majority of the adult capture population.

Age and sex analysis of returns. Of 125 Lincoln's Sparrows banded as adults from 1987 to 1989, 44 (35%) were identified in at least one subsequent year (Table 13). Of these, 15 were captured or observed in three consecutive years, and one was observed in all four years of the study. Some individuals may have escaped identification or recapture. For example, in 1990, two adult Lincoln's Sparrows were spotted near their 1988 capture sites although neither had been seen in 1989. Each season, approximately 50% of the banded adults present the previous year were recaptured or observed to have returned, regardless of sex or year of original capture.

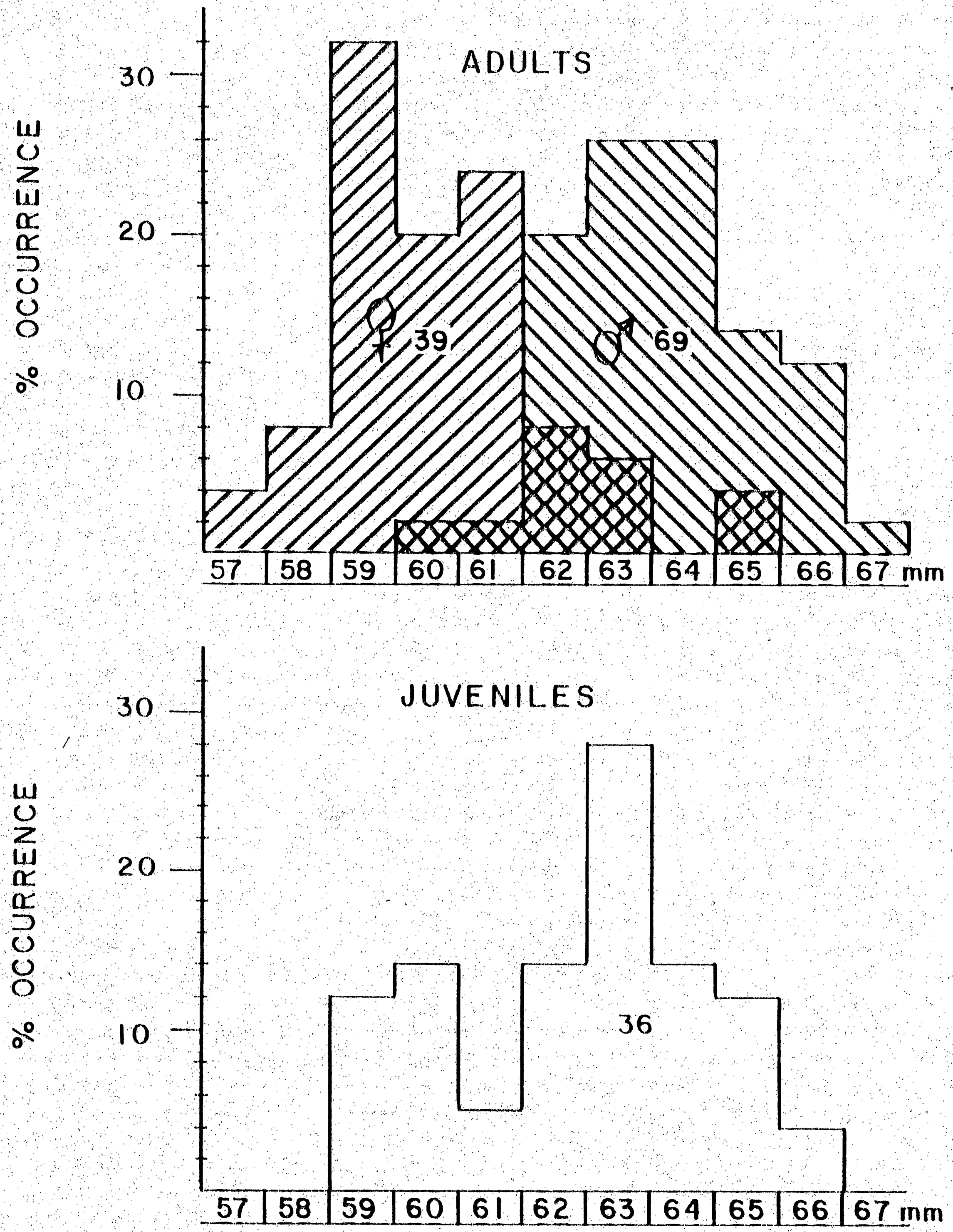

Figure 8.--Wing chord histograms for adult and juvenile Lincoln's Sparrows measured in the San Bernardino and San Jacinto mountains of southern California.

Table 12.--Distribution of field time and Lincoln's Sparrow capture success by sites in the San Bernardino and San Jacinto mountain ranges of southern California.

	Number of visits by month[a]										Number of Lincoln's Sparrows captured, by age and sex class[c]				
Site	A	M	J	J	A	S	O	Field hours	T[b]-net hours	I[b]-net hours	AHY-M	AHY-F	AHY-U	HY-U	L-U
SB01 - Wildhorse Spring															
1987	.	.	.	2	1	1	1	30	...	109	...	...	...	...	...
1988	.	.	1	1	1	1	1	30	...	153	...	...	...	...	...
1989	.	.	1	1	.	.	.	18	...	64	...	...	...	...	...
1990	.	.	.	.	.	.	.	...	...	...	...	...	...	...	...
Total							12	78	0	326	0	0	0	0	0
SB02 - L. Metcalf Meadow															
1987	.	.	.	1	.	.	.	6	...	67	5	2	...	1	...
1988	.	3	2	4	.	.	.	38	6	60	3,[r]2	5	...	3	4
1989	1	1	4	8	5	.	.	81	17	378	4,[r]4	0,[r]5	1	13	9
1990	.	1	1	2	.	.	.	18	3	66	2,[r]2	1,[r]3	...	3	...
Total							33	143	26	571	14	8	1	20	13
SB03 - M. Metcalf Meadow															
1987	.	.	.	1	.	.	.	6	...	60	1	...	1	1	...
1988	.	.	1	2	.	.	.	17	2	65	3	2,[r]1	...	1	1
1989	.	1	2	2	.	.	.	22	4	60	0,[r]4	1,[r]1	...	6	6
1990	.	.	1	1	.	.	.	8	1	60	1,[r]1	2	...	5	0
Total							11	53	7	245	5	5	1	13	7
SB04 - U. Metcalf Meadow															
1987	.	.	.	1	.	.	.	6	...	60	...	1	...	3	...
1988	.	.	.	1	.	.	.	8	...	60	0,[r]1	3	...	0	...
1989	.	1	1	3	.	.	.	20	4	60	4	3,[r]1	...	1	5
1990	.	.	.	1	.	.	.	6	...	60	2,[r]2	1,[r]1	...	6	...
Total							8	40	4	240	6	8	0	10	5
SB05 - Boulder Camp Meadow															
1987	.	.	.	1	.	.	.	6	...	60	...	...	...	1	...
1988	.	1	.	.	.	.	.	1	...	...	...	...	...	...	...
1989	.	.	2	1	.	.	.	4	3	...	1	...	...	...	...
1990	.	.	.	1	.	.	.	1	...	...	...	...	...	...	...
Total							6	12	3	60	1	0	0	1	0

Table 12.--continued.

Site	Number of visits by month[a] A M J J A S O	Field hours	T[b]-net hours	I[b]-net hours	Number of Lincoln's Sparrows captured, by age and sex class[c] AHY-M	AHY-F	AHY-U	HY-U	L-U
SB06 - Far East Bluff Lake Meadow									
1987	. . . . 1 . .	6	...	60	...	...	1	3	...
1988	. 1 . 1 . . .	13	4	60	0,[r]1	1	...	...	...
1989	. . . 1 1 . .	24	25	60	2,[r]2	1,[r]1	...	2	1
1990	. . . 1 . . .	7	...	60	...	...	...	...	...
Total	6	50	29	240	2	2	1	5	1
SB07 - Champion Lodgepole Pine Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. 3 7 4 1 . .	88	18	...	12	5	...	...	15
1989	1 2 5 1 1 . .	37	10	...	3,[r]4	2,[r]1	...	1	5
1990	. . . 2 . . .	6	...	...	...	...	...	...	...
Total	27	131	28	0	15	7	0	1	20
SB08 - East Bluff Lake Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . . 1 . .	1	1	...	...	...	...	...	...
1989	. . . 1 . . .	6	...	60	...	...	...	2	...
1990	. . . 2 . . .	7	...	78	0,[r]1	...	...	...	...
Total	4	14	1	138	0	0	0	2	0
SB09 - North Creek Pocket Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. 1 1	13	2	...	2	1	...	...	...
1989	. . 3	4	2	...	1	1	...	...	...
1990	. . . .	...	...	...	...	...	...	...	...
Total	5	17	4	0	3	2	0	0	0
SB11 - Deer Camp Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . 1 . 1 . .	9	7	...	3	1	...	4	...
1989	. . 2 1 1 . .	16	21	...	...	0,[r]1	...	...	...
1990	. . . 1 . . .	3	5	...	1	...	...	...	...
Total	7	28	33	0	4	1	0	4	0

Table 12.--continued.

Site	Number of visits by month[a] A M J J A S O	Field hours	T[b]-net hours	I[b]-net hours	Number of Lincoln's Sparrows captured, by age and sex class[c] AHY-M	AHY-F	AHY-U	HY-U	L-U
SB12 - Metcalf Spring Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . 2 . . .	7	7	...	1	1	...	...	...
1989	. . 1 1 . . .	8	7	...	1	1	...	3	5
1990	. . 1 1 . . .	3	1	...	1	...	...	...	...
Total	6	18	15	0	3	2	0	3	5
SB13 - Mission Creek Spring Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . 1 . . .	3	1	...	1	1	...	...	...
1989	. . . .	...	...	...	...	...	...	...	...
1990	. . . .	...	...	...	...	...	...	...	...
Total	1	3	1	0	1	1	0	0	0
SB14 - College Camp Verge Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . 1 . . .	4	2	...	1	...	...	...	...
1989	. . . 1 . . .	1	1	...	...	...	...	...	...
1990	. . . .	...	...	...	...	...	...	...	...
Total	2	5	3	0	1	0	0	0	0
SB15 - Big Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . 1 . . .	5	2	...	1	1	...	...	...
1989	. . . 2 . . .	11	9	...	2,[r]1	...	...	1	...
1990	. . . .	...	...	...	...	...	...	...	...
Total	3	16	11	0	3	1	0	1	0
SB16 - Little Cienega Seca									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. 1 . 1 . . .	3	1	...	1	...	...	...	...
1989	. . . 1 . . .	3	2	...	1	1	...	...	...
1990	. . . .	...	...	...	...	...	...	...	...
Total	3	6	3	0	2	1	0	0	0

Table 12.--continued.

Site	Number of visits by month[a] A M J J A S O	Field hours	T[b]-net hours	I[b]-net hours	Number of Lincoln's Sparrows captured, by age and sex class[c] AHY-M	AHY-F	AHY-U	HY-U	L-U
SB17 - Upper Fish Creek Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . 1 1 . .	14	6	...	2	2	2	...	...
1989	. . 2	11	8	...	0,[r]1	2,[r]1	...	...	1
1990	. . . .	...	...	...	...	...	...	...	...
Total	4	25	14	0	2	4	2	0	1
SB18 - Horse Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . . 1 . .	3	1	...	1	1	...	...	...
1989	. . . .	...	...	...	...	...	...	...	...
1990	. . . .	...	...	...	...	...	...	...	...
Total	1	3	1	0	1	1	0	0	0
SB19 - Seca 7000 Verge									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . . 1 . .	2	1	...	1	...	...	...	...
1989	. . . .	...	...	...	...	...	...	...	...
1990	. . . .	...	...	...	...	...	...	...	...
Total	1	2	1	0	1	0	0	0	0
SB20 - Wildhorse Meadows									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . 1 1 . . .	10	5	...	1	1	...	...	...
1989	. . 1 1 . . .	6	5	...	1	1	...	...	3
1990	. . . .	...	...	...	...	...	...	...	...
Total	4	16	10	0	2	2	0	0	3
SB21 - Upper South Fork Meadows									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . . 1 . .	5	1	...	...	...	...	...	...
1989	. . . .	...	...	...	...	...	...	...	...
1990	. . . .	...	...	...	...	...	...	...	...
Total	1	5	1	0	0	0	0	0	0

Table 12.--continued.

Site	Number of visits by month[a] A M J J A S O	Field hours	T[b]-net hours	I[b]-net hours	Number of Lincoln's Sparrows captured, by age and sex class[c] AHY-M	AHY-F	AHY-U	HY-U	L-U
SB25 - Fish Creek Trailhead Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . 1 . . .	1	...	...	...	...	...	...	...
1989	. . 1	3	2	...	1	1	...	...	...
1990	. . . .	...	...	...	...	...	...	...	...
Total	2	4	2	0	1	1	0	0	0
SJ116 - Reed's Trail Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . .	...	...	...	...	...	...	...	...
1989	. . . 2 . . .	4	5	...	2	1	...	...	2
1990	. . . .	...	...	...	...	...	...	...	...
Total	2	4	5	0	2	1	0	0	2
SJ117 - Skunk Cabbage Meadow									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . . 1 . .	6	3	...	1	2	...	1	...
1989	. . 3 1 . . .	28	23	...	5,[r]1	1	...	...	1
1990	. . . .	...	...	...	...	...	...	...	...
Total	5	34	26	0	6	3	0	1	1
SJ118 - Round Valley									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . .	...	...	...	...	...	...	...	...
1989	. . . 2 . . .	13	11	...	4	1	...	...	4
1990	. . . .	...	...	...	...	...	...	...	...
Total	2	13	11	0	4	1	0	0	4
SJ120 - Little Tahquitz Valley									
1987	. . . .	...	...	...	...	...	...	...	...
1988	. . . . 1 . .	1	...	...	...	...	...	...	...
1989	. . . 1 . . .	3	4	...	1	...	...	...	...
1990	. . . .	...	...	...	...	...	...	...	...
Total	2	4	4	0	1	0	0	0	0

[a]Months: April, May, June, July, August, September, October.

[b]Net hours: T = targetted mist netting, I = intensive mist netting.

[c]Age and sex classes: AHY = after hatch year, HY = hatch year; M = male, F = female, U = sex unknown.

[r]Indicates number of previously-banded individuals captured (excluding same-year recaptures).

Table 13.--List of recaptures and resightings[a] of Lincoln's Sparrows in the San Bernardino and San Jacinto mountain ranges of southern California, by date and capture site[b], in numerical order by USFWS[c] band number. Individuals that were not captured in two or more years are not listed.

USFWS band #	Age/sex class[d]	1987 date; site	1988 date; site	1989 date; site	1990 date; site
202103503	AHY-M			5/27; 0202	7/17; 0201
202103508	AHY-F			6/02; 1203 7/24; 1204	6/30; 0399[a]
202103510	AHY-F			6/05; 0901 6/20; 0901	7/17; 0203
202103513	AHY-M			6/12; 0703	7/02; 0705[a]
202103521	AHY-M			6/20; 0406	7/23; 0408
202103568	AHY-M			7/13; 0610	7/23; 0402
202103601	AHY-M		5/27; 0701 6/22; 0701	5/15; 0701[a] 6/30; 0701[a]	
202103603	AHY-M		5/27; 0703	5/29; 0706[a]	
202103604	AHY-M		5/27; 0704		7/02; 0703[a]
202103606	AHY-M		5/27; 0706 6/22; 0704 7/13; 0707	6/12; 0706	
202103610	AHY-M		6/02; 0705	6/12; 0706	7/02; 0703[a]
202103615	AHY-F		6/11; 0209 7/21; 0210	8/30; 0209	
202103616	AHY-F		6/11; 0208 7/21; 0207	7/20; 0205	
202103617	AHY-M		6/21; 0399	5/25; 0399	
202103618	AHY-F		6/21; 0399	6/24; 0399[a]	
202103620	AHY-F		6/21; 0293 7/23; 0298	7/04; 0293	7/17; 0293[a]
202103623	AHY-M		6/25; 0901	5/25; 0308	5/12; 0209[a]
202103624	AHY-M		6/25; 0902	6/30; 0707	
202103627	AHY-F		6/28; 0703 7/13; 0706	6/12; 0706	7/02; 0703[a]
202103628	L(88)-M		6/29; 0701 7/28; 0800[a]	7/13; 0610	7/11; 0801
202103635	L(88)-M		6/29; 0703	6/30; 0702	7/09; 0705[a]
202103637	AHY-M		6/30; 1102 8/10; 1105[a]	7/01; 1103[a]	
202103638	AHY-F		6/30; 1103	7/01; 1103	
202103639	AHY-M		6/30; 1103 7/21; 0201 7/20; 0203	5/27; 0299 6/02; 0599[a]	

Table 13.--continued.

USFWS[a] band #	Age/sex class[b]	1987 date;site	1988 date;site	1989 date;site	1990 date;site
202103643	AHY-M		7/06; 0711	6/30; 0710	
202103644	AHY-F		7/06; 0710		7/02; 0703[a]
202103650	AHY-F		7/12; 0610	7/13; 0610	
202103651	AHY-F		7/13; 0705 6/15; 0703[a]	6/08; 0703[a] 7/09; 0705[a]	7/02; 0705[a]
202103661	AHY-F		7/21; 0201 8/22; 0205	7/20; 0211 7/17; 0201	5/12; 0206
202103662	HY(88)-M		7/21; 0203	7/20; 0205	
202103663	AHY-F		7/21; 0204 7/20; 0209 8/23; 0209	5/27; 0209	
202103667	AHY-M		7/22; 0308 5/25; 0308	4/23; 0398[a]	7/18; 0308
202103668	AHY-M		7/22; 0304 7/21; 0304	5/25; 0303	6/30; 0399[a]
202103674	AHY-M		7/25; 1501	7/18; 1503	
202103678	AHY-M		7/26; 0297	6/03; 0297	
202103682	AHY-F		7/27; 0406	7/04; 0308	
202103683	AHY-F		7/27; 0403	6/20; 0406	7/23; 0409
202103686	AHY-M		7/29; 1702	6/22; 1702	
202103687	AHY-F		7/29; 1702	6/22; 1702	
202103695	AHY-F		8/09; 11702	6/29; 11702[a]	
202103696	AHY-M		8/09; 11702	6/29; 11702	
202103698	AHY-F		8/09; 11703	6/28; 11703[a]	
205117815	AHY-M	7/22; 0206	6/11; 0206 6/21; 0209 7/21; 0209		
205117817	AHY-M	7/22; 0207	7/21; 0204 8/24; 0204	5/27; 0206	7/17; 0206
205117826	AHY-M	7/23; 0310	7/27; 0401		
205117832	AHY-F	7/29; 0403	7/22; 0308		
205117839	AHY-M	8/19; 0608	7/12; 0610	7/13; 0610	

[a]Sightings; noted only where they illustrate movement or survival not documented by recapture.

[b]For capture site codes, see Table 2.

[c]U.S. Fish and Wildlife Service.

[d]Age/sex class codes: AHY = after-hatch-year, HY = hatch-year, L = local, M = male, F = female; numbers in parenthesis after HY and L designations indicate birth year.

In contrast to adult return rates, only three of 109 Lincoln's Sparrows banded as hatch-year birds from 1987 to 1989 were captured or observed in the study area in a subsequent season. All three were banded in 1988: two as nestlings and one as an independent juvenile. All three were identified as male at the time of recapture.

Site fidelity: year-to-year. Of the Lincoln's Sparrows known to have returned, most (90% of males, 92% of females, and 100% of previous-year juveniles) established territories in the same meadow they had used the previous year or a closely-adjacent meadow on the same local drainage (Table 14). All Lincoln's Sparrows identified as returning from migration settled on territories within two kilometers of their original capture sites.

For adults, all relocations to new meadows were from smaller meadows (Deer Camp, Far East, North Creek) to larger meadows (Metcalf, Champion). No adult established in a large, high quality meadow was observed to move to a smaller meadow, but some adults remained faithful to the smaller meadows from year to year.

Of the three returnees banded in their hatch year, two established territories within 50 m of their natal sites at Champion and Metcalf meadows as second-year males, and one moved among meadows adjacent to his natal site as a second-year and third-year male.

Table 14.--Site fidelity of Lincoln's Sparrows based on relationship of recapture to original capture sites in the San Bernardino and San Jacinto mountain ranges of southern California, 1988 through 1990, by age/sex class[a] at time of banding, with n equal to number of individuals (some individuals were recaptured a third and fourth year or repeatedly within a single season).

	Subsequent-year recapture or resighting events			Same-year recapture events		
	AHY-M n=25	AHY-F n=19	HY-U n=3	AHY-M n=15	AHY-F n=8	HY-U n=14
Same net	11 (33%)	13 (52%)	...	7 (32%)	4 (31%)	1 (5%)
Same meadow subsection	15 (46%)	6 (24%)	3 (60%)	13 (59%)	9 (69%)	7 (35%)
Same meadow	2 (6%)	3 (12%)	...	...	...	12 (60%)
Adjacent meadow	2 (6%)	1 (4%)	2 (40%)	1 (5%)	...	...
Same archipelago	3 (9%)	2 (8%)	...	1 (5%)	...	...
Same mountain range	...	...	...	...	...	...
Different range	...	...	...	...	...	...

[a]Age/sex class codes: AHY = after-hatch-year, HY = hatch-year, M = male, F = female, U = unknown.

Site fidelity: within-season. Although a deliberate attempt was made to minimize same-season recaptures, 14% (37 of 259) of the banded Lincoln's Sparrow population were captured more than once in one season. Of these, 70% were captured twice, 24% were captured three times, and 5% were captured four times. The average number of days between same-season recaptures was 26, with a range from 1 to 65 days. Same-day recaptures were not counted.

Same-year recapture data confirmed strong within-season territoriality among adult Lincoln's Sparrows (Table 14). Approximately 91% of adult males and 100% of adult females remained in the same area of a meadow throughout the spring and summer. Juveniles did not exhibit obvious territoriality but did remain in their natal meadows or adjacent meadows at least through the end of August when observations were terminated.

MORPHOMETRIC DATA.

Geographic subgroup comparisons. Morphological variation in wing length (Table 15), deck length (Table 16), bill length (Table 17), bill width (Table 18), and tarsal length (Table 19) of adult Lincoln's Sparrows was not high. The coefficient of variation for adult populations was under 6% for each of the five measured morphological characters, both within and among geographic subgroupings.

Table 15.--Wing chord statistics of newly-captured Lincoln's Sparrows, showing mean ($\bar{x}$) in millimeters $\pm$ one standard deviation (s), sample size (n), range of values, and coefficient of variation (V) by sex and age, year, and geographic subdivisions.

	1988				1989			
	$\bar{x} \pm s$	n	Range	V	$\bar{x} \pm s$	n	Range	V
ADULT MALES:								
Total	63.8 ± 1.4	35	61-67	2%	63.5 ± 1.5	34	60-66	2%
San Bernardinos								
Bluff Mesa	63.8 ± 1.2	26	62-67	2%	63.4 ± 1.7	19	60-66	3%
Santa Ana	63.7 ± 1.9	8	61-66	3%	63.2 ± 1.5	4	62-65	2%
San Jacintos								
Round Valley	...	0	...	...	62.9 ± 1.2	4	62-64	2%
Tahquitz	63.0	1	...	...	64.1 ± 0.6	7	63-65	1%
ADULT FEMALES:								
Total	60.0 ± 1.3	24	58-63	2%	60.1 ± 2.1	15	56-65	3%
San Bernardinos								
Bluff Mesa	60.1 ± 1.4	18	58-63	2%	60.4 ± 2.3	8	58-65	4%
Santa Ana	59.8 ± 0.8	5	61-59	1%	59.9 ± 2.2	5	56-62	4%
San Jacintos								
Round Valley	...	0	...	...	...	0	...	...
Tahquitz	61.0	1	...	...	59.2 ± 0.3	2	59-59.5	1%
HATCH-YEAR BIRDS:								
Nestlings	35.0	1	...	...	40.0	1	...	...
Preflight fledglings[a]	44.0	1	...	...	48.0 ± 2.8	2	46-50	6%
Flight-capable locals[b]	...	0	...	...	57.5 ± 4.3	10	52-63	8%
Independent juveniles[c]	60.6 ± 4.2	9	51-65	6%	62.3 ± 2.0	29	59-66	3%

[a]Individuals that have left the nest but are not capable of sustained flight.

[b]Individuals still being attended by adult(s).

[c]Fully flight-capable individuals that do not appear to be attended by adult(s).

Table 16.--Deck length statistics for newly-captured Lincoln's Sparrows, showing mean ($\bar{x}$) in millimeters ± one standard deviation (s), sample size (n), range of values, and coefficient of variation (V), by sex and age, year, and geographic subdivisions.

	1988				1989			
	$\bar{x}$ ± s	n	Range	V	$\bar{x}$ ± s	n	Range	V
ADULT MALES:								
Total	58.0 ± 2.2	33	54-64	4%	59.2 ± 2.1	30	54-63	4%
San Bernardinos								
Bluff Mesa	58.1 ± 2.2	23	55-64	4%	59.9 ± 2.2	15	54-63	4%
Santa Ana	58.0 ± 2.3	9	54-60	4%	58.0 ± 2.0	5	56-61	3%
San Jacintos								
Round Valley	...	0	...	...	58.0 ± 1.4	4	57-60	2%
Tahquitz	56.0	1	...	...	59.3 ± 2.0	6	56-61	3%
ADULT FEMALES:								
Total	55.8 ± 2.4	23	51-61	4%	55.7 ± 2.4	10	53-60	4%
San Bernardinos								
Bluff Mesa	56.1 ± 2.5	17	51-61	4%	56.3 ± 2.7	6	53-60	5%
Santa Ana	55.0 ± 2.1	5	53-58	4%	55.0 ± 2.0	3	53-57	4%
San Jacintos								
Round Valley	...	0	...	...	...	0	...	...
Tahquitz	55.0	1	...	...	54.0	1	...	...
HATCH-YEAR BIRDS:								
Nestlings	...	0	...	...	10.0	1	...	...
Preflight fledglings[a]	14.0	1	...	...	15.5 ± 2.1	2	14-17	14%
Flight-capable locals[b]	...	0	...	...	36.2 ± 12.7	9	24-55	35%
Independent juveniles[c]	58.7 ± 1.8	6	56-61	3%	57.7 ± 3.5	24	48-63	6%

[a]Individuals that have left the nest but are not capable of sustained flight.

[b]Individuals still being attended by adult(s).

[c]Fully flight-capable individuals that do not appear to be attended by adult(s).

Table 17.--Bill length statistics for newly-captured Lincoln's Sparrows, showing mean ($\bar{x}$) in millimeters ± one standard deviation (s), sample size (n), range of values, and coefficient of variation (V), by sex and age, year, and geographic subdivisions.

	1988				1989			
	$\bar{x}$ ± s	n	Range	V	$\bar{x}$ ± s	n	Range	V
ADULT MALES:								
Total	7.96 ± 0.37	38	7.2-8.9	5%	8.11 ± 0.37	36	7.4-9.0	5%
San Bernardinos								
Bluff Mesa	7.99 ± 0.38	28	7.3-8.9	5%	8.10 ± 0.32	19	7.5-8.9	4%
Santa Ana	7.86 ± 0.36	8	7.2-8.2	5%	7.80 ± 0.45	5	7.4-8.5	6%
San Jacintos								
Round Valley	...	0	...	...	8.40 ± 0.41	4	8.1-9.0	5%
Tahquitz	7.90	1	...	...	8.17 ± 0.34	8	7.7-8.6	4%
ADULT FEMALES:								
Total	7.84 ± 0.40	28	7.2-8.6	5%	7.88 ± 0.39	17	7.1-8.5	5%
San Bernardinos								
Bluff Mesa	7.88 ± 0.43	20	7.2-8.6	5%	7.90 ± 0.43	9	7.1-8.5	5%
Santa Ana	7.75 ± 0.31	6	7.4-8.2	4%	8.06 ± 0.21	5	7.9-8.4	3%
San Jacintos								
Round Valley	...	0	...	...	7.90	1	...	...
Tahquitz	7.65 ± 0.07	2	7.6-7.7	1%	7.35 ± 0.21	2	7.2-7.5	3%
HATCH-YEAR BIRDS:								
Nestlings	...	0	...	...	...	0	...	...
Preflight fledglings[a]	5.60	1	...	...	5.80	1	...	...
Flight-capable locals[b]	...	0	...	...	6.39 ± 0.50	10	5.8-7.1	8%
Independent juveniles[c]	7.22 ± 0.55	8	6.4-8.0	7%	7.55 ± 0.35	28	6.9-8.5	5%

[a]Individuals that have left the nest but are not capable of sustained flight.

[b]Individuals still being attended by adult(s).

[c]Fully flight-capable individuals that do not appear to be attended by adult(s).

Table 18.--Bill width statistics of newly-captured Lincoln's Sparrows, showing mean ($\bar{x}$) in millimeters $\pm$ one standard deviation (s), sample size (n), range of values, and coefficient of variation (V), by sex and age, year, and geographic subdivisions.

	1988[a]	1989			
		$\bar{x} \pm s$	n	Range	V
ADULT MALES:					
Total		4.21 ± 0.19	36	3.8-4.6	5%
San Bernardinos					
Bluff Mesa		4.20 ± 0.19	19	3.9-4.6	4%
Santa Ana		4.22 ± 0.25	5	4.0-4.6	6%
San Jacintos					
Round Valley		4.27 ± 0.05	4	4.2-4.3	1%
Tahquitz		4.21 ± 0.22	8	3.8-4.5	5%
ADULT FEMALES:					
Total		4.16 ± 0.15	17	4.0-4.4	4%
San Bernardinos					
Bluff Mesa		4.18 ± 0.17	9	4.0-4.4	4%
Santa Ana		4.12 ± 0.13	5	4.0-4.3	3%
San Jacintos					
Round Valley		4.00	1	...	...
Tahquitz		4.30 ± 0.00	2	4.3-4.3	0%
HATCH-YEAR BIRDS:					
Nestlings		...	0	...	...
Preflight fledglings[b]		4.10	1	...	...
Flight-capable locals[c]		4.03 ± 0.32	10	3.6-4.5	8%
Independent juveniles[d]		4.36 ± 0.15	28	4.0-4.6	4%

[a]No measurements were taken for this characteristic during 1988.

[b]Individuals that have left the nest but are not capable of sustained flight.

[c]Individuals still being attended by adult(s).

[d]Fully flight-capable individuals that do not appear to be attended by adult(s).

Table 19.--Tarsal length statistics of newly-captured Lincoln's Sparrows, showing mean ($\bar{x}$) in millimeters $\pm$ one standard deviation (s), sample size (n), range of values, and coefficient of variation (V), by sex and age, year, and geographic subdivisions.

	1988[a]	1989			
		$\bar{x} \pm s$	n	Range	V
ADULT MALES:					
Total		19.79 ± 0.64	36	18.2-20.9	3%
San Bernardinos					
Bluff Mesa		20.01 ± 0.56	19	18.6-20.9	3%
Santa Ana		19.80 ± 0.51	5	19.1-20.5	3%
San Jacintos					
Round Valley		19.02 ± 0.35	4	18.5-19.2	2%
Tahquitz		19.64 ± 0.75	8	18.2-20.6	4%
ADULT FEMALES:					
Total		19.27 ± 0.53	16	18.6-20.4	3%
San Bernardinos					
Bluff Mesa		19.46 ± 0.62	8	18.6-20.4	3%
Santa Ana		18.92 ± 0.08	5	18.8-19.0	1%
San Jacintos					
Round Valley		18.70	1	...	...
Tahquitz		19.65 ± 0.21	2	19.5-19.8	1%
HATCH-YEAR BIRDS:					
Nestlings		...	0	...	...
Preflight fledglings[b]		19.30	1	...	...
Flight-capable locals[c]		19.42 ± 0.58	10	18.6-20.4	3%
Independent juveniles[d]		19.78 ± 0.67	28	17.9-21.0	3%

[a]1988 measurements were discarded due to failure to standardize technique during that season.

[b]Individuals that have left the nest but are not capable of sustained flight.

[c]Individuals still being attended by adult(s).

[d]Fully flight-capable individuals that do not appear to be attended by adult(s).

F-statistic analysis of variance among sample means from the four geographic subgroups (Bluff Mesa and Santa Ana River regions of the San Bernardino mountains; Round Valley and Tahquitz Flats regions of the San Jacinto mountains) was conducted at the 0.05 level of significance. No significant differences were found among the populations in wing length, deck length, bill length, or bill width. In the case of male tarsal lengths (Table 19), F-statistic analysis generated the conclusion that differences in the means were too large to be attributed to chance. This conclusion was also generated at the 99% confidence level.

Sexual dimorphism. The most distinct morphological differences seen were between the sexes rather than among geographic units. Wing chord displayed the most distinct dimorphism (Figure 8). Males averaged 2% to 5% larger than females on all measured traits, but considerable overlap existed in all measured traits. T-tests at the 99% confidence level confirmed significant sexual dimorphism in wing chord, deck length, and tarsal length. No significant differences in bill length or bill width were found, even at 95% confidence levels.

The degree of variability in male and female traits was generally similar. Interestingly, coefficients of variation for developmentally-fixed characteristics (tarsal length and bill width) were slightly higher for males than females. In contrast, coefficients of variation were lower for males than females for measures of traits that were potentially alterable as a result of individual activity levels and/or daily or seasonal cycles (wing chord, deck length, and bill length).

Physiological dynamics. The weight of a small passerine may fluctuate several grams over the course of a single day, so this trait was not used in the analysis of variation among geographic subgroups. Coefficients of variation ranged from 4% to 16% for adults and from 6% to 23% for hatch-year birds (Table 20). Seasonal fluctuations in average adult weights were observed (Figure 9). High female weights in May coincided with onset of egg production, while lows coincided with the period when adults would be likely to be feeding young (Figure 10). Pre-migratory weight gains become apparent in early August.

Growth dynamics of immature birds. Data collected from hatch-year Lincoln's Sparrows reflected the dynamic continuum of nestlings fledging, achieving flight, and attaining independence and adult size (Tables 16 through 21). Due to rapid juvenile growth rates, higher coefficients of variation than those seen for adults were found for all traits, even when the data was subdivided by approximate growth stage. Geographic grouping of data from immature Lincoln's Sparrows was not feasible due to the small sample sizes obtained outside of the Bluff Mesa region.

Table 20.--Weight statistics of newly-captured Lincoln's Sparrows, showing mean ($\overline{x}$) in grams $\pm$ one standard deviation (s), sample size (n), range of values, and coefficient of variation (V), by sex and age, year, and geographic subdivisions.

	1988				1989			
	$\overline{x} \pm s$	n	Range	V	$\overline{x} \pm s$	n	Range	V
ADULT MALES:								
Total	17.53 ± 0.87	37	15.5-18.7	5%	17.51 ± 0.95	36	15.7-19.9	5%
San Bernardinos								
Bluff Mesa	17.47 ± 0.89	28	15.5-18.7	5%	17.52 ± 0.74	19	16.3-18.8	4%
Santa Ana	17.60 ± 0.84	8	16.4-18.6	5%	17.64 ± 1.56	5	16.0-19.9	9%
San Jacintos								
Round Valley	...	0	...	...	17.17 ± 1.16	4	15.7-18.5	7%
Tahquitz	18.5	1	...	...	17.55 ± 1.04	8	16.2-19.1	6%
ADULT FEMALES:								
Total	16.71 ± 1.81	28	13.9-20.9	10%	16.71 ± 1.56	17	14.4-20.0	9%
San Bernardinos								
Bluff Mesa	16.81 ± 2.04	20	13.9-20.9	12%	17.27 ± 1.53	9	15.4-20.0	9%
Santa Ana	16.42 ± 1.14	6	14.6-17.4	7%	16.28 ± 1.26	5	15.1-17.7	8%
San Jacintos								
Round Valley	...	0	...	...	14.90	1	...	...
Tahquitz	16.60 ± 1.56	2	15.5-17.7	9%	16.20 ± 2.55	2	14.4-18.0	16%
HATCH-YEAR BIRDS:								
Nestlings	12.42 ± 2.90	18	7.3-17.0	23%	12.73 ± 1.40	30	9.4-15.0	11%
Preflight fledglings[a]	14.10 ± 0.85	2	13.5-14.7	6%	15.40 ± 1.56	2	14.3-16.5	10%
Flight-capable locals[b]	...	0	...	...	15.68 ± 2.14	9	13.2-19.0	14%
Independent juveniles[c]	17.01 ± 1.71	9	14.4-20.5	10%	16.10 ± 0.90	28	14.5-17.8	6%

[a]Individuals that have left the nest but are not capable of sustained flight.

[b]Individuals still being attended by adult(s).

[c]Fully flight-capable individuals that do not appear to be attended by adult(s).

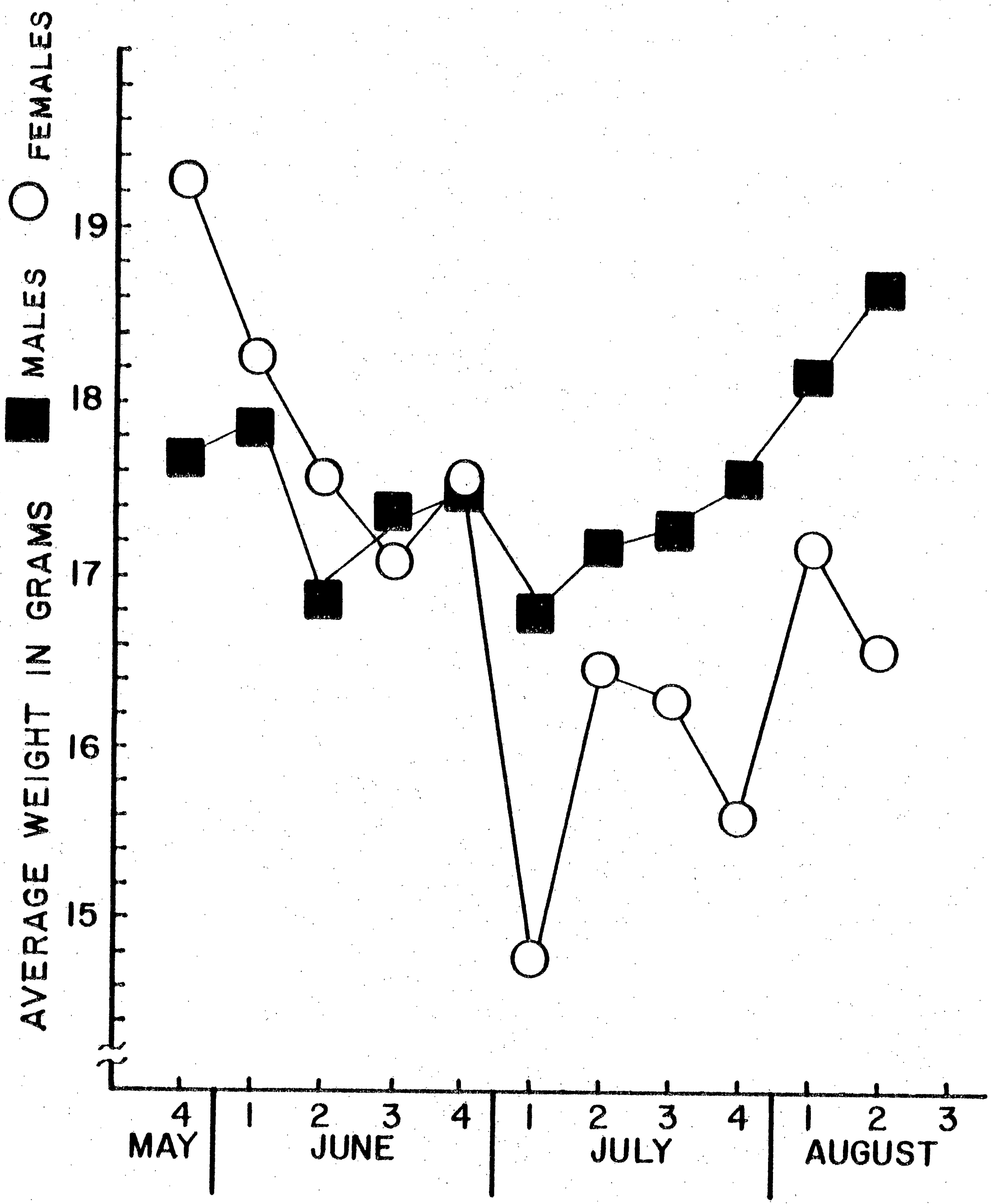

Figure 9.--Changes in average male and female adult Lincoln's Sparrows weights over the course of the breeding season in southern California.

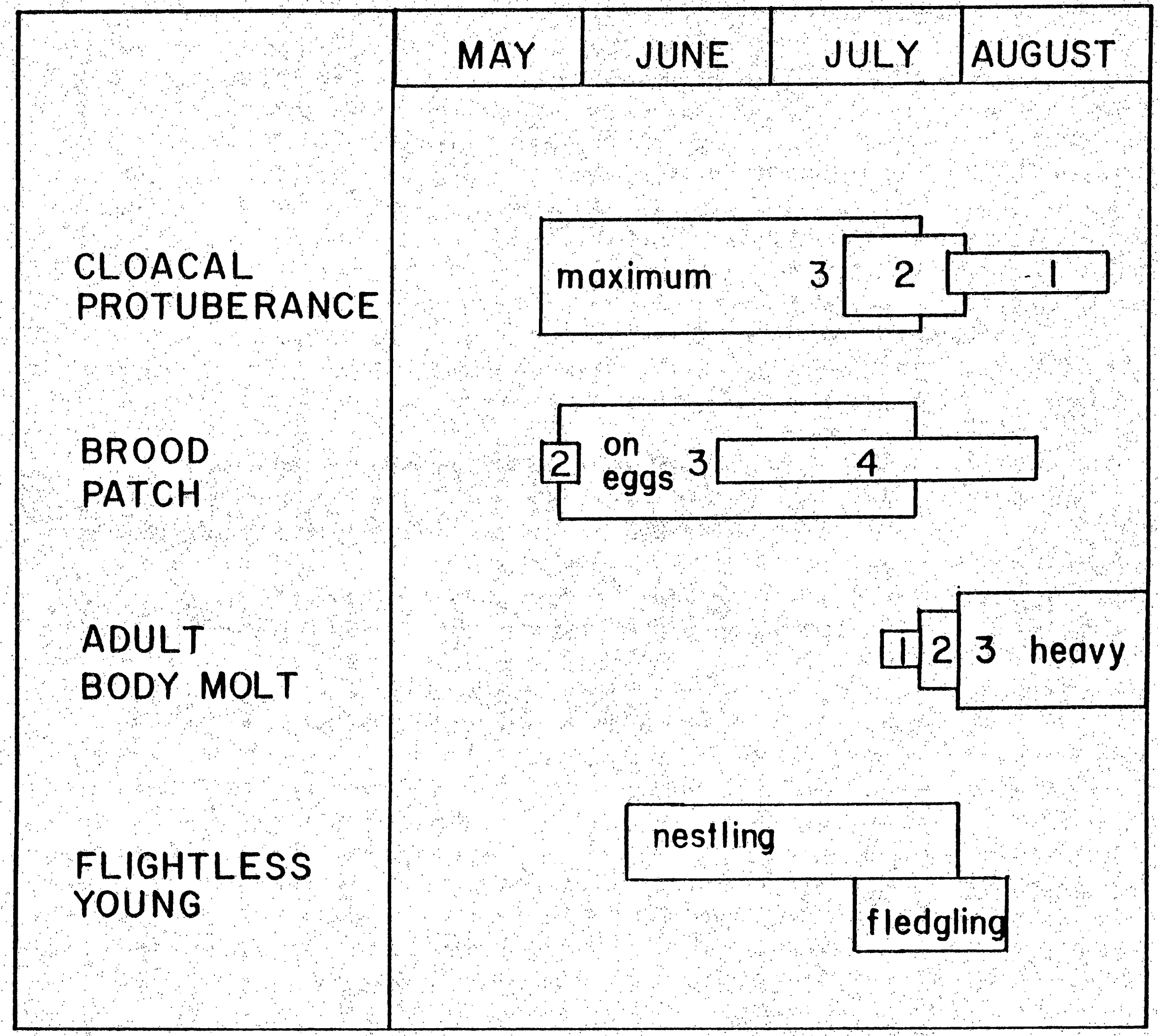

Figure 10.--Timing of events in the summer biology of Lincoln's Sparrows in the San Bernardino and San Jacinto mountains of Southern California.

1. Nestlings. As is typical of altricial birds, growth of nestlings is rapid. In this study, nestlings were not handled until they had attained a bandable age estimated at between 6 to 9 days after hatching. Nestling weights during that four-day time span could double (Table 21). Within-brood variation in weight ranged from 0.3% to 13.0%. Many nestlings had no fat reserves at the time of banding, and only one individual attained a fat class of 4 (refer to Table 9). Additional fat presence did not correlate with increased weight.

2. Fledglings. Young Lincoln's Sparrows leave the nest before they are able to fly well. Fledglings did not appear to be able to take to the air until wing length surpassed 50 mm (Table 15). Tail growth lagged behind wing growth, and flight-capable young birds were captured with deck lengths as short as 24 mm (Table 16). Growth of bony structures, such as tarsus and bill, also continued following fledging (Tables 17, 18, and 19).

3. Independent juveniles. Comparisons with adult population data were handicapped by the inability to sex immature Lincoln's Sparrows. However, the ranges of measurements in the independent juvenile data sets were similar to combined ranges of adult male and female data sets. This suggests that full growth or near to it was achieved by juveniles before their first migration away from their natal sites.

Table 21.--Lincoln's Sparrow nest and nestling statistics, by site, showing date and estimated chick age at time of banding, number of young per nest (n) plus any unhatched eggs (number in parenthesis), mean ($\bar{x}$) weight in grams ± one standard deviation (s), range of weight values, coefficient of variation (V) for weight, and mean and range of fat classifications.

Nest Site Code[b]	Date	Estimated chick age (days)[c]	n	Weight			Fat class[a]	
				$\bar{x} \pm s$	Range	V	$\bar{x}$	Range
0209	6/13/89	8	5	11.56 ± 0.65	10.8-12.4	5.6%	1.2	0-2
0406	6/20/89	8	5	12.18 ± 0.77	11.3-12.9	6.3%	0	0-0
0704	6/20/89	8	4	14.03 ± 0.05	14.0-14.1	0.3%	2.5	2-3
0701	6/29/88	8	5	13.08 ± 0.66	12.0-13.7	5.0%	0	0-0
0703	6/29/88	9	4(1)	16.00 ± 0.91	15.0-17.0	5.7%	2.7	2-4
0390	6/30/89	8	5	14.08 ± 1.00	12.4-15.0	7.1%	3.0	3-3
0710	7/06/88	9	4[d]	13.00 ± 1.41	12.0-14.0	10.9%	2.0	2-2
0705	7/16/88	6	4	7.92 ± 0.58	7.3- 8.6	7.4%	0	0-0
0209	7/21/88	7	3(1)	12.17 ± 0.31	11.9-12.5	2.5%	0.3	0-1
2007	7/23/89	9	3	12.20 ± 0.35	12.0-12.6	2.8%	0.3	0-1
1203	7/24/89	7	5	11.50 ± 1.49	9.4-13.2	13.0%	0	0-0
0209	7/29/89	8	3(1)	14.17 ± 0.74	13.6-15.0	5.2%	1.7	0-2

[a]See Table 10 for fat classification descriptions.

[b]See Table 2 for site locations; first two digits of nest code corresponds to site code.

[c]Days-after-hatch estimated by extent of featherization.

[d]Although there were 4 nestlings in this nest, 2 nestlings escaped into the grass without being banded (and before measurements could be made).

OBSERVATIONAL DATA.

Timing of breeding. My earliest visit to Lincoln's Sparrow breeding habitat was April 23. Males were already singing vigorously from concealed perches in willow clumps and Lodgepole pines and engaging in intermittent territorial skirmishes with conspecifics and congenerics (Song Sparrows, Melospiza melodia). By the time the first Lincoln's Sparrows were captured (May 25), all males had fully-developed cloacal protuberances, and females were in the process of nest-building, egg-laying, or egg-incubation (Figure 10).

Nesting attempts were staggered throughout the breeding season, with egg-laying occurring from mid-May to mid-July. Nestlings were banded as early as June 13 and as late as July 29. Brief outbursts of song persisted throughout August, but for the most part, male singing ended abruptly during the last week of July, along with territorial responses to tape-recorded song. These behavioral observations correlated with the rapid reduction of male cloacal protuberances during the last two weeks of July and the subsidence of active incubation patches in females by the third week of July (Figure 10).

Post-nuptial body molt was observed to begin as early as July 18, molt of primary feathers 1 and 2 as early as July 20, and molt of rectrices by July 27. Body and rectrix molt was still occurring in some individuals and wing feather molt had advanced to primaries 8 and 9 by the end of August. I was not able to discern any sex-specific patterns in molt.

Nest location. All of the Lincoln's Sparrow nests located during this study were well-hidden on the ground in clumps of grass and other low herbaceous meadow vegetation (20 to 40 cm in height), immediately adjacent to narrow, shallow water channels which often braided around the vegetative clump which sheltered the nest. Surface water was generally less than two centimeters deep, but due to soft saturated mud, I often found myself ankle- to calf-deep in water while trying to approach a nest site.

My ability to locate nests improved from 1988 to 1989, as I became familiar with patterns of adult Lincoln's Sparrow behavior and the characteristic vocalizations of their nestlings.

One drawback to locating nests by ear was that Lincoln's Sparrow young do not vocalize noticeably until they have reached an age where fledging is imminent, so that there is a great risk of the chicks "boiling out", perhaps a day or two prematurely, if the nest is disturbed. I found this out the hard way (through the experience of touching a nest and watching helplessly as Lincoln's Sparrow nestlings scattered from a nest and disappeared into the surrounding sea of grass). In subsequent reading, I found a vivid description of this characteristic behavior of young altricial birds (Pettingill 1970):

> Near the time of nest-leaving, [the nestling] will not gape at all; instead it cowers, sinking lower in the nest, sleeking the plumage, and sometimes even closing the eyes. If removed from the nest, it ordinarily "comes alive," giving "fear calls" and attempting escape. The commotion may induce its nest-mates to come alive, burst from the nest, and disperse. Thus alarmed, neither the nestling, taken from the nest, nor its fellows which departed of their own accord can be put back in the nest with the expectation of their staying.

I located a few nests by flushing an incubating female from the nest. However, such discoveries were usually accidental rather than as a result of deliberate meadow transects. Observations of known nest sites revealed that a female Lincoln's Sparrow may stay on her nest even when an intruder (such as myself) is right beside the nest. The female sometimes would not flush until the grass shielding the nest was moved aside. Even when flushed, female Lincoln's Sparrows tended to run away (nearly invisibly) through the grass rather than fly up into the air.

Fecundity. Out of 12 nests discovered and observed during 1988 and 1989 (refer to Table 21), average brood size was 4.2 young, excluding unhatched eggs. Single unhatched eggs were found in one early nest with four hatchlings and two late nests with three hatchlings. Clutch sizes generally declined as the season advanced.

Double-brooding (raising a second clutch after successfully fledging a first clutch) was confirmed in 1989. A breeding pair in Metcalf Meadow (site 0209) nested in late May, fledged five chicks by mid-June, rebuilt atop the previously-used nest, and fledged three more chicks by the end of July (Table 22). Observations of adults in several different meadows attending fledged young in June and then again in July provide evidence that second broods may not be uncommon.

Nest site fidelity. Reuse of specific nest sites was documented both within and between breeding seasons. Relocating nests hidden in a sea of grass was often difficult even from one day to the next, but in several instances I successfully used field notes to locate previous-year nest sites despite changes in the herbaceous landscape. In two cases, I found no nest, although I was confident of being in the correct spot. In two other cases, I found a fresh nest at the old site, despite the fact that a different pair was now occupying the territory.

Adult attendance on young. Only females were observed nest-building and incubating. Both males and females were active in giving alarm calls (a repetitive "tkk" that increased in frequency and volume with the approach of threatening intruders, reminiscent of a Geiger counter). On two occasions, the alarm cries of a flightless fledgling incited a parental distraction display. The adult

Table 22.--Lincoln's Sparrow nesting calendar, based on multiple observations of individual Lincoln's Sparrow nests in the San Bernardino mountain range.

Day	Nest 0204	Nest 0701	Nest 0209a	Nest 0209b
1	6/13-nest started	6/02-nest started		
2				
3	6/15-nest finished			
4				
5	6/17-two eggs			
6				7/08-three eggs
7				
8	6/20-five eggs		5/27-five eggs	
9				
10				
11				
12				
13				
14				
15				
16				
17				7/19-four eggs
18				7/20-four eggs
19	7/01-two eggs,			
20	three chicks		6/08-five chicks	
21				
22				7/24-one egg,
23				three chicks
24				
25			6/13-chicks banded	
26	7/08-nest found			
27	predated		6/15-five chicks	7/29-three chicks
28		6/29-five chicks		banded
29		banded	6/17-two chicks	
30			(others	
31			heard in grass	
32				
33				
34				
35		7/06- fledglings		
36		seen being	6/24- fledglings	
37		fed by adults	seen being	
38			fed by adults	
39				
40				

(unidentified as to whether it was the female or the male) fluttered out into the open with wings spread and dragging within two meters of where I sat with the chick.

Both adults provisioned nestlings and fledged young--as well as themselves--with a steady stream of caterpillars, moths, crane flies, and other unidentified arthropods. Newly-fledged young frequently retreated to shrubs and thickets for shelter, although all nests were found in the open. Adults were observed feeding adult-sized juveniles (wing chord up to 63 mm, deck length up to 55 mm) in response to their juvenile behavior.

Nest predation and parasitism. Of 13 observed broods, one fell prey to a nest predator just prior to attaining banding age. This was the only confirmation of nest predation made during this study, although potential predators (long-tailed weasel, coyote, squirrels, chipmunks, rats, snakes, Steller's Jay, Common Raven, etc.) were regularly observed in study meadows.

No evidence of cowbird parasitism of Lincoln's Sparrow nests was discovered despite Brown-headed Cowbird presence in the habitat.

Some nestlings suffered from myiasis, the condition of having maggot parasites. The large (4 x 18 mm) white dipteran larvae distended the skin as they burrowed in the flesh of the crown, wrists, thighs, and abdominal area near the cloacal vent. No nestling was observed to harbor maggots in more than two areas of its body, and maggot location was fairly uniform among sibling nestlings (Table 23). Parasite load ranged from one to six maggots per individual Lincoln's Sparrow chick. Most parasitized individuals had two or three maggots. When disturbed by an investigator, a maggot often squirmed out of the host's flesh though a small, pre-existing hole in the skin (approx. 1.5 mm diameter) and dropped to the grass. Several pupae were observed encysted in host tissue.

Likelihood of maggot parasitism seemed to increase as the breeding season progressed; a single parasitized fledgling was observed in late June, but all the other myiasis victims were observed during the last week of July.

No parasitized nestlings were recaptured, either later in the season or in a subsequent year. However, some Lincoln's Sparrows captured as independent juveniles had small circular scabs or scars on the skin of their crowns that could have been healed maggot holes.

Mate fidelity. The mating status of banded Lincoln's Sparrows was unknown in many cases. Data from the best-studied meadows indicate that Lincoln's Sparrows can be serially monogamous but that pair bonds are equally likely to be broken from one year to the next (Table 24). Some individuals were "widowed" by the failure of their partners to return following migration. The term "widowed" may be a misnomer if the missing partners emigrated outside the

Table 23.--Distribution of observed maggot presence in individual immature Lincoln's Sparrows captured in the San Bernardino mountains of southern California.

USFWS band number	Age class	Date	MAGGOT DISTRIBUTION			
			Crown	Wrist	Thigh	Abdomen
202103-						
-536	Fledgling	6/24/89	X	...	...	...
-672	Fledgling	7/23/88	X	X	...	...
-593	Nestling	7/24/89	...	...	X	...
-594	" "	" "	...	...	...	X
-595	" "	" "	...	...	X	X
-596	" "	" "	...	...	...	...
-597	" "	" "	...	...	X	...
-600	Fledgling	7/26/89	X	X	...	...
-408	Nestling	7/29/89	X	...	...	...
-409	" "	" "	X	...	...	...
-410	" "	" "	X	...	...	...

Table 24.--Mate fidelity in Lincoln's Sparrows, 1988 through 1990, in selected Bluff Mesa meadows, San Bernardino mountains of Southern California, listing only individuals whose pair bonds were observed; F = female, M = male, * = was not recaptured or observed, S = serially monogamous, W = widowed, D = divorced, U = mate was unbanded.

	PAIR BONDS BY SITE			
	0201 0211	0203 0204	0205	0209
Year	F x M	F x M	F x M	F x M
1988	661 x 659		663 x 817	616 x 815
	W *		D D	W *
1989	U x 503	616 x 662[a]	661 x 817	663 x 514
	W/D	* *	S	* *
1990	(from 0901) 510 x 503		661 x 817	

[a]Second-year male; banded previous year as independent juvenile.

Table 24.--continued.

	PAIR BONDS BY SITE					
	1203	0304	0399	0308	0403	0406 0408
Year	F x M	F x M	F x M	F x M	F x M	F x M
1988	685 x 649	669 x 668	618 x 617	832 x 667	683 x U	682 x U
	* *	* W	S	* W	?	W/D
1989	508 x 507	501 x 668	618 x 617	682 x 667	401 x 502	683 x 521
	W *	* W	* *	* W	* *	S
1990			508 x 668	439 x 667		683 x 521

Table 24.--continued.

Year	0701 F x M	0703 F x M	0704 F x M	0705 F x M	0707 F x M	0710 F x M
1988	621 x 601	627 x 603	U x 604	651 x 610		644 x 626
	* W	S	*	D D		* *
						from 0711
1989	544 x 601	627 x 603	506 x 505	U x 610	651 x 513	U x 643
	* *	W *	* *	W/D	S	*
1990		627 x 610	644 x 604	651 x 513		

study area rather than died, but the fate of missing individuals cannot be determined. In other cases, both mates returned from migration but formed pair bonds with new partners, i.e., "divorce" occurred.

Most serially-monogamous pairs reestablished previously-held territories. In cases of widowing or divorce, male Lincoln Sparrows generally retained custody of their original territory, while widowed or divorced females usually relocated to an adjacent territory in the same meadow. Although females were more likely to change territories than males, males--when they did disperse--relocated greater distances.

Lincoln's Sparrows were not observed to break pair bonds during a breeding season. One instance of an attempted extra-pair copulation was observed. A second-year male repeatedly pounced on a female from an adjacent territory as she tried to attend fledged young in the grass. This second-year male defended a territory and sang regularly during the breeding season, despite his apparent lack of success in attracting a mate of his own.

Habitat use. Adults not only foraged on the ground like "proper" sparrows, but also gleaned Veratrum stalks and tree and shrub branches like warblers, searched bark crevices like creepers, and "sky hawked" like flycatchers. Most activity was concentrated in the meadow or in bordering vegetation. A few birds were spotted as much as

100 meters away from a meadows' edges on dry, chaparral-covered slopes.

METHODOLOGICAL OBSERVATIONS.

Research-linked injury or mortality. Three Lincoln's Sparrows died as a result of capture, all during intensive net deployment. An adult male in 1988 and a juvenile in 1989 were found dead in the net, apparently from heat stress. The juvenile had been banded two weeks earlier as a flightless fledgling. In 1990, a newly-captured juvenile was found to have a shattered tibia; thoracic compression (as recommended by the American Ornithologists' Union 1988) was applied as a method of euthanasia.

In 1990, an adult female Lincoln's Sparrow was found to have had her right leg neatly amputated mid-tarsus. Color bands on her left leg indicated that she had been banded in 1989. The amputation was completely healed and the female was observed attending fledged young. The amputation may have occurred as a consequence of wearing bands or as an unrelated injury. Aside from occasional superficial net cuts (mostly on toes) and loss of body or tail feathers, no other injuries to either newly-captured or recaptured Lincoln's Sparrows were observed.

Use of tape-recorded song. As expected, this technique proved to be most effective with Lincoln's Sparrow males, but it occasionally provoked responses from females and juveniles. The tape recording of male

Lincoln's Sparrow song attracted adult male song sparrows on several occasions and once a song sparrow juvenile. Response to the tape recording was usually rapid. Often, the male Lincoln's Sparrow flew out to challenge the singing "intruder" before I had moved more than a few meters away from the net. In late July, Lincoln's Sparrows abruptly ceased responding to the tape-recorded song, although sporadic songs were heard well into August.

Use of mist nets. Subjects were observed approaching and then swerving away from mist net or (annoyingly) perching on the top trammel or poles. Detection of net presence appeared highest when subjects approached the net from an angle where sunlight reflected from the mesh or when breezes were causing mesh movement. Subjects sometimes hit the net, were caught, and then wiggled through the 1-1/2" mesh to escape in a matter of seconds.

Use of leg bands as markers.

1. Color band fade. Some of the colored-plastic bands underwent color changes after exposure to the elements. I discovered this potential problem early in the summer of 1989, when the first color-banded recoveries from 1988 were made. PINK color bands were found to have faded to a beige or off-white that was difficult to distinguish from yellow during field observations. Other colors shifted slightly under exposure, but not enough to create problems.

PINK bands faded noticeably within a single week of exposure to the elements in the San Bernardino Valley during the month of July, and a month of exposure resulted in color changes similar to those seen in the field on color-banded Lincoln's Sparrows after one year (Figure 11).

Band burden. In banding birds for a field study of demography and population dynamics, researchers are making an assumption that band presence will not affect these processes significantly. This assumption has not been widely tested (Frankel and Baskett 1963, Watt 1982, Burley 1985 and 1988, Hagan and Reed 1988 and 1989, Hill and Carr 1989). Application of any additional mass to a bird's body will presumably affect its energetics (American Ornithologists' Union 1988). In order to estimate the band load being applied to my study subjects, I weighed a random selection of 30 USFWS "size 1" aluminum leg bands and 54 colored-plastic leg bands to the nearest milligram on a Torsion Balance (Table 25). An estimated band burden range of 0.6% to 1.1% of body weight was calculated by comparing maximum and minimum band-load weights (one USFWS band and three colored-plastic bands) to the maximum and minimum values in a representative range of adult Lincoln's Sparrow body weights. Loads of less than 1% of body mass have been considered by researchers to have negligible effects on birds (Caccamise and Hedin 1985).

Figure 11.--Comparison of unexposed and sunlight-exposed color bands. New color bands (A) began color changes within one week of exposure in full sunlight (B). After 30 days of exposure, PINK bands had shifted in color to a faded yellow (C), and after 90 days of exposure, PINK bands had lost all color and were an off-white

Table 25.--Mean weight ($\bar{x}$) in grams of a random sample (n) of size 1 leg bands, showing the range of values and the coefficient of variation (V).

	n	$\bar{x}$	Range	V
Aluminum USFWS bands	30	0.065	0.064-0.066	0.8%
Colored-plastic bands	54	0.025	0.021-0.029	8.5%
Red	4	0.028	0.027-0.028	2.1%
Light blue	10	0.024	0.024-0.026	2.9%
Green	10	0.023	0.022-0.024	3.1%
Yellow	10	0.023	0.021-0.026	8.0%
Violet	10	0.025	0.024-0.026	3.1%
Navy blue	5	0.026	0.026-0.027	2.1%
Orange	5	0.028	0.027-0.029	3.0%

DISCUSSION

<u>PHILOPATRY AND DISPERSAL</u>.

<u>Importance of site fidelity</u>. The extent of reproductive insularity and inbreeding in a wild animal population is dependent on the degree of philopatry (faithfulness to a particular site) exhibited by the species. According to Best and Rodenhouse (1984), patterns of philopatry may vary both between species and between populations within a species. Mayr (1976) suggests that bird populations may be composed of two kinds of individuals, those with strong locality sense (70% to 90% of the population) and others with little or none (10% to 30% of the population).

Variations in philopatry have obvious implications for gene flow and effective population size. Despite the importance of this information to studies of evolutionary and ecological dynamics, estimates of effective population sizes (demes) of birds are in their infancy (Barrowclough 1980) and the factors influencing the dispersal-philopatry dynamic (such as criteria for territory selection, mate selection, mating system determination, and reproductive success) are poorly understood (Greenwood and Harvey 1982).

Determinants of site fidelity. Settlement patterns probably represent a trade-off between preference for areas of high quality and the benefits of site fidelity (Lanyon and Thompson 1986). The ability of birds to precisely relocate specific sites after migrations of hundreds or thousands of miles is remarkable and presumably must confer some selective advantage. Proximate advantages of philopatry include optimization of return times, improved chances for successful territorial acquisition and defense, and foreknowledge of potential food resources and predation risks. Ultimate advantages of philopatry include increasing the likelihood of matching a selected genome to the environment in which it evolved and finding a mate that shares the same adaptive gene complexes (Greenwood 1980).

Natural selection should favor individuals best able to identify, obtain, and retain high-quality habitat. Territory shifts or dispersal to new breeding areas has been correlated to prior reproductive failure in a wide range of bird species (Greenwood and Harvey 1982, Petersen and Best 1987). However, environmentally-unstable conditions, inability to assess habitat quality, or short life expectancy could favor site tenacity over the ability to disperse to potentially more favorable breeding locations (Oring 1982). Instances of continued faithfulness to site despite repeated reproductive failures (Best 1977, Bedard and LaPointe 1984) or habitat alteration

(Wiens and Rotenberry 1986, Knopf and Sedgwick 1987) have been documented.

In a review of the literature on dispersal, Greenwood (1980) found that movement from birthplace to first breeding site (natal dispersal) is usually greater than movement of individuals between successive breeding sites (breeding dispersal). Both natal and breeding dispersal tend to be female biased in bird species, in contrast to the male bias common in mammals (Greenwood 1980). However, exceptions do occur. Male-biased dispersal in American Goldfinches was observed by Middleton (1979).

Patterns observed in Lincoln's Sparrows. Greenwood and Harvey (1982) claim that most passerine species exhibit relatively strong philopatry ("median natal dispersal of both sexes usually less than ten territories from birth site"). Barrowclough (1980) estimated that noncolonial passerines disperse roughly one kilometer per year, with a range of 0.35 km to 1.70 km per year). These claims are supported by the results of this study of montane Lincoln's Sparrow populations in southern California, where the greatest dispersal distance observed was less than two kilometers.

Natal dispersal. Dispersal among juvenile birds is predicted to be more extensive than that of adults, while showing similar patterns of sex specificity (Greenwood and Harvey 1982). Unfortunately, the data set generated by my study was not large enough to support any conclusions regarding natal dispersal of Lincoln's Sparrows. Only three out of 109 Lincoln's Sparrows banded as juveniles in the first three years of this study were relocated within the study area in a subsequent year. It is impossible to know whether nonreturning individuals dispersed or died. Similar low return rates (0% to 11%) of individuals banded as juveniles are common in multi-year banding studies of small passerines (Goodpasture 1977, Wittenberger 1978, Freer 1979, Herlugson 1981, Shields 1984, Bedard and LaPointe 1984, Weatherhead and Boak 1986, Sullivan 1989).

The settlement patterns of the young Lincoln's Sparrows returning after migration support Greenwood and Harvey's (1982) contention that returning young in philopatric passerines usually settle within four to five territories of their natal territory, with a median dispersal distance of less than ten territories. The fact that all three returning young were male fits in well with the expected female-biased dispersal pattern (Greenwood and Harvey 1982). However, the sample size was far too small to be conclusive.

Breeding dispersal.

1. Influence of habitat and/or reproductive success. All instances of adult Lincoln's Sparrow dispersal were from small to large habitat areas, suggesting that the species has a preference for larger meadows. Although some

individuals were observed successfully fledging young prior to dispersing, it is possible that overall reproductive success is reduced in smaller habitat patches. Within-season and particularly between-season reuse of nest sites by Lincoln's Sparrows suggests the existence of highly-specific nest location criteria. Unfortunately, the population was not followed closely enough to yield data on comparative reproductive success. Additional study to determine the factors potentially motivating nest site choice and breeding dispersal is required.

2. Site versus mate fidelity. The issues of site fidelity and mate retention are closely intertwined. It has long been an ornithological maxim that the majority (approximately 90%) of birds mate in monogamous pairs (Lack 1968). The importance of the pair bond to reproductive success has been demonstrated by a number of studies of monogamous passerines, where a lone female will (at best) produce fewer and/or lower-quality offspring and (at worst) experience complete nest failure (Weatherhead 1979, Mead and Morton 1985, Lyon et al. 1987). Greenwood and Harvey (1982) suggest that mate retention from season to season results in enhanced reproductive success, but there is little unequivocal evidence from natural populations.

In order for serial monogamy to occur, both sexes must exhibit high site fidelity and both partners of a pair must survive to the next breeding season. Both of these conditions may be met, however, and individuals may still form new pair bonds. I observed equal occurrence of these outcomes in Lincoln's Sparrow pairs. The factors influencing whether individuals re-establish previous pair bonds or "divorce" and find new mates are poorly understood but believed to be influenced by age, sex, and previous reproductive success (Greenwood and Harvey 1982). Competition may also play a role. Delius (1965) found that male and female Skylarks almost always tried to settle on prior territory but were sometimes displaced by earlier-arriving birds, either one-year-old settlers or other displaced individuals. Detailed observations of individual life histories would be necessary to clarify this issue.

3. Sex biases in breeding dispersal. Gender biases in site fidelity of adult birds presumably originate in the different reproductive imperatives of males and females--i.e., the higher cost of reproductive failure to females (Orians 1969). Most studies of monogamous, open-ground-nesting sparrow species have described stronger site tenacity in males than females (Nice 1937, Walkinshaw 1968, Post 1974, Best 1977, Baker & Mewaldt 1978). In these cases, males remain in the same territories within and between breeding seasons, while a small proportion of females move one or two territories between seasons (Greenwood and Harvey 1982).

Sexually-undifferentiated return rates have been reported recently in Savannah Sparrows (Bedard and LaPointe 1984) and Song Sparrows (Arcese 1989b). In Lincoln's Sparrows, too, observed differences in male and female site tenacity were slight and overall annual return rates were similar (approximately 50%). There appeared to be a trend (following widowing or divorce) for male Lincoln's Sparrows to re-establish previously-held territories while females shifted to adjacent or nearby sites. However, in contradiction to theory, males--when they did disperse--moved slightly greater distances than did females. It is possible that dispersing males were subordinate individuals who had failed to obtain mates. If this is the case, their movements would not be considered breeding dispersal.

Lieberg and von Schantz (1985) predicted that little sexual differentiation in philopatry would exist where the mating system was truly monogamous. If true, sexual biases in dispersal arise from deviation from pure monogamy. In fact, researchers are finding that avian mating systems may be much more complex than previously believed. New genetic testing techniques are revealing frequent extra-pair copulation and intraspecific brood parasitism in an increasing number of outwardly monogamous species (Gowaty and Karlin 1984, Gavin and Bollinger 1985, Westneat 1987a, Westneat 1987b, Sherman and Morton 1988, Arcese 1989a, Petter et al. 1990). Little is known about the role of female sexual behavior (whether she solicits or resists extra-pair copulations) or the dynamics of sperm competition in wild passerines.

I observed only one instance of attempted extra-pair copulation. However, such behavior might be expected to be attempted somewhat furtively and thus be easy to miss even with careful observation. Closer monitoring of the reproductive success of individuals and the dynamics of pair-bonds is needed to shed light on the adaptive imperatives governing of mating systems and breeding dispersal. Ideally, field observations should be augmented by definitive tests, such as "DNA fingerprinting" of young and analysis of sperm samples collected by cloacal lavage from male and female subjects.

Skewed sex ratios. Lack (1954) postulated that a skew toward excess males would exist in most monogamous passerine species, perhaps as a result of higher female mortality. Such imbalances are believed to be an important influence on the dynamics of territoriality, mate choice, and dispersal.

In my study, I captured more male than female Lincoln's Sparrows. It seemed possible that this sex-biased result was an artifact of capture methodology, due to my use of tape-recorded male songs as a lure. However, I was able to capture most observed females using alternative strategies. Furthermore, territorial but apparently-unpaired male Lincoln's Sparrows were observed singing throughout each breeding season. Recapture data also showed that previously-banded birds had equal chances of being recaptured whether male or female. The similar recapture rates for male and female Lincoln's Sparrows negate the idea that the high proportion of males in the sample set is a result of greater female mortality in adults.

Preliminary evidence suggests that the skewed sex ratio may originate in the juvenile population (refer to Figure 8). A 1:1 sex ratio in egg-laying is expected (Gill 1990, p.425), and I observed no evidence of brood reduction (selective nestling mortality) that might affect after-hatch sex ratios. The next investigative step would be to use laparotomy (Fiala 1979) or karyotyping to sex nestlings, in order to determine whether the skewed sex ratios originate in hatch ratios or in differential nestling or post-fledging survival.

Nonreturning individuals. The fate of non-returning individuals in avian population studies is rarely determinable. Few researchers are able to adequately monitor the entire breeding range of a deme, much less a whole species. Identification of returning individuals is dependent on the amount and distribution of time spent in the field. Sites in this study were not treated consistently, due to time and manpower constraints. Nonreturning individuals may have returned but escaped identification, may have dispersed outside the study region, or may have died.

There are also potentially confounding factors due to the use of leg bands. Leg band presence may negatively bias survival, causing an underestimation of normal return rates. It is also possible that some unbanded individuals could be previously-captured birds that had removed their bands (Stedman 1990), leading to underestimation of returns. Therefore, the return rates of Lincoln's Sparrows generated by this study should be considered conservative estimates.

<u>Mortality</u>. Expected mortality rates for small passerines are sufficient to explain the nonreturning portions of both the adult and juvenile populations, although this cannot be established definitively due to the limitations discussed above.

1. <u>Juvenile mortality</u>. The average life expectancy of small passerines in the wild may be as low as one to two years, largely as a result of high first-year mortality (Pettingill 1970). A young passerine's annual chance of survival from fledging to breeding age is about half that of an adult (Gill 1990, p.411). Lack (1954) estimated the mortality rate of first year passerines at 70% to 90%.

Variability in juvenile mortality may be high both between and within populations. Gibbs and Grant (1987) found that different cohorts could have drastically different survivorship curves. Juvenile mortality may be especially high shortly after fledging, with most of the difference between juvenile and adult survival rates arising prior to migration (Lack 1968, Wittenberger 1978). Sullivan (1989) found that while predation was the main cause of mortality in nestling and fledgling juncos, rapid weight loss and death by starvation were widespread in recently-independent juvenile juncos, apparently due to inefficient foraging behavior.

One of the biggest unanswered questions of my research project is what happened to the 106 nonreturning (of 109 banded) juvenile birds. The return rate of juveniles from 1988 to 1989 was 10%, at the low end of predicted survival rates. The return rate from 1989 to 1990 was zero. This could be a result of the limited amount of field work conducted in 1990. However, most of young birds banded in 1989 were captured in the Bluff Mesa region of the San Bernardino mountains, and all of field work carried out in 1991 was done in the same region, so some recoveries were anticipated. None were achieved. Either mortality rates were extremely high or young birds dispersed widely.

2. Adult mortality. Annual survival rates in small temperate zone land birds are estimated to range from 30% to 65% (Gill 1990, p.412). Thus, expected small passerine mortality rates are sufficient to explain the nonreturning

half of the adult Lincoln's Sparrow population. Once individuals reach reproductive age, mortality is generally considered to be age-independent (Ricklefs 1973, Nol and Smith 1987, but see Botkin and Miller 1974), probably because relatively few birds live long enough to experience senescence. The current longevity record for Lincoln's Sparrows is seven years, seven months (Klimkiewicz and Futcher 1987). Survival may vary markedly between subpopulations, between the sexes, and between years (Wittenberger 1978, Gibbs and Grant 1987).

<u>Population recruitment</u>. While mortality may explain the disappearance of banded individuals, it does not account for the appearance of initially-unbanded adult Lincoln's Sparrows among the previously-banded population each year. These unbanded individuals may be immigrants from outside the study area or natives to the area that were missed during the previous year's capture efforts. Since no evidence of emigration over distances exceeding two kilometers was collected, I feel that the most likely source of these unbanded adults was the previous-year's juvenile population.

In the most intensively-studied meadows (within the Bluff Mesa habitat archipelago), I have confidence that in 1988 and 1989, I captured and banded 85% to 90% of the adults present each season. On the other hand, based on the number of breeding pairs present, their possible productivity, and sightings of unbanded juveniles, I estimate that I captured no more than 10% to 50% of the juvenile population, even in the most thoroughly-searched areas. If every nest could be identified and every juvenile Lincoln's Sparrow banded, then the continued appearance of large numbers of unbanded adults in the breeding population would provide support for the immigrant influx hypothesis.

MORPHOMETRIC EVIDENCE OF POPULATION INSULARITY

One third of North American bird species show conspicuous geographical variation in size and color (Gill 1990, p.489). Such morphological differences may exist as a result of genetic variation arising from adaptive selection, genetic drift, population bottlenecks or founder effects, or may be environmental effects without genetic bases.

Comparison to Miller and McCabe (1935). When Miller and McCabe (1935) examined Lincoln's Sparrow museum specimens from the San Bernardino and San Jacinto mountains, they described the San Jacinto population as having very short tarsi compared to the San Bernardino population and exhibiting a decrease in wing length in males but not females. The likelihood of this being an environmental effect or an adaptive genetic variation was dismissed by Miller and McCabe as unlikely in view of the environmental similarities of the two mountain ranges.

Instead, they speculated that the morphological variances arose as a result of the two populations deriving from "small, slightly different, parental stocks" and that these differences would be preserved due to reproductive isolation.

My morphological analysis of currently-existing Lincoln's Sparrow populations in the San Bernardino and San Jacinto mountain ranges failed to support Miller and McCabe's finding of significant differences in male wing length but did find a significant difference in the tarsal lengths of male Lincoln's Sparrows. It is important to keep in mind that these conclusions rest upon extremely small sample sizes and should be tested through additional research.

1. Wing chord. Miller and McCabe's wing length means were higher than mine by 0.7 to 2.6 mm (Table 26). As best I could determine (by estimating Miller and McCabe's standard deviation from their data histograms), these differences are statistically insignificant. Our methodology was very similar (measurement of unstraightened wing chord) except that Miller and McCabe measured both wings of museum skins and averaged the result, whereas I measured the right wing of living sparrows. It would be interesting to know from which meadows the specimens used in Miller and McCabe's analysis were collected. Grinnell (1908) mentions collecting museum specimens from several

Table 26.--Comparison of Lincoln's Sparrow mean wing chord measurements between two studies conducted in the mountains of southern California, where n is the number of individuals included in each sample set.

Category	Miller & McCabe (1935)	Greyraven (this study)
San Jacintos		
Male	64.3 mm (n=10)	63.6 mm (n=12)
Female	62.4 mm (n=6)	59.8 mm (n=3)
San Bernardinos		
Male	65.2 mm (n=15)	63.6 mm (n=57)
Female	62.0 mm (n=7)	60.1 mm (n=36)

locales in the San Bernardinos, but primarily from the Bluff Mesa region. Grinnell and Swarth (1913) describe catching Lincoln's Sparrows (largely caught in traps set for meadow mice and shrews) in Round Valley and Tahquitz Valley in the San Jacintos. Thus, all four geographic subdivisions should have been represented in museum study-skin collections.

2. Tarsal length. My measurements of tarsal length yielded means remarkably similar to those found by Miller and McCabe (Table 27) for males but not for females. Although the differences in tarsal lengths proved statistically significant only for males, similar patterns were seen for females in this study. As with wing chord, knowledge of the specific origins of the specimens examined by Miller and McCabe would be useful, as quite divergent results were generated within each ranges' subdivisions (refer to Table 19). Deme boundaries remain to be determined.

Table 27.--Comparison of Lincoln's Sparrow mean tarsal length measurements between two studies conducted in the mountains of Southern California, where n is the number of individuals included in each sample set.

Category	Miller & McCabe (1935)	Greyraven (this study)
San Jacintos		
Male	19.3 mm (n=13)	19.4 mm (n=12)
Female	19.0 mm (n=7)	19.3 mm (n=3)
San Bernardinos		
Male	20.0 mm (n=16)	20.0 mm (n=24)
Female	19.7 mm (n=7)	19.3 mm (n=13)

BREEDING BIOLOGY.

Seasonal fecundity. Populations are dynamic entities that exist as a function of individual reproductive success. Lifetime fecundity (the number of young successfully raised) depends on the age at which a bird starts to breed and on its life span. Annual fecundity is determined by the number of nesting attempts, the age and experience of the breeding individual, clutch size, success in avoiding nest-predators and destructive climatic events, and the ability to adequately meet the nutritive needs of offspring. Brood parasitism, ectoparasites, disease, and nest-site competition also affect reproductive output (Gill 1990, p.416).

Clutch timing. Some passerine species have been reported to show considerable population synchrony in the timing of clutch initiation (Gavin 1984, Lyon et al. 1987), while others may stagger clutch initiation over many weeks (Mead and Morton 1985, Weatherhead 1989). The latter pattern was seen in this study. Later nests may represent delayed starts, re-nestings following the failure of a first nest, or second nestings following the successful fledging of a first brood.

Double brooding. I confirmed that Lincoln's Sparrows can raise a second brood after successfully fledging their first. Harrison (1978) states that Lincoln's Sparrows are "probably double brooded at times" and Speirs and Speirs

(1968) observed indirect evidence of double brooding (a second courtship cycle in a pair of breeding Lincoln's Sparrows in Ontario, Canada). While replacement of lost clutches is known to be a common occurrence, the brief time span during which ecological conditions support breeding has generally been believed to restrict most species of birds breeding in temperate zones to only one brood a year (Lack 1968, p.302).

Whether or not additional clutches contribute significantly to individual reproductive success depends on comparative post-fledging survival rates of early and late broods. Song Sparrows in Ontario, Canada, reportedly can produce three successful broods in one season (Weatherhead and Boak 1986). However, in a population of Bobolinks where double-brooding was observed closely (Gavin 1984), the second broods were not successful. Mean clutch size was reduced from 5.33 to 3.82 eggs, only 47.8% of the second-clutch eggs hatched compared to 93.7% of first-clutch eggs, and no second-clutch young survived to fledging, due to predation.

Reduced clutch sizes were seen late-season Lincoln's Sparrow nests. Declines in clutch size have been described both in correlation to breeding season progression and as a result of re-nesting (Slagsvold and Lifjeld 1988). In my study, late nests accounted for the single observed instance of nest predation and all but one case of myiasis.

Most Lincoln's Sparrow late clutches did appear to be surviving to fledging. Comparisons of long-term survival between early and late clutches was not possible due to the overall poor return of birds banded as juveniles. However, of the three Lincoln's Sparrows banded as juveniles and recaptured as adults, two were definitely from early clutches (banded in the nest) while the third individual was most probably from a early clutch (based on his wing wear at date of capture).

Clutch size. Small passerines are indeterminate layers, with clutch sizes varying a little above or below an average number of eggs. The evolution of and constraints on clutch size are a topic of considerable current interest and controversy (Slagsvold and Lifjeld 1988, Price and Liou 1989, Gill 1990 p.419). Lincoln's Sparrow clutch sizes in the San Bernardino and San Jacinto mountain ranges were within the range expected for open-nesting small passerine species and previous reports for this species (Harrison 1978, Martin 1988).

Food availability and efficiency of foraging. Lincoln's Sparrows have traditionally been considered ground foragers. On their breeding grounds, however, they show diverse foraging behaviors and forage on a wide range of substrates. Raley and Anderson (1990) classified montane Lincoln's Sparrows in the Rocky Mountain region as generalized foragers, feeding on both seeds and arthropods, both on the ground and in shrubs. In their comparison of the feeding strategies of Lincoln's Sparrows and Wilson's Warblers, Raley and Anderson state:

> Actively-flying prey, or prey that fly in response to disturbances, should be more accessible to warblers, which have the ability to hawk for prey, than to sparrows.

Raley and Anderson evidently did not observe Lincoln's Sparrows flycatching in Wyoming. It may seem a bit unsparrowlike, but Lincoln's Sparrows in the mountains of southern California made regular aerial forays, snapping up flying insects to feed themselves or their young. Flycatching by Lincoln's Sparrows has been previously described in a northeastern population (Speirs and Speirs 1968).

Raley and Anderson (1990) collected Lincoln's Sparrows to examine their stomach contents. They were not able to determine the preferred arthropod prey size of Lincoln's Sparrows because "ingestion of grit and subsequent grinding of food items precluded accurate measurements of lengths." From the information they were able to gather, Raley and Anderson (1990) concluded that the preferred arthropod prey of Lincoln's Sparrows was cryptic but uniformly distributed. Soft-bodied Coleoptera ranked as first choice, followed by Lepidoptera, Diptera, Homoptera, Araneae, and Ephemeroptera. Alternatives to Raley and Anderson's destructive methodology of killing birds during breeding season to find out what they are eating are available (Ralph et al. 1985). My visual observations of arthropod prey items being carried by adults attending young seemed congruent with the findings of Raley and Anderson. Generalized diet and diverse foraging behavior clearly enhance Lincoln's Sparrow access to available food resources and consequently increase adult ability to meet the dietary demands of nestlings.

I found no evidence of brood reduction, a response to inadequate food supply in which the smallest, weakest chicks fail to compete successfully with brood mates and succumb to starvation. Brood reduction is most commonly seen in species with hatch asynchrony. Hatch asynchrony is hypothesized to be a parental manipulation of brood permitting the formation of a stable feeding hierarchy and the potential for efficient brood reduction (Mead and Morton 1985, Slagsvold 1986, Mock and Ploger 1987, Magrath 1988, Slagsvold & Lifjeld 1988 and 1989). Lincoln's Sparrow females lay one egg per day, like most passerines (Gill 1990, p.331). Hatch synchrony is achieved through delaying regular incubation until after the last egg is laid. Lincoln's Sparrow nestlings were observed to hatch and fledge with only slight asynchrony (give or take a day). Nests were not followed closely enough to determine causes of intra-clutch variation in nestling weight (Table 22), which could potentially lead to brood reduction in a season of low food availability or where a widowed parent acts as the sole provider.

Fledging success. The number of young Lincoln's Sparrows raised to fledging seemed high for a passerine bird but not extraordinarily so (Ricklefs 1973, Wittenberger 1978). Nestling mortality can occur from starvation, predation, temperature drops, disease, and unknown causes. In this study, only predation was observed to cause nesting failure. Because of the difficulty of locating nests, few nests were followed from the beginning of incubation until the young fledged. Nest losses are probably understated, possibly by a large margin (Mayfield 1975).

Nest concealment. Pierce (1916) found one nest in a small meadow near Bluff Lake and then "spent considerable time in search but did not find any more nests although there were several of the sparrows apparently nesting there." Speirs and Speirs (1968), too, remarked on the difficulty of locating Lincoln's Sparrows nests. Although my nest-finding skills improved markedly with experience, some nests eluded my most dogged efforts to discover them, and it was not unusual for me to experience difficulty locating a nest I had visited only a week earlier, due to the lack of landmarks in the grassy landscape.

One solution to this difficulty is to place markers at a fixed distance and direction from nests to aid relocation. Because all the meadow areas of the San Bernardino mountains attract recreational visitors, I felt that use of markers might attract visitors to the vicinity of nests. Nest visits, with or without markers, are also known to provide clues for predators (Robertson and Ralph 1975, Bart 1977, Lenington 1979, Mead and Morton 1985, Westmoreland and Best 1985). That risk may have to be taken in the future if nesting outcomes are to be monitored closely enough to permit definitive conclusions regarding seasonal reproductive success.

Nest defense. Lincoln's Sparrows appear to rely primarily on concealment as defense against predators. Other researchers (Speirs and Speirs 1968) also made note of the tendency of incubating females to stick to their nest in the presence of an intruder, and when flushed to slip away into the grass rather than flying up into the air. When approaching the nest, adults would land some meters away and then "mouse" their way invisibly through the grass to their nest site.

Adults became extremely agitated when a nest with young was disturbed or when a predator was in the vicinity, but rarely did anything but "tkk" rapidly from nearby trees or shrubs. In two instances where I had run down and captured a fledged-but-flightless chick, one adult performed distraction displays. Speirs and Speirs (1968) also reported an instance of such behavior in Lincoln's

Sparrows. Parental investment theory predicts that the female parent would be more likely than the male to take the risk of diverting a predator's attention away from her offspring (Weatherhead 1989). Unfortunately, I was not able to read the leg bands of the individuals performing the distraction displays.

Nest parasitism. The expansion of the nest-parasite Brown-headed Cowbird into California during the twentieth century is believed to be responsible for reduced reproductive success in several species of small, open-cup-nesting passerines (Laymon 1987). Brown-headed Cowbirds were not reported in early field studies in the San Bernardino (Grinnell 1908) and San Jacinto (Grinnell and Swarth 1913) mountains but are now common there. Cowbird range expansion has been facilitated by placement of corrals in or adjacent to meadows and grazing of meadows by livestock (Laymon 1987), practices that are widespread in the San Bernardino and San Jacinto mountains. Although I found no evidence of cowbird parasitism of Lincoln's Sparrow nests, montane Lincoln's Sparrows have been recorded as rare cowbird hosts (Rothstein 1978, Hanka 1979, Friedmann and Kiff 1985).

Invertebrate parasites. The effect of maggot parasitism on juvenile Lincoln's Sparrows deserves additional study. The exact identity of the maggot parasite remains to be determined, as no specimens were collected successfully. Growth of infected and uninfected chicks could be monitored in the wild or in captivity (for greater control). Parasites at best represent an increased metabolic burden and at worst may leave hosts open to microbial infections or may cripple hosts through destruction of muscle tissue. Little is known about levels of parasitism in Lincoln's Sparrow populations. Speirs and Speirs (1968) searched the literature and found mention of nematodes, flukes, and louse flies being found as parasites of Lincoln's Sparrows. An excellent study could be made of myiasis in montane Lincoln's Sparrow populations and the factors influencing host infection, such as parental attentivity and grooming, nest placement, and seasonality.

CONCLUSIONS

This study's findings of strong site fidelity and possible morphological differentiation in geographic populations of Lincoln's Sparrows suggest but do not definitively establish that montane Lincoln's Sparrow populations exist as disjunct, insular units in the Southern California mountain ranges.

The extremely small sizes of some apparently-isolated populations (such as the Round Valley subgroup) handicap attempts to carry out biometric analyses. Although geographic variation in tarsal length achieved statistical significance, the observed clustering of morphological traits by geographic area could all too easily be an artifact of small sample size rather than evidence of local genetic homogeneity. Recent advances in the field of molecular biology may provide a solution. "DNA fingerprinting" (Gowaty and Karlin 1984, Burke 1987, Wetton et al. 1987, Petter et al. 1990) has the potential to revolutionize demographic studies of wild populations. Genetic analysis can be used to identify genetic parentage, determine patterns of relatedness in a breeding group, and estimate the extent of heterozygosity in the population. This sort of information would be invaluable as a supplement to continued observation and morphometric analysis.

Reproductive success appears sufficient to sustain local populations, provided existing habitat areas are not degraded. The low recovery rates of birds banded as juveniles leaves the source of population recruitment in question. Continued banding and multi-year observations of the study populations are needed to establish the geographic and numeric size(s) of the deme(s) and to confirm the extent and age-sex specific patterns of philopatry in this species.

Information on wildlife populations is needed to make critical ecosystem management decisions, as well as to shed light on evolutionary processes. Human population pressures are consuming the world's wild lands at a frightening rate. Studies of habitat islands are particularly pertinent as wild lands are increasingly fragmented and surrounded by spreading urbanization and agriculture. All nature reserves are becoming habitat islands. Understanding the dynamics of biogeographical "islands", at both the ecosystem and individual species level, is essential if we hope to be able to manage remaining wild lands for the preservation of wild plant and animal species.

Riparian areas in the western United States are particularly vulnerable to disturbance as a result of grazing, road construction, timber harvesting, mining, watershed modifications, and recreational activities (Blakesley and Reese 1988, Warner and Hendrix 1984). Lincoln's Sparrows, as an obligate breeder in wet, montane meadows, may serve as a useful indicator species for habitat "health." This study advances our knowledge of the population dynamics and behavior of Lincoln's Sparrows and provides a baseline for continued monitoring of Lincoln's Sparrow populations in the Southern California mountains.

TYPE PERMIT
SUBPERMIT PERSONAL

PERMITTEE:

GREYRAVEN C MS
P O BOX 1443
REDLANDS CA 92373

Permit Number:	Action:	Action Date:	Valid Until:
22251-A	ISSUE	03/29/88	02/28/89

Authorized to Band the Following Species:
ALL SPECIES EXCEPT WATERFOWL, EAGLES OR ENDANGERED SPECIES

Authorized to Capture or Mark Birds in the Following States:
*CA *

Special Provisions:
AUTHORIZED TO TRAP, NET, BAND AND MARK ONLY AS DIRECTED BY:

CARLSON B A MS
P O BOX 55419
RIVERSIDE CA 92517

Authorized to Use Mist Nets: YES Maximum Number: NA

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FISH AND WILDLIFE SERVICE
BIRD BANDING LABORATORY
OFFICE OF MIGRATORY BIRD MANAGEMENT
LAUREL, MARYLAND 20708

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Bird Banding Laboratory
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FEDERAL BIRD MARKING AND SALVAGE PERMIT

Under the provisions of Regulations issued under the Migratory Bird Treaty Act of July 3 1918 (40 Stat. 755) as amended or the Bald Eagle Act of June 6, 1940 (54 Stat 250) as amended, the person named hereon is authorized to capture, for scientific banding or marking purposes, those migratory birds described hereon or to salvage birds found dead or accidentally killed during normal banding activities

This authorization is subject to the terms exceptions and restrictions expressed herein or on the reverse side hereof and is further subject to any applicable Territorial, State, or Federal Regulations.

This Permit is invalid unless accompanied by any required State permits or licenses.

George M Jonkel — Acting Chief, OMBM

FORM 3-475
(REVISED APRIL 1986)

GENERAL CONDITIONS

1. The holder of this permit is not authorized to capture or possess migratory birds for any reason other than banding, marking or salvage for scientific purposes NOR IS HE ALLOWED TO HOLD MIGRATORY BIRDS FOR A PERIOD OF MORE THAN 24 HOURS except that he may possess, for the purpose of donating to a public scientific or educational institution, birds which are found dead or die as a result of normal banding activities. Live birds shall be released as soon as practical after capture
2. The holder of this permit shall keep RECORDS accounting for the use of all bands received Periodic REPORTS COVERING THE USE OF THESE BANDS shall be submitted to the Bird Banding Laboratory in accordance with instructions received therefrom The holder of this permit shall keep records on disposition of salvaged birds for a period of five years and shall be reported to the Bird Banding Laboratory only upon request
3. The holder of this permit shall, at all reasonable hours, allow any authorized representative of the U S Fish and Wildlife Service to ENTER and INSPECT the premises where operations authorized by this permit are being conducted and shall allow such representatives to inspect the records relating to such operations
4. This permit may be SUSPENDED or REVOKED by the Director of the U.S Fish and Wildlife Service or his authorized representative, if the permittee violates any of the provisions of the regulations under which this permit is issued or if the permittee fails to render promptly any reports required This permit is at all times, subject to suspension or revocation at the discretion of the Director or his representative
5. This permit is not transferable and must be carried upon the person of the permittee when exercising the authorizations granted herein
6. All traps, nets or other capture devices shall bear a TAG or LABEL showing the name, address and permit number of the permittee or the trapping area shall be adequately marked with POSTERS provided by the Bird Banding Laboratory The permittee's name, address and permit number shall be legibly displayed on such posters
7. This permit DOES NOT authorize the capture of any birds on any property, public or private without the CONSENT OF THE OWNER OR CUSTODIAN THEREOF.
8. Unless specifically noted on the reverse or in an attached "letter of authorization" from the Bird Banding Laboratory the following ARE NOT AUTHORIZED.
   a. The USE OF ANY BAND clip, paint dye, signal-sending device or any marking device other than the official numbered leg bands issued by the Bird Banding Laboratory
   b. The USE OF BIRD NETS or nets similar to the Italian bird net or the Japanese mist net for the purpose of capturing birds.
   c. The use of TRANQUILIZING DRUGS OR OTHER CHEMICALS for the purpose of capturing birds
   d. Trapping for or disturbing the nests or nestlings; for the purpose of banding or marking, of species designated by the Secretary of the Interior as "ENDANGERED."
   e. The handling of any PREVIOUSLY BANDED BIRD in any manner which may bias data on file in the Bird Banding Laboratory which pertain to that bird or which may alter that bird's survival potential behavior or other normal characteristics.

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TYPE PERMIT
SUBPERMIT PERSONAL

PERMITTEE:

GREYRAVEN C MS
P O BOX 1443
REDLANDS CA 92373

Permit Number:	Action:	Action Date:	Valid Until:
22251-A	RENEW	01/03/89	02/28/91

Authorized to Band the Following Species:

ALL SPECIES EXCEPT WATERFOWL, EAGLES OR ENDANGERED SPECIES

Authorized to Capture or Mark Birds in the Following States:

*CA *

Special Provisions:

AUTHORIZED TO TRAP, NET, BAND AND MARK ONLY AS DIRECTED BY:

CARLSON B A MS
P O BOX 55419
RIVERSIDE CA 92517

Authorized to Use Mist Nets: YES Maximum Number: NA

U.S. DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
BIRD BANDING LABORATORY
OFFICE OF MIGRATORY BIRD MANAGEMENT
LAUREL, MARYLAND 20708

Address all inquiries
Bird Banding Laboratory
Office of Migratory
Bird Management
Laurel MD 20708
Telephone — [illegible] 301 498-0205

FEDERAL BIRD MARKING AND SALVAGE PERMIT

Under the provisions of Regulations issued under the Migratory Bird Treaty Act of July 3, 1918, (40 Stat. 755) as amended or the Bald Eagle Act of June 8, 1940 (54 Stat. 250) as amended, the person named hereon is authorized to capture, for scientific banding or marking purposes, those migratory birds described hereon or to salvage birds found dead or accidentally killed during normal banding activities.

This authorization is subject to the terms, exceptions and restrictions expressed herein or on the reverse side hereof and is further subject to any applicable Territorial, State, or Federal Regulations.

This Permit is invalid unless accompanied by any required State permits or licenses.

Acting Chief, OMBM

FORM 3-[illegible]
REVISED APRIL [illegible]

GENERAL CONDITIONS

1. The holder of this permit is not authorized to capture or possess migratory birds for any reason other than banding, marking or salvage for scientific purposes. NOR IS HE ALLOWED TO HOLD MIGRATORY BIRDS FOR A PERIOD OF MORE THAN 24 HOURS except that he may possess, for the purpose of donating to a public, scientific or educational institution, birds which are found dead or die as a result of normal banding activities. Live birds shall be released as soon as practical after capture.

2. The holder of this permit shall keep RECORDS accounting for the use of all bands received. Periodic REPORTS COVERING THE USE OF THESE BANDS shall be submitted to the Bird Banding Laboratory in accordance with instructions received therefrom. The holder of this permit shall keep records on disposition of salvaged birds for a period of five years and shall be reported to the Bird Banding Laboratory only upon request.

3. The holder of this permit shall, at all reasonable hours, allow any authorized representative of the U.S. Fish and Wildlife Service to ENTER and INSPECT the premises where operations authorized by this permit are being conducted and shall allow such representatives to inspect the records relating to such operations.

4. This permit may be SUSPENDED or REVOKED by the Director of the U.S. Fish and Wildlife Service or his authorized representative, if the permittee violates any of the provisions of the regulations under which this permit is issued or if the permittee fails to render promptly any reports required. This permit is at all times subject to suspension or revocation at the discretion of the Director or his representative.

5. This permit is not transferable and must be carried upon the person of the permittee when exercising the authorizations granted herein.

6. All traps, nets or other capture devices shall bear a TAG or LABEL showing the name, address and permit number of the permittee or the trapping area shall be adequately marked with POSTERS provided by the Bird Banding Laboratory. The permittee's name, address and permit number shall be legibly displayed on such posters.

7. This permit DOES NOT authorize the capture of any birds on any property, public or private without the CONSENT OF THE OWNER OR CUSTODIAN THEREOF.

8. Unless specifically noted on the reverse or in an attached "letter of authorization" from the Bird Banding Laboratory, the following ARE NOT AUTHORIZED:

a. The USE OF ANY BAND, clip, paint, dye, signal-sending device or any marking device other than the official numbered leg bands issued by the Bird Banding Laboratory.
b. The USE OF BIRD NETS or nets similar to the Italian bird net or the Japanese mist net for the purpose of capturing birds.
c. The use of TRANQUILIZING DRUGS OR OTHER CHEMICALS for the purpose of capturing birds.
d. Trapping for or disturbing the nests or nestlings, for the purpose of banding or marking, of species designated by the Secretary of the Interior as "ENDANGERED."
e. The handling of any PREVIOUSLY BANDED BIRD in any manner which may bias data on file in the Bird Banding Laboratory which pertain to that bird or which may alter that bird's survival potential, behavior or other normal characteristics.

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