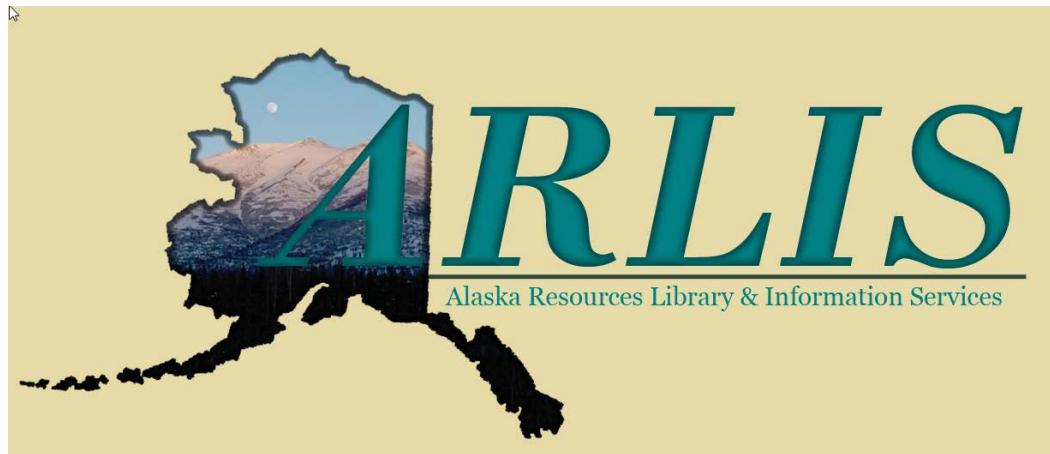


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Breeding ecology of snowy plovers at Great Salt Lake, Utah

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Utah State University, 1994

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BREEDING ECOLOGY OF SNOWY PLOVERS
AT GREAT SALT LAKE, UTAH

by

Peter W. C. Paton

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Fisheries and Wildlife
(Wildlife Biology)

Approved:



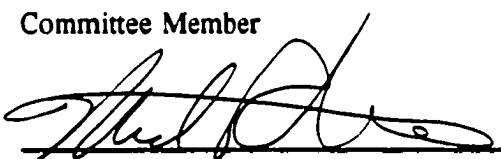
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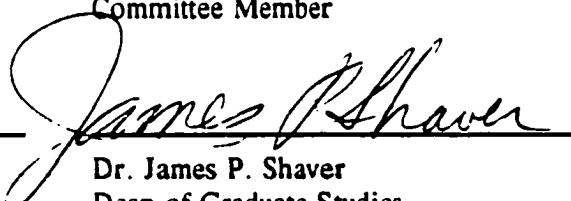
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1994

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DEDICATION

To my parents, for all the support they have provided over the years.

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First, I want to thank the Utah Division of Wildlife Resources, Native Wildlife Section, under the former guidance of Randy Radant and Frank Howe for providing the funds to conduct this study.

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Peter W. C. Paton

CONTENTS

	Page
DEDICATION	ii
ACKNOWLEDGMENTS	iii
LIST OF TABLES	v
LIST OF FIGURES	vii
ABSTRACT	viii
CHAPTER	
1. OVERVIEW	1
2. BREEDING BIOLOGY OF SNOWY PLOVERS AT GREAT SALT LAKE	12
3. SURVIVAL ESTIMATES FOR SNOWY PLOVERS AT GREAT SALT LAKE	36
4. SCALE-MEDIATED EFFECTS OF NEST-SITE SELECTION BY SNOWY PLOVERS ON NEST PREDATION RATES	51
5. EFFECTS OF SITE QUALITY AND PRIOR NEST SUCCESS ON INTERYEAR MOVEMENT PATTERNS OF SNOWY PLOVERS	78
6. SYNTHESIS	105
CURRICULUM VITAE	113

LIST OF TABLES

Table	Page
1.1 Summary statistics for Great Salt Lake at various lake levels	5
2.1 Annual variation in nest success at two focal study sites at Great Salt Lake	27
2.2 Annual variation in the percent of plover nests failing for various reasons at two focal study sites	27
2.3 Estimates of snowy plover annual fledging success.	28
3.1 Capture history matrix for 532 snowy plovers at Great Salt Lake from 1990-1993	40
3.2 Potential survival rate models for adult snowy plovers at Great Salt Lake	41
3.3 Annual survival and resighting probabilities for snowy plovers at Great Salt Lake	43
3.4 Annual variation in the finite rate of population change (λ) for snowy plovers breeding at two focal study sites at Great Salt Lake	44
4.1 Annual variation in snowy plover nest success at two focal study sites . . .	61
4.2 Ground cover at 355 snowy plover nests and paired-random points at four radii from plot center	62
4.3 Mean differences between nests and random points in the percentage of 3 habitat types found at 4 radii from plot center	63
4.4 Snowy plover nest fate as a function of proximity to an object	63
4.5 Temporal variation in nest fate, based on yearly variation in microhabitat selection	64
4.6 Comparison of nest success between habitat patches with high and low densities of potential nest sites underneath dead shrubs	65
4.7 Total number of artificial nest substrates used by snowy plovers to build nest scrapes or initiate nests	66

5.1	Annual variation in adult snowy plover site fidelity patterns	88
5.2	Documented movements of banded snowy plovers around Great Salt Lake	89
5.3	Annual variation in the total amount and individual patch size of potential plover nesting habitat at two focal study sites at Great Salt Lake	90
5.4	Annual variation in snowy plover nest densities (nest per ha) at two focal study sites at Great Salt Lake	93
5.5	Site fidelity patterns of adult plovers in relationship to the overall study site density the preceding year	94
5.6	Adult site fidelity patterns in relationship to prior nest success and nest density the preceding year	95

LIST OF FIGURES

Figure	Page
1.1 Great Salt Lake water elevation over the past 150 years	4
1.2 Topology of Great Salt Lake at various lake levels	6
2.1 Arrival dates for banded snowy plovers at Great Salt Lake	18
2.2 Annual variation in the nest initiation chronology for snowy plovers at two focal study sites	20
2.3 Number of days that banded plovers were observed at the focal study sites within a breeding season	21
2.4 Number of days that adult plovers were seen at the study sites following nest outcome	21
2.5 Distances travelled (m) by foraging or roosting plovers away from their active nests	23
2.6 Intersexual variation in the daily incubation chronology	24
5.1 Distribution of study sites at Great Salt Lake	84
5.2 Distribution of snowy plover nests and potential nesting habitat at two focal study sites at Great Salt Lake	91

ABSTRACT

Breeding Ecology of Snowy Plovers

at Great Salt Lake, Utah

by

Peter W. C. Paton, Doctor of Philosophy

Utah State University, 1994

Major Professor: Dr. Thomas C. Edwards, Jr
Department: Fisheries and Wildlife

I studied the breeding ecology of snowy plovers (*Charadrius alexandrinus*) at Great Salt Lake, Utah, from 1990 to 1993. Plovers began arriving in late March, nests were initiated from mid April to mid July, and most adults departed by late August. Both sexes shared incubation duties, but only males cared for broods. Most plovers in Utah were monogamous, at least one was sequentially polyandrous, and the majority were potentially double-brooded. Annual nest success was poor (range = 5.4%-49.2%). Most nest failures (92.8%) were due to predators, primarily red foxes (*Vulpes vulpes*).

I uniquely color-banded and subsequently resighted 44.7% of the females ($n = 199$) and 52.5% of the males ($n = 162$). Adult annual survival estimates did not differ between the sexes and ranged from .578 to .880 ($\bar{x} = .687$). Resighting probabilities were significantly higher for males (.675) than for females (.518).

Survival estimates for immature birds were imprecise ($\hat{x} = .385$, 95% CI = .048-.885). In only 1 of 4 years was the finite rate in population change (λ) large enough to prevent the population from declining (i.e., $\lambda \geq 1$).

The movement of banded birds around Great Salt Lake implied that snowy plovers breeding there represent a metapopulation. Ecological nest density (i.e., number of nests \div amount of suitable habitat) ranged from .22-.83 per ha. Unsuccessful nesting females were more likely than successful females to subsequently disperse ($P < .001$). Males did not exhibit this nest-success dispersal bias. Familiarity with brood-rearing areas may explain this male-biased fidelity.

Plovers typically nested on salt flats; approximately 75% of the area within a 15-m radius of nests was bare ground. Microhabitat characteristics appeared to affect nest-site selection; 68% were associated with an object (e.g., dead shrub, woody debris). When nest success was relatively high, nests under objects were more successful than those in other microhabitats. Nests situated in habitat patches with high densities of potential nest sites tended to be more successful than those in other patches. Plovers readily used experimental nest substrates and drawdown areas, both of which could be effective management tools.

The primary threat facing plovers today at Great Salt Lake is nest predation by red foxes (*Vulpes vulpes*). A management plan may have to be developed to help alleviate this problem.

(120 pages)

CHAPTER 1

OVERVIEW

The sandplover (*Charadrius alexandrinus*) is one of the most cosmopolitan of the 31 species in the genus *Charadrius*. Seven recognized subspecies occur throughout the world, including Kentish plover (*C. a. alexandrinus*) found throughout Europe and central Asia, Peruvian plover (*C. a. occidentalis*) of coastal Peru and Chile, Javanese plover (*C. a. javanicus*), Ceylonese plover (*C. a. seebohmi*), and the Oriental plover (*C. a. dealbatus*) of eastern China and Japan (Johnsgard 1981). Two subspecies occur in North America. Cuban snowy plovers (*C. a. nivosus*) reside along the beaches of the Gulf of Mexico and islands throughout the Caribbean, with some migratory individuals venturing into the Great Plains during the breeding season (e.g., Kansas, Colorado, and Oklahoma; Boyd 1972, Johnsgard 1981). Western snowy plover (*C. a. tenuirostris*) populations consist of both year-round residents and migratory individuals (Warriner et al. 1986, Stenzel et al. *in press*). Resident birds breed along the Pacific Coast as far north as central Washington, while migratory individuals nest at saline lakes throughout the Great Basin (i.e., Nevada, southeastern Oregon, Utah, and isolated areas in Arizona) (Page et al. 1986, 1991; Paton and Edwards 1990).

Snowy plovers breeding throughout the Great Basin in western North America apparently winter along the Pacific Coast and along beaches at the Gulf of California, based on observations of color-banded individuals (G. Page, M. Stern, and P. Paton, *unpublished data*). Snowy plovers banded in Utah have been found

during the nonbreeding season at three locations; birds were seen in the northeast corner of the Gulf of California (Puerto Penasco), the west coast of Baja California near Scammon's Lagoon, and the near La Paz at the southern tip of Baja (G. Page, M. Stern, P. Paton, *unpublished data*).

In North America, Pacific Coast populations of snowy plover were listed as threatened by the U.S. Fish and Wildlife Service effective 5 April 1993 (Federal Register 1992). This listing was due to population declines and the apparent extirpation of nesting plovers from 59 of 87 documented breeding sites in coastal California, Oregon, and Washington (Federal Register 1992). Crude population estimates from 1977-1980 reported 10,200 snowy plovers nested in Washington, Oregon, California, and Nevada (Page et al. 1991). By 1989, the population estimate for this same area was \approx 7,900 plovers, which suggests a potential 22.5% reduction over a 10 year period. Up to 1988, virtually all snowy plover research conducted in western North America was confined to California and Oregon (Wilson-Jacobs and Meslow 1984, Page et al. 1985, 1991, Warriner et al. 1986, Herman et al. 1988).

A growing concern with western North American snowy plover populations caused the Utah Division of Wildlife Resources to initiate a series of snowy plover surveys in northern Utah in 1988. These surveys were designed to gather baseline data on plover distribution and abundance in Utah (Halpin and Paul 1989, see also Paton and Edwards 1990). Only anecdotal observations were available with regard to its ecology or status in Utah prior to these surveys. Halpin and Paul (1989) used

volunteers to survey selected areas in northern Utah during a 1-week period in early June of 1988 and 1989, when they counted 487 adults and 26 juveniles, and 845 adults and 53 juveniles, respectively (M. Halpin, *personal communication*). However, even after the work by Halpin and Paul (1989), there were no data available on nest-site habitat characteristics, breeding chronology, movement patterns, survival estimates, or site fidelity patterns for plovers breeding in Utah.

Snowy plovers breeding in the interior of North America nest near barren salt or alkali flats adjacent to saline bodies of water (Boyd 1972, Grover and Knopf 1982, Page et al. 1985, 1991). Relatively large interior breeding concentrations include Mono Lake in eastern California (Page et al. 1985), Lake Abert in eastern Oregon (Herman et al. 1988), Stillwater National Wildlife Refuge in Oklahoma (Grover and Knopf 1982), and Great Salt Lake (Halpin and Paul 1989, Paton and Edwards 1990). Plovers nesting at interior areas generally prey on adult brine flies (*Ephydria* spp.), which are abundant at most inland saline water bodies (Purdue 1976, Grover and Knopf 1982).

Great Salt Lake is the largest saline water body in the Great Basin (Murchison 1989). It is an extremely dynamic ecosystem, with constantly fluctuating water levels (Fig 1.1). These fluctuations resulted in dramatic changes of the vegetation. When the adjacent marshes are flooded with hypersaline water, most vegetation is killed (Foote 1991). It is a terminal lake (i.e., it has no outlet to the ocean), and the remains of the Pleistocene era Lake Bonneville. Lake Bonneville regressed approximately 13,000 years before present (BP) (Murchison 1989). Lake Bonneville

was once a freshwater lake that covered most of northwestern Utah and parts of northeastern Nevada. From 9,400 years BP to 5,000 years BP, the lake fluctuated between 1,283.8 m to 1,274.1 m elevation (4,212 ft - 4,180 ft), which was similar to current lake levels. Approximately 2,000 years BP, the lake reached a high elevation of 1,286.6 m (4,221 ft), and then slowly regressed to 1,284.4 m (4,214 ft) 200 years ago (Murchison 1989). Lake levels over the past 150 years have fluctuated between a low of 1,277.52 m (4191.35 ft) in November 1963 and a high of 1,283.77 m in April 1987 [4,211.85 ft] (U.S. Geological Survey, *personal communication*) (Fig. 1.1).

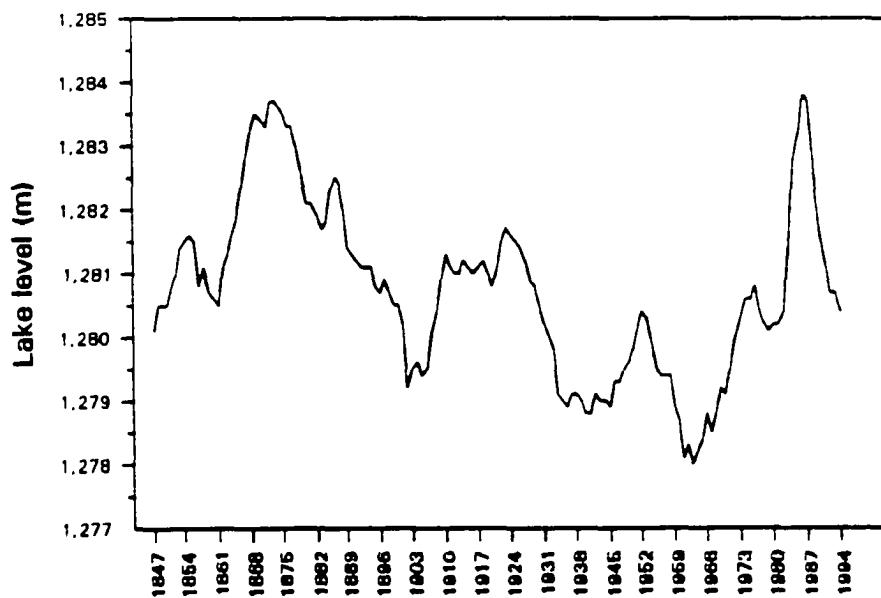


FIG. 1.1 Great Salt Lake water elevation over the past 150 years.

Within the past 10 years, lake levels have fluctuated dramatically, primarily due to a series of heavy snows starting in 1983 (Fig. 1.1). This study was conducted during the summers of 1990-1993, a period when the lake was receding and vegetation was recovering along the newly exposed shoreline (see Foote 1991).

Great Salt Lake is shallow, averaging only 4.3 m depth when the lake is at an average elevation (i.e., 1,280.16 m; Arnott 1984). Relatively minor fluctuations in lake levels result in significant changes in the lake's surface area (Table 1.1, Fig. 1.2). For example, a 1.5 m drop in mean lake levels (i.e., 1,280.16 m down to 1,278.64) results in a 32.8% reduction in the total surface area covered by water and a 39.9% reduction in the shoreline perimeter (Table 1.1). Some of the most dramatic changes take place in Farmington Bay at low lake levels, where virtually all of the bay becomes salt flats or mudflats. In contrast, at peak levels the lake covers 150% as much surface area as average levels, and areas such as the northeast corner of the lake (i.e., Bear River Bay) are inundated with saline water (Fig. 1.2).

TABLE 1.1. Summary statistics for Great Salt Lake at various lake levels.

Lake level (m) [feet]	Area covered (ha) by salt water	Lakeshore perimeter (km)
1,278.64 [4,195]	289,581	513
1,280.16 [4,200]	430,669	853
1,283.82 [4,212]	644,945	906

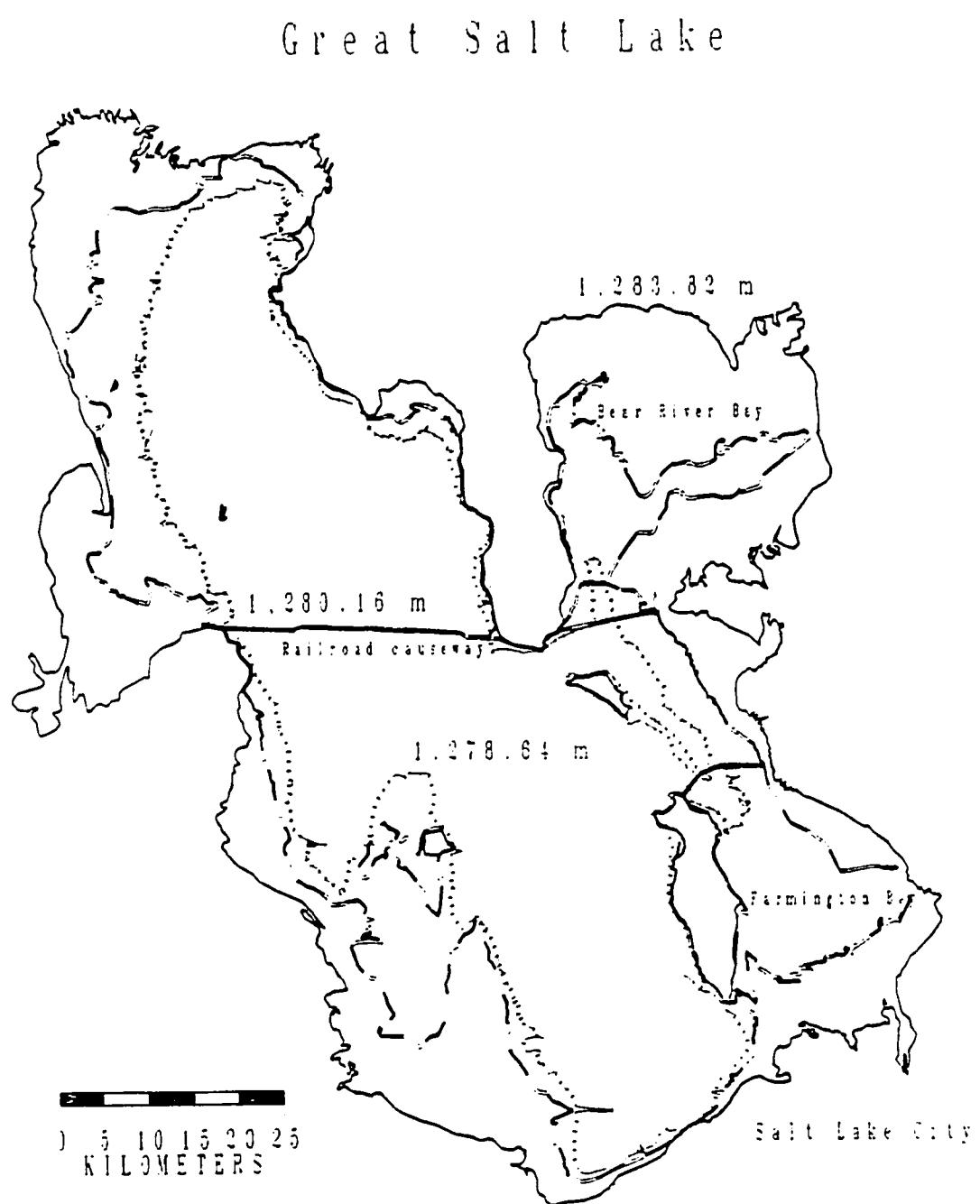


FIG. 1.2. Topology of Great Salt Lake at various lake levels.

There were four primary objectives to this study; a separate chapter is devoted to each objective. Chapter 2 summarizes the breeding biology of snowy plovers at Great Salt Lake. This chapter discusses their migratory chronology, mating system, fecundity rates, and within-year movement patterns. Knowledge of mating systems is critical because variations in mating systems can significantly affect population viability models and estimates of the effective population size.

Chapter 3 summarizes survival estimates of snowy plovers at Great Salt Lake. This analysis was based on the capture-recapture histories of 532 individually color-banded birds followed over a 4-year period. There were no prior survival estimates for this species, even though it has been designated as threatened by the U.S. Fish and Wildlife Service. In addition, this chapter discusses the influence of nest success on estimates of Utah snowy plover population stability (e.g., increasing or decreasing populations), by calculating standard cohort life tables using survival estimates and nest success derived from this study.

Chapter 4 deals with plover nest-site characteristics and the scale at which habitat selection appears to affect nest success. Previous work found that the microhabitats plovers selected provided minimal thermal benefits (Purdue 1976). In addition, plovers nesting beside objects generally had poorer nesting success than those away from or underneath objects (e.g., shrubs; Page et al. 1985). Chapter 4 further explores why plovers appear to select nest sites with microhabitats near objects and investigates the selective advantages or disadvantages that these microhabitats provide to breeding plovers. Experiments with artificial nest

substrates were conducted to determine if preferred microhabitats were limited for plovers at Great Salt Lake.

Chapter 5 provides the first quantitative studies of site fidelity patterns of snowy plovers. This chapter summarizes site fidelity in relation to prior nest success, and discusses the effects of habitat changes on site fidelity patterns.

One objective of this dissertation is to provide baseline data on the breeding ecology of snowy plovers at Great Salt Lake. Studies by Halpin and Paul (1989) and Paton and Edwards (1990) indicate that Great Salt Lake represents one of the largest concentrations of snowy plovers in North America. This study was designed to determine what factors appear to be affecting its populations at Great Salt Lake, and to provide Utah's wildlife managers with information on this species' basic habitat requirements.

A second objective of this study was to provide biologists with some insight into the breeding ecology of a species living in a dynamic environment. I studied snowy plovers at Great Salt Lake during a time period when the amount of potential nesting habitat (i.e., barren salt flats) changed dramatically from year to year. The year I initiated my fieldwork, 1990, the land at my study sites had just been re-exposed because of receding lake levels. Therefore, all the nesting habitat used by plovers in 1990 was unavailable just 2 years earlier. Over the 4 years of this study, the amount of potential nesting habitat declined by about 50% at the two focal study sites. This provided a unique opportunity to monitor the short-term effects of natural habitat fluctuations on an organism. For example, what effect does a

changing environment have on site-fidelity patterns? What scale of habitat selection appears to be most important to this type of species? By creating a series of artificial nest structures, how quickly do birds respond to the availability of the potential nest sites? Those are the types of questions I hope to address in the following chapters that will be of interest to a broad array of ecologists.

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CHAPTER 2

BREEDING BIOLOGY OF SNOWY PLOVERS AT GREAT SALT LAKE

Abstract. I studied the breeding biology of snowy plovers (*Charadrius alexandrinus*) at two focal sites from 1990 to 1993 at Great Salt Lake, Utah. Plovers first arrived at Great Salt Lake in late March, and nests were initiated over a 14-week period from mid April to mid July. Breeding males were first resighted from late March to early May, while breeding females had a more prolonged arrival period from late March through mid June ($n = 256$). Renesting was only observed twice, in part because birds often left the study sites following nest failure. Both sexes foraged in flocks up to 3 km from nest sites. Most females departed the study sites immediately after nests hatched, while males remained to care for broods. A similar mating system was described for coastal California, where sequential polyandry was documented regularly. During this study double-brooding and sequential polyandry were rarely documented, but both strategies were probably more common than I observed. Modal clutch size was 3 eggs, which was similar to other parts of their range. Mayfield-method estimates of annual nest success ranged from 5.4% to 49.2%. Most nest failures were caused by mammalian predators (91%, $n = 188$), principally red fox (*Vulpes vulpes*). Estimates of fledging rates for successful nests averaged 1.87 chicks per brood. These results suggest the breeding strategies of migratory plovers in Utah resemble resident and migratory birds nesting in coastal California, rather than migratory plovers nesting in the Great Plains.

INTRODUCTION

The breeding biology of snowy plovers (*Charadrius alexandrinus*) appears to vary among geographic regions. Warriner et al. (1986) found that plovers nesting in California were double-brooded and sequentially polygamous, while plovers in Kansas were single-brooded and monogamous (Boyd 1972). In coastal California, both sexes shared incubation duties, but only males remained with broods once eggs hatched (Warriner et al. 1986). While males cared for broods, females found new mates and initiated second clutches. If young fledged relatively early in the breeding season, males occasionally initiated second clutches with new females. European studies also found a small percentage of Kentish plovers (*C. a. alexandrinus*) changed mates within a year (i.e., sequential polyandry and polygyny; Rittinghaus 1956, Lessells 1984, Székely and Lessells 1993). In western North America, within-year interclutch movements of >600 km have been documented, which is much farther than reported for other avian species (Stenzel et al. *in press*).

Studies of snowy plover breeding biology in the Great Basin (after Mozingo 1987) primarily have focused on populations in Oregon and California (Wilson-Jacobs and Meslow 1984, Page et al. 1983, 1985, 1991, Warriner et al. 1986). The most comprehensive study has taken place in coastal California, where a large percentage of the population were year-round resident birds (Warriner et al. 1986). Little is known about its breeding biology in the eastern Great Basin in Utah, where plovers are all migratory, with the exception of distributional data (Halpin and Paul 1989) and some preliminary data (Paton and Edwards 1990). Because Pacific Coast

populations were listed as threatened by the U.S. Fish and Wildlife Service in April 1993 (Federal Register 1993), there is a need to examine plover breeding biology throughout its range. The objectives of this paper were to quantify migratory and nesting chronology, mating system, and nest success for snowy plovers at Great Salt Lake, Utah.

STUDY AREA AND METHODS

I studied snowy plovers at two focal sites on Great Salt Lake, Davis County, Utah, from 1990 to 1993: Howard Slough Waterfowl Management Area (350 ha) ($41^{\circ}09'N$, $112^{\circ}09'W$), and West Layton marsh (400 ha) ($41^{\circ}02'N$, $112^{\circ}05'W$). These sites are located approximately 10 km apart on the eastern, central shore of the lake. The Utah Division of Wildlife Resources (UDWR) actively manages Howard Slough for waterfowl production with a series of diked impoundments. UDWR personnel controlled mammalian predators at Howard Slough (red fox [*Vulpes vulpes*], striped skunk [*Mephitis mephitis*], and raccoon [*Procyon lotor*]). West Layton marsh (hereafter Layton marsh) is jointly owned and managed by UDWR and the Nature Conservancy, and predators were not controlled at this site. Layton marsh is located at the western edge of the largest complex of undiked wetlands at Great Salt Lake.

Both study sites were dominated by salt flats, interspersed with patches of salt-tolerant species in the Chenopodiaceae, including greasewood (*Sarcobatus vermiculatus*), iodine bush (*Allenrolfea occidentalis*), seepweed (*Suaeda* spp.),

summer cypress (*Kochia scoparia*), bassia (*Bassia hyssopifolia*), and pickleweed (*Salicornia europaea*). In addition, marsh vegetation increased dramatically over the course of the study and consisted primarily of alkali bulrush (*Scirpus maritimus*), cattail (*Typha* spp.), and phragmites (*Phragmites australis*).

Both areas were surveyed approximately two to three times per week from 15 March through 31 August from 1991 to 1993. In 1990, surveys were initiated at Howard Slough on 4 May and at Layton Marsh on 13 June. I worked by myself in 1990 and had one field assistant from 1991 to 1993. I located nests using the nest-searching techniques of Page et al. (1985), which included scanning potential nesting areas for incubating adults with a 22X spotting scope at distances of 100 to 200 m, or watching for birds returning to nests after observers walked through potential nesting habitat. I determined expected hatching dates using the egg-floatation method (Westerkov 1950), by assuming a 4-d egg laying period and a 27-d incubation period (Warriner et al. 1986, Page et al. 1985). A nest was considered to be successful if ≥ 1 chick hatched. A nest was classified as unsuccessful if it was empty prior to the expected hatching date, if obvious predator signs were found at the nest, or if small egg shell fragments (indicating pipping) were absent from the scrape lining after the expected hatching date. I calculated apparent nest success (i.e., number of successful nests \div total number of nests) and Mayfield-method estimates of nest success (i.e., success based on exposure days; Mayfield 1961, Johnson 1979, Johnson and Shaffer 1990). Only nests active for > 1 week were used in analyses of clutch size because the egg-laying period can take up to 5 d

(Wariner et al. 1986). Eggs with puncture holes were assumed to have been preyed upon by avian predators, while missing or crushed eggs were assumed to have been depredated by mammalian predators (Rearden 1951). Observations of tracks and scat near nests often confirmed predator identifications. Following Page et al. (1983), I defined fledging as the time when juveniles were capable of flight. Therefore, fledging success was estimated from the mean size of broods at 4-weeks posthatching and ready to fledge (Page et al. 1983, Wariner et al. 1986).

I captured incubating birds with a circular funnel trap (Lessells 1984), or herded plovers into two mist nets staked together to form a 'V'. Plovers were uniquely marked with four unicolored leg-bands. Eighty-two adult and 60 immature (i.e., where immature equals both chicks and fledglings) plovers were banded at the sites in 1990, 142 adults and 22 immatures in 1991, and 137 adults and 79 immatures in 1992.

Nesting chronology was analyzed by pooling data into 10, 15- to 16-d periods, from 1 April to 31 August (e.g., 1-15 May, 16-31 May). A likelihood ratio chi-square test (G^2) was then used to compare the goodness-of-fit between the two study sites, and among years at the same study site. To determine how long individual plovers remained at the study sites, I used data for birds resighted only in years subsequent to their initial banding year. I divided these data into two groups: (1) birds definitely known to be breeding individuals because they were captured or observed on a nest (nest confirmed) or (2) birds seen at the focal study sites but never seen on a nest (no nest confirmed). I also determined the number of days

birds remained at the study sites following nest completion (i.e., failure or success), which included data for birds banded in the preceding years and their banding year. Therefore, sample sizes for this latter analysis were larger than for the former analysis.

To monitor daily movements of foraging color-banded adults away from their active nests, I conducted biweekly transect surveys of both study sites. Observations of color-banded individuals were plotted onto field maps of each study site (1 cm = 100 m), while nests were mapped using a satellite-based global positioning system. I used a Mann-Whitney test to compare daily movement distances between the sexes. For this comparison, I used only the mean distance individuals moved within a breeding season to minimize pseudo-replication errors associated with multiple observations on the same bird. P -values $< .05$ were considered significant.

RESULTS

Migratory chronology

Plovers began arriving in northern Utah in late March from 1991 to 1993, with the earliest sighting on 19 March 1992. The majority of banded birds (83.4%, $n = 224$) were first resighted between April and mid June (Fig. 2.1). The migratory chronology of adult males differed significantly from females ($G^2 = 23.9$, 10 df, $P = .008$). Most breeding males tended to arrive in a single peak period from late March through early May. In contrast, females that were confirmed breeders (i.e., a nest was found) had a longer arrival period from late March to mid June. Some

banded adult males and females were not resighted at the focal study sites until after late July, suggesting they possibly nested elsewhere that year or were simply transients (Fig. 2.1). Data on fall departure dates were not complete, as many juveniles were still in northern Utah after systematic fieldwork ended on 31 August (P. Paton, *personal observation*). Few adults were seen during surveys in late August.

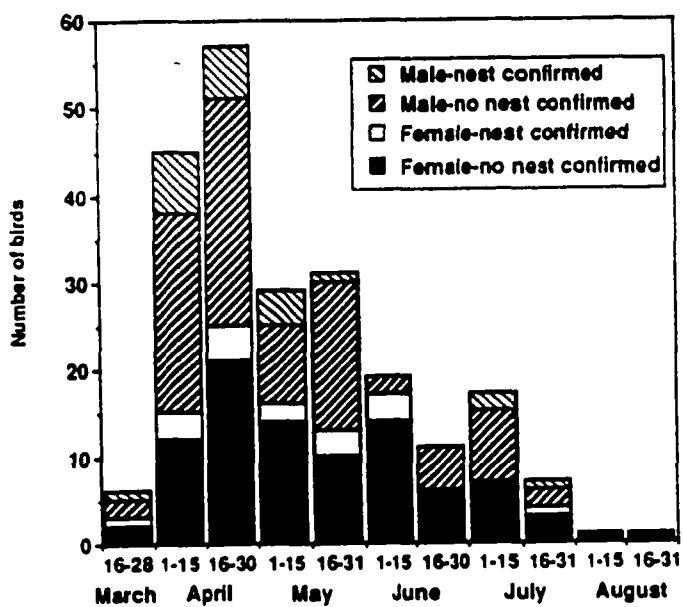


FIG. 2.1. Arrival dates for banded snowy plovers at Great Salt Lake.

Migratory chronology for nonbreeding birds (no nest confirmed) and known breeding birds (nest confirmed) are given.

Nest chronology

The egg-laying period commenced in mid April and continued for 14 weeks until mid July (range = 10 April-18 July). In most years, there were two peak egg-laying periods, one during the first half of May and another from June to early July (Fig. 2.2). As would be expected given typical climatic variation, there was significant annual variation in nest chronology. Based on data collected from 1991 to 1993, the nest initiation period differed significantly among years at both Howard Slough ($G^2 = 29.1$, 14 df, $P = .01$) and Layton marsh ($G^2 = 29.7$, 14 df, $P < .001$) (Fig. 2.2). The timing of nest initiations differed between the two focal sites in 1991 ($G^2 = 15.1$, 6 df, $P = .020$) and 1992 ($G^2 = 19.8$, 7 df, $P = .006$), but not in 1993 ($G^2 = 7.0$, 7 df, $P = .43$).

Breeding adult males had a tendency to remain longer at the study sites than adult females, although this difference was not statistically significant (Mann-Whitney *U*-test, $P = .082$) (Fig. 2.3). Breeding female plovers were seen for a median of 45 d (25%-75% quantiles = 33-65, maximum = 98 d, $n = 17$), whereas breeding males were observed a median of 53.5 d (25%-75% quantiles = 39-80, maximum = 149 d, $n = 22$). A substantial percentage of both sexes left the study sites immediately following nest failure, and were not resighted for the remainder of the year (41.5% of the females, 46.4% of the males; $G^2 = .17$, 1 df, $P = .68$) (Fig. 2.4).

Renesting following nest failure within the boundaries of the study sites was apparently rare, as I only documented renesting twice. If pairs did renest in

northern Utah, they apparently chose to move to other areas rather than remain at the focal study sites. However, a large proportion of unsuccessful breeding birds that apparently never renested was subsequently resighted at the same focal study site for ≥ 50 d (i.e., 29.3% of females and 28.6% males).

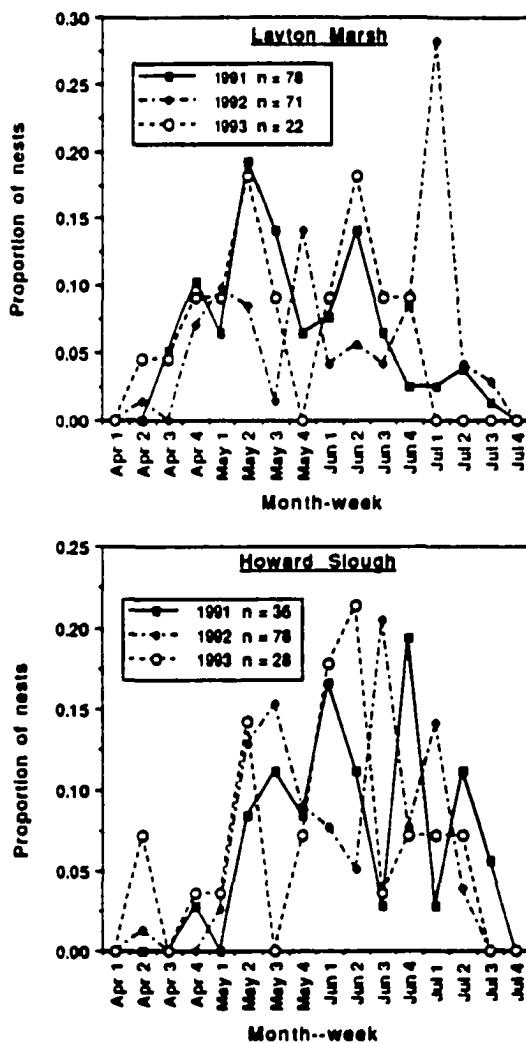


FIG. 2.2. Annual variation in the nest initiation chronology for snowy plovers at two focal study sites.

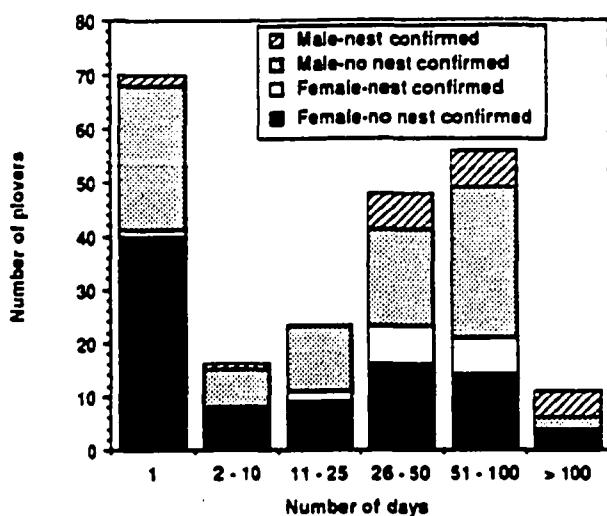


FIG. 2.3. Number of days that banded plovers were observed at the focal study sites within a breeding season. Data are shown by sex for potentially nonbreeding birds (no nest confirmed) and breeding birds (nest confirmed).

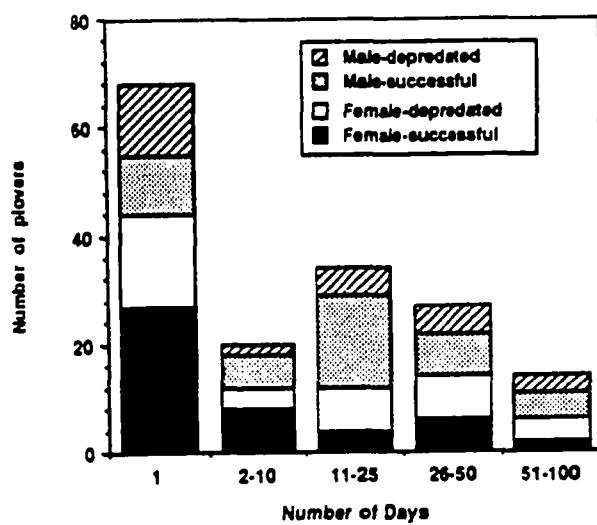


FIG. 2.4. Number of days that adult plovers were seen at the study sites following nest outcome (i.e., either the nest was successful or failed).

Males tended to remain at the focal study sites for longer time periods than females after nests successfully hatched ($G^2 = 17.5$, 4 df, $P = .002$) (Fig. 2.4). The majority of females (57.5%) were never resighted ≥ 2 d after eggs hatched, and only a small percentage of the successful females (16.9% of 47) remained for > 25 d. In contrast, most males (63.8%) remained for ≥ 11 d with their broods. Some males (23.4%) were not resighted ≥ 2 d after nests hatched, apparently leading their broods off the study sites (see also Lessells 1984, Warriner et al. 1986).

Incubation behavior

Plovers at Great Salt Lake appeared to defend only an area immediately around the nest (i.e., 10-20 m radius around the nest). Nonincubating parents foraged in areas separate from nest sites, and I rarely observed birds foraging near nesting areas. Based on observations of color-banded birds known to be associated with active nests, I found that plovers sometimes travelled > 3 km to forage (Fig. 2.5). Females were found as far as 3,770 m from active nests (median = 177 m, 25%-75% quantiles = 64-466 m, $n = 192$ observations), while males were found as far as 2,030 m (median = 272 m, 25%-75% quantiles = 110-580 m, $n = 266$). There was no intersexual variation in distances travelled (Mann-Whitney U -test = -1.2, $n_1 = 60$, $n_2 = 53$, $P = .22$) (Fig. 2.5).

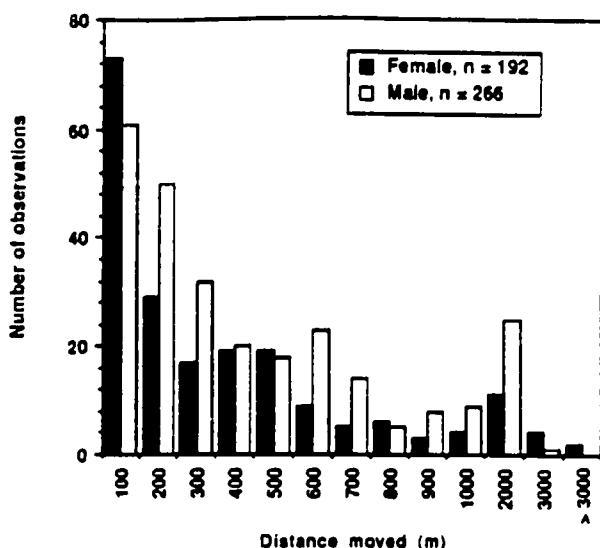


FIG. 2.5. Distances travelled (m) by foraging or roosting plovers away from their active nests.

The daytime incubation chronology differed between the sexes ($G^2 = 23.2$, 6 df, $P = .001$; Fig. 2.6). Females tend to incubate during the morning hours, while males often incubate in the mid-afternoon and late evening. Males and females would often exchange incubation duties on hot afternoons at short intervals (i.e., 10-15 min) (*personal observation*, see also Grant 1982). In addition, males would often relieve females at dusk, when females were observed foraging together in small flocks. No attempts were made to quantify nocturnal incubation behavior.

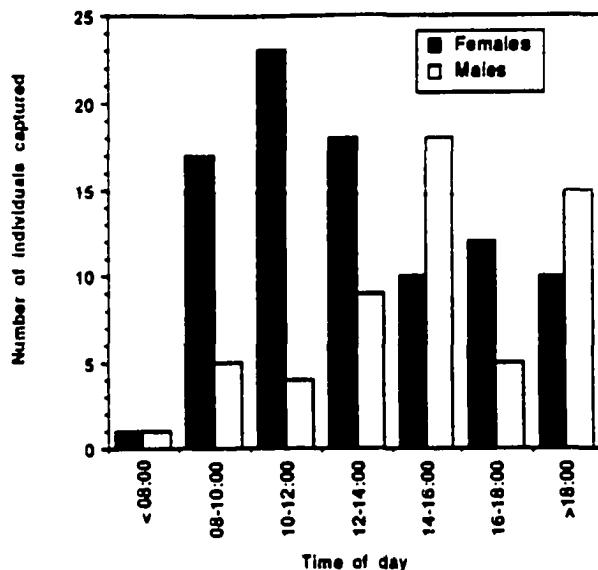


FIG. 2.6. Intersexual variation in daily incubation chronology, based on capture times of incubating adults.

Clutch size

Modal clutch size was 3 eggs (93.3% of 327 clutches). There were 18 nests with 2 eggs, 3 nests with 4 eggs, and 1 nest with 5 eggs. There was little annual variation in clutch size over the 4 years of the study ($G^2 = 7.5$, 9 df, $P = .58$), and clutch size was similar between the two study sites ($G^2 = 2.3$, 3 df, $P = .52$).

Pair retention, double-brooding and polyandry

Snowy plovers in Utah did not exhibit mate fidelity between years. I documented only one occasion when the same pair remated between years, based on

123 nest attempts for 30 pairs initially banded. The pair that remated was originally banded at Layton on an unsuccessful nest in 1990. In 1991, the female mated with another male at Howard Slough, while the original male was seen only once at Layton marsh. In 1992, the 1990 pair nested together successfully at Howard Slough.

I documented double-brooding only twice. One banded male at Layton marsh (mated with an unbanded female) had a clutch hatch successfully on 5 May 1991 and was last seen with this brood on 24 May. This male was then observed building a scrape on 7 June and incubating a second clutch, with an unbanded female, from 13 June to 10 July. In the other instance, the 1-d-old brood of a banded pair died after a cold rainstorm at Howard Slough on 8 May 1993. The female remated with a new banded male, although her original mate was still alive, and initiated a second nest on 10 June. This second clutch was lost to a predator on 20 June. This latter case was also the only example of within-year sequential polyandry I documented during this study.

Nest success

Estimates for mean annual nest success (Mayfield method) ranged from 5.4 to 49.2% at Howard Slough and 11.3 to 38.1% at Layton marsh (Table 2.1). Nest success varied widely from year to year, and the annual fluctuations were not consistent between the two focal study areas ($G^2 = 43.5$, 3 df, $P < .001$; Table 2.1).

At both study sites, mammalian predators were responsible for most nest failures (91%, $n = 188$; Table 2.2) based on tracks and scat near nests, while avian predators (7%) and unknown predators (2%) accounted for the rest of the losses. Red foxes were the primary predators, accounting for 90% of all mammalian nest depredations. Foxes were commonly observed at both Howard Slough and Layton marsh during all 4 years of the study. Striped skunks were observed only in 1993, and raccoons were also rare until 1993. California gulls (*Larus californicus*) apparently preyed upon plover nests only where gulls roosted, and I never observed gulls actively searching for plover nests. Common ravens (*Corvus corax*) preyed upon 10 nests, all at Layton marsh, where flocks of up to 65 ravens were occasionally observed foraging in plover nesting habitat. In contrast, ravens were rarely observed foraging at Howard Slough. Ravens could have been responsible for some of the nest depredations that I attributed to foxes, but tracks, scat, and observations of both predators indicates that foxes had a much greater impact than ravens at the focal study sites.

TABLE 2.1. Annual variation in nest success at two focal study sites at Great Salt Lake.

Howard Slough					Layton Marsh				
Mayfield				Mayfield					
Method ¹						Method			
Year	Mean	95 % CI	Apparent	n	Mean	95 % CI	Apparent	Success	n
1990	.492	.286-.837	.611	18	.381	.247-.585	.623	53	
1991	.197	.101-.379	.314	35	.113	.063-.203	.247	73	
1992	.445	.334-.592	.594	79	.129	.068-.240	.236	55	
1993	.054	.107-.165	.133	30	.345	.168-.695	.471	71	

¹Based on Mayfield (1961) and Johnson (1979).

TABLE 2.2. Annual variation in the percent of plover nests failing for various reasons at two focal study sites.

Year	% depredated					Hatched	n
	Mammalian	Avian	Unknown	Flooded			
<i>Howard Slough</i>							
1990	27.8	5.5	5.5			61.1	18
1991	60.0	5.7	2.9			31.4	35
1992	29.1		1.3	10.1		59.5	79
1993	80.0	3.3				13.3	30
<i>Layton Marsh</i>							
1990	34.0	1.7	1.7			62.3	53
1991	58.9	4.1		12.3		24.7	73
1992	54.5	9.1		12.7		23.6	55
1993	41.2			11.8		47.1	17

Fledging success

I calculated fledging success (i.e., young capable of flight) using the mean size of 4-week-old broods; age was based on plumage characteristics and size of the young (Boyd 1972). Snowy plovers fledge at \approx 30-d posthatching (Boyd 1972, Warriner et al. 1986). There was no annual variation in fledging rates, with an average of 1.87 chicks per brood for successful nests (Table 2.3).

TABLE 2.3. Estimates of snowy plover annual fledging success. Estimates were based on mean brood size as a function of brood age.

Age ¹	1990		1991		1992		1993		<i>F</i> ²	<i>P</i>
	$\bar{x} \pm SE$	<i>n</i>								
1	2.32 \pm .11	50	2.29 \pm .10	49	2.30 \pm .11	53	2.12 \pm .16	23	.2	.89
2	2.36 \pm .18	22	2.19 \pm .16	36	2.06 \pm .10	71	2.03 \pm .15	36	.9	.42
3	2.17 \pm .17	18	1.88 \pm .17	27	2.08 \pm .11	50	1.97 \pm .17	31	.5	.66
4	1.96 \pm .13	57	1.88 \pm .09	36	1.78 \pm .07	54	1.84 \pm .10	57	.7	.56

¹ Brood age in weeks

² ANOVA, comparing brood size among years by brood age.

DISCUSSION

The duration of the breeding season for snowy plovers nesting in Utah (mid-April to mid July; 14 weeks) was intermediate in length between reports from coastal California (Warriner et al. 1986) and Kansas (Boyd 1972). Plovers breeding in Utah are all migratory, as there are no winter records (November through February; Ella Sorensen, *personal communication*). In contrast, plover populations in coastal California consist of both migratory and year-round resident birds, with the egg-laying period encompassing 16 weeks from 23 March to 13 July (Warriner 1986). Birds nesting in the Great Plains are also migratory, but most nests are initiated during a 6-week period from 15 May to 30 June; there is one early record from 23 April (Boyd 1972, Grover and Knopf 1982). Given the relatively short breeding season in the Great Plains, it is not surprising that birds breeding there appear to be exclusively single-brooded and monogamous (Boyd 1972).

The mating system of snowy plovers breeding in northern Utah appears to resemble coastal California populations (Warriner et al. 1986) more than those in the Great Plains (Boyd 1972, Grover and Knopf 1982). Three lines of evidence suggest the possibility that snowy plovers nesting in Utah are regularly double-brooded and sequentially polygamous, although I found little direct evidence to support the existence of either strategy at Great Salt Lake. First, I documented two examples of double-brooding and one case of sequential polyandry. Second, based on a 31-d egg-laying and incubation period (Page et al. 1985, Warriner et al. 1986) and the

fact that only males care for broods, there was ample time for females to produce two clutches during the 14-week nest-initiation period in northern Utah. Third, the migratory and nest initiation chronology of the birds I banded suggested that there were two distinctive nest initiation periods. Plovers have been documented moving as far as 1,140 km between nest sites in western North America (Stenzel et al. *in press*). Therefore, it is possible that the second wave of females arriving in June consisted of birds that nested elsewhere early in the breeding season and attempted their second clutches of the year at my study sites. However, it is unknown if these birds arriving in June came from other areas in northern Utah, or from areas as far away as the Gulf of California where they winter (P. Paton, *unpublished data*).

I was unable to find the nests of the majority of the banded birds resighted at the study sites (i.e., 84.3% of 108 females, 81.0% of 116 males; Fig. 2.3) because of at least five factors. First, an unknown percentage of both sexes could have been "floaters" (i.e., nonbreeding birds that did not nest that year; see Beletsky 1992). Second, many females and males (44.0% and 28.7%, respectively) were observed only on one occasion within a breeding season. This suggests a substantial proportion of the plovers observed at the study sites were transients, or were foraging at the focal study sites but nesting elsewhere. Transients are birds roaming the Great Salt Lake or an even larger region, trying to find either suitable breeding habitat or potential mates. A similar strategy has been reported among the spotted sandpiper (*Actitis macularia*), although its search for breeding sites appears to be more restricted to the postbreeding dispersal period (Reed and Oring 1992). In

addition, because many of the plovers observed at the focal study sites were potentially nonbreeders, biologists should be cautious when trying to determine the number of breeding birds at a particular site from census data alone. Third, breeding plovers were often extremely secretive around their nest and could easily be missed (Boyd 1972, Warriner et al. 1986, *personal observation*). For example, three color-banded breeding adults (1♀ and 2♂♂) were only resighted when they were captured on their nests, and were never seen before or afterwards. Fourth, large numbers of plovers used each study site. This is exemplified by the fact that although I banded 256 adults at both sites, banded birds often accounted for <10% of the birds observed on any given day (P. Paton, *unpublished data*). Finally, plovers in Utah often spent most of the day foraging over 1 km from their nest (Fig. 2.5). These factors made it difficult to determine which individual bird was associated with each nest.

In contrast to results from coastal California (Warriner et al. 1986), Kansas (Boyd 1972) and the European subspecies in Germany (Rittinghaus 1956), I found little evidence that plovers in northern Utah readily renested in the immediate vicinity of their failed nest. Reasons for the apparent absence of renesting in Utah are unclear. It is possible that with so much plover nesting habitat available to breeding birds around Great Salt Lake from 1990 to 1993, pairs that attempted to renest moved off the study sites to maximize the probability of a successful nesting attempt. However, many birds remained at the study sites following nest failure and apparently did not renest, so it appears this dilemma remains unresolved.

Impacts of red foxes on snowy plovers and other ground-nesting species are a growing concern to wildlife managers throughout the United States (e.g., Patterson et al. 1991). Apparent nest success rates found during this study (13.3-62.3%) were lower than reported for plovers in Oklahoma (38-73%; Grover and Knopf 1982), Kansas (55-60%; Boyd 1972), coastal California (50%; Warriner et. al 1986), and eastern, interior California (59.3%; Page et al. 1985). Of all these studies, Utah was the only area where red foxes were the dominant predator. A recent invasion of red foxes to coastal California has had a significant negative impact on plover nest success (G. Page, *personal communication*). Red foxes are the primary predator of piping plover (*C. melanotos*) nesting along parts of the Atlantic coast (Patterson et al. 1991), and have forced managers to adopt short-term solutions, such as fencing off individual nests to reduce depredation problems (Rimmer and Deblinger 1990). However, long-term management strategies need to be developed to minimize nest depredation by red foxes on ground-nesting species throughout North America.

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CHAPTER 3

SURVIVAL ESTIMATES FOR SNOWY PLOVERS

AT GREAT SALT LAKE

Abstract. I estimated annual survival and resighting rates for snowy plovers (*Charadrius alexandrinus*), using data collected from 1990-1993 at Great Salt Lake, Utah. I uniquely color-banded and subsequently resighted 44.7% of 199 adult females and 52.5% of 162 adult males. The most parsimonious Jolly-Seber model postulated that survival rates were time-dependent and resighting probabilities were sex-specific. Annual survival estimates for adults did not vary between the sexes and ranged from .578-.880 ($\bar{x} = .687$). Resighting probabilities were significantly higher for males (.675) than for females (.518). Mean life expectancy for an adult plover (i.e., birds ≥ 1 years old) was 2.7 years. Survival estimates for immature birds were imprecise because few were resighted ($\bar{x} = .385$, 95% CI = .048-.885). Estimates of the finite rate in population change, lambda, suggest that in 1 of 4 years nest success and survival estimates were large enough (i.e., $\lambda > 1.0$) to sustain the population for a number of years. Increases in adult survivorship would have the greatest affect on lambda, although manipulating nest success rates might be an easier management strategy.

INTRODUCTION

Current knowledge of the breeding biology of snowy plovers (*Charadrius alexandrinus*) in North America is primarily confined to studies of their reproductive success (Boyd 1972; Purdue 1976; Grover and Knopf 1982; Wilson-Jacobs and Meslow 1984; Page et al. 1983, 1985; Paton and Edwards 1990), mating system (Boyd 1972, Warriner et al. 1986), dispersal (Stenzel et al. *in press*), and distribution (Herman et al. 1988, Halpin and Paul 1989, Page et al. 1991). Pacific Coast populations of the snowy plover were listed as threatened by the U.S. Fish and Wildlife Service in April 1993 (Federal Register 1993), yet there are no quantitative survival estimates available for this species.

Snowy plovers nesting around Great Salt Lake, Utah, are all migratory. Birds breeding in Utah primarily winter along the coasts of the Gulf of California and the west coast of Baja California (G. Page, M. Stern, and P. Paton, *unpublished data*). Their mating system is primarily monogamous; some individuals in California are sequentially polyandrous (Warriner et al. 1986. Stenzel et al. *in press*), whereas polygamy has rarely been documented in Utah (see Chapter 2). In Utah, there is weak evidence to suggest that plovers are occasionally double-brooded, and apparently seldom renest in the same area following nest failure (see Chapter 2).

Page et al. (1983) calculated a minimum adult annual survival estimate of .743, based solely on return rates for birds in coastal California. However, this likely underestimated actual adult survival rates because it did not use appropriate capture-recapture models (e.g. Cormack 1964, Jolly 1965, Seber 1965). The Jolly-Seber

modeling approach uses information on annual resighting rates to calculate the probability that organisms that were never resighted were actually still alive. The purpose of this paper is to estimate annual survival for snowy plovers breeding in Utah, using a hierarchical modeling approach developed by Lebreton et al. (1992).

METHODS

The study was conducted at eight sites at Great Salt Lake, Utah, from 1990 to 1993: Locomotive Springs Waterfowl Management Area (WMA) ($41^{\circ} 41'N$, $112^{\circ} 55'W$); Harold Crane WMA ($41^{\circ} 20'N$, $112^{\circ} 08'W$); the West Warren area of Harold Crane WMA ($41^{\circ} 18'N$, $112^{\circ} 08'W$); the northwest corner of Ogden Bay WMA ($41^{\circ} 14'N$, $112^{\circ} 14'W$); Howard Slough WMA ($41^{\circ} 09'N$, $112^{\circ} 09'W$); West Layton Marsh ($41^{\circ} 02'N$, $112^{\circ} 05'W$); Farmington Bay WMA ($40^{\circ} 55'N$, $111^{\circ} 55'W$); and 2 km northeast of Saltair Beach ($40^{\circ} 46'N$, $112^{\circ} 08'W$). Fieldwork was centered at 2 focal sites, Howard Slough WMA and West Layton marsh, which were surveyed approximately two to three times per week from 1 April to 31 August, with one observer in 1990 and two observers from 1991 to 1993. The other six sites were visited less frequently at intervals of one to four surveys per month.

Incubating birds were trapped with a circular funnel trap (Lessells 1984); others were captured .1-1 km away from nests by herding birds into two mist nets staked together to form a 'V'. Adults were sexed based on plumage characteristics, while nestlings and juveniles (hereafter immatures) could not be sexed (Warriner et al. 1986). Individual plovers were uniquely marked with four color-bands, two on each

tarsometatarsus (Page et al. 1983). Nestlings were banded with a single U.S. Fish and Wildlife Service (USFWS) band, with two narrow strips of colored automobile pin-striping tape soldered over the band. Each brood had a unique color combination, while fledglings (i.e., young capable of flight) received a USFWS band plus one color-band.

Analysis

I used the Cormack-Jolly-Seber (CJS) modeling approach (Cormack 1964, Jolly 1965, Seber 1965) to calculate annual survival estimates. I used the capture history data for 532 snowy plovers (162 adult males, 199 adult females, and 171 immature plovers) to determine annual survival (S) and resighting probabilities (P) for birds breeding in northern Utah (Table 3.1). I first tested the assumption that every bird had equivalent survival and recapture probabilities using TESTS 2 and 3 in Program RELEASE (Burnham et al. 1987). I did these tests with the full CJS model (i.e. there was an interaction between annual survival, the resighting probability and sex). There was no evidence for heterogeneity of fates within groups (Program RELEASE TEST 3; total $\chi^2_8 = 11.4$, $P = .18$). Therefore, the assumptions of the Jolly-Seber model were met, and data from males and females could be pooled for further analyses (Burnham et al. 1987).

I then used Program SURGE (Lebreton et al. 1992) to determine the minimum Akaike's Information Criterion (AIC), which was calculated using each model's maximum log-likelihood plus the number of estimable parameters. The model with

the smallest AIC was then used to select the best CJS model because it provided an unbiased criterion for model selection (Lebreton et al. 1992). This approach is similar to using Mallow's C_p in multiple regression. Potential survival models examined included 13 combinations of sex, time, and sex \times time interaction terms for survival probabilities and resighting probabilities (Table 3.2). Mean life expectancy was calculated as: $-1/\ln$ (annual survival estimate).

TABLE 3.1. Capture history matrix for 532 snowy plovers at Great Salt Lake from 1990-1993.

Capture history ¹	Adult males	Adult females	Immature
1000	9	18	58
1001	2	1	2
1010	1	8	1
1011	0	4	0
1100	6	12	2
1101	3	2	0
1110	6	2	1
1111	4	4	0
0100	37	48	21
0101	4	7	0
0110	15	11	3
0111	12	8	0
0010	31	44	74
0011	32	30	9

¹Capture or resighting = 1, no sighting = 0.

TABLE 3.2. Potential survival rate models for adult snowy plovers at Great Salt Lake.

Model ¹	<i>np</i> ²	-2 ln <i>L</i> ³	AIC ⁴	Comparison
(1) <i>S, P</i>	2	815.62	819.62	Constant <i>S</i> and <i>P</i>
(2) <i>S_s, P</i>	3	813.64	819.64	Sex differences in <i>S</i> , constant <i>P</i>
(3) <i>S, P_t</i>	3	809.74	815.74	Constant <i>S</i> , time effect on <i>P</i>
(4) <i>S_s, P_t</i>	4	809.44	817.44	Sex differences in <i>S</i> and <i>P</i>
(5) <i>S_t, P</i>	4	805.04	813.04	Time effect on <i>S</i> , constant <i>P</i>
(6) <i>S, P_t</i>	4	814.82	822.82	Constant <i>S</i> , time effect on <i>P</i>
(7) <i>S_t, P_t</i>	5	803.50	813.50	Time effect on <i>S</i> and <i>P</i>
(8) <i>S_t, P_s</i>	5	798.96	808.96	Time effect on <i>S</i> , sex differences in <i>P</i>
(9) <i>S_s, P_t</i>	5	812.86	822.86	Sex differences in <i>S</i> , time effect on <i>P</i>
(10) <i>S, P_{sxt}</i>	7	807.04	821.04	Constant <i>S</i> , time\sex interaction on <i>P</i>
(11) <i>S_t, P_{sxt}</i>	8	796.96	812.96	Time effect on <i>S</i> , time\sex interaction on <i>P</i>
(12) <i>S_s, P_{sxt}</i>	8	807.03	823.03	Sex differences in <i>S</i> , time\sex interaction on <i>P</i>
(13) <i>S_{sxt}, P_{sxt}</i>	10	794.24	814.24	Time\sex interaction on <i>S</i> and <i>P</i>

¹Model notation: *S* = survival probability, *P* = resighting probability, *s* = sex, *t* = time, *x* = interaction term.

²Number of estimable parameters

³*L* = likelihood function

⁴Akaike's Information Criterion = 2*np* + -2 ln *L*

I used standard cohort life table calculation formulae to determine the finite rate of population change (λ). I categorized plover survival rates into two age-classes: immatures (probability of surviving from hatching to 1 year old), and adults (i.e., ≥ 1 year old; Warriner et al. 1986). Using data from Gary Page (*personal communication*), I assumed that age at first reproduction was 1 year, plovers lived for 15 years, reproductive senescence did not occur, modal clutch size was 3 eggs (see Chapter 2), the sex ratio was 1:1 at hatching, and therefore there were 1.5 female

chicks per successful nest. There was little evidence that plovers at Great Salt Lake renested at the same study site following depredation events, but there was weak evidence for double-clutching (see Chapter 2). Therefore, when I calculated lambda, I assumed that 10% of females double-clutched.

RESULTS

Of the 13 survival models tested, one model (Model 8) clearly had the smallest AIC (Table 3.2). This model postulated that survival rates were time-dependent and resighting rates were sex-specific (i.e., S_t, P_t). Using this model, survival rates were high during the winters 1990-91 and 1992-93, and low in the winter of 1991-92 (Table 3.3). It is possible that the low survival estimates for the winter of 1991-92 were due to permanent emigration from Great Salt Lake, rather than higher mortality rates, but I could not differentiate between these two processes. In addition, males had a higher probability of being resighted than females; .675 versus .518, respectively (Table 3.3).

The best estimate for the mean annual survival probability for an adult plover was .687, which I calculated using a CJS model with constant survival and sex-specific resighting probabilities (i.e., S, P). Given this average overall survival estimate, mean life expectancy for an adult plover was 2.7 years. Few resightings of immature plovers resulted in an imprecise survival estimate, due to the large confidence interval around the mean survival estimate of .385 (Table 3.3).

Annual estimates of the finite rate in population change (λ) ranged from .075 to

2.0 (Table 3.4). In only the first year of the study (1990) was the finite rate of population change large enough (i.e., $\lambda > 1$) to prevent the population from declining. This was the only year when nest success rates were relatively high (i.e. 38-49% successful) and adult survivorship was also relatively high (.88; SE = .076; Table 3.3).

The model I used to calculate lambda had relatively simple assumptions; survivorship remained constant for birds once they became adults, nest success did not vary by age-cohort, and all cohorts double-clutched with equal probability. Given these assumptions, a sensitivity analysis found that variations in all parameter

TABLE 3.3. Annual survival and resighting probabilities for snowy plovers at Great Salt Lake.

Age/Sex	Years	Estimate ¹	SE	95% CI
<i>Survival rates</i>				
Adults	1990-91	.880	.076	.640-.968
Adults	1991-92	.578	.050	.478-.672
Adults	1992-93	.732	.071	.573-.848
Immatures	pooled	.385	.304	.048-.885
<i>Resighting rates</i>				
Adult males	pooled	.675	.061	.547-.781
Adult females	pooled	.518	.050	.420-.615
Immatures	pooled	.213	.171	.036-.666

¹ Parameter estimates were based on the Jolly-Seber model that survival rates time-dependent and resighting probabilities were sex-specific.

TABLE 3.4. Annual variation in finite rate in population change (λ) for snowy plovers breeding at two focal study sites at Great Salt Lake.

Year	Annual survival estimate	Howard Slough		Layton Marsh	
		Nest Success ^a	λ^b	Nest Success	λ
1990	.880	.492	2.00	.381	1.54
1991	.578	.197	.171	.113	.098
1992	.732	.445	.767	.129	.222
1993	.687	.054	.075	.345	.480

^aMayfield method estimate (see Chapter 2)

^bAssumes 10% of females double-clutch and first-year survival was .385.

estimates (i.e., immature survivorship, percent of adults double-clutching, nest success) affected lambda equally, with the exception of adult survivorship. For example, based on my model, a 20% increase in adult survivorship would result in a 49.9% increase in lambda, whereas all other parameters would only increase lambda by 20%.

DISCUSSION

The mean survival estimate I calculated for snowy plovers breeding at Great Salt Lake (.687) was lower than the survival estimate for snowy plovers breeding in coastal California (.743, Page et al. 1983). Annual variations in survival estimates at Great Salt Lake (i.e., survival estimates ranged from .578-.880; Table 3.3) were within the range for coastal California estimates. The mean and range of survival estimates for snowy plovers at Great Salt Lake were similar to Jolly-Seber survival

estimates for a migratory population of piping plovers (*Charadrius melanotos*) in North Dakota (i.e., $\lambda = .664$, range = .563-.933; Root et al. 1992).

There were not enough resightings of first-year plovers at Great Salt Lake to calculate a precise survival estimate for that age-class. The only other published survival estimate for immature plovers comes from Page et al. (1983), who subsequently resighted 9 of 14 (.643) fledglings banded in coastal California. Page et al.'s (1983) survival estimate was based solely on fledglings (i.e., young capable of flight); therefore, it was higher than the survival estimate that I calculated for immature plovers (i.e., both nestlings and fledglings combined) in Utah. However, after I recalculated the survival estimates for immature plovers for California data, the estimates were similar between the two locations. Page et al. (1983) estimated fledging rates for Mono Lake of 1.64 chicks fledged per successful clutch of 3 eggs or .547 for each nest. This results in an survival estimate for immature birds at Mono Lake of approximately .352 (i.e., .547 x .643), which is close to the immature survival estimate I determined for northern Utah birds of .385. Because variations in immature survival estimates can affect estimates of the finite rate of population change (e.g., a 20% increase in immature survivorship could increase lambda by 20%), it would be helpful to gather more data to obtain a more precise estimate of immature snowy plovers survival rates in western North America.

As with piping plovers in the Great Plains (Root et al. 1992, Ryan et al. 1993), little is known about mortality factors affecting either immature or adult snowy plovers at Great Salt Lake. I observed one instance of immature mortality, when an

American kestrel (*Falco sparverius*) captured a 2-week-old chick. Red foxes (*Vulpes vulpes*) and northern harriers (*Circus cyaneus*) were other common, potential predators for immatures in northern Utah (*personal observation*). In addition, peregrine falcons (*Falco peregrinus*) have been reintroduced to northern Utah by the Division of Wildlife, using a series of 10 hack towers around Great Salt Lake. The remains of several adult snowy plovers have been found at the base of these towers (Don Paul, Utah Division of Wildlife Resources, *personal communication*).

Ryan et al. (1993) found that both survivorship and nest success rates for piping plovers needed to be increased for piping plover populations to persist. Because little was known about factors influencing adult and immature survivorship in piping plovers, they suggested the most appropriate management strategy would be to increase nest success rates (e.g., Mayer and Ryan 1991). My calculations suggest that increases in adult survivorship would have the greatest influence on snowy plover populations in northern Utah, whereas changes in immature survivorship, nest success, or the percent of adults double-brooding would have less influence. However, I used a simple modeling approach and violations of any of the assumptions could change these results. For example, nest success rates and survival rates vary from year to year, but my modeling approach assumed no annual variation in these parameters. In addition, older adults may have higher nest success rates than younger individuals (Thomas and Coulson 1988), but I assumed constant fecundity for each cohort.

The most parsimonious Jolly-Seber model suggests that either plover survival

estimates vary dramatically annually, or that there occasionally is substantial permanent emigration from my Utah study sites. These fluctuations in survival rates, in combination with variations in annual nest success, result in large variations in estimates of lambda. In addition, my analyses suggest that among Utah plovers, in some years lambda occasionally increases much greater than 1.0, which would allow the population to persist for a number of years. This strategy makes sense given the highly ephemeral environment in which this species exists (see Chapters 1 and 5) and may explain its nomadic nature (Stenzel et al. *in press*).

It appears that snowy plovers are a pioneering species that move rapidly into suitable nesting habitat when it becomes available. For example, due to flooding of Great Salt Lake from 1983-1987, all of my study sites were underwater up until two years before I initiated my study. Snowy plover's ability to take advantage of ephemeral habitats may partially explain why plovers are double-brooded in parts of their range (i.e., California, Warriner et al. 1986) because this strategy would dramatically increase fecundity rates during ideal years. Snowy plovers are a long-lived species (15 yrs, G. Page, personal communication); therefore, one successful cohort could help the population persist through several poor years. The mean survival rate for an adult is 2.7 years, suggesting that as long as there is a "good" reproductive year at intervals of every 3 to 5 years, the population probably would persist. If conditions are ideal for breeding (i.e., low nest predation rates and a substantial percentage of the population double-clutches) and survival (i.e., high immature and adult survival rates), it appears that snowy plover populations are

adapted to respond rapidly.

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CHAPTER 4

SCALE-MEDIATED EFFECTS OF NEST-SITE SELECTION BY SNOWY PLOVERS ON NEST PREDATION RATES¹

Abstract. I studied factors affecting nest-site selection by snowy plovers (*Charadrius alexandrinus*) from 1990 to 1993 at Great Salt Lake, Utah. At both a mesohabitat scale (i.e., < 15-m radius from nests) and a microhabitat scale (i.e., < 1-m radius from nests), plovers selected nest-sites in habitats devoid of vegetation (i.e., 73-78% bare ground). Birds appeared to select specific nest-sites based on microhabitat characteristics because I only found significant differences in vegetation attributes between nests and random points at this scale. The majority of nests, 68%, were \leq 15 cm from an object (e.g., dead shrub, woody debris, bones). There were no significant relationships between nest fate and proximity to an object in 3 of 4 years ($P > .5$). In 1990, however, nests under objects were 4.3 times (95% CI = 1.5-12.7) more likely to be successful than nests beside objects or in the open. This supports the hypothesis that nest concealment may increase nest success. There was also weak evidence supporting the hypothesis that birds might select mesohabitats with high densities of potential nest sites to maximize predator search time. I found that plovers readily used artificial nest substrates which mimicked the size and color of plover eggs, suggesting that preferred microhabitats may be scarce at Great Salt Lake.

¹Coauthored by Peter W. C. Paton and Thomas C. Edwards Jr.

INTRODUCTION

Predation is the major cause of nest failures for most avian populations (Ricklefs 1969, Martin 1988a, 1992a). Some ecologists have hypothesized that predation is the primary selective force determining nest-site selection (e.g., Martin 1988b, 1992b, Steele 1993). However, other authors believe physiological constraints are of utmost importance (e.g., Walsberg 1985, With and Webb 1993), or have focused on foraging considerations (e.g., MacArthur et al. 1962, Gibbs et al. 1987). Relatively few studies of natural nests have quantified how specific habitat attributes influence reproductive success (e.g., Best and Stauffer 1980, Haensly et al. 1987, Leonard and Picman 1987, Riley et al. 1992), but these habitat features should be most pertinent to biologists concerned with managing populations (Van Horne 1983, Martin 1992a, Vickery et al. 1992).

If predation is one of the most important factors shaping nest-site habitat selection, the scale at which there are quantifiable differences in the environment that minimize predation risk remains ambiguous. The importance of "microhabitat," that is the area immediately surrounding the nest (i.e., within a 1-m radius from the nest for this study), is suggested by evidence that increasing foliage density at the nest is positively correlated with nest success (e.g., Dwernychuk and Boag 1972, Jones and Hungerford 1972, Sugden and Beyersbergen 1986, Crabtree et al. 1989, Martin 1992a, but see Krasowski and Nudds 1986, Haensly et al. 1987).

Recent studies with passerines, however, found stronger evidence for the importance of "mesohabitat," that is the habitat patch where the nest is located

(Martin 1988c). For the purposes of this study, mesohabitat encompasses an area within a 15-m radius of the nest (see Kelly 1993, Knopf and Sedgwick 1992). For example, Martin and Roper (1988) suggested that hermit thrush (*Catharus guttatus*) select habitat patches with relatively high densities of potential nest sites (e.g., small trees), thereby increasing predator search time and decreasing the probability that predators locate the nest (see also Bowman and Harris 1980). Other studies have suggested that birds select nest sites based on mesohabitat characteristics, while simultaneously choosing microhabitats which increase concealment from potential predators and nest parasites (Knopf and Sedgwick 1992, but see Holway 1991). Finally, others have hypothesized that "macrohabitat," that is the entire home range, can play an important role in determining predation rates. At a macrohabitat scale, birds may select territories that have relatively low predation probabilities (Fretwell and Lucas 1969).

I studied the breeding ecology of snowy plovers (*Charadrius alexandrinus*) in northern Utah to determine if habitat attributes at microhabitat or mesohabitat scales affected reproductive success. Snowy plovers are ground-nesters and generally select areas devoid of vegetation, which makes it relatively simple to quantify structural complexity near nest sites (Purdue 1976; Grover and Knopf 1982; Wilson-Jacobs and Meslow 1984; Page et al. 1983, 1985). Determining what influences snowy plover reproductive success is important because Pacific Coast populations were listed as threatened by the U. S. Fish and Wildlife Service in April 1993 (Federal Register 1993).

Snowy plovers experience relatively high nest depredation rates (e.g., 40% in eastern California [Page et al. 1983], and 68% on the Oregon coast [Wilson-Jacobs and Meslow 1984]), therefore, plovers are probably under strong selective pressure to select habitats that minimize depredation rates. Page et al. (1985) found that nests beside objects (e.g., woody debris, dead shrubs) had higher depredation rates than nests underneath objects or in the open (see also Grover and Knopf 1982, Wilson-Jacobs and Meslow 1984). Previous research found that snowy plovers nested near objects that were too small to provide effective thermal benefits to incubating adult plovers (Purdue 1976, Purdue and Haines 1977). This implies that plovers were potentially selecting objects for reasons other than energetic considerations.

Snowy plovers are potentially less constrained than many other avian taxa, in terms of nest location in relationship to distance to foraging sites, when making nest-site placement decisions. At Great Salt Lake, plovers often travel far from nests to forage (i.e., up to 3.7 km; Chapter 2). In addition, anti-predator behavior can play an important role in determining where to locate a nest-site. The primary anti-predator strategy incubating plovers employ, when a potential predator approaches, is to scurry away from the nest when the predator is within 100 to 200 m. Then the adult relies on cryptic eggs to avoid detection (Boyd 1972, Warriner et al. 1986).

The objectives of this paper were to: (1) determine the scale at which habitat attributes differ between nests and random points, (2) investigate the relationship between nest fate and microhabitat or mesohabitat, and (3) based on the empirical

results of the previous objectives, establish artificial nest substrates at the most significant scale to determine if plovers will readily use artificially altered habitats.

METHODS

Study area

I studied nesting plovers during four breeding seasons from 1990 to 1993 at two focal study sites on the eastern shores of Great Salt Lake, in northern Utah; Howard Slough Waterfowl Management Area (WMA)(41°08'N, 112°09'W) and West Layton Marsh (41°02'N, 112°05'W). Focal sites were surveyed two to three times per week by one observer in 1990 and two observers from 1991 to 1993. Field work typically took place from 1 April to 31 August.

The marshes and adjoining upland habitat of Great Salt Lake were a dynamic ecosystem, with the vegetation characteristics at each site constantly changing between years. Fieldwork took place following 6 years of severe flooding (Arnow and Stephens 1990, Foote 1991). During the flood years, 1983 to 1987, the lake increased 3.7 m in depth. At its peak in 1987, the lake covered 5940 km², compared to a recent historic low in 1963 when it covered 2470 km².

All areas where plovers nested were dominated by salt flats, interspersed with sparse patches of salt-tolerant members of the Chenopodiaceae, including greasewood (*Sarcobatus vermiculatus*), iodine bush (*Allenrolfea occidentalis*), seepweed (*Suaeda spp.*), summer cypress (*Kochia scoparia*), bassia (*Bassia hyssopifolia*), and pickleweed (*Salicornia europaea*). Nest predators included red

foxes (*Vulpes vulpes*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), common ravens (*Corvus corax*), and California gulls (*Larus occidentalis*). Eggs with puncture holes were assumed to be depredated by avian predators, while missing or crushed eggs were categorized as being taken by mammalian predators (Rearden 1951). Observations of tracks and scat near depredated nests often substantiated predator identifications.

Field procedures

Nests were found using nest-searching techniques outlined in Page et al. (1985). From 1991 to 1993, 28% of the nests were discovered by walking through nesting habitat and looking for plovers flushing off nests; 29% were detected by standing > 150-200 m away from potential nesting areas, scanning with a 22X spotting scope for incubating adults; 32% were found by walking systematically through potential nesting habitat scanning the ground for nests; and 11% were accidentally found each year. Nests that I found were marked with 10-cm tall, wooden stakes, which were placed 15 m to the south of each nest.

I used the same criteria as Page et al. (1985) to categorize the proximity of nests to objects (e.g., bushes, dead or live plants, sticks, bones, dried cow dung). Page et al. (1985) did not explicitly define "objects"; I defined objects as anything \geq 7-cm diameter by \geq 2-cm tall (i.e., large enough to partially conceal plover eggs when viewed at a 45° angle from 5 m). Nest scrapes \leq 15 cm from an object, but not covered by any part of the object, were categorized as "beside" an object. Nests

beside an object and had $\geq 5\%$ of the upper surface area of the eggs covered by the object were categorized as "under" an object. Nests > 15 cm from an object were "in the open."

Estimated hatching dates for clutches were calculated using the egg-floatation method (Westerkov 1950, Page et al. 1985). I assumed a 4-d egg-laying period and a 27-d incubation period (Warriner et al. 1986). Nests were checked at 1-week intervals during the first 3 weeks of incubation, and daily near expected hatching dates. Nests were classified as successful if ≥ 1 chick hatched. Nests were categorized as failing if the nest was empty prior to its expected hatching date, obvious predator signs were found at the nest (e.g., large egg shell fragments [> 25 mm²], predator tracks, or predator scat), or small egg shell fragments were absent from the scrape lining after the expected hatching date. Nest success estimates based on exposure days were calculated using the Mayfield method (Mayfield 1961), with a 95% confidence interval as outlined by Johnson (1979).

Vegetation attributes were quantified at 355 nests and paired-random points using a line-intercept method (Hays et al. 1981). Random points were located 50 m in a random direction from each nest. I estimated vegetation coverage at both nests and random points along four, 15-m long transects, with transects oriented in the four cardinal directions. Random points were placed only in potential plover nesting habitat, which was based on three criteria: (1) a width of > 33 m (i.e., 0.1 ha in size), (2) vegetation, live or dead, accounted for $< 50\%$ of the total coverage within a habitat patch; and (3) vegetation within a 15-m radius of the nest or random point

was predominately < 5 cm tall (plovers only nest in barren habitats based on Wilson-Jacobs and Meslow 1984, Grover and Knopf 1982, Page et al. 1985, Paton and Edwards 1990). Random points located in habitat without regard to suitability can result in data suggesting nest-site selection occurred, when in fact no real selection occurred (see Edwards and Collopy 1988). Each 10-cm segment was classified as either live vegetation, dead vegetation, or barren ground, based on the dominant habitat type touching the transect measuring tape (i.e., > 50% of the 10-cm segment). Plant species were recorded for live and dead vegetation categories, with taxa pooled for the analyses presented here. I then calculated the proportion of ground cover for each of the three habitat types (live and dead vegetation, and bare ground) for four radii from plot center (0-1 m, 0-5 m, 0-10 m, and 0-15 m).

To investigate the effect of nest-site selection on depredation rates, I defined eight microhabitat types. Nests in the open (i.e., > 15 cm from an object) were categorized in one of four microhabitats: (1) barren salt flats; (2) rough terrain (e.g., barren areas with obvious topographic features such as deep cracks, uneven terrain, hoof prints [from domestic cattle *{Bos taurus}*, antelope *{Antilocapra americana}*], and tire tracks); (3) live or dead vegetation; and (4) gravel (i.e., roads or natural rock formations). The four microhabitats beside or under objects included: (5) brine fly (*Ephydria spp.*) exuviae (i.e., tan-colored mats formed from the exoskeletons of larval brine flies); (6) live and dead plants; (7) dead shrubs, which were usually the remnant woody stems of iodine bush and greasewood; and (8) miscellaneous objects, which included the bones of domestic cattle ($n = 7$), a duck carcass [*Anas spp.*] (n

= 1), carp [*Cyprinus carpio*] bones ($n = 1$), goose [*Branta canadensis*] feathers ($n = 1$), and white piece of plastic ($n = 1$).

Statistical analyses

I was interested in the relative differences of three vegetation types (i.e., the amount of dead vegetation, live vegetation, and bare ground) between nest-sites and paired random points at four spatial scales (i.e., 0-1, 0-5, 0-10, and 0-15 m radius from plot center). To statistically compare nests to random points, I used a paired multivariate analysis of variance (MANOVA) design (Hotelling's T^2 statistic) with 95% simultaneous confidence intervals (Johnson and Wichern 1988:214), which is the multivariate equivalent of a paired-*t* test. The level of statistical significance was $\alpha = .05$ for all comparisons.

To analyze the relationship between nest fate and proximity to an object, I used a log-linear modelling approach with a backward selection process (BMDP statistical software, Dixon et al. 1990). I further analyzed nest fate in relation to microhabitat, based on the eight potential microhabitats listed above, using a likelihood-ratio chi-square test (G^2) (Agresti 1990). Analyses of nest success in relationship to proximity to objects, based on daily survival rates (Mayfield 1961, Johnson 1979), revealed similar trends as the categorical analyses and are not presented here.

Artificial nest substrates

To test whether plovers would nest on artificial microhabitats, I initiated two

sets of experiments using artificial nest substrates (ANS) at Howard Slough WMA in 1993. ANS consisted of 0.2 m³ of gravel, spread over a 1-m diameter area, and were established on barren, salt flats that were approximately 3 ha in size. ANS were spaced approximately 30 m apart, which was similar to the spatial distribution pattern of active plover colonies (see Chapter 5). The first set of 75 ANS consisted of multicolored, medium- to large-grained (3-10 cm diameter) gravel, with 20% of the material composed of light brown-colored soil. These were established on 13 and 14 May. A second set of 32 ANS used tan-colored, uniformly small-grained gravel (2-3 cm diameter), which contained no soil. The second set was established on 22 June, also on a 3 ha salt flat at Howard Slough.

RESULTS

Snowy plover annual nest success ranged from 5-49% (Mayfield method estimates), with dramatic fluctuations between years (Table 4.1). Predation was the primary cause of nest failures, accounting for 87.9% of all nest losses. A small percentage of nests was lost to stochastic events, such as inclement weather (12.1%). Nests failing due to inclement weather were all destroyed by flooding after rain storms. Of the nests lost to predators, 91% were depredated by mammals, 7% were taken by avian predators, and 2% were taken by unknown predators. Red foxes were responsible for most mammalian nest losses (85%), based on observations of tracks and scat at depredated nests. Avian predators (gulls and ravens) were rarely observed near habitat patches where plovers nested.

TABLE 4.1. Annual variation in snowy plover nest success at two focal study sites.

Year	Howard Slough			Layton Marsh		
	Mean ¹	95% CI	n	Mean	95% CI	n
1990	.492	.286-.837	18	.381	.247-.585	53
1991	.197	.101-.379	35	.113	.063-.203	73
1992	.445	.334-.592	79	.129	.068-.240	55
1993	.054	.017-.165	30	.345	.168-.695	71

¹Mayfield Method estimate (Mayfield 1961, Johnson 1979).

Nest site habitat characteristics

Snowy plovers breeding at Great Salt Lake selected barren, salt flats for nest-sites, with an average of 73-78% of the ground \leq 15 m from nests devoid of vegetation (Table 4.2). Vegetative cover near nests consisted equally of live and dead plants. There were no significant differences between nests and paired-random plots in the relative amounts of dead vegetation, live vegetation, and barren ground at the two largest mesohabitat scales (i.e., 10- and 15-m radii) (Table 4.3). Nests and random plots differed to some degree at the smallest mesohabitat scale (i.e., 5-m radius) ($T^2 = 8.4$, $P = .041$), although no individual habitat type was significantly different between nests and random points at this scale.

Only at the microhabitat scale (i.e., \leq 1-m radius from the nest) were vegetative differences readily apparent between nests and random points ($T^2 = 31.2$, $P < .001$; Table 4.3). Nest microhabitats had significantly more dead vegetation than random points, while random points had more barren ground. Differences in

microhabitat vegetation between nests and random plots were due to the majority of nests (67.6%) being beside or under an object. In 3 of 4 years (i.e., 1991 to 1993), there was no significant relationship between nest fate and proximity to an object (Table 4.4). However, in 1990 when nest success was relatively high, nests under objects were 4.3 times more likely to be successful (95% CI = 1.5-12.7) than nests beside or away from objects.

TABLE 4.2. Ground cover at 355 snowy plover nests and paired-random points at four radii from plot center.

Radii (m)	Type ¹	% cover ($\bar{x} \pm SE$)		
		Barren ground	Dead vegetation	Live vegetation
1	N	73.5 \pm 1.6	16.8 \pm 1.3	9.4 \pm 1.2
	R	80.0 \pm 1.7	9.1 \pm 1.3	12.8 \pm 1.2
5	N	78.2 \pm 1.5	11.5 \pm 1.2	10.0 \pm 1.1
	R	78.8 \pm 1.7	9.0 \pm 1.2	11.7 \pm 1.2
10	N	77.8 \pm 1.5	11.0 \pm 1.2	10.8 \pm 1.1
	R	77.9 \pm 1.6	9.0 \pm 1.1	12.4 \pm 1.3
15	N	77.4 \pm 1.5	11.0 \pm 1.2	11.3 \pm 1.1
	R	77.3 \pm 1.6	9.2 \pm 1.1	12.8 \pm 1.2

¹N=nest plots, R = random plots.

TABLE 4.3. Mean differences between nests and random points ($\bar{x} \pm SE$) in the percentage of 3 habitat types found at 4 radii from plot center.

Plot radius (m)	Dead vegetation*	Live vegetation	Barren ground	T^2	P
1	7.7 \pm 1.4	-0.9 \pm 1.5	-6.4 \pm 1.9	31.2	< 0.001
5	2.6 \pm 1.2	-1.7 \pm 1.3	-0.4 \pm 1.5	8.4	0.041
10	2.0 \pm 1.1	-1.6 \pm 1.2	0.1 \pm 1.5	6.5	0.092
15	1.7 \pm 1.0	-1.6 \pm 1.2	-0.1 \pm 1.4	4.9	0.183

*Positive values signify the habitat is more common at nests than random plots, whereas negative values signify the habitat is more common at random plots.

TABLE 4.4. Snowy plover nest fate as a function of proximity to an object.

Year	Number of nests						G^2	P*		
	Beside object		No object		Under object					
	Fail	Hatch	Fail	Hatch	Fail	Hatch				
1990	28	31	4	5	5	21	6.1	0.038		
1991	61	31	14	11	14	8	0.9	0.640		
1992	30	28	44	46	7	8	0.2	0.917		
1993	52	18	32	7	9	3	0.9	0.636		

*There was not a significant 3-way interaction term between nest fate, year, and proximity to an object ($G^2 = 5.78$, 6 df, $P = .45$). However, there were significant 2-way interactions terms between year and nest fate ($G^2 = 35.5$, 3 df, $P < .001$) and between year and proximity to an object ($G^2 = 79.7$, 6 df, $P < .001$).

TABLE 4.5. Temporal variation in nest fate, based on yearly variation in microhabitat selection.

Habitat type	Number of nests								G^2	P	
	1990		1991		1992		1993				
	Fail	Hatch	Fail	Hatch	Fail	Hatch	Fail	Hatch			
<i>No object</i>											
Barren, salt flat	1	2	3	3	10	6	1	1	1.0	.800	
Rough terrain	3	1	5	4	10	17	20	1	20.0	.001*	
Vegetation	2	2	8	6	29	28	13	5	2.7	.440	
Gravel	1	0	16	13	9	9	30	11	4.8	.180	
<i>Object</i>											
Exuviae	17	22	20	5	3	6	1	0	11.8	.008*	
Plants ¹	1	5	1	3	2	1	1	1	---		
Dead shrub	10	25	32	15	18	14	23	8	17.9	.001*	
Other ¹	0	0	4	1	0	1	4	1	---		
Total	42	55	101	50	99	82	102	28	35.6	.001*	

¹Insufficient data for analysis.

* $P < 0.01$

There was a significant 2-way interaction term between year and nest fate in the overall model investigating microhabitat attributes ($G^2 = 35.6$, $P < .001$; Table 4.5). Of six microhabitats with adequate data, nest success rates in three varied significantly over time. The microhabitat plovers used most consistently each year was dead shrubs (Table 4.5), where most nests under objects were found (83.8%, $n = 99$) .

One possible reason for the relatively high success of nests underneath woody shrubs was because they were located in patches with a high density of potential nest sites. Most shrubs occurred in patches that were killed during the 1983-1987 floods.

At Howard Slough, there was one 6-ha patch of dead iodine bushes (approximately 4.9% of the total available potential habitat). Nest success rates in this area tended to be higher than other habitat patches at Howard Slough from 1990-1992, although the differences were not statistically significant due to large confidence intervals around nest success estimates (Table 4.6). At Layton marsh, there was also one 4.2-ha patch of dead iodine bushes (2.6% of the total available potential habitat). Nest success rates were greater in patches with high densities of potential nests sites in only 2 of 4 years at Layton marsh (Table 4.6).

TABLE 4.6. Comparison of nest success between habitat patches with high and low densities of potential nest sites underneath dead shrubs.

Year	Site ¹	High density			Low density			<i>n</i>
		Mean ²	95% CI	<i>n</i> ³	Mean	95% CI		
1990	HS	.935	.85-1.0	7	.856	.75-.97	12	
1991		.401	.23-.69	15	.274	.13-.56	21	
1992		.600	.40-.91	15	.497	.38-.65	67	
1993		.036	.01-.60	5	.150	.06-.34	25	
1990	LM	.630	.37-1.0	8	.541	.41-.71	48	
1991		.488	.27-.87	11	.440	.35-.55	69	
1992		.183	.04-.80	7	.314	.22-.46	57	
1993		.001	ND ⁴	1	.606	.44-.83	19	

¹Howard Slough and Layton Marsh.

²Nest success was based on Mayfield method estimates (Mayfield 1961, Johnson 1979).

³Sample sizes refer to the total number of nests in each patch type.

⁴Insufficient data to calculate a confidence interval.

Artificial nest substrates

Plovers built scrapes and nests on small-grained (2-3 cm) gravel structures more than large-grained structures (i.e., use of scrapes [$G^2 = 34.1, P < .001$] and nests [$G^2 = 2.0, P = .15$]; Table 4.7). However, due to my study design, I could not statistically separate the effects of timing of nest structure placement from structure type. The large-grained structures were established during the peak egg-laying period, whereas the small-grained structures were established at the end of the egg-laying period. This implies large-grained structures should have been used more often if they were a desirable substrate, but they were not. In contrast, after 20 d, 50% of the small-grained nest structures had plover scrapes and three nests. One clutch was started 5 d after the gravel was in place, the second nest started after 15 d and the third nest after 17 d. One of three nests on small-grained structures successfully hatched, while the other two were depredated.

TABLE 4.7. Total number of artificial nest substrates used by snowy plovers to build nest scrapes or initiate nests.

Pebble size ¹	Scrapes	Nests	<i>n</i> ²
Large	2	2	75
Small	16	3	32

¹Large=3- to 6-cm diameter gravel; small=2- to 3-cm diameter gravel.

²Total number of artificial nest substrates established.

DISCUSSION

All snowy plover habitat selection studies have found relatively similar habitat attributes near nest sites throughout their range (Wilson-Jacobs and Meslow 1984; Grover and Knopf 1982; Page et al. 1985, 1991; this study). Plovers select mesohabitat devoid of vegetation near saline bodies of water; nest-sites in northern Utah had <25% vegetative coverage within 15 m of nests (Table 4.2). Nests in coastal Oregon were described as flat, sandy beaches with an average of 26% driftwood cover and <1% live vegetation within 20 m of the nests (Wilson-Jacobs and Meslow 1984). At Mono Lake, California, nests were located on barren, sand-gravel or alkali substrates (Page et al. 1985), while breeding birds at Salt Plains National Wildlife Refuge nested on barren salt flats (Purdue 1976, Grover and Knopf 1982). Microhabitat characteristics were also remarkably similar among the three studies that quantified the percentage of nests associated with objects (68% in Grover and Knopf 1982; 58% in Page et al. 1985, and 68% in this study).

My results from Great Salt Lake do not concur with Page et al. (1985), who found that snowy plover nests beside objects had lower hatching rates than nests under objects. In only 1 of 4 years did microhabitat characteristics affect nest success at Great Salt Lake, when nests under objects had higher hatching rates than nests in the open or beside objects (Table 4.4). In this study, mammals accounted for most nest failures, while Page et al. (1983, 1985) studied plovers at Mono Lake, California, where birds were the primary predators (i.e., California gulls and ravens). Apparent nest success rates were greater in California than at Great Salt Lake (51-67% versus

21-58%, respectively; Table 4.1). Page et al. (1985) reasonably hypothesized that hatching success decreased for nests beside objects because objects provided a visual-cue for avian predators.

There are a number of possible explanations for plovers' selection of specific microhabitats at Great Salt Lake. First, plovers might have selected microhabitats to minimize depredation rates. During this study, nest depredation rates were decreased when plovers nested under an object, but only in one year when nest success rates were relatively high. However, it is unclear what mechanism shrubs provide to prevent predators from finding nests, especially nocturnal mammalian predators such as red foxes using olfactory cues. Nesting under or beside an object in northern Utah never resulted in higher depredation rates, as predators never appeared to be selecting objects to find nests. It is therefore unclear why the use of objects was not more frequent than I observed.

Second, another potential reason plovers selected certain microhabitats was to minimize the heat stress associated with incubating on barren salt flats during the mid-summer months (Grant 1982). Work by Purdue and Haines (1977) found little evidence to support this hypothesis. However, I did not explicitly test the thermal environment of nest sites compared to random points. The microhabitats at Great Salt Lake could have provided physiological benefits to incubating adults that I did not quantify. In addition, there could have been some interaction between thermal benefits and predation benefits that would help to explain plovers' association with objects.

Up until this point, my discussion has assumed that there are adaptive explanations for plovers' use of specific microhabitats at Great Salt Lake. However, problems do exist with these arguments. First, I studied nest site characteristics just after the lake started to recede following 6 years of flooding. Many of the habitat patches where plovers nested during this study had just been reexposed. Given the typical fluctuations in Great Salt Lake water levels (see Chapter 1), large patches of dead shrubs near the lake's shoreline probably only occur once every 50 years. Therefore, if one were to study nest-site characteristics over a 100-year time span at Great Salt Lake, the probability of finding plovers nesting under dead shrubs would be a rare event.

A second explanation for microhabitat selection is that nest-sites may be adaptive only under certain environmental conditions or in specific habitat types. Snowy plovers are double-brooded and extremely mobile, moving up to 660 km within a year between clutches and over 1000 km between years (Warriner et al. 1986, Stenzel et al. *in press*). Plovers may only select specific microhabitat attributes that minimize depredation rates or thermal stress in one area (e.g., coastal California where birds are the key predator). When plovers move within or between years to a new nesting area to initiate a second clutch, they may select a microhabitat similar to their original nesting area, even though the microhabitat in the new area might not have a selective advantage. Therefore, microhabitat attributes I quantified may have been an artifact of plovers' past selection pressure or predation pressure at other locations.

Evidence gathered during this study tends to support Martin's (1988c) hypothesis

that mesohabitats with high densities of potential nest sites may have higher nest success than patches with relatively few potential nest sites. In the case of snowy plovers, nests under objects were located in dense patches of dead shrubs, making it difficult to separate the effects of microhabitat and mesohabitat on depredation rates. This point deserves further research.

Empirical and experimental information from Great Salt Lake suggests that plovers were selecting specific microhabitats for nest sites, but only when the microhabitat occurred within suitable mesohabitat. For example, plovers only would nest under a dead shrub if the surrounding habitat was generally devoid of vegetation, while a dead shrub in tall, live vegetation would not provide the suitable mesohabitat characteristics. In addition, experimental evidence gathered during this study suggests that suitable microhabitats were sometimes lacking for plovers at Great Salt Lake. At Howard Slough, establishing artificial nest structures in an area with suitable mesohabitat resulted in plovers immediately using the patch. However, birds apparently used the artificial microhabitats only when the gravel was similar in color and size to plover eggs (see Burger 1987, Prindiville Gaines and Ryan 1988, Flemming et al. 1992). Therefore, one potential management strategy for this species might be to spread small-grained gravel over large expanses of barren salt flats to get plovers to nest in specific areas.

The importance of microhabitat as a means of reducing predation rates is not confined to plovers. Cavity-nesting species generally have lower nest predation rates than open-nesting species (Ricklefs 1969). Martin (1992a) reviewed factors affecting

nest success in neotropical migrants, and found that concealment of the nest-site appears to improve nest success rates. Among waterfowl, dense, tall nesting cover immediately near the nest can improve hatching rates (e.g., Dwernychuk and Boag 1972, Duebbert and Kantrud 1974). Thus, microhabitats can be critical to species because they help reduce predation pressure and are often limited (e.g., the number of cavities; Mannan et al. 1980, Raphael and White 1984). However, although nest-site microhabitats appear to be important, unless the microhabitat is located in the appropriate mesohabitat, the microhabitat may not be used by a breeding birds or affect nest success rates (Martin 1992a).

Finally, this paper points out the importance of taking a hierarchical approach to scale-dependent factors affecting nest-site selection. At broader spatial scales, such as a biogeographic scale, factors such as the distribution of prey and resources (e.g., fresh water for juveniles) may be of primary importance in determining potential nesting locations. In the case of the snowy plover in western North America, birds are found almost exclusively at saline water bodies. Once birds select a particular lake to utilize, they then have to decide exactly in which potential habitat patch to locate their nest (e.g., a barren mesohabitat). The final decision is exactly where to locate the nest in the mesohabitat, and only then does microhabitat probably play an important role in a bird's nest placement decision.

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CHAPTER 5

EFFECTS OF SITE QUALITY AND PRIOR NEST SUCCESS ON INTERYEAR MOVEMENT PATTERNS OF SNOWY PLOVERS

Abstract. I studied the interyear movement patterns of 532 uniquely banded snowy plovers (*Charadrius alexandrinus*) at Great Salt Lake, Utah, from 1990 to 1993. Plovers breeding at Great Salt Lake nested in a dynamic environment; suitable nesting habitat declined by \approx 50% at two focal study sites in 4 years. There was no gender bias in the return rates of adult plovers to northern Utah; 53% of females and 60% of males were resighted. I found no significant relationship between site quality the previous year and subsequent site fidelity (i.e., where site quality was measured as either the overall nest success or nest density for an entire study site), with the exception that unsuccessful nesting females breeding at high-density sites dispersed ($P = .003$). Although site quality for the most part did not appear to influence site fidelity, an individual's prior nest success did affect return rates. Females that nested unsuccessfully were 12 times less likely than successful females to return to the same site the following year ($P < .001$), while males did not exhibit this nest-success bias ($P = .75$). Both sexes shared incubation duties, but only males cared for broods. Familiarity with the brood-rearing area was one potential explanation for the male-biased fidelity. However, I could not eliminate an alternative explanation that both focal study sites represented high-quality breeding sites, and male plovers preferred to use the same area rather than disperse.

INTRODUCTION

Migratory birds face a dilemma when returning to their breeding grounds: Should an individual breed at the same site as the previous year or disperse to a new area? Individuals faithful to their preceding breeding grounds presumably have some knowledge concerning the distribution of essential resources, predation risks, and potential mates (Shields 1982, Oring and Lank 1984, Gratto et al. 1985, Wiens and Cuthbert 1988). On the other hand, dispersing individuals have the opportunity to find a new territory or new mate, either of which could increase or lower reproductive output (Ollason and Dunnet 1978, Cuthbert 1988), but they also face considerable new risks. Birds typically exhibit female-biased natal and breeding dispersal (i.e., females disperse farther and more often; Greenwood 1980, Greenwood and Harvey 1982, but see Oring and Lank 1984). The proximate and ultimate causes for this sex-biased dispersal are still under debate (e.g., Lessells 1985, Bollinger and Gavin 1989).

Greenwood (1980) hypothesized that the type of mating system determines gender biases in dispersal. In resource-defense mating systems (i.e., territorial species), the sex defending the resource is less prone to disperse, whereas in mate-defense systems, the sex competing for a mate is more apt to disperse. For many avian species, males compete for females via intrasexual competition for vital resources, and females select mates based on the quality of the territory each male controls. Resource defense mating systems often occur in monogamous species (i.e., 90% of avian species [Oring 1982]), with both parents helping to raise

offspring (Greenwood 1980, Greenwood and Harvey 1982). This hypothesis assumes that site-faithful males have a competitive advantage over dispersing males (Hinde 1956). Females tend to be the more mobile sex in birds because females in most species do not have the responsibility for establishing the territory, thus allowing females to obtain the highest quality territory or mate.

Previous studies of avian populations have found a strong tendency for individuals whose nest was successful the preceding year to exhibit a higher degree of site fidelity the subsequent year than individuals whose nest was unsuccessful (e.g., Greig-Smith 1982, Oring and Lank 1982, Gratto et al. 1985, Cuthbert 1988, Pärt and Gastafasson 1989, Hepp and Kennamer 1993; but see Haig and Oring 1988a, Schamel and Tracy 1991). In addition, experienced birds are more likely to return than younger birds (e.g., Oring et al. 1983, Oring and Lank 1984, Thompson and Hale 1989, Montalvo and Potti 1992). Site quality can also affect return rates, with higher return rates to better quality sites regardless of prior nest success (e.g., Bollinger and Gavin 1989, Montalvo and Potti 1992).

Plovers of the genus *Charadrius* provide a unique opportunity to investigate the proximate causes for dispersal, due to the large interyear dispersal distances and variety of mating systems documented within this genus (e.g., Haig and Oring 1988b, Stenzel et al. *in press*). Adult piping plovers (*C. melanotos*) exhibit varying degrees of site fidelity (25-69% of birds returned to same area), are almost exclusively monogamous, and have biparental care of young (Haig and Oring 1988a, 1988b). Haig and Oring (1988b) postulated that in areas with limited suitable

nesting habitat, piping plovers should show a high degree of site fidelity, whereas in areas with many potential breeding sites, birds should show less site fidelity. Little has been published on site fidelity patterns for snowy plovers (*C. alexandrinus*) in North America or the European Kentish plover (*C. a. alexandrinus*). Both subspecies exhibit monogamy and sequential polyandry within the same population (Ritterhaus 1956, Boyd 1972, Lessells 1984, Warriner et al. 1986, Székely and Lessells 1993, Stenzel et al. *in press*). Dispersal distances are extreme in these two subspecies, with individuals moving as far as 1,140 km between breeding seasons (Stenzel et al. *in press*). No study of the *Charadrius* specifically investigated the influence of changes on the amount of suitable nesting habitat on site fidelity. Therefore, the reasons for the relatively large dispersal distances found within this genus remain unresolved.

Snowy plovers nesting in northern Utah are all migratory and apparently winter along the coasts of the Gulf of California and the Pacific side of Baja California (G. Page, M. Stern, and P. Paton, *unpublished data*). Snowy plovers exhibit little resource defense, either at foraging sites or near their nest, although males will defend females from other males near the nest (Ritterhaus 1956, Boyd 1972, Warriner et al. 1986, *personal observation*). Great Salt Lake has the largest concentration of snowy plovers in North America (Paton and Edwards 1990, P. Paton, *unpublished data*).

For this study, I investigated the effects of three factors on adult snowy plover site fidelity patterns at Great Salt Lake, Utah: (1) the overall nest density of a study

site; (2) the overall hatching success of a study site; and (3) an individual's prior nest success. The first two factors relate to site quality. Research with Bobolinks (*Dolichonyx oryzivorus*) found that adults were more prone to return to high-quality breeding sites, where quality was measured in terms of production of fledglings (Bollinger and Gavin 1989). I was unable to quantify fledging rates for the most part during this study, but I was able to determine the annual density of nests at each of my study sites, as well as nest hatching rates. Stenzel et al. (*in press*) investigated the third factor with snowy plovers breeding in coastal California, and did not find a significant relationship between prior nest success and site fidelity for either sex. I first examine the general interyear movement patterns of snowy plovers at Great Salt Lake, Utah. I then describe changes in the abundance of potential nesting habitat at two focal study sites. Finally, I investigate the relationship between site quality and prior nest success on adult site fidelity.

STUDY AREA AND METHODS

Great Salt Lake has a mean depth of 4.3 m at typical lake levels and is terminal (i.e., it has no outlet; Arnow and Stephens 1990). Lake levels therefore oscillate dramatically with precipitation levels (Murchison 1989, Arnow and Stephens 1990, see Chapter 1). From 1983 to 1987, the lake rose 3.7 m, inundating approximately 2,100 km² of marsh and upland habitat (see Chapter 1). Thousands of hectares were left denuded as the lake receded starting in 1988, which created potential nesting habitat for snowy plovers. These barren areas were eventually revegetated by salt-

tolerant species within the Chenopodiaceae, including greasewood (*Sarcobatus vermiculatus*), iodine bush (*Allenrolfea occidentalis*), seepweed (*Sueda spp.*), summer cypress (*Kochia scoparia*), bassia (*Bassia hyssopifolia*), and pickleweed (*Salicornia europaea*). In addition, marsh vegetation increased dramatically over the course of the study, and consisted primarily of alkali bulrush (*Scirpus maritimus*), cattail (*Typha spp.*), and phragmites (*Phragmites australis*) (see also Foote 1991).

Plovers were banded and monitored at eight study sites at Great Salt Lake, Utah, from 1990 to 1993: Locomotive Springs Waterfowl Management Area (WMA; $41^{\circ} 41'N$, $112^{\circ}55'W$ [21 birds banded at this site]); Harold Crane WMA ($41^{\circ} 20'N$, $112^{\circ}08'W$ [86 banded]); the West Warren area of Harold Crane WMA ($41^{\circ} 18'N$, $112^{\circ}08'W$ [16 banded]); the northwest corner of Ogden Bay WMA ($41^{\circ}14'N$, $112^{\circ}14'W$ [21 banded]); Howard Slough WMA ($41^{\circ}09'N$, $112^{\circ}09'W$ [211 banded]); West Layton marsh ($41^{\circ}02'N$, $112^{\circ}05'W$ [151 banded]); Farmington Bay WMA ($40^{\circ}55'N$, $111^{\circ}55'W$ [8 banded]); and 2 km northeast of Saltair Beach ($40^{\circ}46'N$, $112^{\circ}08'W$ [18 banded]; Fig. 5.1). Fieldwork focused on two focal sites that were 10 km apart; Howard Slough (a diked, managed marsh) and Layton marsh (an undiked, unregulated marsh). Focal sites were surveyed two to three times per week by one observer in 1990 and two observers from 1991-1993. The other six sites were visited less frequently, approximately one to four surveys per month. The study took place from 1 April to 31 August, with the exception of 1990, when Howard Slough was not visited until 19 May and Layton marsh was not surveyed until 13 June.

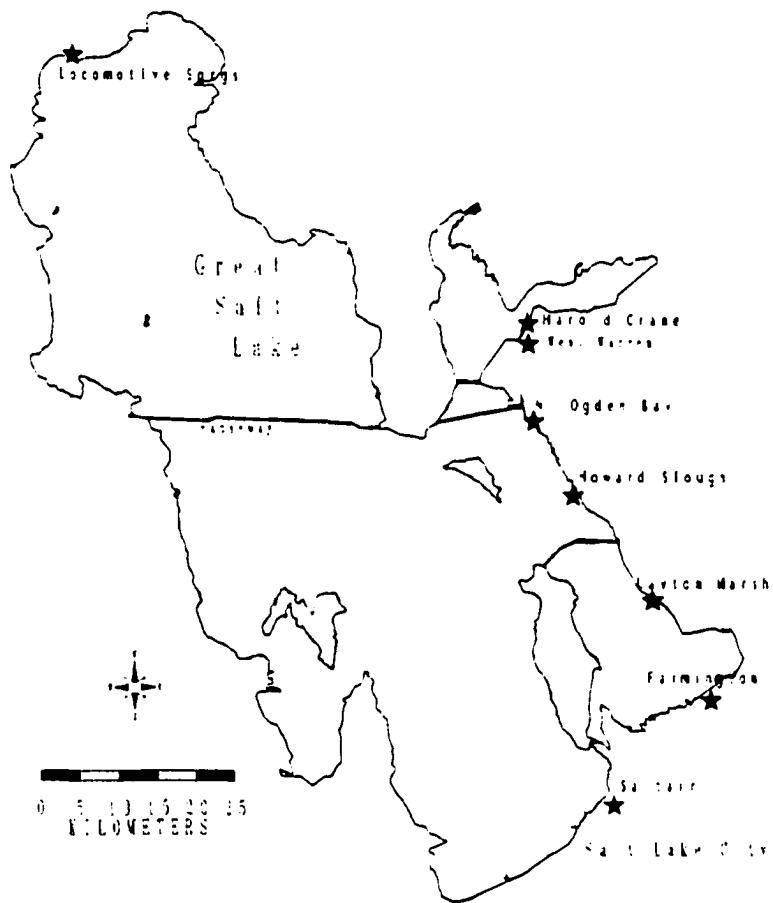


FIG. 5.1. Distribution of study sites (stars) at Great Salt Lake.

Yearly changes in the distribution of plover nesting habitat at the focal sites were quantified by taking black and white aerial photographs (photo scale: 1 cm = 100 m) in mid-June from 1990 to 1993. Potential nesting habitat patches were delineated based on two criteria: (1) a width of >33 m (i.e., 0.1 ha in size), and (2) live or dead vegetation accounted for <25% of the ground cover in a habitat patch (Wilson-Jacobs and Meslow 1984, Page et al. 1985, Paton and Edwards 1990).

(Wilson-Jacobs and Meslow 1984, Page et al. 1985, Paton and Edwards 1990). Barren areas that consisted of soft mud (e.g., adjacent to the lake shoreline, or deltas formed where ditches met the lake) were not classified as potential nesting habitat because plovers only nest on hard, dry substrates (*personal observation*). Potential nesting habitat was then digitized from the aerial photographs and analyzed using ARC/INFO software (Environmental Systems Research Institute, Redlands, California). Nest density estimators for each focal study site included crude density (i.e., total number of nests found within one breeding season/total area surveyed), ecological density (i.e., total number of nests found within one breeding season/amount of potential nesting habitat available), and maximum ecological density (i.e., maximum number of nests active on one day/amount of potential habitat available).

Eggs were floated to determine expected hatching dates using methods described in Westerkov (1950). I assumed a 4-d egg laying period and a 27-d incubation period (Warriner et al. 1986, Page et al. 1985). I classified successful clutches as having ≥ 1 chick hatch, and failed nests were empty prior to expected hatching dates (Page et al. 1983, 1985, see Chapter 2). Nest predators were primarily red fox (*Vulpes vulpes*) (see Chapter 2).

Incubating adults were captured with a chicken-wire drop trap in 1990 (Paton and Edwards 1990) and a circular funnel trap from 1991 to 1993 (Lessells 1984). In addition, breeding and nonbreeding plovers were trapped .1-1 km from nesting areas by herding birds into two mist nets, which were staked together to form a 'V'.

Adults were sexed based on plumage characteristics (Page et al. 1983, Warriner et al. 1986). Capture technique did not significantly affect resighting probabilities for females (i.e., 61/112 caught on nests versus 12/25 in mist nets were subsequently resighted; $G^2 = .34$, $P = .56$). However, there was a marginally significant trend for males captured while incubating, 42/60, to be resighted at a higher rate than ones captured in nets, 29/57 ($G^2 = 3.52$, 1 df, $P = .061$).

Plovers were uniquely marked with three uncolored plastic-bands (A. C. Hughes Ltd., Middlesex, England; band size = XCL) and a U.S. Fish and Wildlife Service (USFWS) metal band (special size = 1AA). Two bands were placed on each tarsometatarsus. Colored automobile pin-striping tape was then soldered over all four bands.

Movements of color-banded plovers were determined to the nearest 30 m by plotting daily observations onto field maps of each study site (1 cm = 100 m). Universal Transverse Mercator (UTM) coordinates were then determined for each observation and used for further distance calculations. Nest locations at the focal study sites were accurate to ± 10 m using a satellite-based Global Position System (Magellan Systems Corporation, Monrovia, California), and reverified by manually plotting nests onto high-resolution orthophotoquads of the focal study sites (1 cm = 25 m). Nearest-neighbor distances between synchronous nests were measured to the nearest 0.5 m for nests < 100 m from each other.

Interyear movement patterns for individual plovers were based on the arithmetic mean for all UTM coordinates within a year, and compared to the arithmetic mean

for the UTM coordinates for previous year. Intersexual variation in interyear movement patterns (both between annual home ranges and nest sites) was compared with a Mann-Whitney *U*-test. I compared the relationship between an individual's site fidelity and study site nest density, study site nest success, and the nest success for a specific individual using a log-linear model with a backward selection approach (Agresti 1990). Because some cell counts were equal to zero, I added 0.5 to each cell before calculating likelihood-ratio chi-square statistics (Agresti 1990). Alpha levels < .05 were considered significant.

RESULTS

Interyear movement patterns

Adult males and females from the focal study sites did not differ in their return rates to Great Salt Lake; 59.7% of the males ($n = 119$) and 53.3% of the females ($n = 137$) were subsequently resighted ($G^2 = 1.06$, $df = 1$, $P = .304$). Males tended to be resighted more than females, although this difference was statistically significant only in 1 of 3 years (Table 5.1). Males tended to become less site faithful over the course of the study, whereas females returned at a relatively constant rate (Table 5.1). In addition, adult males were generally resighted annually, only 11.3% of 71 adult males were missing for 1 year and then subsequently resighted. In contrast, 24.7% of 73 females were missing for at least 1 year. This difference between the sexes in resighting consistency was significant ($G^2 = 3.7$, 1 df, $P = .054$; see also Chapter 2).

TABLE 5.1. Annual variation in adult snowy plover site fidelity patterns. Data are for birds banded at focal study sites.

Resighting year	% resighted							G^2*	P		
	Males			Females							
	Same site	Different site	Number banded ¹	Same site	Different site	Number banded					
1991	60.0	12.0	25	37.2	7.0	43	.01	.94			
1992	50.0	0.0	44	29.5	6.8	44	3.90	.05			
1993	44.0	8.0	50	32.0	14.0	50	1.50	.22			

¹Number banded previous year.

*Likelihood ratio statistic, comparing gender differences in annual site fidelity.

The interyear movement of color-banded plovers around Great Salt Lake was considerable (Table 5.2). Birds moved readily between study sites, which was especially evident between Howard Slough and Layton marsh. The geographic center of the home ranges of adult females moved about 1.5 km between years (median = 1.64 km, 25-75% quantiles = .59-11.99 km, range = .05 - 101.4 km, n = 95) while males moved about 1 km (median = 1.11 km, 25-75% quantiles = .54-7.21 km, range = .1 - 69.7 km, n = 94). However, the sexes did not differ in interyear movement patterns (Mann-Whitney U -test, P = .21). Females moved ≈ 1 km between yearly nesting attempts (median = .90 km, range = .06 - 23.7 km, n = 12), whereas males did not move as far (median = .58 km, range = .06 - 12.7 km, n = 10). Again, this intersexual variation was not significant (P = .97).

TABLE 5.2. Documented movements of banded snowy plovers around Great Salt Lake. See Fig. 5.1 for locations of study sites.

Banding location ¹	Bird years ²	Resighting location ³								
		FB	HC	HS	SB	LM	LS	NO	WW	Misc
FB	8	1				2				
HC	209			3	1	2	1		2	1
HS	307			61	7	21		1		
SB	31				7	1				
LM	304	1	1	21	3	91		2		1
LS	28					2	1			
NO	26					2		1		1
WW	14				1				7	
Misc	38					2				

¹FB = Farmington Bay WMA; HC = Harold Crane WMA; HS = Howard Slough WMA; SB = NE of Saltair Beach; LM = Layton Marsh; LS = Locomotive Springs WMA; NO = North end of Ogden Bay WMA; WW = West Warren access to Harold Crane; Misc. = Miscellaneous sites around Great Salt Lake.

²cumulative number of years banded birds could have been subsequently resighted from 1991-1993.

³Each datum represents one bird year at the resighting location.

Habitat changes

Snowy plovers breeding at Howard Slough and Layton marsh typically nested in only certain habitat patches, and the specific habitat patches with nests varied annually (Fig. 5.2). The number of synchronous nests in close proximity to each other (i.e., < 100 m apart) ranged in size from three to nine nests, with nearest-neighbor distances averaging 36.2 m (SD = 20.0, range = 7.5 - 90 m, n = 79 nests).

The distribution and availability of potential nesting habitat at the focal study

sites changed substantially during the 4 year study period, primarily due to the reestablishment of vegetation. At Howard Slough, 349 ha were surveyed annually. The amount of potential nesting habitat at Howard Slough declined 56% over 4 years (Table 5.3, Fig. 5.2), with the exception of 1992 when potential nesting habitat increased due to a series of experimental drawdowns designed to augment existing shorebird nesting habitat (P. Paton, *unpublished data*). At Layton Marsh, I increased the study area boundaries from 171 ha in 1990 to 400 ha in 1991 to incorporate more potential nesting habitat (Fig. 5.2). In 1990, 75 ha (i.e., 43.9% of the entire Layton study area) were classified as potential nesting habitat, which by 1993 had declined to only 19 ha (a 74.7% reduction) of potential nesting habitat. The 1991 expanded study area at Layton marsh encompassed 188 ha of potential habitat (i.e., 47% of the entire study site), which declined by 52.1% from 1991-1993 (i.e., 188 to 90 ha; Table 5.3, Fig. 5.2).

TABLE 5.3. Annual variation in the total amount and individual patch size of potential plover nesting habitat at two focal study sites at Great Salt Lake.

Howard Slough					Layton Marsh				
Year	Total		Patch size (ha)			Total	Patch size (ha)		n
	area	Median	Range	n			Median	Range	
1990	147	31.7	1.1-114.1	3		75	2.4	.4-21.9	10
1991	85	2.6	.9 -43.5	11		188	3.8	.1-78.2	19
1992	102	2.4	.2 -45.0	15		156	.5	.03-81.3	22
1993	64	1.5	.2 -32.2	18		90	.6	.01-46.7	22

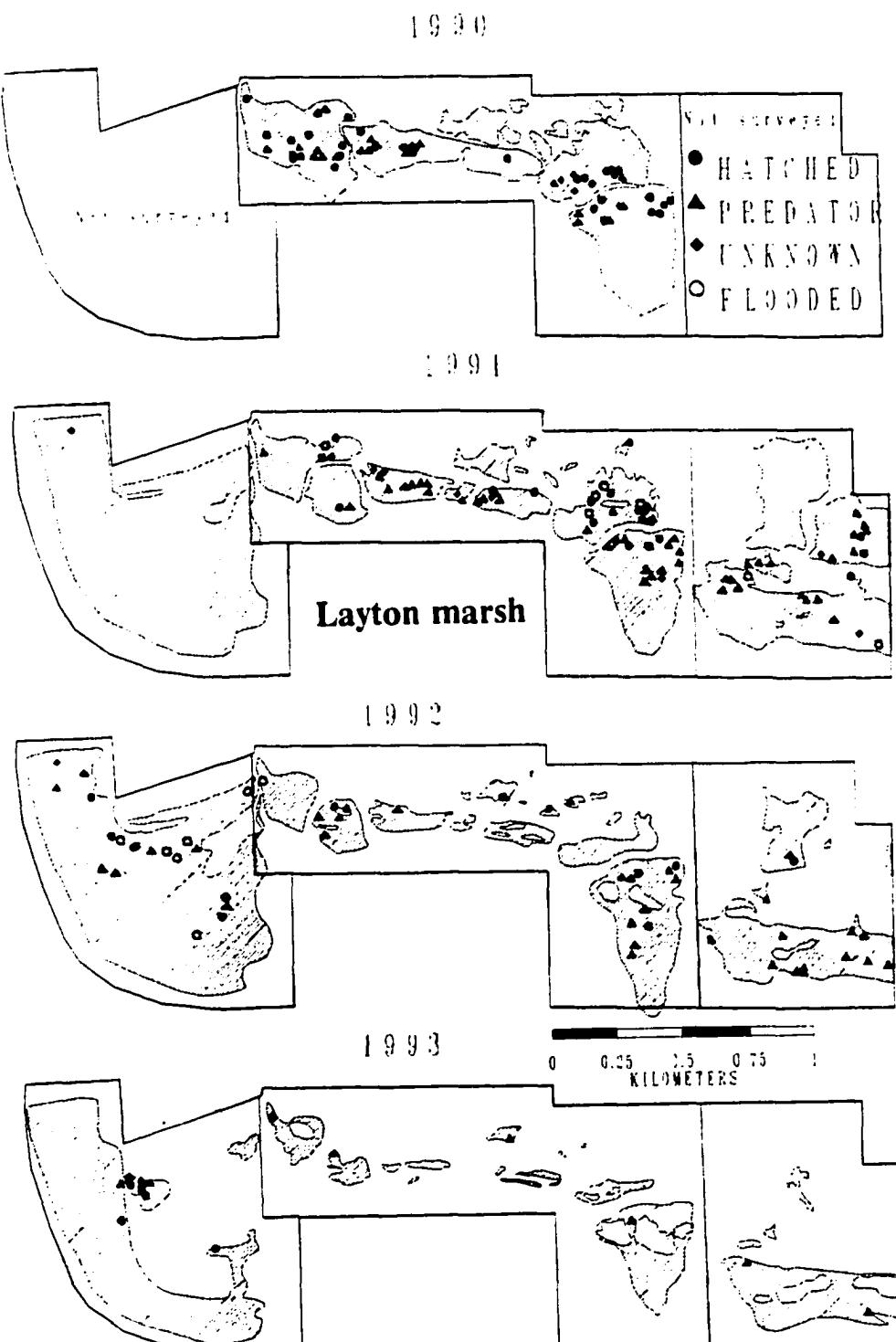


FIG. 5.2. Distribution of snowy plover nests and potential nesting habitat (striped areas) at two focal study sites at Great Salt Lake.

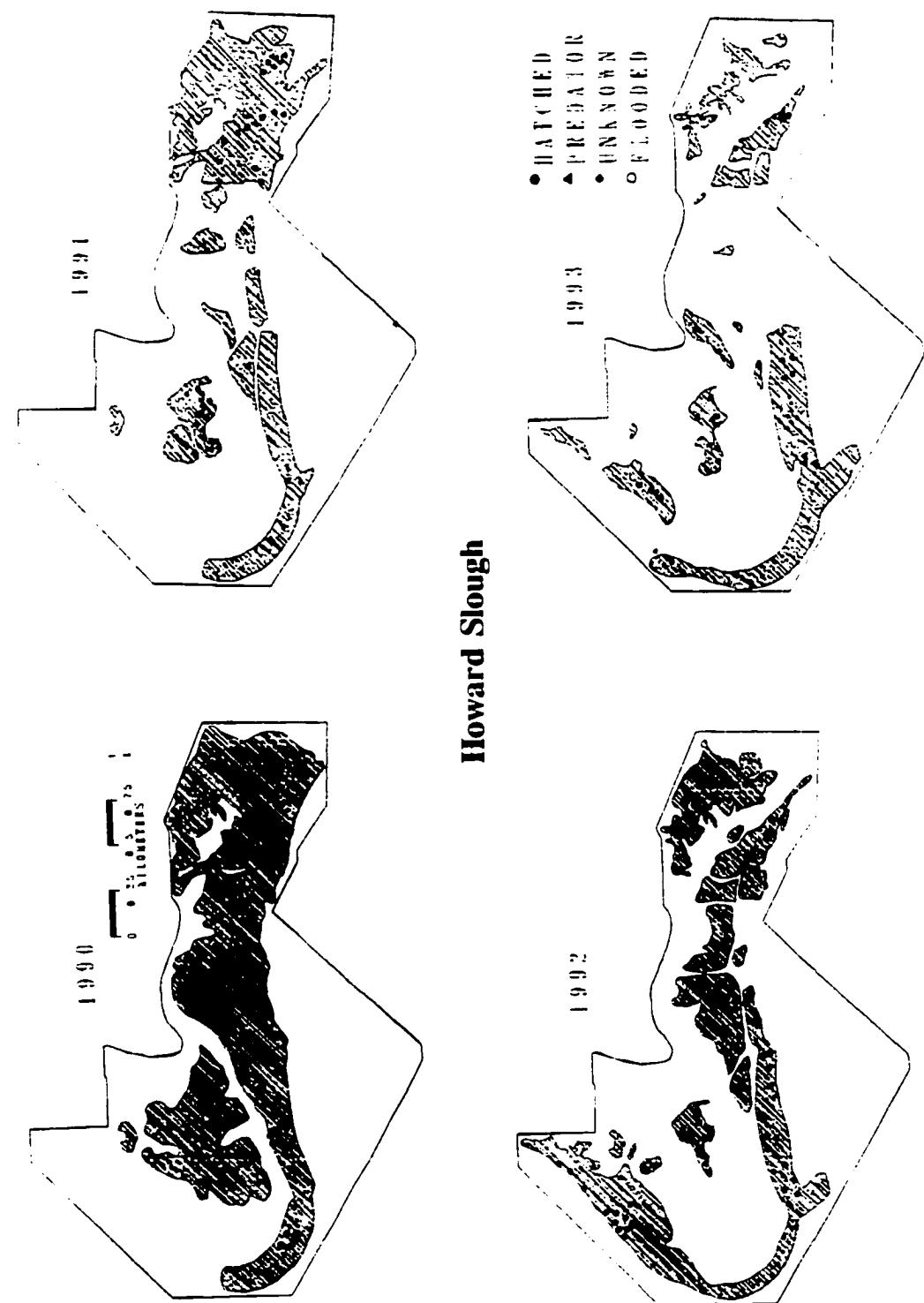


FIG. 5.2. continued

TABLE 5.4. Annual variation in snowy plover nest densities (nests per ha) at two focal study sites at Great Salt Lake.

Year	Howard Slough				Layton marsh			
	Crude ¹	Ecological ²	Max/day ³	n	Crude	Ecological	Max/day	n
1990	.097	.232	.054	34	.339	.773	.493	57
1991	.106	.435	.129	37	.208	.441	.112	83
1992	.232	.833	.275	81	.140	.359	.154	56
1993	.089	.484	.141	31	.050	.222	.078	20

¹Annual total number of nests ÷ total area surveyed regardless of habitat type.

²Annual total number of nests ÷ amount of potential habitat.

³Maximum number of nests active on 1 day ÷ amount of potential habitat.

Although both focal study sites experienced significant declines in the amount of potential nesting habitat, there was not a concomitant reduction in the number of plovers nesting at Howard Slough. In fact, nest density estimates and the total number of nests at Howard Slough increased from 1990 to 1992 and then density decreased in 1993 (Table 5.4). In contrast, both the nest density estimates and the total number of nests at Layton marsh declined over the study period (Table 5.4).

I found no significant relationship between a study site's ecological nest density and site fidelity patterns for either sex ($G^2 = .33$, 1 df, $P = .56$; Table 5.5). There was also no significant relationship between a study site's overall nest success and the number of adults that were site faithful ($G^2 = .02$, 1 df, $P = .88$).

TABLE 5.5. Site fidelity patterns of adult plovers in relationship to the overall study site nest density the preceding year. Data presented are the total number of uniquely banded birds in each category.

Density ¹ at study site the previous year	Site faithful the next year		Resighted at another study site the next year	
	Male	Female	Male	Female
Low ²	39	36	4	8
High	43	26	8	6*

¹Ecological density: total number of nests ÷ amount of potential nesting habitat.

²Low = < .5 nests per ha; High = > .5 nest per ha.

*Return rates did not differ based on density ($G^2 = .03$, 1 df, $P > .5$).

I further explored the effects of nest density on adult site fidelity patterns by simultaneously comparing return rates of adults to both their nest success the previous year and also the overall study site nest density the previous year (Table 5.6). At high nest densities, successful females were more likely to return to the same study site than unsuccessful females ($P = .003$). However, at low densities an individual's prior nest success did not appear to affect site fidelity patterns ($P = .11$). Males were not affected by site quality, as measured by overall nest densities ($P = .25$).

TABLE 5.6. Adult site fidelity patterns in relationship to prior nest success and nest density the preceding year. Data presented are the number of plovers in each category.

Sex	Preceding year study site nest density ¹	Site faithful the next year		Resighted at another site the next year		G^2*	<i>P</i>
		Nest failed	Nest hatched	Nest failed	Nest hatched		
F	High ²	3	16	5	1	8.6	.003
	Low	7	13	5	2	2.6	.11
M	High	6	22	2	4	.50	.48
	Low	7	13	0	0	.08	.78

¹Ecological density; annual total number of nests ÷ amount of potential habitat.

²High = > .5 nests per ha; Low = < .5 nests per ha.

*0.5 was added to each cell for likelihood ratio analyses.

I found a marginally significant three-way interaction between an individual's nest success the previous year, gender, and site fidelity ($G^2 = 3.55$, 1 df, $P = .059$) (Table 5.6). In other words, site fidelity patterns differed between the sexes based on the preceding year's nest success. Nest success the prior year did not affect the probability that males returned the subsequent year to the same focal study site (i.e., 89.7% of 39 successful males returned compared to 86.7% of 15 unsuccessful males; $G^2 = .101$, 1 df, $P = .75$; Table 5.4). However, nest success the previous year did affect female's site fidelity patterns ($G^2 = 13.58$, 1 df, $P < .001$). Of 32 females that had a successful nest the previous year, 90.6% return to the same focal study site. In contrast, only 45.5% of 22 unsuccessful females returned to the same

study site. Site fidelity patterns were similar between successful males and females ($G^2 = .015$, 1 df, $P = .901$), whereas unsuccessful females dispersed compared to males ($G^2 = 6.98$, 1 df, $P = .008$).

DISCUSSION

This study revealed at least four movement patterns for snowy plovers nesting at Great Salt Lake, Utah. First, males were consistently site faithful, with 44-60% of adult males returning annually to the same focal study site. Male's nest success the preceding year did not appear to affect this pattern among Utah birds, and Stenzel et al. (*in press*) also found the same relationship in California. I also found no significant relationship between site quality (either overall nest density or overall nest success) and preceding year's nest site density or overall site nest success for male plovers. However, there was an indication that as the amount of suitable habitat declined at the focal study sites (Table 5.3), the percentage of males that were site faithful declined as well (Table 5.1). In contrast, the percentage of females that returned yearly remained relatively constant.

Second, females tend to be less site faithful than males (i.e., 29.5-37.2% returned between years; Table 5.1), although return rates were statistically different between the sexes in only 1 of 3 years. Overall, 53% of banded females and 60% of banded males from the focal study sites were eventually resighted, and estimates of survival rates did not differ between males and females (see Chapter 3). However, 23% of females were not resighted in one or more years and then

subsequently resighted, while only 11% of banded males were missing at least one year (see also Chapter 3). This pattern agrees with the findings of Stenzel et al. (*in press*), who found that approximately 50% of females were absent from their study sites in western North America for part or all of a breeding season, while only 25% of the males were not consistently resighted.

Third, female site fidelity patterns, in contrast to males, appeared to be affected by prior nest success. Successful females were 11.6 times (95% CI = 2.7-49.7) more likely to return to the same study site compared to unsuccessful females. This was the first time this pattern has been reported for this species (see Stenzel et al. *in press*). Reasons for the discrepancy between this study and work in California are unclear. One possible explanation is the relatively high depredation rates found during this study (5-49% nest success) compared to >60% nest success rates found by Warriner et al. 1986. Females nesting at Great Salt Lake may be under greater selection pressure to find sites to minimize predation rates, and therefore tend to disperse more readily following a failed nesting attempt.

Finally, unsuccessful females nesting at sites in years with high nest densities were more likely to disperse to other sites in subsequent years, compared to females who nested in low density years (Table 5.6). This latter pattern may be explained by the hypothesis of Page et al. (1983) that plovers in eastern California maximize the distance between nests to minimize depredation rates. Therefore, plovers in Utah may be moving to areas with lower nest densities following nest failure. However, this conclusion should be interpreted with caution as the data were

limited, and detailed work at a larger number of focal study sites is needed to conclusively answer this hypothesis.

One obvious question this study presents is why are male snowy plovers more site-faithful than females. Parental care appears to play an important role in determining gender-biases in adult site fidelity patterns (Greenwood 1980, Greenwood and Harvey 1982, Oring and Lank 1984, Reynolds and Cooke 1988). Oring and Lank (1984) reviewed site fidelity patterns of adult sandpipers (family Scolopacidae), and found that monogamous species (i.e., ones with biparental care of the young and both sexes were territorial) had the highest degree of site fidelity. In contrast, species which were nonterritorial and had uniparental care of young were less site faithful (e.g., Red Phalaropes *Phalaropus fulicaria* [Schamel and Tracy 1977, 1991]). Lessells (1985) argued that parental care played an important role in the evolution of female-biased philopatry within ducks (Anatidae), one of the few avian taxa in which females are more site faithful than males. Female ducks are responsible for rearing the brood, and individuals familiar with a site may have selective advantage over inexperienced individuals (Shields 1982).

A similar hypothesis may explain male site fidelity in snowy plovers. Both sexes share incubation duties in snowy plovers, but only the male parent usually remains with the brood (Lessells 1984, Warriner et al. 1986, this study; but see Boyd 1972). If familiarity with the brood-rearing area provides a selective advantage to the parent(s) responsible for brood care, males should exhibit a higher degree of site fidelity, which is what I observed. Greenwood's (1980) arguments

about the importance of resource defense do not seem applicable to snowy plovers.

Male snowy plovers generally exhibit little resource defense. Males forage together at sites away from nesting areas when they were not incubating (see Chapter 2) and intraspecific disputes generally occur only near to active nests (Warriner et al. 1986, *personal observation*).

One alternative explanation for male-biased fidelity among Utah snowy plovers was that the focal study sites were relatively high-quality nesting areas compared to many other breeding sites around Great Salt Lake (i.e., nest densities were estimated to be at least two to three times greater at the focal study sites; Paton and Edwards 1990, P. Paton, *unpublished data*). Bollinger and Gavin (1989) found that bobolinks returned consistently to a high-quality site, regardless of nest success the preceding year, while birds were less likely to return to relatively low-quality sites following nest failure. Snowy plovers can live for 10-15 years (G. Page, *personal communication*); therefore, males may continue to return to the same high-quality site waiting for a productive breeding season (see Chapter 3). Unfortunately, the number of visits and the number of banded birds at the six satellite study sites were too few to adequately assess nest densities or return rates of plovers to areas that were potentially low-quality sites.

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CHAPTER 6

SYNTHESIS

The breeding biology of snowy plovers at Great Salt Lake resembles plovers nesting in California (Wilson-Jacobs and Meslow 1984, Page et al. 1983, 1985, Warriner et al. 1986, Stenzel et al. *in press*). Similarities between the two populations include: (1) both monogamous and sequentially polyandrous individuals, although polyandry was only documented once in Utah, (2) a relatively long breeding season which potentially permitted double-brooding, (3) incubation by both sexes, but males generally cared for broods, and (4) extreme mobility and movement over large distances between clutches and between years (see Stenzel et al. *in press*).

The breeding biology of snowy plovers nesting west of the Rocky Mountains is apparently divergent from plovers breeding in the Great Plains states, which apparently are monogamous and single-brooded (Boyd 1972). Further research is needed to clarify the subspecific designations of Gulf of Mexico and western North America populations. In addition, further research is needed to determine reasons for the apparent differences in plover breeding biology between the two regions.

Based on resightings of color-marked birds, plovers breeding in northern Utah potentially represent a separate population from plovers breeding in California, Oregon, and eastern Nevada. Only .8% of 532 banded snowy plovers from Great Salt Lake (i.e., 2 adults, 2 immatures) were resighted during the winter months in Mexico (G. Page, M. Stern, and P. Paton, *unpublished data*). I found an adult male in December 1991 and an immature bird in December 1992 at Puerto Penasco,

Sonora (i.e., the northeast corner of the Gulf of California, 1,100 km from Great Salt Lake). An adult female was found near Guerrero Negro in January 1993, on the west coast of Baja California, 1,513 km from Utah, and an immature bird was found in December 1991 near La Paz at the southern tip of Baja California (1,870 km from the banding location). One Utah-banded bird was seen with an Oregon banded bird at Guerrero Negro, Baja California in 1993. No Utah-banded birds were ever seen in coastal California during the winter months or the breeding season, when there was an extensive system of volunteers searching for banded plovers (G. Page, *personal communication*). In contrast, of the birds banded at Lake Abert, southwestern Oregon, 16% of adult males, 24% of adult females, and 10% of immature birds were resighted in coastal California ($n = 370$; M. Stern, *personal communication*). In addition, although several hundred plovers were banded in California and Oregon during the 1980s (G. Page and M. Stern, *personal communication*), I never saw any of those birds that were banded on the west coast during my 4 years of fieldwork at Great Salt Lake.

The depredation of avian nests by red fox (*Vulpes vulpes*) is the primary threat currently facing upland, ground-nesting shorebirds breeding at Great Salt Lake. Plover nest success found during this study was poor, ranging from 5-49%. Only in 1 of 4 years were nest success rates great enough to sustain plover populations in northern Utah, and fox depredation of nests was the primary cause of nest failures. Detrimental impacts of foxes were not confined to snowy plovers, as only 2 of 10 long-billed curlew (*Numenius americanus*) nests were successful at my study sites

(Paton and Dalton 1994). In addition, other upland, ground-nesting species that historically were common are now rare breeding birds on the east side of Great Salt Lake (e.g., northern harriers [*Circus cyaneus*], short-eared owls [*Asio flammeus*], and willets [*Catoptrophorus semipalmatus*]; [Paton et al. 1992, Val Bachman, Ogden Bay Waterfowl Management Area manager, *personal communication*]).

The only strongholds I found for curlew, harriers, short-eared owls, and willets at Great Salt Lake were on Antelope Island and near Locomotive Springs. Antelope Island has a well-established coyote (*Canis latrans*) population, and according to park rangers, no red foxes have been observed on the island. Recent research suggests there is a negative correlation between coyote and red fox populations (Johnson et al. 1989), and red foxes probably take more avian nests than coyotes (Sargeant et al. 1984). The interactions between red foxes and coyotes deserve further research, and more detailed studies of the impacts of fox on ground-nesting species are needed.

I agree with Reynolds and Cooke (1988) that any hypothesis attempting to explain dispersal patterns needs to distinguish between natal philopatry and adult site fidelity. This is especially true among migratory birds. Greenwood (1980) believed that mating systems were the main determinant for future intersexual variation in dispersal patterns, yet as Reynolds and Cooke postulated, this idea may only be relevant to natal philopatry. Adult site fidelity is presumably the result of many selective forces, of which experience (i.e., prior nest success and age) may be of primary importance (Ollason and Dunnet 1978, Shields 1982, 1984, Gratto et al.

1985, Cuthbert 1988, Reynolds and Cooke 1988, Bollinger and Gavin 1989, Thompson and Hale 1989). Natal philopatry may be the ecological equivalent of adult site fidelity, but only for adults that successfully fledged young the previous year. Obviously a juvenile's experience indicates the natal site is potentially an adequate breeding site (Oring and Lank 1984). The data from this study on juvenile dispersal patterns were too limited to explore differences between adult and juvenile snowy plover dispersal patterns.

The eastern North American congener of the snowy plover, piping plover, has a monogamous mating system, biparental care of young, and a high degree of nest-site tenacity (e.g., 84% nested within 200 m of previous nest sites in Minnesota [Wiens and Cuthbert 1988], and 67% of adults were site faithful in Manitoba [Haig and Oring 1988a]). However, potential nesting habitat apparently was scarce for piping plovers, therefore dispersal opportunities appear to be limited (Haig and Oring 1988a). In contrast, snowy plovers breeding at Great Salt Lake had thousands of hectares of potential nesting habitat during this study. There were many areas that appeared to have potential nesting habitat, but no plovers bred there (*personal observation*). Because there was ample nesting habitat available during the study period, snowy plovers breeding in northern Utah were potentially able to move to alternative locations, an option apparently not available to many piping plover populations. This may explain why female snowy plovers tend to move to alternative locations following nest failure (this study), while piping plovers generally remain at the same site following unsuccessful nesting attempts (Haig and

Oring 1988a).

An unresolved question is why plovers disperse such long distances within and between seasons (e.g., Haig and Oring 1988b, Székely and Lessells 1993, Stenzel et al. *in press*). I documented birds moving as far as 101 km between years, although I only searched Great Salt Lake for banded birds. The maximum dispersal distance I could have detected was only 125 km, an order-of-magnitude smaller than the 1,140 km movement documented by Stenzel et al. (*in press*). One possible explanation for large movements found within this taxon is that many of the sites where plovers nest throughout the Great Basin Desert are ephemeral. Snowy plovers double-clutch (Warriner et al. 1986, see Chapter 2), and both adults probably share incubation duties due to the harsh weather conditions birds have to endure. As breeding sites dry up, females are forced to find alternative nesting areas, which often are relatively far apart. Given the ephemeral nature of lakes throughout the Great Basin, it is probable that females that moved large distances between broods had a selective advantage over sedentary females. Schamel and Tracy (1991) found that red-necked phalaropes (*Phalaropus lobatus*) nesting at northern latitudes, a relatively unstable nesting habitat, were less site faithful than birds nesting at more stable, southerly latitudes. In other words, shorebirds can be plastic in nest-site selection under dynamic environmental pressure. It is not too difficult to envision female plovers moving throughout the Great Basin Desert, trying to take advantage of the best available habitat, while males care for the brood.

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