ABUNDANCE AND CONSERVATION OF ENDANGERED INTERIOR LEAST TERNS NESTING ON SALT FLAT HABITAT

By

SARA HANNAH SCHWEITZER

Bachelor of Science in Biology
University of North Carolina
Chapel Hill, North Carolina
1985

Master of Science in Wildlife Science
Texas Tech University
Lubbock, Texas
1988

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Thesis Approved:

D.M. Leslie, Jr.

Thesis Advisor

Anthony A. Echelle

W Scott Fargo.

James H. Shaw

Thomas C. Collins

Dean of the Graduate College

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PREFACE

The interior population of least terns (Sterna antillarum) was listed as endangered by the U.S. Fish and Wildlife Service in 1985 due primarily to loss of nesting habitat along inland riverine systems and alkaline flats. Direct (dredging, channelization, damming, recreation) and indirect (introduction of prolific plant species such as salt cedar [Tamarix chinensis Lour.]) human activities have reduced the quantity and quality of available nesting habitat for this population. We developed a standardized census method; quantified spatial use of the salt flat, and nest site selection criteria; examined foraging behavior and requirements; assessed stage-specific survival rates determined from earlier and current studies on the salt flat; and evaluated physical conditions of least terns found dead. Our purposes were to monitor and encourage the recovery of the least tern population nesting at Salt Plains National Wildlife Refuge. This thesis comprises 4 manuscripts formatted for submission to The Condor (Chapter I), Journal of Wildlife Management (Chapter II), The Southwestern Naturalist (Chapter III), and Colonial Waterbirds (Chapter IV). Manuscripts are complete as written and need no supporting material.

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CHAPTER I

EVALUATION OF CENSUS TECHNIQUES FOR NESTING CHARADRIIFORMES

Abstract.--Census methods used to obtain statistically valid population data must be compatible with target species and their habitat, provide quantitative abundance estimates, and be used consistently. Variable Circular Plot (VCP) and Purdue, and VCP and Colony Point Count (CPC) census methods were evaluated during the Least Tern (*Sterna antillarum*) and Snowy Plover (*Charadrius alexandrinus*) breeding seasons in 1992 and 1993, respectively. Field work was conducted in and adjacent to colony sites of these species on the salt flat of Salt Plains National Wildlife Refuge, Oklahoma. Objectives were to assess: (1) ability of methods to detect changes in species' density estimates among census strata and census periods, (2) density estimates among methods within and between years, and (3) the efficiency of each method. The VCP density estimates of species differed among census strata in 1992 but not in 1993. In 1992, Least Tern densities differed among Purdue census strata; Snowy Plover densities were homogeneous. The CPC estimates did not differ among census strata. The VCP and CPC density estimates differed among census periods; Purdue estimates did not. Overall density estimates of each species did not differ between methods within each breeding season. However, overall densities were greater in 1992 than 1993. Evaluated methods quantified spatial and temporal use of salt flat habitat by breeding Least Terns and Snowy Plovers. The CPC census technique was the most efficient to implement.

Key Words: *Charadrius alexandrinus*, inland salt flat, Least Tern, Oklahoma, Snowy Plover, *Sterna antillarum*

INTRODUCTION

Quantitative census techniques are needed to assess population abundances, and these methods must be compatible with species of concern and their habitat. Although censuses of breeding Charadriiformes at Salt Plains National Wildlife Refuge (NWR) have been conducted at various times in the past (Purdue 1974, Grover 1979, Downing 1980, Hill 1985, Boyd 1986), no standardized method has been applied. Interior Least Terns (*Sterna antillarum*) and Snowy Plovers (*Charadrius alexandrinus*) concentrate at Salt Plains NWR during their breeding seasons (April through August; Downing 1980, Hill 1985, Sidle and Harrison 1990). Quantitative spatial and seasonal comparisons of Least Tern and Snowy Plover numbers are unreliable unless a standardized census method is used. Precise data are needed to determine distribution and habitat use, breeding chronology, and population trends (Kirsch 1992, Savereno 1992).

We evaluated the Variable Circular Plot (VCP) and Purdue census methods in 1992, and VCP and Colony Point Count (CPC) methods in 1993. Our objectives were to assess: (1) ability of methods to detect changes in species' density estimates among census strata and census periods, (2) density estimates among methods within and between years, and (3) the efficiency of each method. Our overall goal was to select a standardized census method sensitive to spatial and temporal distributions and compatible with behaviors of adult, nesting Least Terns and Snowy Plovers, open salt plain habitat, and Refuge management capabilities.

STUDY AREA, SPECIES' CHARACTERISTICS, AND METHODS

STUDY AREA

Our study area was the 4,050-ha salt flat west of Great Salt Plains Reservoir of Salt Plains NWR, Alfalfa County, Oklahoma (Fig. 1). The salt flat is barren and seasonally encrusted with precipitated salt (Reed 1978) from brine drawn to the surface by capillary action (Grover and Knopf 1982). The land is level to gently sloping and is part of stream flood plains. The salt flat is crossed by the West Branch of the Salt Fork of the Arkansas River, Clay Creek, Cottonwood Creek, and intermittent streams. Frequent flooding occurs in spring and fall. Floodwaters may remain for long periods (Williams and Grover 1975) and carry debris onto the flats (Hill 1985). Near the margins of the salt flat there are hummocks of windblown sand anchored by vegetation.

Summers are long and usually hot (Ortenburger and Bird 1933). Average maximum daily air temperature recorded in Cherokee (about 5 km west of the salt flat) is 36°C in July and August (Williams and Grover 1975). Prevailing winds are from the south (Ortenburger and Bird 1933), and average wind speed is about 21 km/hr. Spring is the windiest season; gusty southwesterly winds of 48 to 72 km/hr are not uncommon (Williams and Grover 1975).

SPECIES' CHARACTERISTICS

Least Terns.--The interior population of Least Terns migrates northward (late March to early May) from wintering habitat along the east coasts of Central and South America to breeding habitat on sand bars, sandy islands and shorelines of inland riverine systems, and alkaline flats (Sutton 1967). Least Terns nest at Salt Plains NWR from late May through August (Grover and Knopf 1982, Hill 1985). Breeding colonies of Least Terns can range in size from a few to several hundred nesting pairs and may be divided into subcolonies (Massey 1974). Because nesting sites are frequently unstable (due to inundation, vegetation encroachment, human disturbance, or predation), Least Terns have been described as having strong group adherence and weak site tenacity (McNicholl 1975) and hence, may relocate colonies to less disturbed nesting sites.

When a threatening intruder enters the nesting territory of a Least Tern, the tern will dive at and attempt to defecate on the intruder while making alarm calls (Hill 1985, Burger 1987, Sidle and Harrison 1990). Nesting territories often overlap, thus an intruder is frequently mobbed. Attack flights become more intense and defended territory increases in size as incubation and hatching proceed (Hardy 1957, S. Schweitzer, pers. obs.). Colonies on the salt flat can be located by initiation of this attack behavior by nesting Least Terns (Sidle and Harrison 1990).

The interior population of Least Terns was federally listed as endangered in 1985 (U.S. Fish and Wildl. Serv. [USFWS] 1985). The apparent non-cyclic population decline of interior Least Terns is due primarily to human manipulation of waterways and shorelines affecting breeding habitat (Sidle and Harrison 1990). Natural factors affecting breeding success include predation, flooding, and catastrophic weather events (Grover 1979). Natural unchecked succession of plant species on formerly barren shorelines, sandbars, and alkaline flats has reduced quality and quantity of breeding habitat (Faanes 1983).

Snowy Plovers.--Migratory Snowy Plovers winter on beaches along the Gulf of Mexico, Gulf of California, and Pacific Ocean (Paton and Edwards 1990) and may be found at some brackish or saline lakes (Hayman et al. 1986). They are primarily coastal breeding birds but some inland populations occur on alkaline flats (Purdue 1976a). Inland, Snowy Plovers nest on highly saline habitats where they are exposed to extremes of continental climates (Purdue 1976a). Most birds are found around water, especially along creeks and at creek mouths (Page and Stenzel 1981).

Nesting areas often overlap those of Least Terns (Sutton 1967). Open habitat and access to water seem to be key requirements for nest placement (Page and Stenzel 1981). Nests are often several hundred meters from vegetation (Purdue 1976b) but near small objects (Boyd 1972, Page and Stenzel 1981, Page et al. 1985). In response to a potential predator, an adult Snowy Plover often performs a broken wing display to divert the threat from its nesting territory (Simmons 1951, 1952).

The migratory, inland population of Snowy Plovers is considered Category 2 (USFWS 1991) indicating possible endangered or threatened status, but conclusive data on biological vulnerability and threat are not currently available to support listing. The Pacific Coast population of Snowy Plovers was federally listed as threatened in 1993 (USFWS 1993).

METHODS

Techniques.--We used the VCP and Purdue methods in 1992 and the VCP and CPC methods in 1993 to census adult Least Terns and Snowy Plovers on the salt flat. The VCP technique was used in both years to enable direct comparisons of (1) total density estimates between years and (2) equality of density means in (a) strata commonly-used between years and (b) census periods common between years.

Because of the endangered status of the Least Tern, it was our species of primary concern. We placed census transects and points through Least Tern nesting areas. Snowy Plovers nested in and adjacent to Least Tern colonies and thus were included by our sampling procedure. All counts were conducted with 10 x 50 binoculars. To investigate effects of abiotic factors on density estimates, we recorded air temperature (°C), relative humidity, wind speed, wind direction, time of day (morning [< 1100 hr], afternoon [1100 - 1700 hr], and evening [1700 - 2000 hr]), and date before all counts.

The VCP census method, described in detail by Ramsey and Scott (1979) and Reynolds et al. (1980), is an adaptation of line transect methodology. Although it has been used successfully in various habitats (DeSante 1981, Scott et al. 1981, Hamel 1984, DeSante 1986), it has not been used previously on a salt flat. We established a series of transects across target regions or strata (active and potential Least Tern colony sites) on the salt flat (Fig. 1). The number and length of parallel transects in each stratum depended on stratum size. Distance between transects (250 m) was determined by the "maximum-accurate-distance" or maximum distance an observer could confidently identify species (125 ± 10 m; mean ± SD), which was ascertained after 2 weeks of trial estimations and measurements with decoys and target species. Wind-blown sand and heat waves within 0.5 m of the ground surface adversely affected visual identification of birds, and aural detection of birds was reduced by high winds. Before each census, we used a random number generator to select the point from which we conducted a count on each transect.

Advantages of the VCP method were: (1) the observer remained at a point for a fixed period of time, enhancing his/her ability to detect all birds within the maximum-accurate-distance (Ramsey and Scott 1979); (2) because the observer was relieved of survey duty between points, he/she could move quickly and safely through the colony site (safety of observer and ground-nesting birds; Ramsey and Scott 1979); (3) the observer was stationary and therefore spent more time searching for birds and less time watching the path of travel, improving density estimates (Reynolds et al. 1980); (4) stationary observers had less effect on bird activity (Reynolds et al. 1980); (5) fixing the census time (8 min) at each point aided in standardizing the time spent counting (Reynolds et al. 1980); and (6) statements could be made concerning abundance of bird species and habitat variables along transects (Reynolds et al. 1980, Scott et al. 1981).

The following assumptions were associated with the VCP method: (1) all birds had an equal likelihood of occurring anywhere within the habitat being censused; (2) all birds seen or heard were in the exact position that they occupied when the census point was first occupied by the observer; (3) all individuals actually in the area bounded by the point of inflection (distance from point where number of birds observed began to decline) were detected (Reynolds et al. 1980); (4) the observer correctly estimated the distance between herself and each bird; and (5) individuals using the area were adult breeding birds. Assumptions 1 and 2 were not met due to the tendency of Least Terns and Snowy Plovers to occur in aggregated distributions associated with waterways on the salt flat (Talent and Hill 1985) and to terns' mobbing defense behavior of their nesting territory. Assumption 3 was met and 4 was corrected by 2 weeks of training with decoys before actual censusing began. Placing points through nesting areas reduced the probability of violating assumption 5. To reduce the effect of violating assumption 1, transects were placed perpendicular to waterways in or adjacent to strata (Ramsey and Scott 1979, Scott et al. 1981). To conduct the VCP census, the observer walked to the previously-selected random point along a transect and waited for 1 min (Szaro and Jakle 1982) to allow birds to acclimate to her presence. Distance to each bird was estimated the first instant it was sighted to reduce effects of violating assumption 2. Estimated distances were used to calculate the point of inflection for each species in each year (Ramsey and Scott 1979, Reynolds et al. 1980). We censused 13 strata in 1992 and 11 strata in 1993 with the VCP technique.

Purdue (1976a) censused Snowy Plovers by walking transects parallel to flowing water courses on the salt flat. He counted all Snowy Plovers present along the stream and counts were converted to number/km. Our "Purdue census," similar to the strip transect described by Verner (1985), was a modification of the original in that we standardized all components of the procedure. Transects were established parallel to and 150 m from the complete length of 5 waterways (Fig. 1) flowing throughout the 1992 season. Each Purdue census was initiated at a previously-selected random point and covered 1 km of the waterway. All adult birds actively using the area between the transect line and waterway were counted.

Advantages of Purdue censuses were: (1) transects were established quickly and easily; (2) little training was necessary before conducting censuses; and (3) nesting colonies were not disturbed by observers. Assumptions associated with this method were: (1) all birds had an equal likelihood of occurring anywhere within the habitat being censused; (2) all individuals actually in the area bounded by the fixed 150-m width were detected; and (3) individuals using the area were adult breeding birds. Because assumption 1 may have been violated by birds aggregating along portions of waterways, we initiated each census from a random point to increase the portion of each waterway censused and reduce bias. Assumption 2 was affected by adverse weather and uneven topography. Use of waterways by nonbreeding adults for resting and foraging impacted assumption 3.

Design of the CPC method, a fixed-radius point count technique (Verner 1985, Hutto et al. 1986), was based on our knowledge of the size and elliptical configuration of Least Tern colonies on the salt flat and behavioral responses of Least Terns and Snowy Plovers to observers. This method entailed bisecting each colony (stratum) lengthwise with 1-m stakes (fixed points) placed 300 m apart. First and last points were at edges of strata. Points were placed 300 m apart to reduce the possibility of double-counting birds. Number of points through strata varied due to differences in colony sizes. We considered "colonies" strata with >2 Least Tern nests. Count time in preliminary trials (n = 70) averaged 11.1 ± 0.2 min. We rounded our standardized time to 10 min. To conduct the CPC, the observer walked to the first point, waited for 1 min to allow birds to acclimate to her presence, and then counted, for 10 min, all adult birds actively using the area within a 150-m radius (area censused/point = 70,686 m^2). When the count was complete, the observer walked to the next point, and continued the process until birds had been counted from all points. Nine strata were censused with the CPC method in 1993.

Advantages of the CPC method were: (1) the observer remained at a fixed point, enhancing his/her ability to detect confidently all birds within the 150-m radius; (2) because the observer was relieved of survey duty between points, he/she could move quickly and safely through the colony site; (3) the stationary observer spent more time searching for birds and less time watching the path of travel improving density estimates; (4) stationary observers had less effect on bird activity; (5) statements could be made concerning abundance of bird species and habitat variables along transects; (6) placing points through nesting colonies was completed quickly and easily; and (7) little observer training was necessary before initiation of censuses.

Assumptions associated with the CPC method were: (1) all birds had an equal likelihood of occurring anywhere within the habitat being censused; (2) all individuals actually in the fixed 150-m radius were detected; and (3) individuals using the area were adult breeding birds. Assumption 1 may have been violated by birds defending their nesting territories with attack flights or displays. Assumption 2 may have been affected by adverse weather conditions. We reduced impacts of violating assumptions 2 and 3 by only counting birds that were positively identified within the 150-m radius and actively using the area. Placing points through nesting areas reduced the probability of violating assumption 3.

Statistical Analyses.--All counts of terns and plovers were converted to densities to correct for different areas covered by the 3 census methods and enable direct comparisons among density estimates. After subjecting all data to diagnostic tests (e.g., residual plots [Neter et al. 1989], Shapiro-Wilk's test [Shapiro and Wilk 1965, SAS 1990], and Levene's test [Snedecor and Cochran 1980]), we determined that they did not meet the assumptions of parametric statistics even with appropriate transformations (Zar 1974). Data were therefore ranked for analyses (Conover and Iman 1981). Results of statistical tests were considered significant if $\underline{P} \leq 0.05$.

To determine if density estimates differed among strata or waterways for each year, census method, and species, we applied the general linear model of SAS (GLM procedure [ANOVA]; SAS 1990) to density estimates. If the test statistic of the overall model was significant, density estimates were separated using the LSMEANS procedure (Conover and Iman 1981, SAS 1990). This procedure computed least-square estimates of marginal means for unbalanced designs (SAS 1990). Taylor's Power Law regression models (Taylor 1961, 1984) were used to assess spatial distribution of each species among strata and waterways. Secondly, we applied the general linear model of SAS to density estimates to determine if means differed among census periods for each year, census method, and species (i.e., if each census method detected changes in species density over the breeding season; 'census period' was defined as the amount of time required to census all strata and waterway transects once). Differences among density estimates were determined using the LSMEANS mean separation procedure, if the overall model was significant.

Overall density estimates were analyzed using the general linear model to determine if density estimates obtained by each method differed within each year and between years. Because 9 strata and all census periods were common between VCP and CPC methods in 1993, we applied the general linear model to data first sorted by strata then by census period. The test statistic (*F*-value = t^2-value) determined whether means of VCP and CPC methods were different in strata and census periods. Density means from 1992 and 1993 VCP estimates were tested for equality in strata and census periods using the procedure described for 1993 VCP and CPC means.

Optimally, to provide the best estimate of number of adult breeding birds on the salt flat, censuses should be conducted when most birds are in the nesting area, not feeding, or roosting away from the nest site. We used the all-possible-regressions selection procedure (Neter et al. 1989, SAS 1990) to choose the model that best predicted density with census period, stratum, time-of-day, temperature, relative humidity, wind direction, and wind speed as independent variables. Models were developed for each method used in 1992 and 1993. Criteria for selecting "best" models were maximum adjusted R^2 and minimum mean square error (Neter et al. 1989). We examined the suitability of models selected by the all-possible-regressions procedure with an overall *F*-test (Neter et al. 1989). Whether or not a variable contributed significantly to the model was determined by a partial *F*-test (Neter et al. 1989).

We recorded the amount of time required to establish each method's transects and to conduct censuses using each method. We assessed the quality (e.g., compatibility with Least Tern and Snowy Plover behavior and with the open habitat of the salt flat) and quantity of work accomplished by each method given the required time to complete it, enabling estimation of efficiency.

RESULTS

A census period averaged 5.5 days (±0.7 SE; range=2 to 13 days). Adverse weather affected timely completion of censuses. A complete Purdue census covered 98 ha. Inflection points for the VCP technique in 1992 were 105 m and 120 m for Least Terns and Snowy Plovers, respectively. In each census period, counts were taken from 54 random points along transects; thus, areas covered by VCP censuses of Least Terns and Snowy Plovers in 1992 were 187 ha and 244 ha, respectively. In 1993, counts were taken from 46 random points along transects in each census period; Least Tern and Snowy Plover inflection points were 125 m, and the area covered was 226 ha. Because new random points were used on each VCP transect during each census period, over the course of the breeding season we covered the entire area of all strata: 989 ha and 539 ha in 1992 and 1993, respectively. There were 34 points in a complete CPC census covering 240 ha in each census period.

Spatial use of salt flat habitat by adult birds was not uniform. Least Tern density estimates from the Purdue method differed among waterways, but densities of Snowy Plovers did not (Table 1). Both Least Tern and Snowy Plover densities differed among VCP strata in 1992, but densities did not differ among strata in 1993 (Table 2). Densities estimated from the CPC technique in 1993 were not different among strata (Table 3). Taylor's Power Law regression models determined that the spatial distributions of both species among VCP and CPC census strata were negative binomials (Table 4). Among Purdue waterways, both species followed Poisson and negative binomial distributions, respectively (Table 4).

Although densities of adult birds along waterways on the salt flat were consistent over the breeding season, densities in colony sites differed. Neither Least Tern nor Snowy Plover density estimates from the Purdue method differed among census periods (Table 1). In 1992 and 1993, VCP density estimates of Least Terns and Snowy Plovers differed among census periods (Table 2), as did CPC estimates of both species (Table 3).

Purdue and VCP total density estimates did not differ in 1992 (Table 5), nor did the VCP and CPC total density estimates of Least Terns in 1993 (Table 5). Within strata and census periods common to VCP and CPC methods, densities of Least Terns did not differ (Tables 6 and 7). In 1993, overall VCP density estimate of Snowy Plovers was greater than that of the CPC method (Table 5); however, no differences were found between VCP and CPC density estimates of Snowy Plovers in common strata (Table 6) or census periods

(Table 7). Overall density estimates of terns and plovers differed among methods and between years (Table 5).

Six VCP strata were used for nesting in 1992 and 1993. The primary cause of colony relocation was flooding; several sites that were available in 1992 were under water during most of the 1993 breeding season. Total densities from VCP estimates were greater in 1992 than in 1993 for both species (Table 8). The VCP estimates of Least Tern density were greater during 1992 than 1993 in 3 strata; only 1 stratum had a significantly greater Least Tern density in 1993 than 1992 (Table 9). Densities of both species from the VCP method were greater in 1992 than 1993 during 3 of 10 census periods (Table 10). The VCP estimates of Snowy Plover densities were greater in 1992 than 1993 in only 1 stratum (Table 9).

"Best models" for estimating densities of Least Terns and Snowy Plovers differed among methods (Table 11). In 62% of Least Tern and Snowy Plover models taking all 7 possible independent variables into consideration, the independent variable "census period" best explained the most variation in "density." No consistent set of environmental variables predicted density estimates. The greatest amount of variation in density explained by any model was 62%; 75% of models explained <40% of the variation in density. Models with only environmental variables explained less of the variation in density than models with all independent variables.

DISCUSSION

It is difficult to census open, seemingly featureless habitats like the salt flat of Salt Plains NWR (Boyd 1981, Warriner and Warriner 1981, Boyd 1990). However, it is imperative to obtain reliable assessments of population trends (Scott et al. 1981, Hill 1993). Census methods used should be standardized and compatible with the species of concern, their associated habitat, and available logistics. If these criteria are not met, results are apt to be unreliable and inconsistent.

Ideally, census procedures produce estimates of density in selected strata, describe spatial patterns of species in the study area, and provide the possibility of understanding underlying distributions and regulatory mechanisms (Pank 1981). For Least Terns, VCP and Purdue methods both detected spatial differences in 1992; for Snowy Plovers, however, spatial differences in 1992 were detected only by the VCP method. Failure to find spatial differences in Least Tern and Snowy Plover densities in 1993 by VCP and CPC methods may be explained by movements of breeding birds among strata and to new strata due to loss of nest sites by flooding. This disturbance resulted in increased movement among strata, use of sites not used previously, and no significant selection for one stratum over another. Others have found that Least Terns (Nisbet 1973, Massey 1974, Boyd 1993) and Snowy Plovers (Boyd 1972, Warriner et al. 1986) will relocate and renest if nests fail during the breeding season. Because the salt flat is expansive, yet a habitat of intermediate stability, terns and plovers may have adopted the strategy described by McNicholl (1975) of combining nest site tenacity with group adherence. If a formerly-used site is temporarily unsuitable, the group will nest elsewhere until the familiar site is again available.

Taylor's Power Law regression models determined that distribution of Least Terns and Snowy Plovers among strata tended to be clumped or aggregated; use of the salt flat was not uniform. The negative binomial distribution (clumped spatial pattern) implied that some constraints influenced use of habitat by terns and plovers. The Poisson distribution among waterways suggested that species were randomly dispersed over homogeneous habitat or did not select among heterogeneous habitat types (Ludwig and Reynolds 1988). Knowledge of spatial distribution patterns of nesting Least Terns and Snowy Plovers on the salt flat will help guide placement of future census strata and results from censuses can be used to investigate underlying influences on habitat selection. Additionally, our results suggest that the method used to census these birds should be flexible and its transects or census points quick to establish in newly colonized sites.

Estimates of densities by the Purdue method did not differ significantly over the breeding season, indicating a consistent use of waterways. Slight increases in densities of both species in early August followed by a decline in mid-

August reflected birds leaving nesting colonies and aggregating along waterway shorelines. This behavior is common on the salt flat; adults, chicks, and fledglings of both species use waterway and reservoir shorelines for thermoregulation (Purdue 1976b, Hill 1985) and feeding (Grover and Knopf 1982, Talent and Hill 1985, Hill 1993) before their migration to wintering sites.

The VCP and CPC census procedures were sensitive to temporal changes in Least Tern and Snowy Plover densities on the salt flat. Peak densities in 1992 and 1993 occurred from mid-June to late-July for both species. Densities declined significantly in the second week of August 1992 and during the third week of July 1993. Talent and Hill (1985) estimated that the greatest percentage of Least Terns and Snowy Plovers engaged in breeding activity on the salt flat occurred from late-May to mid-July 1982. Although the length of the breeding season of both species on the salt flat may vary due to weather conditions, the peak of the breeding season (mid-June to mid-July) appears consistent among years. Density estimates of the VCP and CPC methods accurately reflected the breeding chronology of Least Terns and Snowy Plovers on the salt flat.

There were twice as many rainfall events of ≥3 cm in 1993 ($n = 12$; May through August) as in 1992. Such events caused frequent sheet-flooding of the salt flat, nest failure, and lower overall densities of Least Terns and Snowy Plovers. Changes in densities of Least Terns in VCP strata used in 1992 and 1993 reflected movements of birds due to flooding. Densities declined in 3 strata adjacent to the Salt Fork of the Arkansas River and Great Salt Plains Reservoir. These bodies of water exceeded their normal mean high waterline for most of the 1993 season. A significant increase in Least Tern densities in stratum H, approximately 5 km west of flooded areas, and nesting at 2 new sites, probably reflected relocated birds from flooded strata.

Activity patterns and detection of many avian species are affected by environmental conditions (Nettleship 1976), time of day (Shields 1977), habitat (Ornelas et al. 1993), and season (Recher 1981, Robbins 1981). Effects of these variables on census results influence timing of field work and selection of census method. We investigated effects of census period (seasonal effect), census stratum (spatial effect), and environmental parameters on observed variation in density estimates for each year, method, and species. Environmental variables appeared to have minimal influence on species density. The most important variables were census period (stage of the breeding season) and census stratum (nesting site); however, 75% of models containing all measured effects explained <40% of variation in mean density estimates. Least Terns and Snowy Plovers have adapted physiological (Howell 1959, Purdue and Haines 1977) and behavioral traits (Boyd 1972, Purdue 1976b, Hill 1985) making them tolerant of environmental conditions on the salt flat. In general, the peak breeding period and nest site selection pattern exhibited by the two species are consistent between years on the salt flat. Knowledge of these patterns will benefit an annual census program: initial surveys for colonies will be expedited and guided by knowledge of preferred habitat and repeated censuses can be conducted during the peak breeding period to get the best estimate of breeding birds.

Portnoy (1980) compared 5 census methods of inventorying colonial waterbirds along the coast of the Gulf of Mexico (aerial photography, aerial estimates from aircraft, transect sampling of active nests, total ground-nest counts, and ground estimates of adult birds). He concluded that ground estimates of adult birds were the most easily applied and reliable methods to use for species such as Least Terns, which nest in small colonies. Our assessment of ground estimates of adult Least Terns and Snowy Plovers by the VCP, Purdue, and CPC methods exhibited the strengths and weaknesses of each and allowed us to select a method suitable for use on the salt flat. Strengths shared by VCP and CPC methods included placement of points in nesting areas, relieving the observer from census duties between points, waiting 1 min upon arrival at each point, remaining stationary during each count, and allowing habitat data to be collected in association with census points. Placing points in nesting areas improved the probability of counting only adult breeding birds. The 1-min "rest" period reduced the possibility of double-counting birds because birds that may have mobbed the observer at one point returned to their nesting territory as she moved to and stopped at the next point. Between points, the observer could safely avoid disturbing cryptic nests and remaining stationary increased counting accuracy. Habitat descriptions could be related to densities for each nesting stratum and increase understanding of Least Tern and Snowy Plover distribution on the salt flat.

Because the VCP method used new random points for each census on established transects, it covered more area than either the CPC or Purdue method. This advantage did not result in density estimates greater than those of Purdue or CPC techniques. Establishing transects for the VCP method required more time (10 days) than transects and points for the Purdue (2 days) and CPC (6 days) methods. In addition, not considering travel time between strata, it took 13 hr ± 18 min (mean ± SE) to complete a VCP census compared to 6 hr ± 8 min and 3 hr ± 5 min for complete CPC and Purdue censuses, respectively.

Primary advantages of the Purdue method were ease with which transects were established and reduced disturbance to nesting strata due to placement of transects along waterways. Disadvantages of this method however, out-weighed its advantages. Counting birds along waterways increased the probability of counting nonbreeding adults and double-counting birds that followed the observer, and some birds may have been missed along uneven creek banks.

In conclusion, the strengths or advantages of VCP and CPC methods outweighed those of the Purdue technique. Results of the VCP method were not different than those of the CPC method, and the latter was more efficient. The CPC census method was sensitive to spatial and temporal distributions, and compatible with the behavior of adult, breeding Least Terns and Snowy Plovers, open salt plain habitat, and Refuge time budgets.

The peak breeding period for Least Terns and Snowy Plovers on the salt flat occurred from mid-June to late-July. To assess population trends of these species, annual censuses must be conducted. Censuses should be conducted during the peak breeding period to obtain the most accurate estimate of adult breeding birds on the salt flat. If a census is conducted once every 2 weeks beginning in mid-June, 4 censuses will encompass the breeding season and provide the best estimate of the season's peak numbers of breeding birds. Annual use of the CPC census method will provide reliable population estimates of Least Terns and Snowy Plovers. These estimates provide essential feedback on recovery management efforts and data for building predictive population trend models.

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Table 1. Means and standard errors of Least Tern and Snowy Plover densities (birds/ha) obtained using the Purdue census method along 5 waterway transects and in 8 census periods in 1992. Means (within columns) followed by different letters are different (*P* ≤ 0.05); determined by ANOVA conducted on rank-transformed means followed by LSMEANS mean separation procedure.

	Least Tern		Snowy Plover	
Grouping	$\bar{x}$	SE	$\bar{x}$	SE
Waterway Transect				
1	0.80a	0.15	1.34	0.41
2	0.44ab	0.05	0.44	0.15
3	0.29b	0.10	1.00	0.24
4	0.26b	0.12	1.73	0.25
5	1.10a	0.27	0.64	0.20
Census Period[a]				
4	0.88	0.24	1.91	0.54
5	0.50	0.17	1.02	0.46
6	0.53	0.12	0.79	0.60
7	0.40	0.14	1.57	0.58
8	0.60	0.20	0.78	0.34
9	0.64	0.39	1.06	0.20
10	0.92	0.36	0.88	0.45
11	0.16	0.04	0.22	0.16

[a] Census Periods 1 through 3 were not sampled because transects were not yet established.

Table 2. Means and standard errors of Least Tern and Snowy Plover densities (birds/ha) obtained using the Variable Circular Plot census method in nesting strata and census periods. Means (within columns) followed by different letters are different ($\underline{P} \leq 0.05$); determined by ANOVA conducted on rank-transformed means followed by LSMEANS mean separation procedure.

	1992					1993			
	Least Tern		Snowy Plover			Least Tern		Snowy Plover	
	$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE
Stratum					Stratum				
A	1.02ab	0.24	1.13abc	0.35	A	0.61	0.26	0.42	0.20
B	0.99abc	0.29	0.81abcde	0.28	C93	0.76	0.26	0.59	0.15
C92	0.77bcd	0.24	0.30de	0.13	Dc	0.40	0.07	1.73	0.72
Da	0.35de	0.12	0.14e	0.44	E	0.37	0.12	0.40	0.15
Db	0.68bcd	0.17	0.23cde	0.07	F	0.47	0.12	0.64	0.21
E	0.79abc	0.17	1.10abcd	0.42	G	0.22	0.07	0.71	0.23
F	0.72bc	0.12	0.44cde	0.20	H	0.33	0.08	0.69	0.34
G	0.49bcd	0.08	0.56bcde	0.23	Ja	0.19	0.03	0.68	0.24
H	0.01f	0.01	1.35abcde	0.64	Jb	0.41	0.08	0.74	0.17
I	0.12ef	0.03	1.58ab	0.46	K/L	0.61	0.13	1.62	0.55
J	0.44cd	0.11	0.72abcde	0.26	M	0.39	0.13	0.29	0.08
K	1.24a	0.14	1.81a	0.47					
L	0.71bcd	0.16	1.29ab	0.32					

Table 2. Continued.

	1992					1993			
	Least Tern		Snowy Plover			Least Tern		Snowy Plover	
	$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE
Census Period					Census Period				
1	0.55cd	0.27	1.41b	0.41	1	0.86a	0.25	2.38a	0.70
2	0.80ab	0.16	2.06a	0.41	2	0.90a	0.25	1.72a	0.32
3	1.04a	0.20	1.21ab	0.28	3	0.68a	0.14	1.11ab	0.13
4	0.72ab	0.12	0.74bc	0.32	4	0.52ab	0.14	0.97bc	0.41
5	0.72abc	0.16	1.08ab	0.30	5	0.41ab	0.05	1.22ab	0.34
6	0.62abc	0.13	1.04bc	0.39	6	0.38ab	0.08	0.50cd	0.15
7	0.77abc	0.17	0.82bc	0.29	7	0.35ab	0.08	0.24de	0.06
8	0.68abc	0.14	0.36cd	0.13	8	0.26bcd	0.08	0.21de	0.08
9	0.41bc	0.11	0.22de	0.11	9	0.28bc	0.07	0.16ef	0.06
10	0.10	0.04	0.09e	0.06	10	0.13cd	0.05	0.52de	0.39
					11	0.11d	0.06	0.04f	0.02

Table 3. Means and standard errors of Least Tern and Snowy Plover densities (birds/ha) obtained using the Colony Point Count census method in nesting strata and census periods in 1993. Means followed by different letters (within columns) are different ($\underline{P} \le 0.05$); determined by ANOVA conducted on rank-transformed means followed by LSMEANS mean separation procedure.

	Least Tern		Snowy Plover	
	$\bar{x}$	SE	$\bar{x}$	SE
Stratum:				
A	0.33	0.13	0.20	0.08
C93	0.61	0.20	0.80	0.30
Dc	0.30	0.05	0.69	0.18
E	0.22	0.08	0.25	0.09
F	0.41	0.11	0.39	0.18
G	0.26	0.11	0.45	0.20
Jb	0.28	0.06	0.30	0.10
K/L	0.63	0.15	1.14	0.37
M	0.31	0.10	0.09	0.05
Census Period:				
1	0.98a	0.20	1.32a	0.38
2	0.86ab	0.17	1.37a	0.36
3	0.67abc	0.18	0.83a	0.34
4	0.53abcd	0.18	1.16a	0.35
5	0.38cd	0.10	0.54a	0.12
6	0.42bcd	0.08	0.36b	0.21
7	0.16ef	0.08	0.22b	0.10
8	0.23de	0.08	0.16b	0.08
9	0.16ef	0.04	0.12b	0.05
10	0.11ef	0.05	0.14b	0.09
11	0.04f	0.03	0.00c	0.00

Table 4. Spatial distribution patterns of nesting birds determined by variance-mean relationships, analyzed using Taylor's Power Law regression models. Density estimates were obtained using Variable Circular Plot (VCP) and Purdue census methods during the 1992, and VCP and Colony Point Count (CPC) methods during the 1993 breeding seasons.

Census Method (year)	Species	b_1	Standard Deviation	n	calculated t-value	*P*-value[a]	Distribution	b_o
VCP	Least Tern	1.3287	0.1538	13	7.7048	<0.0001	Negative Binomial	0.9048
(1992)	Snowy Plover	1.9189	0.1628	13	20.3554	<0.0001	Negative Binomial	0.2152
Purdue	Least Tern	1.2181	0.8388	5	0.5814	0.6018	Poisson	0.9996
(1992)	Snowy Plover	1.8323	0.2566	5	7.2532	0.0054	Negative Binomial	0.1864
VCP	Least Tern	2.7703	0.4206	11	13.9580	<0.0001	Negative Binomial	0.1433
(1993)	Snowy Plover	2.3030	0.3264	11	11.9755	<0.0001	Negative Binomial	0.7502
CPC	Least Tern	1.9674	0.6746	9	4.3023	0.0036	Negative Binomial	-0.0810
(1993)	Snowy Plover	1.8158	0.1785	9	13.7125	<0.0001	Negative Binomial	0.0754

[a] H_o: $\beta_1=1$ (birds were normally distributed [followed a Poisson distribution] among locations censused on the salt flat).

Table 5. Overall means and standard errors of Least Tern and Snowy Plover densities (birds/ha) obtained using Variable Circular Plot (VCP), Purdue, and Colony Point Count (CPC) census methods during 1992 and 1993 breeding seasons. Means (within column and year: lower-case; within column: upper-case) followed by different letters are different ($P \leq 0.05$); determined by ANOVA conducted on rank-transformed means followed by LSMEANS mean separation procedure.

Census Method	Least Tern		Snowy Plover	
	$\bar{x}$	SE	$\bar{x}$	SE
	1992			
VCP	0.64 A	0.05	0.89 A	0.10
Purdue	0.58 AB	0.08	1.03 A	0.16
	1993			
VCP	0.43 BC	0.04	0.80 a AB	0.11
CPC	0.38 C	0.04	0.51 b B	0.08

Table 6. Means and standard errors of Least Tern and Snowy Plover densities (birds/ha) obtained using the Variable Circular Plot (VCP) and Colony Point Count (CPC) census methods in 1993. *P*-values are given for mean comparisons between methods, within strata.

	Least Tern					Snowy Plover				
	VCP		CPC			VCP		CPC		
Stratum	$\bar{x}$	SE	$\bar{x}$	SE	*P*-value	$\bar{x}$	SE	$\bar{x}$	SE	*P*-value
A	0.61	0.26	0.33	0.13	0.56	0.42	0.20	0.20	0.08	0.77
C	0.76	0.26	0.61	0.20	0.68	0.59	0.15	0.80	0.30	0.60
Dc	0.40	0.07	0.30	0.05	0.40	1.73	0.72	0.69	0.18	0.35
E	0.37	0.11	0.22	0.08	0.21	0.40	0.15	0.25	0.09	0.84
F	0.47	0.12	0.41	0.11	0.92	0.64	0.21	0.39	0.18	0.28
G	0.22	0.07	0.26	0.11	0.79	0.71	0.23	0.45	0.20	0.39
J	0.30	0.05	0.28	0.06	0.82	0.71	0.14	0.30	0.10	0.15
K/L	0.61	0.13	0.63	0.15	0.92	1.62	0.55	1.14	0.37	0.93
M	0.39	0.13	0.31	0.10	0.54	0.29	0.08	0.09	0.05	0.10

Table 7. Means and standard errors of Least Tern and Snowy Plover densities (birds/ha) obtained using the Variable Circular Plot (VCP) and Colony Point Count (CPC) census methods in 1993. *P*-values are given for mean comparisons between methods, within census periods.

	Least Tern					Snowy Plover				
	VCP		CPC			VCP		CPC		
Census Period	$\bar{x}$	SE	$\bar{x}$	SE	*P*-value	$\bar{x}$	SE	$\bar{x}$	SE	*P*-value
1	0.86	0.25	0.98	0.20	0.35	2.45	0.78	1.32	0.38	0.59
2	0.90	0.25	0.86	0.17	0.71	1.80	0.34	1.37	0.36	0.28
3	0.68	0.14	0.67	0.18	0.92	1.16	0.14	0.83	0.34	0.06
4	0.52	0.14	0.53	0.18	0.73	1.07	0.44	1.16	0.35	0.55
5	0.41	0.05	0.38	0.10	0.49	0.94	0.23	0.54	0.12	0.30
6	0.38	0.08	0.42	0.08	0.71	0.55	0.15	0.36	0.21	0.18
7	0.35	0.08	0.16	0.08	0.06	0.26	0.06	0.22	0.08	0.64
8	0.25	0.08	0.23	0.08	0.91	0.22	0.09	0.16	0.10	0.37
9	0.28	0.07	0.16	0.05	0.32	0.15	0.07	0.12	0.05	0.70
10	0.13	0.05	0.11	0.05	0.91	0.57	0.43	0.14	0.09	0.34
11	0.11	0.06	0.04	0.03	0.60	0.04	0.03	0.00	0.00	0.17

Table 8. Means and standard errors of Least Tern and Snowy Plover densities (birds/ha) obtained using the Variable Circular Plot census method. Means are from 6 strata and 10 census periods common between years. Means (within column and species) followed by different letters are different ($P \leq 0.05$); determined by ANOVA conducted on rank-transformed means followed by LSMEANS mean separation procedure.

	$\bar{x}$	SE
Least Tern		
1992	0.71a	0.07
1993	0.41b	0.06
Snowy Plover		
1992	1.10a	0.15
1993	0.64b	0.13

Table 9. Mean densities (birds/ha ± SE) of Least Terns and Snowy Plovers obtained using the Variable Circular Plot census method during the 1992 and 1993 breeding seasons. *P*-values are results from applying the general linear model to data within strata and species. Census strata are locations used for nesting during both breeding seasons.

	Least Tern					Snowy Plover				
	1992		1993			1992		1993		
Stratum	$\bar{x}$	SE	$\bar{x}$	SE	*P*-value	$\bar{x}$	SE	$\bar{x}$	SE	*P*-value
A	1.02	0.24	0.48	0.24	0.05	1.13	0.35	0.30	0.18	0.03
E	0.79	0.17	0.35	0.12	0.02	1.10	0.42	0.43	0.16	0.22
F	0.72	0.12	0.43	0.13	0.07	0.44	0.20	0.54	0.21	0.62
G	0.49	0.08	0.21	0.07	0.02	0.56	0.23	0.58	0.21	0.98
H	0.01	0.01	0.36	0.07	0.00	1.35	0.64	0.58	0.36	0.36
K/L	0.97	0.12	0.63	0.14	0.16	1.55	0.28	1.38	0.55	0.24

Table 10. Mean densities (birds/ha ± SE) of Least Terns and Snowy Plovers obtained using the Variable Circular Plot census method during the 1992 and 1993 breeding seasons. *P*-values are results from applying the general linear model to data within census periods and species. A census period was the amount of time required to census all strata once; dates ranged from 23 June to 21 August.

	Least Tern					Snowy Plover				
	1992		1993			1992		1993		
Census Period	$\bar{x}$	SE	$\bar{x}$	SE	*P*-value	$\bar{x}$	SE	$\bar{x}$	SE	*P*-value
1	0.43	0.11	0.99	0.30	0.12	1.45	0.64	1.71	0.54	0.30
2	0.76	0.20	0.82	0.21	0.85	2.60	0.61	1.28	0.19	0.10
3	1.14	0.28	0.60	0.19	0.20	1.43	0.43	1.00	0.70	0.27
4	0.72	0.17	0.42	0.06	0.24	0.86	0.58	1.59	0.51	0.12
5	0.88	0.25	0.33	0.14	0.12	1.64	0.47	0.37	0.20	0.02
6	0.63	0.16	0.32	0.10	0.23	0.94	0.26	0.18	0.07	0.01
7	1.09	0.25	0.23	0.12	0.02	1.15	0.47	0.06	0.02	0.01
8	0.89	0.22	0.23	0.10	0.04	0.48	0.24	0.08	0.05	0.09
9	0.44	0.17	0.09	0.05	0.04	0.24	0.12	0.10	0.08	0.36
10	0.12	0.06	0.05	0.05	0.32	0.16	0.10	0.00	0.00	0.11

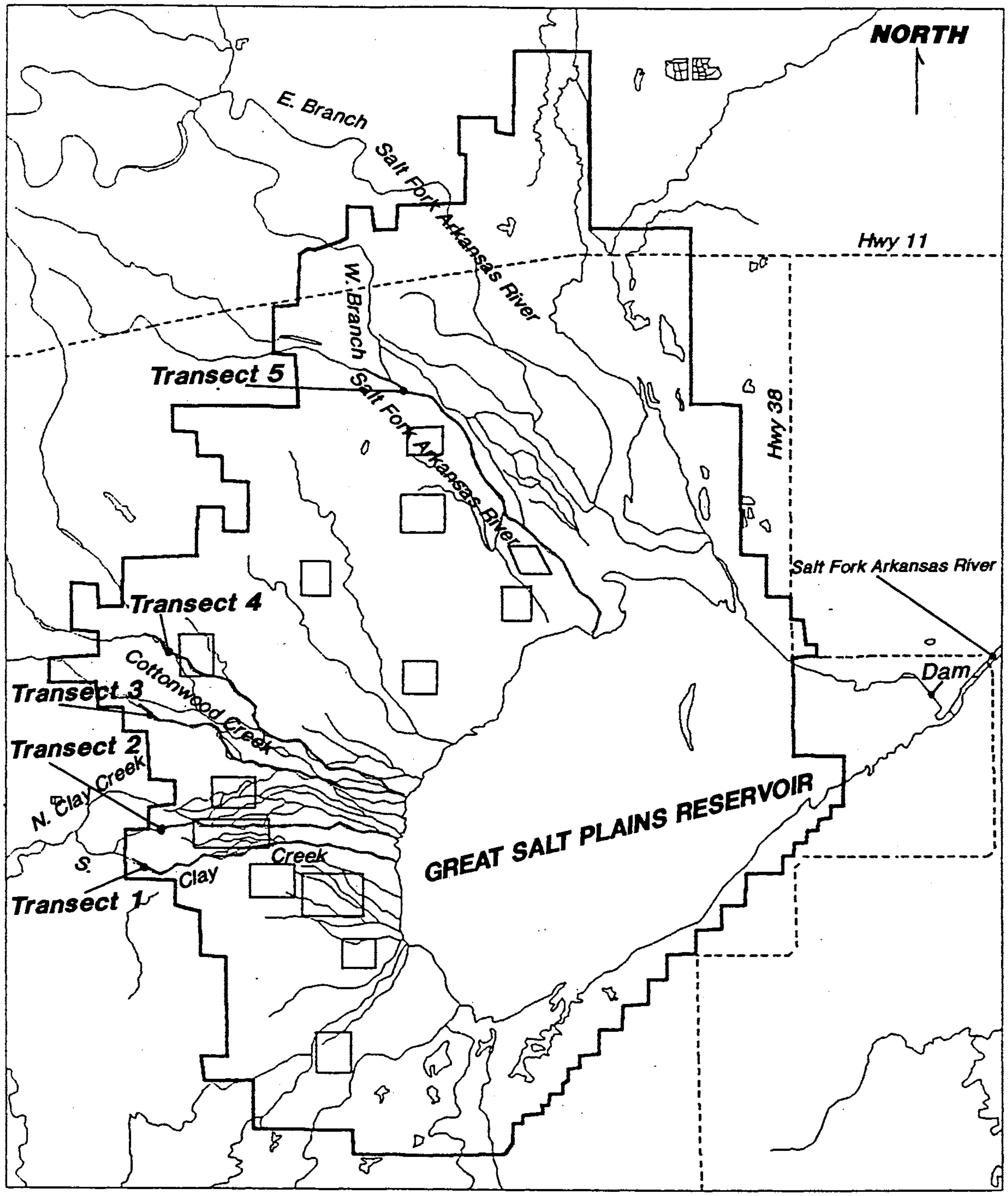
Table 11. Results of all-possible-regressions model selection procedure determining which variables best predicted variation in Least Tern and Snowy Plover density estimated by Variable Circular Plot (VCP), Purdue, and Colony Point Count (CPC) methods. Independent variables were X1: temperature, X2: relative humidity, X3: wind speed, X4: wind direction, X5: time of day, X6: census period, and X7: census stratum.

Species	Method	Year	Variables in Best Model	Model *P*-value	Adjusted R^2	Mean Square Error
-------------------- *All Independent Variables (X1 through X7)* --------------------						
Least Tern	VCP	1992	X6	0.0101	0.0434	1329.0232
	Purdue	1992	X6	0.1156	0.0609	135.4296
	VCP	1993	X6	0.0001	0.2378	848.3729
	CPC	1993	X6 X7	0.0001	0.4801	350.1836
Snowy Plover	VCP	1992	X2 X6 X7	0.0001	0.4126	801.2402
	Purdue	1992	X6	0.0252	0.1291	123.9049
	VCP	1993	X1 X6 X7	0.0001	0.6255	424.4641
	CPC	1993	X6	0.0001	0.5689	289.7993
------------------- *Environmental Variables Only (X1 through X5)* -------------------						
Least Tern	VCP	1992	X3	0.0817	0.0160	1367.1381
	Purdue	1992	X3 X5	0.4450	-0.0220	147.3756
	VCP	1993	X2 X4	0.0020	0.0895	1013.4766
	CPC	1993	X1 X2 X3	0.0001	0.2394	512.3197

Table 11. Continued.

Species	Method	Year	Variables in Best Model	Model *P*-value	Adjusted R^2	Mean Square Error
Snowy Plover	VCP	1992	X1 X3 X4 X5	0.0586	0.1464	121.4472
	Purdue	1992	X2	0.0111	0.0425	1306.1235
	VCP	1993	X1 X2 X3 X4 X5	0.0001	0.3673	717.1559
	CPC	1993	X1 X2 X3	0.0001	0.3643	427.3071

Figure 1. Salt Plains National Wildlife Refuge, the boundary of which is indicated by a bold line. Least Tern colony sites (Variable Circular Plot and Colony Point Count census strata) are indicated by rectangles. Transects 1 through 5 were parallel to waterways and censused for adult Least Terns and Snowy Plovers with the Purdue method. Scale: 1 cm = 1 km.


NORTH
E. Branch
Salt Fork Arkansas River
Hwy 11
W. Branch
Salt Fork Arkansas River
Transect 5
Hwy 38
Salt Fork Arkansas River
Transect 4
Cottonwood Creek
Dam
Transect 3
Transect 2
N. Clay Creek
GREAT SALT PLAINS RESERVOIR
S.
Creek
Clay
Transect 1

CHAPTER II

HABITAT SELECTION BY NESTING LEAST TERNS

Abstract: The interior population of least terns (*Sterna antillarum*) was listed as endangered in 1985 due primarily to loss of nesting habitat. To ensure recovery, habitat of primary importance must be identified, enhanced, protected, and/or restored. We identified macro- (among colony sites) and microhabitat (within colony sites) components of a salt flat selected by least terns for nesting. Nesting least terns followed a negative binomial distribution (clumped) among colony sites. Sites with relatively greater numbers of nests had predominantly bare ground with well-scattered, small pieces of driftwood or debris, coarse soils, and slightly elevated positions. Within colony sites, nests were either randomly or uniformly distributed. Overall mean distances between conspecific nests were 80.2 ± 3.5 (SE) m and 61.5 ± 6.3 m in 1992 and 1993, respectively. Overall, nests were significantly closer to driftwood or debris and on coarser soils than random points. Infrequently and sparsely used colony sites on the salt flat can be enhanced and restored by adding "pads" of coarse (sandy to sandy loam) soil and widely scattered, small

objects. If predators are attracted to improved sites, electric fencing and objects providing shelter for chicks should be added for protection.

The interior population of least terns has received increased attention for ≥10 yr due to its apparent non-cyclic decline (Sidle and Harrison 1990). Decreased numbers of breeding birds have been attributed to loss and degradation of riverine nesting habitat. Channelization, irrigation, construction of reservoirs, human recreational activities, and controlled flows by dams have adversely affected breeding habitat (Sidle and Harrison 1990). Natural factors affecting breeding success include predation, flooding, and catastrophic weather events (Grover 1979). Natural unchecked succession of plant species on formerly barren shorelines, sandbars, and alkaline flats has reduced quality and quantity of breeding habitat (Faanes 1983). In response to these threats, the U.S. Fish and Wildlife Service listed the interior population as endangered in 1985 (U.S. Govt. 1985).

Least terns nest on an alkaline flat at Salt Plains National Wildlife Refuge (NWR), Oklahoma, from late May to August (Grover and Knopf 1982, Hill 1985). Historically, the salt flat covered 11,137 ha (Ortenburger and Bird 1933). In 1941, 3,564 ha (32%; Purdue 1976) of the salt flat were flooded when the U.S. Army Corps of Engineers completed a dam across the Salt Fork of the Arkansas River creating the Great Salt Plains Reservoir. Since dam construction, silt and other fine soils have accreted upstream, filling the reservoir, river, and intermittent streams west of the dam (S. Schweitzer, pers. obs.). Increased flooding and soil deposition amenable to establishment of plant species (especially exotic salt cedar [_Tamarix_ _chinensis_ Lour.]; plant names according to Correll and Johnston 1970) have reduced salt flat area available for nesting least terns (Hill 1993). Although the remaining salt flat is expansive, a relatively small percentage is used for nesting by terns.

We hypothesized that (1) distribution of nesting least tern colonies over the salt flat was not random; (2) habitat features associated with locations used by nesting least tern colonies (colony sites) differed from features associated with locations not used by colonies; (3) nest scrapes in colony sites were not randomly distributed; and (4) least terns selectively placed nest scrapes relative to microhabitat features in colony sites. Tests of these hypotheses could increase our understanding of breeding habitat requirements of least terns in a salt flat environment and allow us to enhance and increase quality of remaining colony sites. Increasing the quantity of habitat meeting least tern requirements during breeding can potentially increase numbers of breeding adults on the salt flat through immigration and enhanced reproductive success, thereby increasing recruitment to the interior population.

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STUDY AREA

Our study was conducted on the salt flat of Salt Plains NWR, Alfalfa County, Oklahoma. The salt flat is mostly barren and seasonally encrusted with precipitated salt (Reed 1978) from brine drawn to the surface by capillary action (Grover and Knopf 1982). The land is level to gently sloping and is part of stream flood plains (Ortenburger and Bird 1933). The salt flat is crossed by the West Branch of the Salt Fork of the Arkansas River, Clay Creek, Cottonwood Creek, and intermittent streams. Frequent flooding occurs in spring and fall. Floodwaters may remain for days (Williams and Grover 1975) and carry debris onto the flats (Hill 1985). Hummocks of windblown sand anchored by vegetation occur near margins of the salt flat. Remnants of military structures (e.g., jeep trails, strafing targets) and debris (e.g., bullet encasements, metal shrapnel, "dummy" bombs) are present on the salt flat from its use as a bombing range in the 1940s.

Summers are long and usually hot (Ortenburger and Bird 1933). Average maximum daily air temperature recorded in Cherokee (about 5 km west of the salt flat) is 36°C in July and August (Williams and Grover 1975). Prevailing winds in summer are from the south (Ortenburger and Bird 1933), and average about 21 km/hr (Williams and Grover 1975). Spring is the windiest season; gusty southwesterly winds of 48 to 72 km/hr are common (Williams and Grover 1975).

METHODS

Macrohabitat Scale

In 1992 and 1993, we assessed habitat features in stratified areas of the salt flat northwest of Great Salt Plains Reservoir. We delineated colony sites used (>2 nests) in 1992 and 1993, and those documented as having been used in the past (Grover 1979, Hill 1985, Boyd 1990). Thus, colony sites were not compared to random sites but represented selected and unselected (during our study) sites. Transects were established through least tern colony sites and oriented perpendicular to any adjacent waterway. If there was no adjacent waterway, we randomly selected a north-south or east-west orientation for transects. Number (≤6) and length (≤500 m) of transects (placed 250 m apart) were determined by size of colony site.

Taylor's Power Law regression models (Taylor 1961, 1984) were applied to density estimates (birds/ha) to determine spatial distribution patterns of nesting least terns on the salt flat. Densities of breeding least terns were estimated from points on transects using variable circular plot and colony point count census methods during a concurrent part of this study (Schweitzer 1994). In Taylor's regression models, variance is related to the mean by a simple power law, $s^2 = am^b$, where a and b are characteristic of the population in question (Taylor 1961). The a is largely a sampling or computing factor, which is dependent on size of sampling unit and on the estimate of variance used. The b is an index of aggregation describing an intrinsic property of the population and follows a continuous gradation from near-regular ($b \rightarrow 0$) through random ($b = 1$) to highly aggregated ($b \rightarrow \infty$) (Taylor 1961).

To evaluate ground cover in colony sites, we placed a 10-point frame (Cook and Stubbendieck 1986) every 50 m, starting at a randomly selected point along each transect. At each point, we recorded whether each pin touched bare ground, driftwood, vegetation, or debris; results were expressed as percentages. To assess substrate type of the soil surface (top 3 to 6 cm) in colony sites, we estimated moist soil color using a Munsell Soil Color Chart (Anon. 1990) and soil texture using the "feel" method (Brady 1974:48) at each point along transects.

Microhabitat

We applied the nearest-neighbor procedure (Clark and Evans 1954, Krebs 1989) to measurements of distances between nearest conspecific nest scrapes to estimate spatial distribution patterns of nesting least terns in colony sites.

This procedure quantified the degree to which the distribution of nesting least terns in each colony site departed from random. The ratio of observed mean distance to expected mean distance served as the measure of departure from randomness (Krebs 1989).

We measured distances from the center of each nest to nearest water, vegetation, and driftwood or debris to determine if least terns selectively placed nest scrapes relative to microhabitat features in colony sites. Moist soil color and texture of each nest scrape were estimated in the field, and a sample was collected for particle-size analysis using the pipette method (Gee and Bauder 1986). The same measurements, except inter-nest distance, were recorded for a random point paired with each nest (Ratti and Garton 1994). Each random point was 10 m from its paired nest scrape in a random cardinal direction. All measurements were taken immediately after each colony site was abandoned and therefore did not exactly reflect features present when least terns selected the nest site. However, the only feature observed to change during the breeding season was placement of driftwood or debris. Error may have been introduced due to movement of these items during sheet-flooding of the salt flat.

We separated colony sites into "high" and "low" sites based on number of nests present to evaluate whether habitat features of colony sites with greater numbers of nests differed from colony sites with fewer nests. Colony sites with ≥11 nests were categorized as high sites and those with <11 nests were low sites. This categorization scheme divided 1992 and 1993 data sets into 2 equally-sized groups.

Statistical Analyses

Application of Taylor's Power Law regression models (Taylor 1961, 1984) entailed regressing variances against means on a log-log scale. Appropriateness of the null hypothesis--nesting least terns were normally distributed among colony sites on the salt flat--was tested with a t-test.

We examined associations between mean least tern density and soil color, density and soil texture, and soil color and soil texture using Spearman rank correlation (Pearson product-moment correlation coefficient based on ranked data; Neter et al. 1989:539). Significant associations were determined using a test statistic based on the t-distribution (Neter et al. 1989:540).

Spatial distribution of least terns in colony sites was assessed using nearest-neighbor analyses (Clark and Evans 1954, Krebs 1989). The index of aggregation (i.e., ratio of observed to expected mean distance to nearest neighbor) was tested for significant departure from the null hypothesis (H_0: $\rho = 1$, random distribution) with a z-test (Krebs 1989:128).

After subjecting all percent ground cover, soil, and distance measurement data to diagnostic tests (e.g., residual plots [Neter et al. 1989], Shapiro-Wilk's test [Shapiro and

Wilk 1965, SAS 1990], and Levene's test [Snedecor and Cochran 1980]), we determined that they did not meet the assumptions of parametric statistics even with appropriate transformations (Zar 1974). These data were therefore analyzed using nonparametric procedures. We used the rank transformation approach of Conover and Iman (1981), which applied parametric tests (e.g., t-test, F-test) to data ranked from smallest to largest. If tests for homogeneity among ≥2 means were significant ($P \leq 0.05$), we separated ranked means with least significant difference tests corrected for unequal sample sizes (LSMEANS option; SAS 1990).

RESULTS

Macrohabitat

Estimated slopes (b_1) of Taylor's Power Law regression models, developed using density estimates of breeding least terns in colony sites from variable circular plot and colony point count census methods (Schweitzer 1994), deviated significantly from 1.0 ($P < 0.01$). Therefore, data did not support the null hypothesis that least terns were normally distributed among colony sites on the salt flat. Least terns followed a negative binomial distribution (were clumped) among colony sites in 1992 and 1993.

In colony sites ($n = 16$), percent ground cover was predominantly bare ground (99.4 ± 0.1 [SE]%; range = 96.7-100.0%; $n = 654$). A small percentage of ground cover in colony sites was driftwood (0.1 ± 0.04%; 0.0-0.4%), vegetation (0.1 ± 0.1%; 0.00-1.2%), and debris (0.4 ± 0.1%; 0.0-1.1%). Means of percent ground cover variables (bare ground, driftwood, vegetation, debris) were not different among colony sites. Sea purslane (Sesuvium verrucosum Raf.) was the only species recorded as vegetative ground cover in colony sites.

Soil textures and colors differed among colony sites (Table 1). Textures ranged from sandy clay to sandy (smallest to largest particle-size), and Munsell colors ranged from 5YR 3/2 (dark reddish brown) to 7.5YR 4/4 (dark brown) (darkest to lightest colors). There were no significant associations between densities of least terns and soil colors or textures in colony sites. Soil color and texture were positively associated (r_s = 0.64, P = 0.0001); soil texture became more coarse as soil color became lighter.

Microhabitat

Nearest-neighbor analyses indicated that least tern nests were randomly distributed in 58% of colony sites (Table 2). Nests were uniformly distributed in 42% of colony sites. Assessment of the mean distance between nests of all colony data suggested that overall, nests were randomly distributed in colony sites (Table 2).

Overall mean distance between least tern nest scrapes was greater (P = 0.0001) in 1992 than 1993 (Fig. 1). In each year, mean distances between least tern nest scrapes and nearest vegetation and water were not different from those of random points (Fig. 1). However, nest scrapes were (P =

0.0001) closer to nearest driftwood or debris than were random points in each year (Fig. 1).

Mean soil texture of least tern nest scrapes was coarser ($P < 0.01$) (larger particle-size) than that of random points (Table 3). No difference was found between moist soil color of nests and random points in 1992, but soil color of nests was lighter ($P = 0.03$) than random points in 1993.

In 1992 and 1993, differences in mean inter-nest distances occurred among colony sites (Table 4). No differences were found in mean distances to nearest water and nearest driftwood or debris from nest scrapes among 1992 colony sites; differences were detected among colony sites for all other variables in 1992. There were differences from nest scrapes and random points to each habitat feature among colony sites in 1993. Within colony sites, only mean distance to nearest driftwood or debris differed between nest scrapes and random points (Table 4).

In colony sites with a high number of nests ($n \geq 11$; high sites), inter-nest distance was smaller than in colony sites with a low number of nests ($n < 11$; low sites); however, this difference was only significant ($P < 0.05$) in 1992 (Fig. 2). Mean distances from nest scrapes and random points to nearest vegetation were not different in or between high and low sites (Fig. 2). In 1993, nest scrapes and random points in high sites were farther from water than those in low sites (Fig. 2). Least tern nest scrapes were consistently closer to driftwood or debris than were random points (Fig. 2).

In high and low sites, nest scrapes tended to be placed on soils consisting of larger particle sizes than that of random points (Table 5). No soil color differences were found among nest scrapes and random points in high and low sites in 1992. In 1993, nest scrapes in high sites were on the lightest-colored soils (Table 5). Soils associated with nest scrapes and random points in high sites were lighter than those in low sites (Table 5).

DISCUSSION

When studying habitat use of colonial-nesting waterbirds, 2 aspects of distribution should be considered: (1) distribution of colony sites over broad geographic regions and (2) distribution of nests within a colony site (Speich 1986). Habitat selection and distribution patterns of colonial ground-nesting birds (e.g., least terns on the salt flat) are constrained by factors such as substrate suitability; distance to foraging sites; and protection from flooding, exposure (to high winds and temperatures, blowing sand, hail), and predators (Burger and Lesser 1978, Soots and Landin 1978, Grover and Knopf 1982, Carreker 1985, Speich 1986). After habitat requirements and factors limiting population growth are identified, managers can direct efforts toward enhancement, protection, and restoration with the ultimate goal of increasing numbers and reproductive success of nesting birds and achieving recovery of the species.

In our study, least terns exhibited an aggregated distribution pattern among sites evaluated on the expansive salt flat of Salt Plains NWR. Grover and Knopf (1982) observed that nesting least terns occurred in a clumped distribution on the salt flat "near" inflow streams or standing bodies of water present at the time of nest initiation. During their study, overall mean distance to nearest water from least tern nests was 69.5 ± 7.7 (± SE) m, which was significantly different from mean distance to water from random points (616.0 ± 39.8 m). Our measurements of distances from nests to nearest water ranged from 84.9 ± 12.8 to 599.1 ± 54.1 m (overall $\bar{x}$ = 316.4 ± 22.7 m). Thus, least terns did not nest immediately adjacent to waterways but closer than would be expected if nests were placed at random on the salt flat. Such nest placement provided direct access to foraging sites yet reduced nest loss due to flooding of waterways beyond their shorelines.

Percent ground cover did not differ among sites and was predominantly bare ground. We observed that least terns nested in areas with sparse, widely scattered driftwood, vegetation, and debris. Grover and Knopf (1982) also found driftwood and debris widely distributed in least tern colony sites and few least tern nests among aggregations of driftwood and debris along stream shorelines (wrack lines). Coyotes frequently followed linear configurations provided by wrack lines and old military jeep trails on the salt flat

(Grover and Knopf 1982, Hill 1985). Birds nesting in these areas often lost nests to coyote predation (Hill 1985).

Studies along interior, riverine sand bars and islands and man-made sand pits found that least terns selected sites with ≤10% vegetative cover (Kirsch 1990, Smith and Renken 1991, Dirks et al. 1993, Wilson et al. 1993). This percentage may increase over the breeding season but should be ≤10% while terns are selecting nesting sites (Soots and Landin 1978). It is essential for terns to have clear, unobstructed visibility from their nest site (Faanes 1983). The small amount of vegetation recorded in colony sites on the salt flat was low-growing (<10 cm) and did not create a visual barrier.

Although soil textures and colors differed among sites and were positively associated, lack of significant associations between these features and least tern densities suggested that they did not have a strong effect on selection of colony sites. Terns nesting on inland riverine sandbars, islands, and shorelines tended to select fine to coarse sand (Kirsch 1990, Wilson et al. 1993). Swickard (1974) found that potential nesting sites on a California salt flat were composed of clay-silt soils that had poor permeability and an increased potential for flooding nests. In our study, soil samples from nest scrapes in colony sites with a relatively high number of nests ($n \geq 11$) tended to be coarser suggesting that least terns preferred nest sites with more permeable, friable, and camouflaging soils, which would enhance nest success and chick survival. In addition, Krey et al. (1993) found that sand was significantly cooler than other substrates tested during afternoon and evening hours on the salt flat.

Colony sites with relatively greater numbers of nests tended to remain unflooded after precipitation events of ≥3 cm. This amount of precipitation inundated other sites. Colony sites containing greater numbers of nests may have remained drier due to their coarse, permeable soils and slightly greater elevations. Least tern use of salt flat habitat appeared to be constrained by availability of coarse soils and elevated sites. Flooding is the primary cause of nest loss on this salt flat (Grover and Knopf 1982, Hill 1985, Utych 1993) and many riverine (Faanes 1983, Smith and Renken 1991) habitats. Selection by least terns for slight elevations in the microhabitat of colony sites has been well-documented in riverine and coastal habitats (Soots and Landin 1978, Thompson and Slack 1982, Faanes 1983, Sidle et al. 1992, Renken and Smith 1993) and also appeared to be a behavioral trait of terns in the salt flat environment that we examined.

Spatial distributions of nest scrapes in colony sites were either random or uniform. A random distribution implied existence of environmental homogeneity and/or nonselective behavioral patterns, and a uniform distribution suggested that there were constraints on the population and/or negative interactions between individuals (Ludwig and Reynolds 1988).

On the salt flat, least terns formed loose colonies with large distances (21.4 ± 4.6 to 101.7 ± 2.1 m) between conspecifics. The smaller overall inter-nest distance in 1993 (61.5 ± 3.3) was probably a reflection of less available habitat during that nesting season. Twice as many ≥3-cm precipitation events occurred in 1993 than 1992, and many sites available for nesting in 1992 were flooded during all or part of the 1993 nesting season. Secondly, 1993 nest distribution patterns in colony sites tended to be more uniform than in 1992. These results reflect the ability of terns to use available habitat opportunistically but to maintain relatively large inter-nest distances. Burger (1988) reported least terns nesting as close as 0.5 m on the New Jersey coast, and Massey (1974) recorded California least terns nesting 3 m apart. On the Platte River, Kirsch (1990) reported inter-nest distances of 17.8 ± 6.5 m on sand bars and 19.5 ± 8.0 m on spoil sites. Inter-nest distances of terns at Salt Plains NWR were greater, perhaps an adaptation to the expansive salt flat habitat.

Nest scrapes in colony sites were placed closer to small pieces of driftwood or debris more frequently than would be expected if they were placed at random. The selection for placement of nests near small objects must be strong considering the small percentage of ground cover in colony sites that was driftwood or debris. The placement of nests near small objects was also observed by Grover and Knopf (1982) and Hill (1985) on the salt flat. Terns nesting along riverine systems of the interior United States also tend to place nests near small objects (Smith and Renken 1991, Dirks et al. 1993, Renken and Smith 1993). Such nest placement provides a more prominent search image for terns on a generally featureless salt flat and gives increased protection to eggs and chicks from predators (especially avian predators that search visually for prey), wind, rain, hail, blowing sand, and intense heat (Burger and Lesser 1978, Dinsmore and Dinsmore 1989, Smith and Renken 1991).

Previous studies on the salt flat did not quantify soil textures using standardized methods. Hill (1985) determined soil type (alkaline, sand/stone, and clay) by observation and reported that 76.6% of least tern nests were on alkaline soils. No previous studies examined selection for soil color. We found that least terns scraped nests out of significantly coarser soils (e.g., loamy sand, sandy loam) than would be expected if nests were placed at random in colony sites. Because overall means of Munsell soil colors were significantly different between nest scrapes and random points in only one year, soil texture appeared to be a stronger cue for site selection. Terns nesting in riverine environments selectively place nests on small gravel, coarse sand, and fine sand (Faanes 1983, Renken and Smith 1993, Wilson et al. 1993). Soils available along rivers and on coastlines are predominantly sands and may not be a primary factor in nest site selection. In colony sites along the Mississippi River adjacent to Missouri, Renken and Smith

(1993) did not find differences between soil texture of nests and random points.

Least tern colonies were clumped on the salt flat but nest scrapes within colony sites were either randomly or uniformly distributed. Distribution on a macrohabitat scale appeared to be influenced primarily by proximity to foraging sites, unobstructed visibility, and reduced probability of flooding (slightly greater elevations, coarser soils with greater permeability). In colony sites on a microhabitat scale, least terns placed nests >20 m from nearest conspecific nest, close to small objects (driftwood or debris), and on coarser soils than that of random points.

MANAGEMENT IMPLICATIONS

About 32% of the original salt flat of Salt Plains National Wildlife Refuge was inundated when a dam was constructed on the Salt Fork of the Arkansas River (Purdue 1976). Recently, >400 ha of open salt flat habitat has been replaced by salt cedar (Hill 1993). Of the remaining habitat, sites with slightly elevated topography, coarse soils, and a small percentage of randomly dispersed driftwood or debris is selected by nesting least terns.

To attract additional nesting least terns to the salt flat and to increase nesting success, colony sites with low numbers of nests could be enhanced by supplementing and slightly elevating the habitat with coarse (sandy to sandy loam) soils. Swickard (1974) successfully enhanced a salt flat nesting area for least terns in California. She provided an elevated, sandy area for terns in a previously-used site and increased the number and success of nests. Boyd (1990, 1993) increased nest success of terns on a salt flat at Quivira NWR, Kansas, by providing nest mounds of egg-sized stone and sand. Enhancing colony sites on the salt flat of Salt Plains NWR with sandy to sandy loam soils and widely scattered (≥20 m apart) small pieces of driftwood and debris would provide better camouflage and protection for tern eggs and chicks, greater permeability (reduced probability of flooding), and increased friability (reduced effort associated with nest construction). Enhanced sites may appear novel to coyotes and thus, attract them. Predation by coyotes can be minimized or eliminated by surrounding enhanced sites with electric fences (Massey 1988, Boyd 1990, Mayer and Ryan 1992, Utych 1993) when necessary and feasible.

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Table 1. Field-estimated textures[a] and colors[b] of soil in habitat available to nesting least terns at Salt Plains National Wildlife Refuge, Oklahoma.

Colony	Soil texture			Soil color								
	Score			Score		Hue		Value		Chroma		
Site	$\bar{x}^{c}$	SE	Class	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	Munsell color
A	6.6f	0.5	SCL	12.6def	0.2	5.3	0.2	3.7	0.1	3.5	0.1	5YR 4/4
B	4.6h	0.3	SC	12.6def	0.2	5.0	0.0	3.7	0.1	3.9	0.2	5YR 4/4
C92	6.2f	0.4	SCL	11.8f	0.3	5.6	0.2	3.5	0.1	2.7	0.2	5YR 3/3
C93	5.4ef	0.2	SC	12.2ef	0.2	5.0	0.0	4.1	0.1	3.1	0.1	5YR 4/3
Da	4.9gh	0.2	SC	11.4f	0.4	5.7	0.2	3.3	0.1	2.4	0.2	5YR 3/2
Db	6.1f	0.3	SCL	12.4def	0.2	5.0	0.0	3.7	0.1	3.7	0.2	5YR 4/4
Dc	6.8de	0.3	SL	12.5ef	0.3	5.6	0.2	4.0	0.1	3.0	0.1	5YR 4/3
E	7.0e	0.3	SL	12.9d	0.2	6.4	0.1	3.7	0.1	2.8	0.1	7.5YR 4/3
F	8.6bc	0.2	S	13.7b	0.1	6.0	0.2	4.0	0.0	3.6	0.1	5YR 4/4
G	8.6bc	0.2	S	12.8de	0.1	5.2	0.1	4.0	0.0	3.6	0.1	5YR 4/4
H	5.1gh	0.2	SC	13.1cd	0.2	5.5	0.1	4.1	0.0	3.5	0.1	5YR 4/4
I	8.9b	0.3	S	13.9b	0.3	6.9	0.2	4.0	0.1	3.0	0.2	7.5YR 4/3
J	7.6cd	0.4	LS	13.9b	0.2	7.2	0.1	3.8	0.1	2.9	0.2	7.5YR 4/3
K	9.5a	0.2	S	15.8a	0.2	7.4	0.1	4.5	0.1	3.8	0.2	7.5YR 4/4
L	8.5bc	0.4	LS	13.9b	0.3	6.5	0.2	4.1	0.1	3.3	0.2	7.5YR 4/3
M	5.6fg	0.4	SCL	13.6bc	0.2	5.4	0.2	4.0	0.0	4.2	0.2	5YR 4/4

Table 1. Continued.

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[a] Soil texture class abbreviations are (from smallest to largest particle-size): SC, sandy clay; SCL, sandy clay loam; SL, sandy loam; LS, loamy sand; and S, sandy.

[b] Soil color estimates were aided by a Munsell Soil Color Chart. A soil sample's hue indicated its relation to red, yellow, green, blue, and purple; value indicated its lightness; and chroma indicated its strength (or departure from a neutral of the same lightness).

[c] Mean scores in a column followed by ≥1 similar letter(s) are not different ($P > 0.05$); determined by analysis of variance of ranked data followed by LSMEANS mean separation procedure.

Table 2. Spatial distribution pattern from nearest-neighbor analyses of nesting least terns in colony sites at Salt Plains National Wildlife Refuge, Oklahoma.

Colony Site	Number of Nests	Area (m^2)	Density (nests/m^2)	Mean dist. Between Nests (m)	Expected dist. Between Nests (m)	Index of Aggregation (R)	SD	Test Statistic (z)	Spatial Pattern
					1992				
F	11	400,000	2.75x10^{-5}	93.96	95.35	0.98	15.03	-0.09	random
G	12	160,000	7.50x10^{-5}	71.18	57.74	1.23	8.71	1.54	random
K	20	375,000	5.33x10^{-5}	66.35	68.46	0.97	8.00	-0.26	random
L	15	375,000	4.00x10^{-5}	90.60	79.06	1.15	10.67	1.08	random
M	5	75,000	6.67x10^{-5}	70.48	61.24	1.15	14.32	0.64	random
N	6	87,500	6.86x10^{-5}	101.67	60.38	1.68	12.88	3.20	uniform
					1993				
Dc	10	275,000	3.64x10^{-5}	90.80	82.92	1.10	13.70	0.58	random
F	25	108,750	2.30x10^{-4}	56.03	32.98	1.70	3.45	6.69	uniform
FC	14	270,000	5.18x10^{-5}	89.54	69.44	1.29	9.70	2.07	uniform
G	7	20,000	3.50x10^{-4}	44.74	26.73	1.67	5.28	3.41	uniform
KL	10	295,132	3.39x10^{-5}	62.39	85.90	0.73	14.20	-1.66	random
CH	11	11,000	1.0x10^{-3}	21.38	15.81	1.35	2.49	2.24	uniform
Totals	12	204,365	5.95x10^{-5}	71.59	64.80	1.10	9.71	0.70	random

Table 3. Soil textures and colors of least tern nests and paired random points over all colony sites at Salt Plains National Wildlife Refuge, Oklahoma.

	Nest scrape			Random point			
Soil characteristic	$\bar{X}$	SE	n	$\bar{X}$	SE	n	*P*-value[a]
Texture							
1992							
Score	7.6	0.2	69	6.6	0.2	69	0.0033
Class	loamy sand			sandy loam			
1993							
Score	7.3	0.2	76	6.2	0.2	77	0.0024
Class	sandy loam			sandy clay loam			
Color							
1992							
Score	15.1	0.1	69	14.7	0.2	69	0.2839
Hue	7.2	0.1		7.0	0.2		
Value	4.5	0.1		4.2	0.1		
Chroma	3.4	0.1		3.5	0.1		
Closest Munsell color	7.5YR 4/3, dark brown			7.5YR 4/4, dark brown			
1993							
Score	15.2	0.2	76	14.8	0.2	77	0.0266
Hue	7.3	0.1		7.3	0.1		
Value	4.6	0.1		4.2	0.1		
Chroma	3.3	0.1		3.3	0.1		
Closest Munsell color	7.5YR 5/3, brown			7.5YR 4/3, dark brown			

[a] Means in rows are different if $P \le 0.05$; determined by *t*-tests on ranked data.

Table 4. Distances (m) between nearest habitat features and least tern nest scrapes or paired random points in colony sites at Salt Plains National Wildlife Refuge, Oklahoma.

	1992											
	Site F (n = 11)		Site G (n = 12)		Site K (n = 20)		Site L (n = 15)		Site M (n = 5)		Site N (n = 6)	
Habitat Feature	$\bar{x}$[a]	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Conspecific nest &												
Nest scrape	94.0a	6.2	71.2ab	10.9	66.4b	6.5	90.6a	4.9	70.5ab	14.2	101.7a	2.1
Water &												
Nest scrape	>100.0	0.0	98.9	4.3	>100.0	2.3	>100.0	0.0	84.9	12.8	>100.0	0.0
Random point	>100.0a	0.0	98.9ab	4.2	>100.0a	2.2	>100.0a	0.0	84.2b	12.8	>100.0a	0.0
Vegetation &												
Nest scrape	>100.0a	0.0	47.1c	12.0	78.5b	7.7	>100.0a	0.0	21.4c	7.2	>100.0a	0.0
Random point	>100.0a	0.0	49.3c	11.8	79.7b	7.5	>100.0a	0.0	21.2c	6.8	>100.0a	0.0
Driftwood/Debris[b] &												
Nest scrape	0.0A	0.0	9.2A	4.4	1.9A	0.8	0.3A	0.3	0.1A	0.1	0.6A	0.6
Random point	3.9cB	1.0	15.8aB	3.7	4.1cB	0.8	3.8bcB	0.7	1.8cB	0.6	7.1abB	1.4

[a] Means in rows (among sites) followed by ≥1 similar lowercase letter(s) are not different ($P > 0.05$); determined by analysis of variance of ranked data followed by LSMEANS mean separation procedure.

[b] In each colony site, nest scrape and random point means are different ($P < 0.05$) if followed by different capital letters; determined by *t*-tests on ranked data.

Table 4. Extended.

Habitat Feature	1993											
	Site CH (n = 11)		Site Dc (n = 10)		Site F (n = 25)		Site FC (n = 14)		Site G (n = 7)		Site KL (n = 10)	
	$\bar{X}$[b]	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Conspecific nest &												
Nest scrape	21.4b	4.6	90.8a	21.2	56.0a	4.9	89.5a	26.3	44.7a	5.2	62.4a	9.6
Water &												
Nest scrape	120.0cd	0.0	349.0b	31.4	352.9b	17.9	599.1a	54.1	205.4c	0.0	90.8d	11.5
Random point	120.0cd	0.0	349.0b	31.4	352.9b	17.9	599.5a	54.1	205.4c	0.0	91.5d	12.4
Vegetation &												
Nest scrape	18.2c	4.6	468.0a	37.9	159.1b	37.3	543.8a	47.1	19.4c	7.0	101.8b	31.5
Random point	18.0c	4.1	468.0a	38.0	158.1b	37.4	544.9a	46.5	20.4c	5.0	102.6b	30.4
Driftwood/Debris[b] &												
Nest scrape	4.3a	2.2	0.6bA	0.5	0.2bA	0.2	0.0bA	0.0	7.0a	3.8	0.4bA	0.3
Random point	4.5a	1.4	2.7abB	1.1	1.5bB	0.4	3.1aB	0.5	4.9a	1.3	3.4aB	0.8

[a] Means in rows (among sites) followed by ≥1 similar lowercase letter(s) are not different ($P > 0.05$); determined by analysis of variance of ranked data followed by LSMEANS mean separation procedure.

[b] In each colony site, nest scrape and random point means are different ($P < 0.05$) if followed by different capital letters; determined by t-tests on ranked data.

Table 5. Soil characteristics of least tern nest scrapes and random points in colony sites with high (≥11) and low (<11) numbers of nests at Salt Plains National Wildlife Refuge, Oklahoma.

	Soil texture			Soil color			
	Score		Class[a]	Score		Munsell color	
Grouping	$\bar{x}$[b]	SE		$\bar{x}$	SE	Notation	Name
1992							
High (*n* = 47)							
Nest scrape	8.3a	0.3	LS	15.1a	0.2	7.5YR 4/3	dark brown
Random point	6.9b	0.3	SL	14.8a	0.2	7.5YR 4/4	dark brown
Low (*n* = 22)							
Nest scrape	6.3b	0.4	SCL	15.1a	0.2	7.5YR 4/3	dark brown
Random point	5.9b	0.4	SCL	14.6a	0.4	7.5YR 4/3	dark brown
1993							
High (*n* = 49)							
Nest scrape	7.4a	0.3	SL	15.5a	0.1	7.5YR 5/3	brown
Random point	6.4b	0.3	SCL	15.1b	0.2	7.5YR 4/3	dark brown
Low (*n* = 27)							
Nest scrape	7.1ab	0.5	SL	14.5c	0.3	7.5YR 4/3	dark brown
Random point	5.8b	0.4	SCL	14.2c	0.3	7.5YR 4/3	dark brown

[a] Soil texture class abbreviations are (from smallest to largest particle-size): SCL, sandy clay loam; SL, sandy loam; and LS, loamy sand.

[b] Within year and column, means followed by ≥1 similar letter(s) are the same (*P* > 0.05); determined by analysis of variance of ranked data followed by LSMEANS mean separation procedure.

Figure 1. Mean distances (SE) between nearest conspecific nests, and between nest scrapes or random points and nearest habitat feature. Asterisks (**) above bars indicate significant difference between means ($\underline{P} < 0.01$); determined by $\underline{t}$-tests of ranked data.

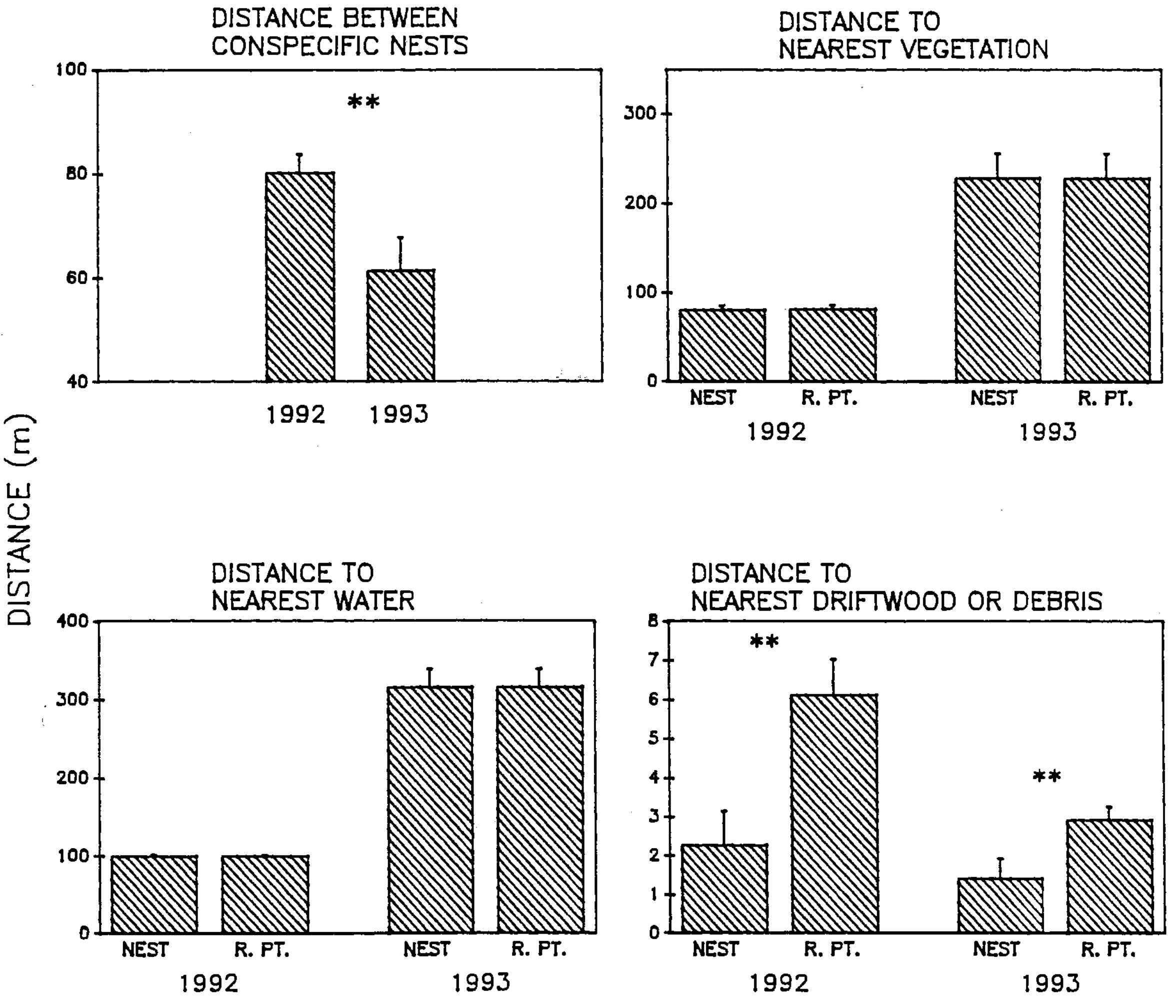
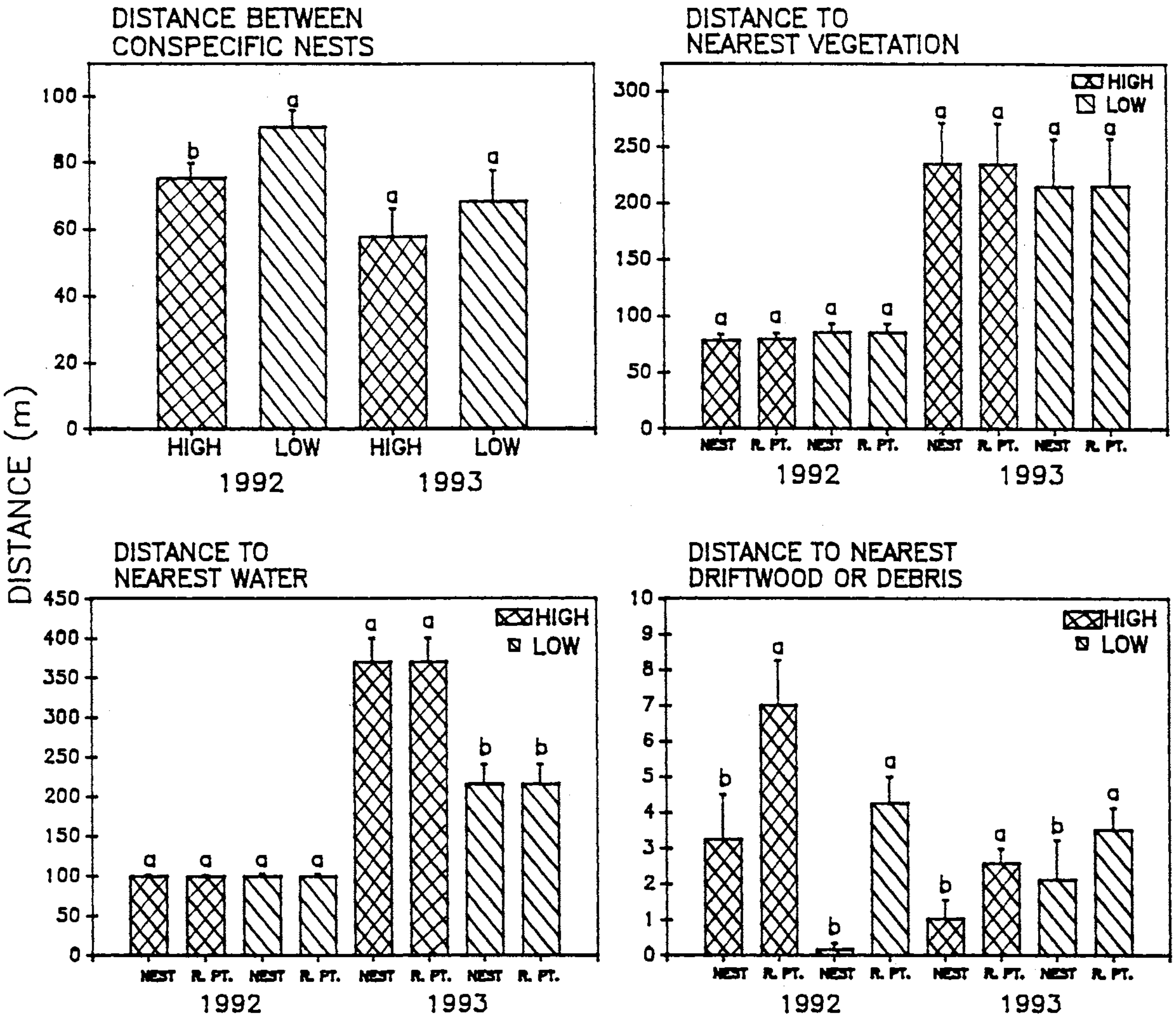

DISTANCE (m)
DISTANCE BETWEEN CONSPECIFIC NESTS
100
80
60
40
**
1992
1993
DISTANCE TO NEAREST VEGETATION
300
200
100
0
NEST
R. PT.
NEST
R. PT.
1992
1993
DISTANCE TO NEAREST WATER
400
300
200
100
0
NEST
R. PT.
NEST
R. PT.
1992
1993
DISTANCE TO NEAREST DRIFTWOOD OR DEBRIS
8
7
6
5
4
3
2
1
0
**
**
NEST
R. PT.
NEST
R. PT.
1992
1993

Figure 2. Mean distances (SE) between nearest conspecific nests, and between nest scrapes or random points and nearest habitat feature in colony sites with high ($\underline{n} \geq 11$) and low ($\underline{n} < 11$) numbers of nests. In each year, different letters above bars indicate differences among means ($\underline{P} < 0.05$); determined by analysis of variance of ranked data followed by LSMEANS mean separation procedure.


DISTANCE (m)
DISTANCE BETWEEN CONSPECIFIC NESTS
0
20
40
60
80
100
b
a
a
a
HIGH
LOW
HIGH
LOW
1992
1993
DISTANCE TO NEAREST VEGETATION
HIGH
LOW
0
50
100
150
200
250
300
a
a
a
a
a
a
a
a
NEST
R. PT.
NEST
R. PT.
NEST
R. PT.
NEST
R. PT.
1992
1993
DISTANCE TO NEAREST WATER
HIGH
LOW
0
50
100
150
200
250
300
350
400
450
a
a
a
a
a
a
b
b
NEST
R. PT.
NEST
R. PT.
NEST
R. PT.
NEST
R. PT.
1992
1993
DISTANCE TO NEAREST DRIFTWOOD OR DEBRIS
HIGH
LOW
0
1
2
3
4
5
6
7
8
9
10
b
a
b
a
b
a
b
a
NEST
R. PT.
NEST
R. PT.
NEST
R. PT.
NEST
R. PT.
1992
1993

CHAPTER III

LEAST TERN FORAGING PATTERNS ON AND ADJACENT TO A SALT FLAT IN NORTH-CENTRAL OKLAHOMA

ABSTRACT--Because the endangered interior population of least terns (Sterna antillarum) is piscivorous, locations of colony sites and reproductive success are strongly influenced by distance to bodies of water with available forage. We examined foraging success and patterns of least terns nesting on the salt flat in north-central Oklahoma during the 1992 and 1993 breeding seasons. Our objectives were to:
(1) estimate whether there were limited quantities of forage available to breeding least terns; (2) examine least tern use of bodies of water adjacent to the salt flat; and
(3) identify fish species brought to colony sites and in bodies of water adjacent to the salt flat. Chicks were fed smaller fish than were brooding adults and chicks were offered more fish than they consumed. Adults did not forage off the salt flat during incubation and brooding (peak hatching). Foraging success of terns observed fishing off the salt flat from May to June was increased by fingerlings available at a fish hatchery approximately 12 km from the salt flat. During incubation, brooding, and fledging (July),

the only location off of the salt flat where terns were observed feeding was the eastern shoreline of the Great Salt Plains Reservoir. Collections of fish dropped and left uneaten by least terns in colony sites contained six species. These collections served as an index of species selected by least terns. The six species of dropped fish were present in all samples seined from adjacent waterways. Sizes of fish in seine samples and of fish brought to nests were smaller than those of fish found dropped and uneaten in colony sites. These uneaten fish may have been too big to consume. Quantity and quality of fish available to least terns during our study were adequate and did not appear to limit reproductive success. Forage availability may only be a limiting factor to reproductive success during drought years.

The endangered interior population of least terns (Sterna antillarum) nests on sandy islands, sandbars, and shorelines of inland waterways, and a small percentage (7%; Boyd, 1989; Sidle and Harrison, 1990) nests on alkaline flats in Kansas and Oklahoma. Least terns are primarily piscivorous, only occasionally feeding on invertebrates (McDaniel and McDaniel, 1963; Wilson et al., 1993). Locations of colony sites and reproductive success are strongly influenced by distance to bodies of water with available forage (Moseley, 1976; Atwood and Kelly, 1984; Massey and Atwood, 1984; Carreker, 1985). Factors determining prey availability include fish size, behavior, and quantity.

In general, adult least terns consume fish ranging in size from 2.0 to 9.0 cm long (Massey, 1974; Moseley, 1976; Massey and Atwood, 1980; Atwood and Kelly, 1984), and chicks <10 days old are fed smaller fish from 1.5 to 4.0 cm long (Moseley, 1976; Atwood and Kelly, 1984). In addition to length, fish rotundity or body depth influences availability of fish to terns (Courtney and Blokpoel, 1980). Fish with body depths >1.5 cm were considered unsuitable by Atwood and Kelly (1984) because the maximum horizontal gape width of adult least terns was 1.5 cm. Hulsman (1981) found a strong positive association between width of gape and size of prey consumed by terns.

Species of fish captured by least terns tend to be surface schoolers (Wilson et al., 1993) that are found in shallow water. Consequently, shallow-water habitats are primary foraging sites for least terns (Atwood and Minsky, 1983; Massey and Atwood, 1984; Carreker, 1985). Talent and Hill (1985) found that least terns nesting on the salt flat of Salt Plains National Wildlife Refuge (NWR) in north-central Oklahoma selectively foraged in bodies of water ≤62 cm deep. Terns opportunistically forage in suitable waters as close as 100 m from sandy island colony sites (Faanes, 1983) and ≤6.4 km from salt flat colony sites (Talent and Hill, 1985).

Terns are categorized as "surface plungers" (Eriksson, 1985) because they search for prey while flying or hovering 5 to 10 m above the water surface and plunge into water to capture or pursue detected prey (Moseley, 1976). Eriksson (1985:2) explained that surface plungers could only "exploit the volume of water closest to the surface" because they were constrained by their search height, visual angle, and maximum diving depth. Terns, in general, have a maximum diving depth of <1 m (Salt and Willard, 1971; Eriksson, 1985). Therefore, a decline in density of surface-schooling fish, water transparency, or an increase in aquatic vegetation would reduce suitability of a site for foraging least terns.

As indicators of forage availability to terns nesting on the salt flat of Salt Plains NWR, we examined chick feeding rates, sizes of fish brought to nests, foraging sites used throughout the breeding season, and foraging success. In addition, we collected fish dropped and left uneaten by least terns in colony sites and sampled fish in bodies of water adjacent to the salt flat to identify selected and available fish species. Our objectives were to: (1) estimate whether there were limited quantities of forage available to breeding least terns; (2) examine least tern use of waters adjacent to the salt flat; and (3) identify and compare fish species brought to colony sites with those in waters adjacent to the salt flat.

MATERIALS AND METHODS--Our study was conducted during the 1992 and 1993 least tern breeding seasons at Salt Plains

NWR. The salt flat at the refuge originally covered 11,137 ha (Ortenburger and Bird, 1933). In 1941, 3,564 ha (32%; Purdue, 1976) of the salt flat was flooded when the U.S. Army Corps of Engineers completed a dam across the Salt Fork of the Arkansas River creating the Great Salt Plains Reservoir (Fig. 1). Since dam construction, silt and other fine soils have accreted upstream, filling the reservoir, river, and intermittent streams west of the dam (S. Schweitzer, pers. obs.). Salt Plains NWR manages several shallow-water ponds east of the salt flat. Additionally, Byron State Fish Hatchery is about 12 km northeast of the salt flat (distance estimated from center of salt flat). Habitats adjacent to the salt flat are predominantly grazed rangeland and cultivated fields.

The salt flat is mostly barren and seasonally encrusted with precipitated salt (Reed, 1978) from brine drawn to the surface by capillary action (Grover and Knopf, 1982). The land is level to gently sloping and is part of stream flood plains (Ortenburger and Bird, 1933). The salt flat is crossed by the West Branch of the Salt Fork of the Arkansas River, Clay Creek, Cottonwood Creek, and intermittent streams. Frequent flooding occurs in spring and fall. Floodwaters may remain for days (Williams and Grover, 1975) and carry debris onto the flats (Hill, 1985).

Summers are long and usually hot (Ortenburger and Bird, 1933). Average maximum daily air temperature recorded in Cherokee (about 5 km west of the salt flat) is 36°C in July and August (Williams and Grover, 1975). Prevailing winds are from the south (Ortenburger and Bird, 1933), and average about 21 km/h (Williams and Grover, 1975). Spring is the windiest season, during which gusty southwesterly winds of 48 to 72 km/h are common (Williams and Grover, 1975).

Least terns arrive in the area from mid- to late-May from their wintering grounds in Central and South America. Breeding activities extend from late-May through early to mid-August. Terns use the reservoir shoreline as a staging site before migration in August.

Observations (1.5 h at each nest) of chick feeding rates, number and size of fish brought to nests, and behavior were conducted with a 10 to 60 x zoom spotting scope from a blind (i.e., white sheet covering observer and tripod) located ≥50 m from nests. Sizes of fish brought to nests were estimated relative to adult bill length (2.6 cm ± 0.4 SE; Schweitzer, 1994) and placed into the following size classes: ≤1.3, 1.4-2.0, 2.1-2.6, 2.7-3.0, and >3.1 cm.

Preliminary surveys were conducted in mid- to late-May to locate least tern feeding sites off of the salt flat. We conducted observations of feeding terns at these sites from late May through the second week of August. We counted number of fishing terns, dives, and fish-captures from fixed stations at each site to estimate relative use among sites and fishing success. We established four stations at the Byron State Fish Hatchery, four at Refuge ponds, and seven along the reservoir shoreline. All observations were conducted with 10 by 50x binoculars. Data were summarized in the following periods of the breeding season: arrival (1 to 31 May); early (incubation: only eggs present in nests, 1 June to 4 July); middle (incubation and brooding: eggs and chicks present in nests, 5 to 20 July); and late (incubation, brooding, and fledging: eggs, chicks, and fledglings present in nest areas, 21 July to 15 August).

All fish found on the substrate within colony sites were collected. These fish were presumed dropped and left uneaten by least terns (Atwood and Kelly, 1984; Massey and Atwood, 1984). In addition, samples of fish were collected by seining from waterways upstream of the salt flat, the southwestern shallow-water shoreline of the Great Salt Plains Reservoir, and downstream of the Great Salt Plains dam. Each location's sample consisted of ≥2 hauls with a 4 by 0.5-m, 3-mm mesh seine, parallel to the shoreline. All seine samples were collected on 12 July 1992. Fish were counted, identified by species, and measured for length and depth.

Differences in mean feeding frequencies (fish/h) at least tern nests with one or two chicks, overall mean foraging success of adult least terns among periods of the breeding season, and lengths and depths of fish between samples collected in colony sites and upstream of the salt flat were examined using Kruskal-Wallis Tests (Chi-Square Approximation; SAS, 1990). Tests were significant if $\underline{P} < 0.05$.

RESULTS--We observed feeding behavior at 17 nests for 26 hours. Mean number of chicks per nest was 1.2 ± 0.1 SE. Mean age of chicks observed was 3.0 days ± 0.8 SE. Chicks >3 days old leave nests (Massey, 1974; Moseley, 1976; Carreker, 1985) and are difficult to relocate on the salt flat; hence, observations were conducted on only three chicks >3 days old. Mean feeding rate was 2.0 fish/h ± 0.3 SE, and overall time between feedings was 24.5 min ± 2.2 SE. Fish were brought to nests containing two chicks more frequently than to nests with one chick (Fig. 2). Of fish brought to nests, 58.4% ± 10.8 SE was offered directly to a chick. In 36.9% ± 9.4 SE of the observations, a fish was transferred to the brooding adult then to a chick. Chicks did not always take fish offered to them, but 59.5% ± 8.6 SE of fish were taken and consumed. Brooding adults consumed 33.4% ± 8.6 SE of fish brought to nests. The sum of these two percentages did not equal 100% because in a couple of instances the bird delivering a fish either ate or flew away with it before offering it to either a chick or brooding adult. Mean estimated length of fish brought to nests was 2.9 cm ± 0.4 SE. Young chicks (<2 days old) were offered and consumed a greater percentage of small fish than older chicks (≥3 days old; Table 1). The three chicks ≥10 days old were only offered 2.6-cm long fish. Only adults ate fish >3.1 cm long.

More least terns foraged off the salt flat during arrival, early, and late periods than during the middle period of the breeding season (Table 2). No terns were observed feeding off the salt flat during the middle (peak hatching) period. During the late period (late July to mid-August), the only area off of the salt flat terns were observed feeding (except one tern at the hatchery) was the eastern shoreline of the reservoir. Foraging success varied among periods and locations (Table 2). The greatest overall success (21.1% ± 14.5 SE) occurred during the early period and was strongly influenced by the success rate (50.0%) at fish hatchery ponds.

Twelve species of fish were identified in all waterway and colony site collections (Table 3). The lowest number of species identified from a body of water was nine, in the Salt Fork of the Arkansas River, downstream of the Great Salt Plains Reservoir dam. Six species of dropped and uneaten fish were collected from the substrate within colony sites. Upstream of the salt flat, plains minnows (Hybognathus placitus) were most common in seine samples. In the reservoir and downstream of the dam, inland silversides (Menidia beryllina) dominated samples.

Overall mean length (3.7 cm ± 0.2 SE) and depth (0.8 cm ± 0.0 SE) of fish collected in waterways by seining were less than the length (6.7 cm ± 0.2 SE) and depth (1.6 cm ± 0.1 SE) of fish collected in colony sites ($P = 0.0001$). Overall mean length of fish collected in colony sites (6.7 cm ± 0.2 SE) was greater than that of fish brought to nests by adult least terns (2.9 cm ± 0.4 SE; $P = 0.0001$). Gizzard shad (Dorosoma *cepedianum*) had the greatest mean body depth (Table 4) and represented the greatest percentage of fish dropped in colony sites (Table 3). Plains killifish (*Fundulus zebrinus*), plains minnows, and inland silversides had body depths <1.5 cm and represented small percentages of dropped fish collected from colony sites. Of fish collected by seining, only common carp (*Cyprinus carpio*) and gizzard shad had body depths >1.5 cm (Table 4).

DISCUSSION--Migration, courtship, egg-laying, and brood-rearing increase the seasonal energy requirements of birds (Arnold, 1994). Life history strategies of least terns (e.g., long-lived, small clutch sizes) likely evolved to compensate for these energetic costs. Interior populations of least terns typically select nesting sites in ephemeral habitat (Gochfeld, 1983) subject to frequent flooding (Schulenberg and Ptacek, 1984). Consequently, least terns often have the added energetic cost of renesting after floods.

Our observations during the 1992 and 1993 breeding seasons at Salt Plains NWR suggested that because chicks did not consume all fish offered to them, adult least terns supplied chicks with enough small (<4 cm) fish at suitable intervals (2 fish/h) to meet their energy requirements. Wilson et al. (1993) in Nebraska and Courtney and Blokpoel (1980) in Canada came to similar conclusions when chicks did not accept 100% of small fish brought to nests by adults.

Brubeck et al. (1981) in Texas recorded the same feeding interval (2 fish/h) as our study. Foraging adults were adept at selecting and offering appropriately-sized fish to chicks and adults; chicks were fed smaller fish than were brooding adults. Atwood and Kelly (1984) observed this behavior in California least terns.

Terns nesting at Salt Plains NWR were opportunistic foragers, feeding off of the salt flat during all but one period of the breeding season. They flew farther from their nesting area (≤12 km) than terns in Nebraska (1.5 km; Wilson et al., 1993) or California (3 km; Atwood and Minsky, 1983). In addition, we observed terns foraging farther from the salt flat (≤12 km) than reported by Talent and Hill (6.4 km; 1985). Terns made a "fish call" (Moseley, 1976) immediately after catching a fish and upon arrival to their nest site. This call may have alerted other terns to their success and directed them to the foraging site.

Peak breeding efforts (e.g., brooding, chick-feeding) of birds usually coincide with greatest food abundance (Perrins, 1970); however, timing of migration, courtship, and egg formation may not coincide with adequate forage availability (Arnold, 1994). We observed a small number (≤18) of least terns foraging at Byron State Fish Hatchery from their arrival (mid-May) through incubation (June). Due to management protocols of the fish hatchery (S. Spade, pers. comm.), fry of smallmouth bass (<u>Micropterus dolomieu</u>), largemouth bass (<u>M. salmoides</u>), palmetto bass (<u>Morone</u>

chrysops x M. saxatilis), and saugeye (Stizostedion canadense x S. vitreum; common and scientific names according to Robins et al. 1991) were maintained in holding ponds from May through June until they reached 2.5 to 6.4 cm, depending on species. Thus, a localized concentration of suitable prey (2.0 to 9.0 cm long with ≤1.5 cm body depth) was available to terns during these months. Monaghan et al. (1989) found that food supply had a strong effect on reproductive effort and breeding success of Arctic terns (Sterna paradisaea). If food was in short supply, adults sometimes abandoned a breeding attempt, or laid fewer and/or smaller eggs, reducing breeding success (Atwood and Kelly, 1984; Massey and Atwood, 1984). Hatchery fish provided a possible energy source to least terns as they prepared to lay eggs and rear young.

During incubation and brooding (middle period) in July, no terns were observed feeding off of the salt flat. Although at this time hatchery fish were transferred from holding ponds to reservoirs outside of our study area (S. Spade, pers. comm.), our seine samples on and adjacent to the salt flat contained numerous fish of appropriate sizes for least terns. Only two species (common carp and gizzard shad) had body depths greater than the gape of least terns. Talent and Hill (1985) also found increased numbers of juvenile fish in July and August in the reservoir and streams of the salt flat. The six fish species collected from substrate in colony sites, an index of fish species selected by least terns (Courtney and Blokpoel, 1980; Atwood and

Kelly, 1984; Massey and Atwood, 1984), were abundant in tributaries to, downstream of, and in the reservoir during our sampling. Fish dropped in colony sites may have been too large for terns; their lengths and depths were greater than fish sampled by seining, and lengths were greater than those of fish brought to nests. Massey and Atwood (1984) cautioned that sizes of dropped fish did not correlate with those of fish eaten by least terns. However, this index is a good, but crude, measure of the principal prey species selected by terns (Atwood and Kelly, 1984). Courtney and Blokpoel (1980) and Atwood and Kelly (1984) suggested that, when feasible, results from this index should be confirmed by observations of fish species brought to nests and identification of stomach contents of terns found dead.

During the late period of the breeding season (late July to mid-August), we observed a greater number of terns foraging along the eastern reservoir shoreline than elsewhere off the salt flat. This increase in foraging activity along the reservoir shoreline reflected movement of adults, fledglings, and older chicks to the reservoir from colony sites. Terns congregated at various points along the shoreline, foraging and resting in preparation for their migration to winter habitats in mid- to late-August. The greatest number of loafing least terns was found at the confluence of streams and reservoir. Talent and Hill (1985) determined that these sites supported the greatest number of fish late in the season.

Our data suggest that during the 1992 and 1993 breeding seasons, food was available in adequate quantities to support least tern energy demands. Bodies of water on and adjacent to the salt flat remained full throughout both the 1992 and 1993 seasons due to above average rainfall (52 and 62 cm, respectively). During dry seasons, however, intermittent streams crossing the salt flat become dry and terns must travel farther to forage (Hill 1985). Therefore, drought years would pose a particular hardship for least terns due to reduced forage availability.

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Table 1--Percentage (consumed/offered) of fish in different size classes consumed by different-aged least tern chicks.

	Size class of fish (cm)[1]				
Age (days) of chicks	≤1.3 (_n_ = 9)	1.4-2.0 (_n_ = 6)	2.1-2.6 (_n_ = 17)	2.7-3.0 (_n_ = 1)	>3.1[2] (_n_ = 5)
1 (_n_ = 7)[3]	100	100	50	0	-
2 (_n_ = 7)	100	100	71.4	-	-
3 (_n_ = 4)	100	100	100	-	-
10 (_n_ = 2)	-	-	100	-	-
12 (_n_ = 1)	-	-	100	-	-

[1] Size (length) of fish estimated relative to bill length of adults.

[2] All fish in this size class brought to nests were consumed by an adult.

[3] Number of chicks.

Table 2--Number and success (%) of least terns foraging off the salt flat during different periods of the breeding season.

		Number of	Number of	Number of	Success (no. captures	Overall Success[1]	
Period	Location[2]	Birds	Dives	Captures	÷ no. dives)	$\bar{X}$	SE
Arrival	A	0	-	-	-		
	B	18	44	5	11.4	10.4	1.0
	C	10	85	8	9.4		
Early	A	15	50	2	4.0		
	B	8	8	4	50.0	21.1	14.5
	C	15	32	3	9.4		
Middle	A	0	-	-	-		
	B	0	-	-	-	-	-
	C	0	-	-	-		
Late	A	54	70	19	27.1		
	B	1	2	0	0.0	13.6	13.6
	C	0	-	-	-		

[1] Overall means were not different among periods of the breeding season (Kruskal-Wallis Test, P = 0.8984).

[2] Fixed-point observation stations were, A: Great Salt Plains Reservoir shoreline east of the salt flat (7 stations); B: Byron State Fish Hatchery (4 stations); and C: Salt Plains National Wildlife Refuge moist soil unit ponds (4 stations).

Table 3--Species and number (% of total) of fish collected by seining in bodies of water adjacent to, and of fish dropped by least terns in colony sites on the salt flat.

	Upstream of salt flat		Colony sites on salt flat		Great Salt Plains Reservoir		Downstream of Great Salt Plains dam	
Scientific name (Common name)[1]	n	%	n	%	n	%	n	%
Cyprinella lutrensis (Red shiner)	891	2.4	3	11.5	1	0.1	0	0
Cyprinus carpio (Common carp)	78	27.5	5	19.2	43	3.8	5	0.1
Dorosoma cepedianum (Gizzard shad)	102	3.2	10	38.5	153	13.7	686	8.6
Fundulus zebrinus (Plains killifish)	107	3.3	2	7.7	4	0.4	0	0
Gambusia affinis (Western mosquitofish)	152	4.7	0	0	115	10.3	11	0.1
Hybognathus placitus (Plains minnow)	1,080	33.3	1	3.8	272	24.4	381	4.8
Ictalurus punctatus (Channel catfish)	83	2.6	0	0	103	9.2	1	0.0
Lepomis humilis (Orangespotted sunfish)	1	0.0	0	0	1	0.1	0	0
Menidia beryllina (Inland silverside)	136	4.2	5	19.2	415	37.2	6,903	86.0
Notropis atherinoides (Emerald shiner)	38	1.2	0	0	7	0.6	17	0.2
Notropis stramineus (Sand shiner)	485	15.0	0	0	0	0	1	0.0
Pimephales promelas (Fathead minnow)	90	2.8	0	0	2	0.2	22	0.3

[1] Names of fish according to Robins et al. 1991. Common and scientific names of fishes from the United States and Canada. Amer. Fish. Soc. Special Pub. 20. Fifth Edition.

Table 4--Length and body depth[1] (cm) of fish collected in colony sites and waterways upstream of the salt flat. Common names are given in Table 3.

	Colony sites on the salt flat					Upstream of the salt flat				
		Length		Depth			Length		Depth	
Scientific name	*n*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	*n*	$\bar{x}$	*SE*	$\bar{x}$	*SE*
Cyprinella lutrensis	3	5.9	0.6	1.6	0.2	10	4.3	0.6	1.1	0.2
Cyprinus carpio	5	5.9	0.6	1.8	0.2	4	5.6	1.2	1.5	0.4
Dorosoma cepedianum	10	6.4	0.2	1.9	0.1	9	6.4	0.1	1.8	0.0
Fundulus zebrinus	2	6.9	0.1	1.2	0.2	10	3.1	0.3	0.5	0.1
Gambusia affinis	0	.	.	.	.	10	2.5	0.1	0.5	0.0
Hybognathus placitus	1	9.0	-	1.1	-	10	2.4	0.1	0.5	0.0
Ictalurus punctatus	0	.	.	.	.	10	2.8	0.2	0.4	0.0
Menidia beryllina	5	7.7	0.6	1.2	0.1	10	4.4	0.5	0.6	0.1
Notropis atherinoides	0	.	.	.	.	10	4.5	0.6	1.0	0.2
Notropis stramineus	0	.	.	.	.	11	3.1	0.3	0.6	0.1
Pimephales promelas	0	.	.	.	.	11	3.1	0.2	0.6	0.0

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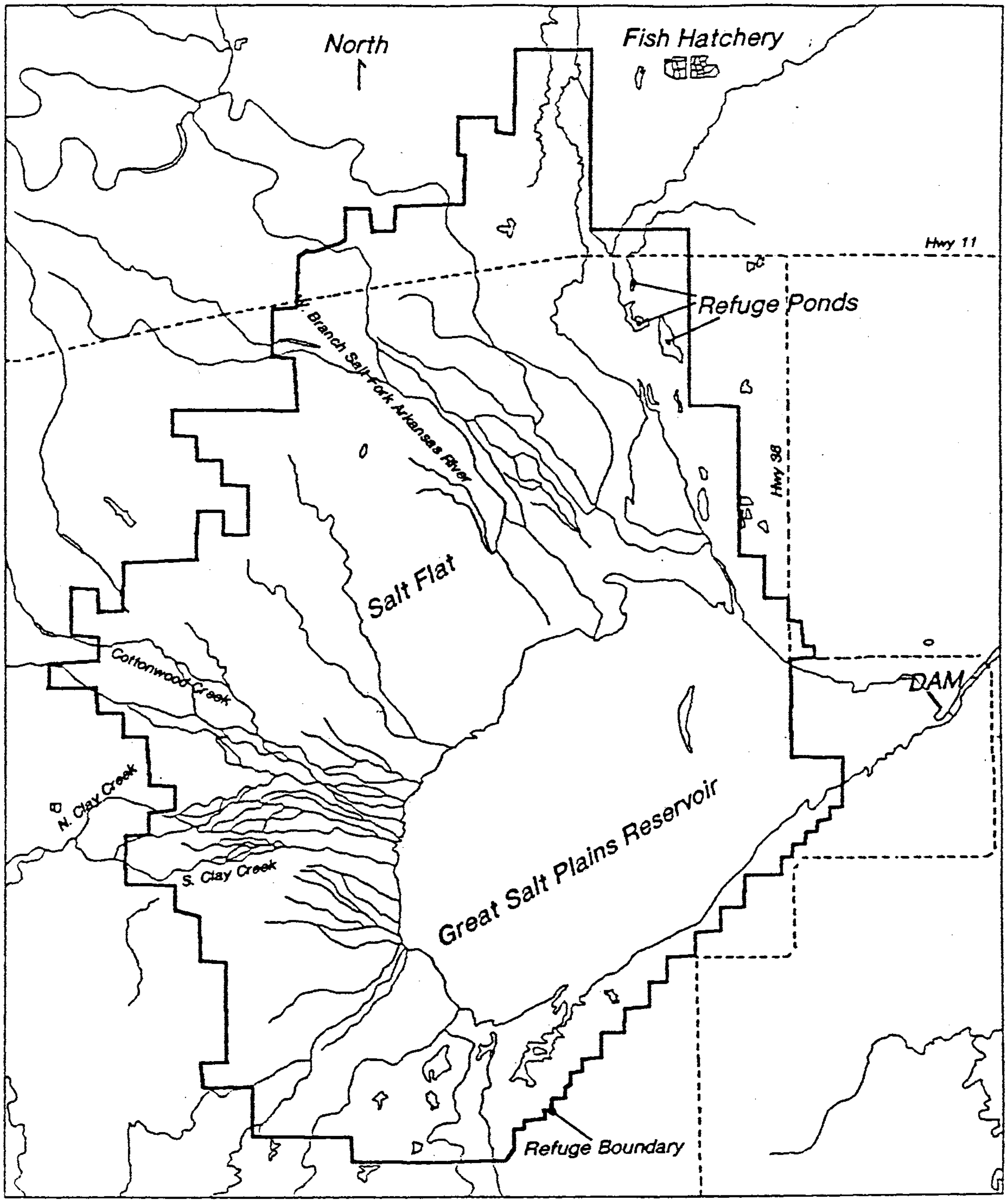
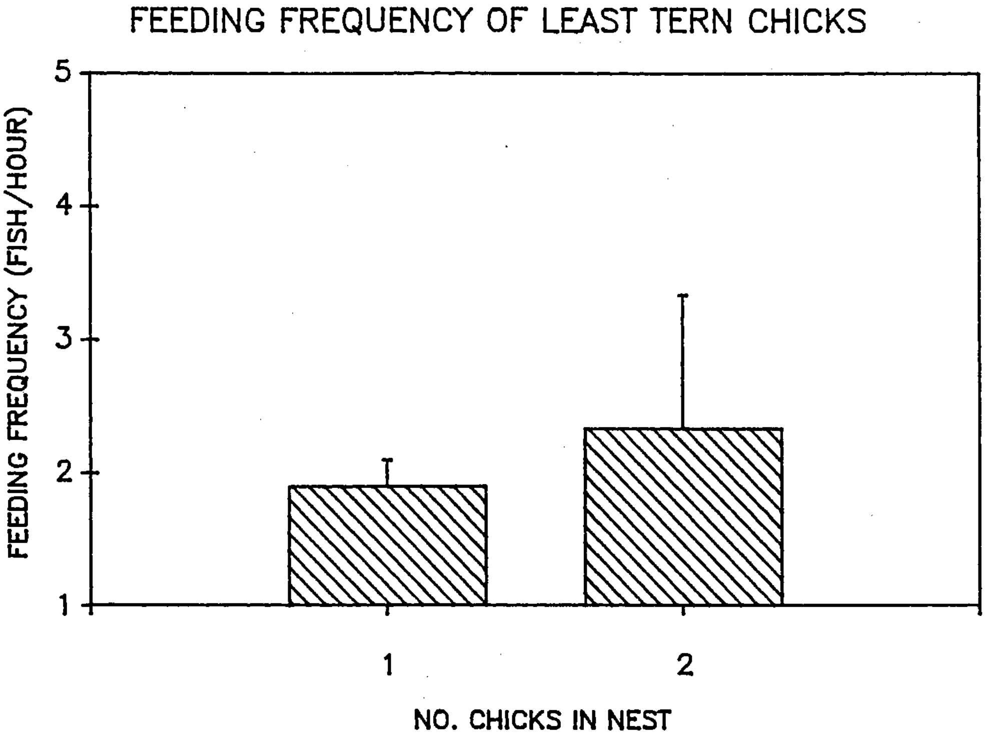
[1] Measured at widest point.

Fig. 1--Boundary of Salt Plains National Wildlife Refuge, Alfalfa County, Oklahoma shown by solid dark line. The salt flat is the area north and west of the Great Salt Plains Reservoir and south of the West Branch of the Salt Fork of the Arkansas River.



Scale: 1 cm = 1 km

Fig. 2--Frequency (fish/h) at which adult least terns brought fish to nests containing one and two chicks. Means were not different (Kruskal-Wallis Test, *P* = 0.5076).


FEEDING FREQUENCY OF LEAST TERN CHICKS
FEEDING FREQUENCY (FISH/HOUR)
5
4
3
2
1
1
2
NO. CHICKS IN NEST

CHAPTER IV

STAGE-SPECIFIC SURVIVAL RATES OF LEAST TERNS NESTING AT SALT PLAINS NATIONAL WILDLIFE REFUGE, OKLAHOMA

Abstract.--The endangered interior population of Least Terns (Sterna antillarum) nests as subpopulations in riverine and alkaline flat habitats. Small populations (N < 500) are at increased risk of extinction. We summarized estimates of survival for egg, chick, young adult (<2 yr), and adult (≥2 yr) developmental stages of Least Terns nesting at Salt Plains National Wildlife Refuge (NWR) from past and present research. In addition, causes of mortality, physical condition, and morphological measurements were recorded. The egg developmental stage had the lowest mean survival of all stages on the salt flat. Data on survival from fledgling to young adult stages were scant. Adult terns were in good condition at time of death. Mortality of eggs and chicks was primarily attributed to mammalian predation and flooding. Additional attention should be directed to more precise estimates of survival of fledgling to young adult stages and to protection of eggs on the salt flat.

Key Words.--developmental stage, Least Tern, Oklahoma, salt flat, Sterna antillarum, survival rates

The interior population of Least Terns was listed as endangered by the U.S. Fish and Wildlife Service (USFWS) in 1985 (USFWS 1985). The perceived decline in its numbers was attributed primarily to loss of breeding habitat along inland riverine systems and alkaline flats (USFWS 1990).

Interacting demographic, genetic, environmental, and catastrophic processes determine the vulnerability of a population to extinction (Clark et al. 1991). Increasingly, managers are using simulation models to explore the dynamics of small populations (generally, $N < 500$; Brussard 1985, Clark et al. 1991, Lacy 1993). Some of the most powerful of these mathematical methods are based on stage-structured models (Ferson 1990). Such demographic models typically are matrix models where elements are important population processes such as maturation, reproduction, survival, and mortality (Ferson 1990).

Various life history traits of the Least Tern population nesting at Salt Plains NWR, Oklahoma, have been studied intermittently since 1977. However, no unified effort has been made to summarize life history traits gathered by previous researchers. Accordingly, we summarized these data to obtain best estimates of stage-specific survival rates, identify primary causes of mortality at each stage, and distinguish the most sensitive stage(s) for Least Terns. We also recorded measurements characterizing physical conditions of Least Terns in different developmental stages during the 1992 and 1993 breeding seasons.

STUDY AREA AND METHODS

Least Terns nest on an alkaline flat at Salt Plains NWR, north-central Oklahoma, from late May to August (Grover and Knopf 1982, Hill 1985). Historically, the salt flat covered 11,137 ha (Ortenburger and Bird 1933). In 1941, 3,564 ha (32%; Purdue 1976) of the salt flat were flooded when the U.S. Army Corps of Engineers completed a dam across the Salt Fork of the Arkansas River creating the Great Salt Plains Reservoir. Since dam construction, silt and other fine soils have accreted upstream, filling the reservoir, river, and intermittent streams west of the dam (S. Schweitzer, pers. obs.). Increased flooding and soil deposition amenable to establishment of plant species (especially introduced salt cedar [*Tamarix chinensis* Lour.]; plant names according to Correll and Johnston 1970) have reduced salt flat area available for nesting Least Terns (Hill 1993).

The salt flat is mostly barren and seasonally encrusted with precipitated salt (Reed 1978) from brine drawn to the surface by capillary action (Grover and Knopf 1982). The land is level to gently sloping and is part of stream flood plains (Ortenburger and Bird 1933). The salt flat is crossed by the West Branch of the Salt Fork of the Arkansas River, Clay Creek, Cottonwood Creek, and intermittent streams. Frequent flooding occurs in spring and fall. Floodwaters may remain for days (Williams and Grover 1975) and carry debris onto the flats (Hill 1985). Hummocks of windblown sand anchored by vegetation occur near margins of the salt flat.

Summers are long and usually hot (Ortenburger and Bird 1933). Average maximum daily air temperature recorded in Cherokee (about 5 km west of the salt flat) is 36°C in July and August (Williams and Grover 1975). Prevailing winds are from the south (Ortenburger and Bird 1933), and average about 21 km/hr (Williams and Grover 1975). Spring is the windiest season, during which gusty southwesterly winds of 48 to 72 km/hr are common (Williams and Grover 1975).

We defined developmental stages of terns as eggs, chicks (hatched but unable to fly), fledglings (able to fly but dependent on parents), young adults (<2 yr, sexually immature, independent), and breeding adults (≥2 yr, sexually mature). Delineation of stages was based on behavioral and physical development (Massey 1974).

We obtained data from five research projects conducted from 1977 to 1993, and our 1992 and 1993 studies. We were concerned primarily with estimates from studies on the salt flat, but where data were lacking, we used estimates from research on other populations.

The estimate of mean survival of eggs to hatching was based on estimates of egg success (number of eggs hatched/total number of eggs monitored) reported by Grover and Knopf (1982), Hill (1985), Boyd (1987, 1989, 1990), Utych (1993), and Koenen (1994). Fledgling counts and number of eggs that successfully hatched reported by Hill (1985), Boyd (1989, 1990), Utych (1993), Koenen (1994), and recorded by us during the 1992 and 1993 seasons were used to estimate mean chick survival rate (number of fledglings/number of eggs hatched). Least Terns rarely migrate to nesting sites until ≥2 yr (Boyd and Rupert 1991, Boyd 1993), and there are no reported sightings of banded Least Terns on wintering grounds in Central and South America; thus, the survival rate of the fledgling to young adult developmental stage is uncertain. We reviewed return rates of terns banded as chicks by Boyd (1992) in Kansas and Oklahoma, and data reported by Atwood and Massey (1988), Kirsch (1992), and Massey _et al_. (1992) to estimate survival of this developmental stage. Estimates of annual survival of breeding adults (≥2 yr) were summarized from returns of banded adults reported by Boyd (1987, 1993), Kirsch (1992), Massey _et al_. (1992), and Renken and Smith (1993).

The percentage of eggs lost to different factors on the salt flat was summarized from Grover and Knopf (1982), Hill (1985), Boyd (1987, 1989, 1990), and Utych (1993). During the 1992 and 1993 breeding seasons, all coyote scats found in colony sites were collected and examined for egg shell fragments, feathers, bones, and keratin structures (e.g., bill, nails). All chicks found were weighed and fitted with a USFWS aluminum band on the right tarsometatarsus, and the date of hatching was estimated. All chicks recaptured were weighed. All chicks and adults found dead were collected; causes of death was determined and physiological indices (e.g., fat deposition, presence of parasites, histopathological abnormalities) were determined (USFWS, National Wildlife Health Research Center, Madison, Wisconsin). Morphological features (culmen length, wing chord, tail length, tarsus length, and total length) were measured on all collected adult terns.

RESULTS

Least Tern egg survival rates on the salt flat were obtained for 12 years and ranged from 12 to 64.3% (Table 1). The overall mean (± SE) was 31.8 ± 4.8%. Survival rates of chicks were summarized over eight years; overall mean chick survival was 41.8 ± 5.8% and ranged from 27.4 to 68.6% (Table 2).

Boyd (1993) banded 537 Least Tern chicks from 1980-1991 in Kansas and Oklahoma and recaptured seven as adults (1.3% return rate). Kirsch (1992) used a post-fledging survival rate of 85% in her population trend models of Least Terns nesting along the Platte River, Nebraska. A total of 5,425 Least Tern chicks from four colony sites in California was banded from 1973 to 1983, and 328 were recovered as adults (6.0% return rate; Atwood and Massey 1988). Massey et al. (1992) reported return rates of adult Least Terns banded as chicks at Venice Beach, California, from 1978 to 1986, and the overall mean was 6.3 ± 1.1%.

The return rate of adult Least Terns on the salt flat, based on banding studies from 1980 to 1991 (Boyd 1993) was 13.3% (14 recovered/105 banded adults). In the Kansas/Oklahoma region, the return rate was 33.6% (Boyd 1993).

Renken and Smith (1993) estimated an adult survival rate of 85 ± 5.7% for terns nesting along the Mississippi River adjacent to Missouri. Kirsch (1992) used annual adult survival rates of 80, 85, and 90% in her deterministic population models of Least Terns nesting along the Platte River. Overall adult survival rate of Least Terns in California was 88% (Massey *et al*. 1992). The reported "old age" for breeding Least Terns ranged from 10 (Boyd 1987) to 16 yr (Kirsch 1992).

Mammalian predation and flooding were the greatest threats to egg survival on the salt flat (Table 3). A *t*-test on ranked means (Conover and Iman 1981) determined that percentages of eggs lost to mammalian predation and flooding were not different ($t = -0.32$, df = 20, $P = 0.75$; Table 3). A simple linear regression model ($Y = 69.5 - 0.98b_1$) appropriately ($F = 8.62$, df = 1,8, $P = 0.02$) described the relation between seasonal egg survival and precipitation (Fig. 1). Other factors reducing egg survival were addling (incubated but did not hatch), abandonment by adults, hail storms, and cracked shells (presumably due to abnormally thin shells; Hill 1985). Chick survival was reduced by drowning (Boyd 1987, 1989), heat stress (Hill 1985), and starvation (Hill 1985), but most losses were likely due to predation (Hill 1985). No authors reported causes of mortality for fledglings. Adult mortality was due to hail and predation (Boyd 1992). Egg shell fragments were found in 2 of 14 coyote scats collected in colony sites. All other remains were of mammals, insects, or plant material.

We banded 102 Least Tern chicks during the 1992 and 1993 nesting seasons on the salt flat. Eleven were recaptured and one was found dead. Weights increased linearly over time (Fig. 2) and were similar to those of Kansas and California Least Tern chicks as reported by Boyd (1983) and Massey (1974), respectively.

In 1992, one adult at Salt Plains NWR and five adults at Quivira NWR, Kansas (about 150 km north of Salt Plains NWR), were killed by hail storms in June. Salt Plains NWR obtained a special permit to have a taxidermist mount the adult found on the salt flat. R. L. Boyd obtained a special permit to perform necropsies on terns collected at Quivira NWR and was assisted by S. Schweitzer. No parasites were found in gastrointestinal tracts, and the terns appeared to be in good condition with visible amounts of subcutaneous, abdominal, and coronary fat present. Four of the Kansas terns were banded (Table 4). Two adults and three tern chicks were found dead in 1993. One adult and two chicks were too decomposed to determine cause of death or physiological condition. The second adult appeared to have died from trauma, possibly from avian predation. A puncture wound in the right pectoral muscle suggested it was attacked by a raptor. At the time of death, it was in good condition with adequate subcutaneous, abdominal, and coronary fat (N. Thomas, USFWS, National Wildlife Health Research Center, pers. comm.). The chick was in good body condition but had wet lungs and may have died from drowning or hypothermia. Measurements of morphological features were recorded for all adult Least Terns collected (Table 4).

DISCUSSION

Small populations are particularly vulnerable to extinction due to heightened stochasticity in processes such as mating, reproduction, migration, disease, and predation (Clark et al. 1991, Lacy 1993). In addition, gene frequencies in a small population are subject to random fluctuations, producing random drift and increased differentiation among subpopulations, uniformity within subpopulations, and homozygosity (Falconer 1989). Knowledge of stage-specific survival rates of a population allows use of models to study population dynamics. Although models are abstracts of reality, they help identify life stages that most strongly influence population size over time, and they can help direct management efforts.

Mean survival of eggs (31.8%) on the salt flat was lower than survival at riverine (41 to 65.5%, Kirsch 1992; 74 to 98%, Smith and Renken 1993) and coastal (79.2%, Massey 1974) sites. Mean survival from chick to fledgling stage on the salt flat (41.8%) was greater than on sand bars of the Platte River (11.8 to 31.2%, Kirsch 1990) and the California coast (10.7 to 33.3%, Massey 1974). However, chick survival on the Mississippi River (64 to 82%, Renken and Smith 1993) was greater than on the salt flat. Risks to egg and chick survival on the salt flat that have not been reported elsewhere were frequent sheet-flooding and hail storms. Colony sites on salt flats are not protected from mammalian predators by water barriers as are sandy islands in rivers. Salt cedar has replaced ≥400 ha of formerly barren salt flat at Salt Plains NWR (Hill 1993) and provided additional cover for predators, especially coyotes. California Least Terns have been managed intensively (e.g., fencing around colony sites, predator control, substrate supplementation) since the late 1970s (Kirsch 1992) and consequently, have experienced slight increases in numbers.

Our estimate of survival of chicks to fledgling stage was calculated using counts of fledglings present on the Great Salt Plains Reservoir shoreline (Boyd 1990). Accurate fledgling counts are difficult to obtain (Massey 1988, Smith and Renken 1993) and may be biased by arrival and staging of fledglings from other colony sites (Thompson and Slack 1984, Kirsch 1990). Without identification of individuals, this bias can not be removed.

Better estimates of survival of the fledgling to young adult stage are needed. Accurate documentation of the wintering range of Least Tern subpopulations is sparse (Kirsch 1992, Massey et al. 1992, Thompson et al. 1992). There are no data available on mortality factors affecting terns during their first 6 months on their migratory route and wintering grounds (USFWS 1990). Existing data and modeling efforts (Kirsch 1992) indicate that survival during this stage may exert the greatest influence on population trends.

Banding return rates of adults are affected by fluctuating banding and resighting effort. The salt flat is expansive and colony site locations shift annually making banding and resighting or recapture efforts difficult. Return rates reported by Boyd (1993) were lower than those recorded in Missouri (Renken and Smith 1993), possibly an artifact of the difficulty of resighting and capturing banded terns on salt flat habitats. More precise estimates of returns are probably obtained at riverine and coastal colony areas because colony sites are restricted to discrete areas (e.g., sand islands and bars, linear beaches).

Physiological conditions of Least Terns have not been reported by others. Adult terns from salt flats were in good condition at the time of death. Catastrophic events such as hail storms and predation were the only causes of mortality determined for adults. Morphological measurements of terns collected at Salt Plains NWR and Quivira NWR were similar to those of Least Terns from other regions (Boyd and Thompson 1985, Kirsch 1990). Additional morphological data should be accumulated to increase our understanding of suspected differences among Least Tern subpopulations (Boyd and Thompson 1985, Thompson et al. 1992).

Our summaries of stage-specific survival rates suggest that survival from fledging to breeding adult may be the most difficult, but additional data are needed to substantiate this hypothesis. During the breeding season on the salt flat, survival of the egg was lower than that of the other developmental stages. Management techniques such as enclosing colony sites with electric fences and providing elevated mounds or ridges for placement of nests have successfully decreased mammalian predation (Massey 1988, Boyd 1990, Mayer and Ryan 1992, Utych 1993) and washing-out of eggs from sheet flooding (Boyd and Rupert 1991). Unfortunately, eggs cannot be protected from sporadic, catastrophic events such as hail storms.

MANAGEMENT RECOMMENDATIONS

Our review of existing data suggested that the egg developmental stage was at greatest risk on the salt flat; thus, efforts to protect this stage should be incorporated into management plans for this Least Tern subpopulation. Continued monitoring of egg success, fledgling numbers, and returns of banded terns will increase the precision of survival estimates. An intensive banding and recapturing program would provide much-needed information on survival and return rates of young adults. These data could be applied to simulation models to obtain better estimates of the viability of the Salt Plains NWR population.

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Table 1. Mean survival (%) of Least Tern eggs on the salt flat of Salt Plains National Wildlife Refuge, Oklahoma.

Source[1]	Year	No. hatched/No. monitored
Grover and Knopf 1982	1977	64.3
Grover and Knopf 1982	1978	16.7
Hill 1985	1982	33.7
Hill 1985	1983	24.7
Hill 1985	1984	53.0
Boyd 1987	1986	38.0
Boyd 1987	1987	12.0
Boyd 1989	1989	37.0
Boyd 1990	1990	46.0
Utych 1993	1991	25.7
Utych 1993	1992	17.8
Koenen 1994	1993	35.6
Overall mean (SE):		31.8 (4.8)

[1] See Literature Cited for full citation.

Table 2. Mean survival (%) of Least Tern chicks on the salt flat of Salt Plains National Wildlife Refuge, Oklahoma.

Source[1]	Year	No. fledged/No. hatched
Hill 1985	1982	27.4
Hill 1985	1983	47.3
Hill 1985	1984	29.3
Boyd 1989	1989	39.8
Boyd 1990	1990	56.2
OCFWRU[2] 1993	1991	46.2
Utych 1993	1992	68.6
Koenen 1994	1993	19.2
Overall mean (SE):		41.8 (5.8)

[1] See Literature Cited for full citation.

[2] OCFWRU: Oklahoma Cooperative Fish and Wildlife Research Unit.

Table 3. Percentage (number lost/number monitored) of Least Tern eggs lost to predation or flooding on the salt flat of Salt Plains National Wildlife Refuge, Oklahoma.

Source[1]	Year	Mammalian Predation	Flooding
Grover and Knopf 1982	1977	57.7	42.3
Grover and Knopf 1982	1978	32.8	67.2
Hill 1985	1982	24.2	8.1
Hill 1985	1983	31.1	6.0
Hill 1985	1984	15.9	0.0
Boyd 1987	1986	5.0	15.0
Boyd 1987	1987	1.0	38.0
Boyd 1989	1989	10.4	23.7
Boyd 1990	1990	12.3	23.3
Utych 1993	1991	45.0	0.0
Utych 1993	1992	33.3	33.3
Overall means[2] (SE):		24.4 (5.3)	23.4 (6.2)

[1] See Literature Cited for full citation.

[2] Means were not different (*P* = 0.75); determined by *t*-test on ranked data.

Table 4. Morphological measurements of adult Least Terns found dead on the salt flat of Salt Plains National Wildlife Refuge (SPNWR), Oklahoma, and Quivira National Wildlife Refuge (QNWR), Kansas.

Date Collected	Location Collected	Sex	USFWS Band No.	Age (yr)	Culmen Length (mm)	Wing Chord (mm)	Tail Length (mm)	Tarsus Length (mm)	Total Length (mm)
19 Jun 92	SPNWR	unknown	none	unk.	26	168	74	17	220
26 Jun 92	QNWR	male	1411-24899	3+	28	173	79	14	199
26 Jun 92	QNWR	female	none	unk.	27	165	85	14	205
26 Jun 92	QNWR	female	1331-60701	9+	25	169	76	15	199
26 Jun 92	QNWR	female	1331-60719	9+	26	170	80	15	197
26 Jun 92	QNWR	female	1331-60902	8+	25	169	75	15	190
30 Jun 93	SPNWR	unknown	none	unk.	28	171.5	82	14.5	197
10 Aug 93	SPNWR	female	none	unk.	25	169	73	14.5	167
Overall means (SE):					26.2 (0.4)	169.3 (0.8)	78.0 (1.5)	14.9 (0.3)	196.8 (5.3)

Figure 1. Seasonal Least Tern egg survival (%) regressed against precipitation (cm) received at the Great Salt Plains Reservoir Dam during ten breeding seasons (May - August 1982 to 1993; 1985 and 1988 not included).

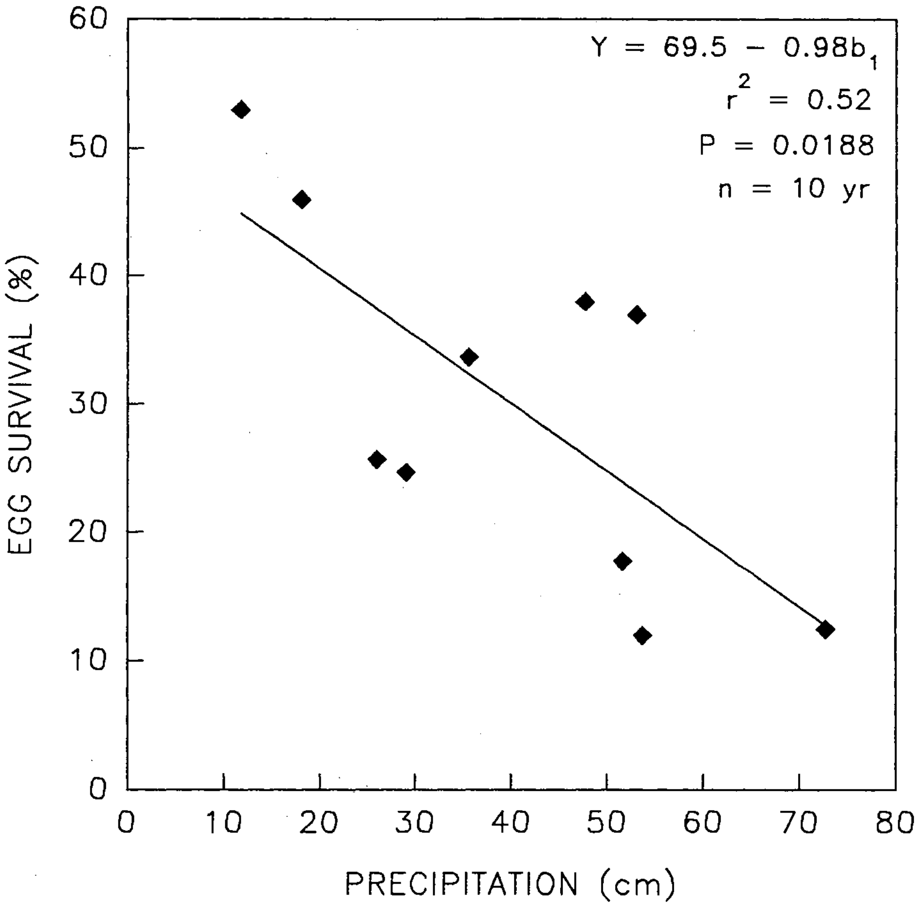
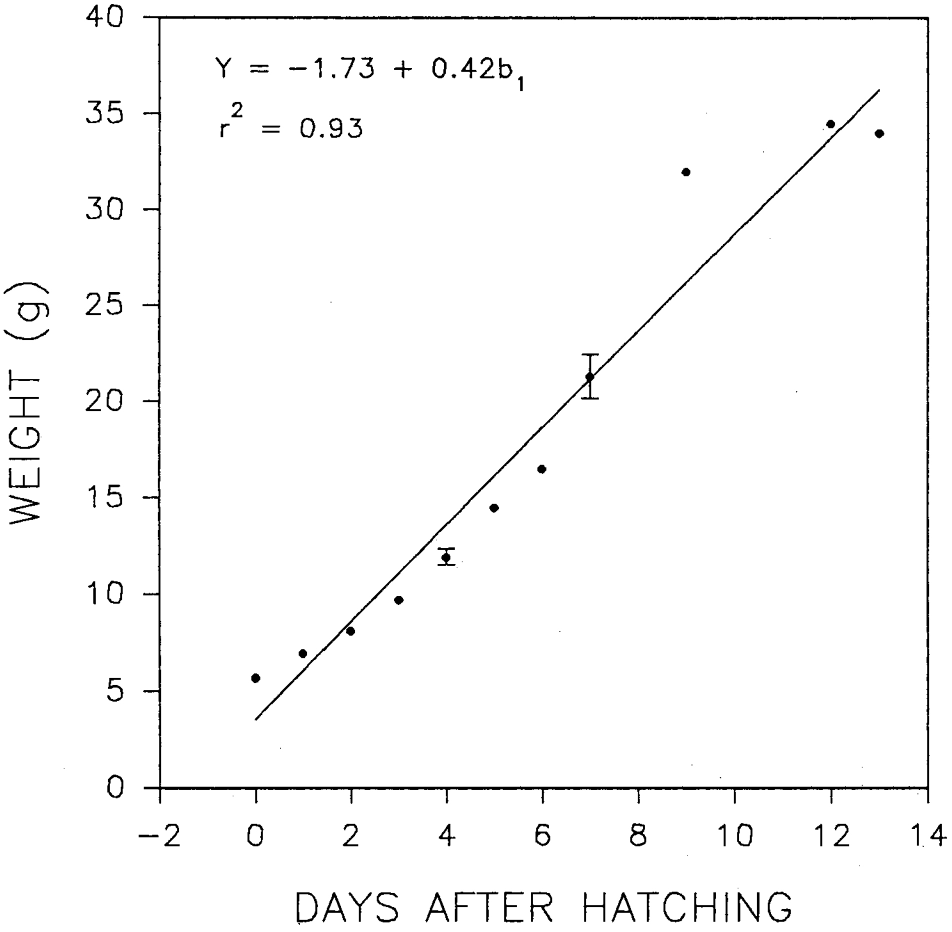

Y = 69.5 − 0.98b$_1$
r^2 = 0.52
P = 0.0188
n = 10 yr
EGG SURVIVAL (%)
PRECIPITATION (cm)
0
10
20
30
40
50
60
70
80

Figure 2. Weight (g) regressed against age of Least Tern chicks captured on the salt flat of Salt Plains National Wildlife Refuge, Oklahoma. A simple linear regression model appropriately (F = 1,435.4, df = 1,112, P = 0.0001) predicted weight given age, up to 13 days after hatching.


Y = −1.73 + 0.42b₁
r² = 0.93
WEIGHT (g)
0
5
10
15
20
25
30
35
40
−2
0
2
4
6
8
10
12
14
DAYS AFTER HATCHING

VITA

Sara Hannah Schweitzer

Candidate for the Degree of

Doctor of Philosophy

Thesis: ABUNDANCE AND CONSERVATION OF ENDANGERED INTERIOR LEAST TERNS NESTING ON SALT FLAT HABITAT

Major Field: Wildlife and Fisheries Ecology

Biographical:

Personal Data: Born in Decatur, Illinois, October 22, 1962.

Education: Graduated from Hillcrest High School, Dallas, Texas, May 1981; received Bachelor of Science degree in Biology from the University of North Carolina, May 1985; received Master of Science degree in Wildlife Science from Texas Tech University, August 1988; completed requirements for Doctor of Philosophy degree in Wildlife and Fisheries Ecology from Oklahoma State University, December 1994.

Professional Experience: Graduate Research Assistant, Department of Zoology, Oklahoma State University (1991-1994); Graduate Teaching Assistant, Department of Zoology, Oklahoma State University (1990-1991); Environmental Scientist, U.S. Army Corps of Engineers (1988-1990); Research Technician, Applied Marine Research Laboratory, Old Dominion University (1988-1989); Graduate Research Assistant, Department of Range and Wildlife Management, Texas Tech University (1986-1988).

Professional Organizations: American Ornithologists' Union, Society for Field Ornithologists, Society for Range Management, The Wildlife Society.