MANAGEMENT IMPLICATIONS OF POPULATION GENETICS AND DEMOGRAPHICS OF LEAST TERNS (*STERNA ANTILLARUM*)

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PREFACE

Chapters in this dissertation are written in manuscript formats suitable for submission to selected scientific journals. Chapter I and II are formatted for *The Auk*; Chapter III for *The Journal of Wildlife Management*; and Chapter IV for *Wilson Bulletin*.

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CHAPTER I

LACK OF GENETIC VARIATION AMONG SUBSPECIES OF LEAST TERN (*STERNA ANTILLARUM*): IMPLICATIONS FOR CONSERVATION

ABSTRACT.—DNA sequence variation from two nuclear introns and part of the mitochondrial cytochrome-*b* gene was used to evaluate population structure among three subspecies of Least Terns in the United States (California [*Sterna antillarum browni*], Interior [*S. a. athalassos*], Eastern [*S. a. antillarum*]). Sequence variation was highest for nuclear intron XI (Gadp) within the glyceraldehyde-3-phosphate dehydrogenase gene. The second nuclear intron was fixed for the same allele in all subspecies. Fixation indices, F_{ST} and $\Phi_{ST,}$ for Gadp indicated genetic divergence between California and Interior subspecies ($P < 0.05$). Estimates of gene flow ranged from 2 - ∞ individuals/generation. Genetic indices for mitochondrial DNA (mtDNA) did not differ among subspecies. Gene flow for mtDNA was 10 - 83 individuals/generation. The contrasting variation between nuclear and mtDNA may indicate gene flow via female dispersal. Limited genetic variation suggests that outcrossing would not be a conservation issue.

Least Terns are long-distance migrants that breed in North America and winter in South America (Thompson et al. 1997a). Five subspecies have been described (*Sterna antillarum antillarum* [Lesson 1847], *S. a. browni* [Mearns

1916], *S. a. mexicana* [van Rossem and Hachisuka 1937], *S. a. staebleri* [Brodkorb 1940], and *S. a. athalassos* [Burleigh and Lowery 1942]; Fig. 1). Taxonomic status within Least Terns has been debated for several years (Thompson et al. 1992, Patten and Erickson 1996, Massey 1998). The American Ornithologists' Union (AOU) recognizes three subspecies: California, *S. a. browni*; Eastern, *S. a. antillarum*; and Interior, *S. a. athalassos*; AOU 1998). California and Interior populations are designated as federally endangered as a result of population declines related to habitat loss (United States Fish and Wildlife Service [USFWS] 1980, 1985). The USFWS, who oversees endangered species management, does not recognize subspecies of Least Tern and manages the California and Interior Least Tern as distinct geographic variants (USFWS 1985).

Criticisms of original descriptions for subspecies have focused on inadequacies of qualitative and variable characteristics, such as feather color and number of black flight feathers, used to describe type specimens (Massey 1976, Thompson et al. 1992, Patten and Erickson 1996). In separate studies, Burleigh and Lowery (1942), Massey (1976), and Thompson et al. (1992) could not differentiate Eastern and California subspecies using morphology, behavior, or vocalizations. Allozyme electrophoresis also failed to differentiate between Eastern and Interior Least Terns (Thompson et al. 1992), but all specimens came from Texas, where the two subspecies may overlap, and sample size of the Interior population was small ($n = 4$). Furthermore, identification is complicated by potential interbreeding between Eastern and Interior Least Terns (e.g., one Least Tern banded as a juvenile in Texas in 1980 was found nesting at

Quivara National Wildlife Refuge, Kansas, in 1984 and 1985; Boyd and Thompson 1985). However, spectrophotometric examination of feather color identified distinguishing characters for each subspecies (Johnson et al. 1998).

Advances in molecular genetics have allowed inclusion of genetic information into management plans for conservation (Mace et al. 1996). The most appropriate use of genetic data to define conservation units is debatable (Parker et al. 1999). Moritz et al. (1993) proposed using variation in allele frequencies for either mtDNA or nuclear DNA to describe management units for conservation. Recognizing that small or large sample sizes could mask or inflate designation of distinct units, Moritz et al. (1993) suggested combining genetic and biological evidence to support designation of management units.

Mitochondrial DNA frequently is used to elucidate recent genetic differentiation between populations (Brown et al. 1979) because divergence can occur in a shorter timeframe than for nuclear DNA. Because mtDNA is maternally inherited, effective population size is smaller than for nuclear DNA, which means fewer generations are required for divergence to occur. Effective population size refers to the ideal number of individuals that would exhibit the same rate of genetic drift as the entire population (Hartl and Clark 1989). Essentially, it is an indication of the number of individuals contributing to the gene pool. In addition, mitochondrial DNA lacks the efficient repair mechanisms of nuclear DNA, and therefore, mutations are more likely to be maintained. Cytochrome-*b* gene (cyt-*b*) within mtDNA is a protein-coding gene that is subject to selection but has distinguished subspecies in other studies (Birt-Friesen et al. 1992). Krajewski et al. (1992) developed cyt-*b* primers that have been used to amplify DNA segments in diverse taxa, including cranes and dasyuroid marsupials.

An advantage of using nuclear DNA to evaluate population structure is that multiple sites that are evolutionarily independent can be examined. Mitochondrial DNA is contained in a single circular chromosome, and therefore the various sites are assumed to be subject to the same selective forces. Genes are composed of coding regions called exons and non-coding regions called introns. Coding regions are subject to selection pressures that may conserve nucleotide arrangement across taxa allowing very little variation; introns are free from selective pressure and therefore are more variable. Exon priming-intron crossing (EPIC) methods for nuclear DNA target regions of variability in genomic DNA by annealing to conserved regions of a nuclear gene bordering an intron (Palumbi and Baker 1996).

Exon priming-intron crossing primers have not been used extensively because few universal EPIC primers have been developed. Friesen et al. (1997) developed four sets of universal primers to amplify nuclear introns in a wide range of vertebrate taxa. These successfully amplified DNA in three mammal, one reptile, and five bird species. A detailed study of Marbled Murrelet (*Brachyramphus marmoratus*) revealed subspecific variation patterns that corresponded with results from a previous study using a section of cyt-*b* (Friesen et al. 1996a).

Our understanding of metapopulation dynamics among Least Terns breeding in the United States is limited. Philopatry estimates are 5 - 82% with about 95% of banded chicks that returned to breed nesting ≤75 km of their natal colony

(Massey et al. 1992, Boyd 1993, Lingle 1993, Renken and Smith 1995). Only one instance of dispersal between Interior and Eastern Least Terns has been documented (Boyd and Thompson 1985). Attempts to examine how the three subspecies interact on wintering grounds have been difficult due in part to uncertainty of wintering locations (Thompson et al. 1997a). The objective of this study was to examine taxonomic structure and relative level of interaction for Least Terns breeding in the United States using molecular genetic techniques. DNA sequences from two nucleic introns and a section of cyt-*b* were examined for the three breeding populations. These data were compared with other studies of Least Tern population structure based on morphology, behavior, and allozyme analysis. Genetic diversity was compared with intraspecific studies of other Charadriiformes.

METHODS

Sample collection.—Several cooperators collected blood or tissue samples from various sites within each subspecies breeding range of Least Terns in the United States (Fig. 1). For the Eastern breeding population, samples were collected from three sites in Georgia, one in Mississippi, and one in Massachusetts. Interior population samples were collected from one site in Oklahoma, one in Missouri, and two in North Dakota. California samples were collected from sites in four counties in California (Alameda, Orange, San Diego, and Ventura). Because breeding ranges of Interior and Eastern populations may overlap (Fig. 1), no samples were taken from Texas to avoid problems with potential interbreeding and misclassification.

DNA extraction.—Genomic DNA was extracted from tissue and blood samples using standard protocols (Longmire et al. 1997). Feather pulp and muscle samples were finely chopped and placed into tubes of lysis buffer. Blood samples were added directly to lysis buffer. Proteins were digested with proteinase-K and extracted from buffer solution with phenol. DNA samples were dialyzed in a 1XTE solution to remove lysis buffer and excess phenol. The 1XTE solution was replaced with fresh 1XTE at least three times over 24 h before samples were removed.

Intron amplification.— I used intron primers that were sensitive to genetic variation in Marbled Murrelets (Friesen et al. 1997). Intron VIII within ∝-enolase (EnolL731 and EnolH912) and a section of intron XI within glyceraldehyde-3-phosphate dehydrogenase (GadpH950 and GadpLT [5'-CCAGGTTGGCAATGTGGGGTGATA-3']) genes were amplified by PCR (Mullis and Faloona 1987). The Gadp primers developed by Friesen et al. (1997) did not amplify clean product in all samples so the GadpLT primer was developed. The thermal profile for Enol primers was 94°C for 3 min for initial denaturation, followed by 35 cycles of denaturation (94°C, 30 s), annealing (60°C, 30 s), and extension (72°C, 45 s) with a final extension of 15 min at 72°C. The Gadp thermal profile began with 3 min at 94°C, followed by 35 cycles of denaturation (94°C, 45 s), annealing (54°C, 45 s), and polymerase extension (72°C, 45 s) with a final extension of 15 min at 72°C. Amplifications were conducted in 25 µl of a mixture containing a final concentration of 2.5 mM $MgCl_2$, 0.2 mM dNTPS, 0.4 µM primers, and 0.5 unit of *Taq* DNA polymerase (Promega, Madison, Wisconsin).

Cytochrome-b amplification.—Part of the cyt-*b* gene was amplified using primers L15136 and H15498 developed by Krajewski et al. (1992). Amplifications were conducted with 50 µl of a mixture containing a final concentration of 4.0 mM $MgCl_2$, 0.2 mM dNTPS, 0.4 µM primers, and 1.0 unit of *Taq* DNA polymerase. Initial denaturation was conducted at 94°C for 3 min, followed by 35 cycles of denaturation (94°C, 45 s), annealing (51°C, 45 s), and extension (72°C, 45 s) with a final extension of 15 min at 72°C.

Separation of alleles.—Number of alleles for each amplified region was determined using single-stranded conformation polymorphism analysis (SSCP; Orita et al. 1989). PCR product for SSCP was radiolabeled by substituting 0.1 mM dNTP and 1.0 µCi $\propto^{32}$P-dCTP in the amplification protocol. Radiolabeled product was denatured at 95°C for 2 min and placed in ice water to cause single-stranded DNA to form secondary structures. These samples were electrophoresed through a 5% non-denaturing polyacrylamide gel (acrylamide:bis-acrylamide = 49:1) containing 10% glycerol for 24 h at ambient temperature and 300 volts. Autoradiography was used to identify variants.

Specimens were selected for sequencing if they were homozygous or heterozygous with a rare allele. PCR product from Enol primers produced a single band that could be sequenced directly (described below). Amplified product from Gadp and cyt-*b* primers required cloning to isolate the segment of interest because, in both cases, multiple bands were amplified. PCR product was cleaned with Wizard PCR Prep DNA Purification System (Promega) and cloned using pGEM-T cloning system (Promega). Clones were compared with the original PCR product using the SSCP protocol described above. Clones that migrated the same distance as the original sample were sequenced.

Sequencing.—Sequencing was conducted on samples or clones reamplified as described above without P^{32}. Amplified product was cleaned to remove PCR solutions and sequenced using an automated sequencer (ABI Prism® 377 DNA Sequencer, Applied Biosystems, Foster City, California). Sequences were verified by comparing complementary strands and sequencing two individuals for each allele. Rare alleles that occurred in single individuals were sequenced at least twice using PCR product from separate amplifications.

Statistical analysis.—Sequences from Least Terns were aligned with corresponding sequences from Marbled Murrelet (available through GenBank; accession no. AF306887) and Common Guillemot (accession no. U37307) using ClustalX (version 1.81, Thompson et al. 1997b) to verify amplification of the correct regions. Genotype frequencies were tested for deviation from Hardy-Weinberg equilibrium using the exact probability test of Haldane (1954) with complete enumeration (Louis and Dempster 1987) in GENEPOP genetics analysis software (version 3.2a, Raymond and Rousset 1995a). Allele frequencies were tested for differences between subspecies using a Markov chain (GENEPOP version 3.2a, Raymond and Rousset 1995a). Estimates of *F*-statistics were calculated using a weighted ANOVA (Weir and Cockerham 1984) with haplotype frequencies (GENEPOP version 3.2a, Raymond and Rousset 1995a). Because *F*-statistics may underestimate population divergence by not including sequence divergence (Friesen et al. 1996a), population genetic structure also was investigated using AMOVA in the computer program Arlequin (version 2.000, Schneider et al. 2000) to incorporate information on variation between haplotype sequences (Excoffier et al. 1992). That test calculated *F*-statistic analogs (Φ-statistics) using proportion of distances and tested significance of the variance components using a randomization approach (Excoffier et al. 1992). Gene flow was calculated from the Φ_{ST}-values (Wright 1965, Birky et al. 1983).

RESULTS

Nuclear.—Enol primers amplified 332 base pairs (bp) consisting of 80 bp of the bordering exons and 257 bp of Intron VIII. Examination of SSCP gels indicated that all 53 Least Terns (17 California, 22 Interior, 14 Eastern) examined were fixed for the same allele (Table 1). Sequence data from four individuals verified the presence of a single allele. Because Least Terns were monomorphic at this amplified region, no tests of population structure were relevant.

Gadp primers amplified 289 bp. Three alleles were found among 50 Least Tern (16 California, 19 Interior, and 15 Eastern; Table 1). Those differed by 16 polymorphic sites consisting of one or two substitutions and 13 indels in 289 bp. The rarest allele was found in single individuals from the California population and the Interior population (Fig. 1). Genotypic frequencies for the three breeding populations were in Hardy-Weinberg equilibrium (exact probability test, $P > 0.150$) despite the absence of the homologous state for a common allele in the Interior breeding population (Fig. 1). Genotypic distribution was identical across populations (modified *G*-test [Goudet et al. 1996]; $P = 0.120$). Allele distribution also was the same across populations (unbiased probability test [Raymond and Rousset 1995b]; $P = 0.08$).

Genotypic variation (F_{ST}) and sequence variation (Φ_{ST}) among breeding populations indicated a significant level of geographic differentiation (AMOVA, $P < 0.001$ for both; Table 2). Pairwise comparisons for both variation indices indicated that the California and Interior breeding populations differed from each other (permutation test, $P < 0.05$), but neither differed from the Eastern population ($P > 0.100$; Table 3). Overall, 6% of the total nucleotide variation was distributed among the breeding populations. Gene flow was highest (∞ individuals/generation) between Interior and Eastern Least Terns and lowest (1.9 individuals/generation) between Interior and California terns (Table 3).

Mitochondrial.—A 362 bp segment of the cytochrome-*b* gene was obtained for 52 individuals (18 California, 21 Interior, 12 Eastern). Three haplotypes were found that differed from each other by one substitution. The Interior population was monomorphic for the most common haplotype, while a single individual in each coastal population possessed a unique haplotype (Table 1). Haplotype distribution did not differ across subspecies (unbiased probability test [Raymond and Rousset 1995b]; $P = 0.23$). Analyses of haplotypic and sequence variation indicated no difference among all three breeding populations (AMOVA, $P > 0.05$; Table 2). Gene flow was highest (82.8 individuals/generation) between California and Eastern Least Terns and lowest (9.7 individuals/generation) between Interior and Eastern terns (Table 3).

DISCUSSION

Analyses of nuclear and mtDNA sequences indicated that Eastern Least Terns did not differ genetically from California or Interior Least Terns. These data concurred with findings of most researchers who explored variation among Least Terns (Table 4). Conclusions from nuclear and mtDNA analyses were contradictory for differences between the California and Interior Least Terns. Results from analysis of nuclear DNA suggested that Interior and California Least Terns differed from each other and exhibited low rates of gene flow while mtDNA suggested no difference and frequent gene flow. However, the difference observed in the nuclear DNA data should be treated cautiously because the lack of one of the homozygous states for the most common heterozygote may indicate an artifact of sample size in the Interior population.

Band-return data suggest that Least Tern populations conform to the stepping-stone model of distribution (Kimura 1953) because dispersal of first-time breeders and adults was greatest to nearby colonies (Atwood and Massey 1988, Renken and Smith 1995). Crow and Aoki (1982) estimated that for stepping-stone dispersers, 2 - 4 migrants/generation would be sufficient to prevent population divergence due to genetic drift. Genetic material is being exchanged between Eastern and California and between Eastern and Interior at sufficient rates (>3 migrants/generation) to prevent divergence. The lower rate of genetic exchange (1.9 migrants/generation) between Interior and California may not be adequate to prevent divergence. Based on mtDNA analyses, none of the geographic regions differed. Of the three haplotypes found, one occurred in 96% of the samples, while the remaining two haplotypes were found in single individuals from each coastal population. Gene flow was high between all regions.

Limited variation in both nuclear and mitochondrial DNA can be suggestive of recent expansion or a bottleneck (Halley and Hoelzel 1996). However, Thompson et al. (1992) found that allozyme variation for Least Terns was not lower than an expected range for birds. Genetic variation for a species within the Charadriiformes, the Marbled Murrelet, has been assessed for cyt-*b* and the Gadp intron. Compared with Least Terns (Φ_{ST} = 0.02), Marbled Murrelets (Φ_{ST} = 0.02) possessed the same levels of divergence in cyt-*b* over a smaller geographic range (coastline from Oregon to Alaska; Friesen et al. 1996b). However, Marbled Murrelets from the same geographic range possessed less nuclear variation (Φ_{ST} = 0.03) at the Gadp intron (Friesen et al. 1997) than Least Terns. Nucleotide sequences have been examined for segments of cyt-b and the control region in three gull species (Caspian Gull, *Larus cachinnans*; Herring Gull, *L. argentatus*; Black-headed Gull, *Chroicocephalus ridibundus*; Crochet and Desmarais 2000); only one haplotype was found in 12 Caspian Gulls and three haplotypes were found in eight Herring Gulls. Black-headed Gulls were the most diverse with six haplotypes in 12 samples. Contrary to expectations, domain III of the control region in 32 Larids was no more variable than domain II or cyt-*b* (Crochet and Desmarais 2000). The levels of variation observed for Least Terns tend toward the low end of variation observed for Laridae with similar life histories but are not unusually low.

Although no variation was found in the Enol intron, F_{ST}-values for the Gadp intron indicated significant genetic divergence between California and Interior breeding populations. This contradicted mtDNA data that showed no population structure. A pattern of significant variation between populations based on nuclear DNA that is not supported by mtDNA suggests that females disperse while males return to nest near their natal colony. Female-biased dispersal has been documented for many bird species (Johnson and Gaines 1990). Estimates of nest-site fidelity and philopatry of Least Terns vary, and sex of dispersing or non-dispersing individuals is rarely reported, which is expected due to the lack of dimorphic traits between tern adults (Thompson et al. 1997a). Various studies have found that some adult Least Terns banded as adults nested ≤80 km of the banding site and that 95% of banded chicks that returned to breed were found ≤75 km of their natal colony (Massey et al. 1992, Boyd 1993, Lingle 1993, Renken and Smith 1995). It is not surprising that Least Terns rarely are relocated at the same location where they were banded. Strict philopatry and breeding site fidelity would be detrimental to this species because breeding grounds of Least Terns are highly susceptible to alteration and destruction by flooding, particularly those of Interior Least Terns nesting on islands within major river drainages (Sidle and Harrison 1990, Thompson et al. 1997a). Measurements of dispersal distance may be biased because relocations of banded individuals would be limited to within a study's boundaries or reports from other observers. The single reported instance of dispersal from coastal Texas to Kansas may reflect difficulties in relocating banded Least Terns, not an indication of rarity. Genetic data suggest that many Least Terns are dispersing between populations and that those dispersers may be predominately female. A recent study on population trends in Interior Least Terns also concluded that dispersal may be common from the Eastern to the Interior breeding population because productivity estimates for Interior terns were too low to account for the increase in population estimates (Kirsch and Sidle 1999).

Lack of genetic and biological variation among breeding populations suggests that none of them exhibit unique adaptations that would limit survival at sites far from natal regions. Based on gene flow estimates, Least Terns possess the mobility to recolonize suitable breeding habitat if it becomes available. Habitat loss remains a problem for endangered populations of Least Terns (Thompson et al. 1997a), but if this trend can be reversed, Least Terns should be able to recolonize previously abandoned sites.

The only definitive measurement distinguishing subspecies is breeding location and even that measurement is vague where Interior and Eastern subspecies likely overlap. Although conclusions in this study are based on historically derived characters, gene flow estimates concur with recent estimates of dispersal between Eastern and Interior Least Terns (Kirsch 1999). At this time, Least Tern subspecies cannot be differentiated consistently based on genetics, morphology, or behavior (Massey 1976, Thompson et al. 1992). I reiterate the request of Thompson et al. (1992) for additional evaluation of the subspecific status for Least Terns.

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Table 1. Haplotype frequencies for two nuclear introns (Enol and Gadp) and part of the cytochrome-*b* (cyt-*b*) gene in three breeding populations of Least Tern. Three haplotypes were found in one intron and the cyt-*b* gene; second intron was monomorphic.

	Breeding Populations		
Haplotype	California	Interior	Eastern
Enol			
n	17	22	14
Enol-A	1.00	1.00	1.00
Gadp			
n	16	19	15
Gadp-A	0.56	0.29	0.37
Gadp-B	0.41	0.68	0.63
Gadp-C	0.03	0.03	0.00
Cyt-*b*			
n	12	21	18
Cytb-1	0.92	1.00	0.94
Cytb-2	0.08	0.00	0.00
Cytb-3	0.00	0.00	0.06

Table 2. Estimates of population differentiation in Least Tern using a nuclear intron (Gadp) and part of the cytochrome-*b* (cyt-*b*) gene. AMOVA analysis (Arlequin, version 2.000; Schneider et al. 2000) detected differences between breeding populations for the Gadp intron at both the genotypic (F_{ST}) and the nucleotide (Φ_{ST}) measurements.

Genetic Indices	Gadp	Cyt-*b*
F_{ST}	0.0556[a]	0.000
F_{IS}	-0.0641	na[b]
F_{IT}	-0.0049	na
Φ_{ST}	0.0622[a]	0.0169
Φ_{IS}	-0.1045	na
Φ_{IT}	-0.0357	na

[a] $P < 0.0001$.

[b] na = not applicable.

Table 3. Population pairwise F_{ST}- and Φ_{ST}-values for cyt-*b* (bottom left of each matrix) and Gadp intron (upper right of each matrix) for subspecies of Least Tern in North America. Pairwise comparisons of the nuclear intron revealed that the California population differed from the Interior although neither population differed from the Eastern. Gene flow was calculated from Φ_{ST}-values (second number in the Φ_{ST}-matrix).

	California	Interior	Eastern
F_{ST}-values			
California		0.111[a]	0.054
Interior	0.000		0.0
Eastern	0.000	0.000	
Φ_{ST}-values			
California		0.119[a]/1.9	0.068/3.4
Interior	0.009/55.1		0.0/∞
Eastern	0.006/82.8	0.049/9.7	

[a] $P < 0.05$.

Table 4. Review of taxonomic studies of Least Terns that evaluated whether or not subspecies (California, Interior, and Eastern) of Least Tern could be differentiated. Original subspecific classifications are not included.

	Pairwise Comparisons of Subspecies			
	California-Interior	California-Eastern	Eastern-Interior	Technique
Thompson et al. 1992	No	No	No	Morphology
Thompson et al. 1992			No	Protein analysis
Massey 1976		No		Vocalizations
Burleigh and Lowry 1942	Yes	No	Yes	Morphology
Johnson 1998	Yes	Yes	Yes	Colorimetrics
This study	Yes	No	No	Nuclear
This study	No	No	No	Mitochondrial

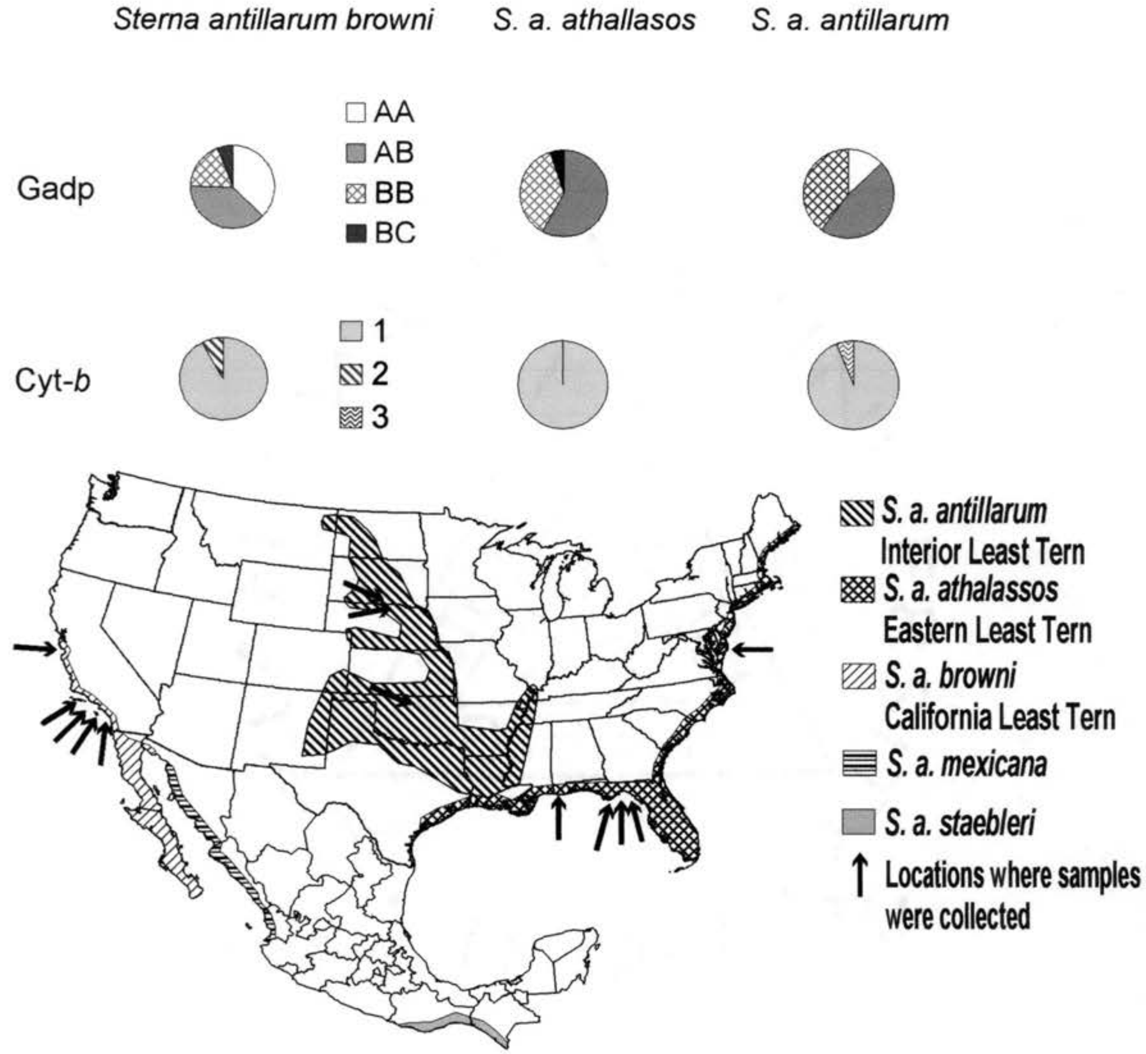

Fig. 1. Breeding ranges for subspecies of Least Tern (*Sterna antillarum*). Genotype frequencies for the nuclear intron, Gadp, and haplotype frequencies for cytochrome-*b* are diagramed for each of the three subspecies examined in this study.

Chapter II

LONG-TERM MONITORING OF ANTHROPOGENIC IMPACTS ON REPRODUCTION OF INTERIOR LEAST TERNS

Abstract: Interior least terns (*Sterna antillarum athalassos*) nest on an extensive salt flat at Salt Plains National Wildlife Refuge (SPNWR) in Oklahoma. This refuge was designated as a critical site for the recovery of this federally endangered species. During the tern's nesting season, 60 ha of the salt flats are open to public access for collecting unique selenite crystals. The objective of this 8-year study was to examine anthropogenic impacts on reproductive success of nesting least terns at SPNWR. Nests were monitored at a reference site and the public access site. Annual visitation to the public access site averaged 25,000 people from 1991 to 1998. Nest success and number of chicks hatched per successful nest differed between study sites ($P < 0.05$); however, both were greater at the public access site. Predation was greater ($P = 0.021$) at the reference site suggesting that reference nests were more vulnerable to predators. Nest success and other reproductive parameters did not increase or decrease relative to distance from human activity. Aside from predators, environmental factors exerted similar influences on nest success between sites. Distribution of nests around the public access site did not appear to be determined solely by distance from human activity; however, no least terns nested $\leq$300 m of human activity. Because the public access site at SPNWR opened prior to arrival of least terns, terns probably placed their nests at an

adequate distance from the human disturbance so that adverse impacts were avoided.

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Key words: colonial waterbird, endangered, human disturbance, least tern, Oklahoma, reproduction, *Sterna antillarum athalassos*

Interior least terns are migratory birds that nest along interior river systems of North America (Kirsch and Sidle 1999). Their nesting habitat consists of riverine sandbars and shorelines and alkaline flats with vegetative cover generally <25% (Thompson and Slack 1982, Faanes 1983, Schweitzer and Leslie 1999). Shoreline development and changes to the normal flood regime have reduced available nesting habitat for this species (Faanes 1983, Gochfield 1983, Thompson et al. 1997). Reduced flooding prevents scouring of sandy islands and shores, allowing vegetation to grow and making the habitat unsuitable for nesting terns (Leslie et al. 1997, 2000; Thompson et al. 1997). In 1985, the interior population of least terns was added to the federal endangered species list (U.S. Fish and Wildlife Service 1985). A recovery plan established SPNWR in Oklahoma as a critical site for recovery of interior least terns because the salt flats area at SPNWR provided nesting habitat for the greatest concentration of breeding least terns in Oklahoma (Sidle and Harrison 1990).

Historically, the salt flats at SPNWR covered about 11,000 ha until a reservoir was built in 1941 that reduced the size of the salt flats by about 30% (Purdue 1976). Prior to designation as a national wildlife refuge, the salt flats were used by the public for collecting salt and the U.S. Army Air Corps for target practice, and picnickers drove onto the flats for recreation and to collect the selenite crystals that form along the creeks. Unlike other federal lands, the National Wildlife Refuge System is managed primarily for wildlife (General Accounting Office 1989). Under the Refuge Recreation Act of 1962, refuge lands can be used for other purposes as long as those uses are compatible with the original intent of the refuge (Curtin 1993). Public access to the salt flats at SPNWR is important to the local economy because of a unique crystal formation sought by tourists and rock collectors. For this reason, crystal collecting is allowed in a 62-ha site located at the southern end of the refuge. The site is divided into 6 units about 10 ha each that are cycled so that only 1 unit is open each year from 1 April to 15 October, which coincids with the least tern nesting season. Crystals are collected by digging shallow pits with shovels or trowels. Although the process of collecting crystals is sedentary and subdued, an average of >200 people/day collect crystals during the tern's nesting season (Koenen 1995). In addition, private vehicles and commercial tour busses are allowed to drive directly to an open dig site. Crystals form on the salt flats in the same areas used by least terns for nesting. Because human disturbance of colonial nesting least terns has been shown to reduce reproductive success (Burger 1984), a study was initiated in 1991 to examine anthropogenic impacts of the crystal collecting activity on least terns at SPNWR.

Anthropogenic impacts fall into 2 categories: direct and indirect (Burger 1981). Direct impacts physically destroy nests while indirect impacts disrupt normal nesting activity and may lead to nest failure. Nests of interior least terns may be impacted directly because they are ground nesters whose cryptic nests are placed in habitats amenable for public recreation and development. Their nests have been destroyed by off-road vehicles and trampling by people and domestic animals (Massey 1977, Burger 1984, Thompson et al. 1997).

Indirect disturbance of least tern colonies can result in temporary abandonment of nests (Burger 1981), exposing adults to aerial predation and eggs and chicks to predation and inclement environmental conditions. During the peak of summer, ground temperatures at SPNWR can reach 50°C (Krey et al. 1993). Under these conditions, if adults remain away from their nest for an extended period, eggs can addle and very young chicks can die of exposure (Moreng and Shaffner 1951, Drent 1967, Grant 1982). Indirect human disturbance has been linked to colony abandonment in least terns (Kotliar and Burger 1986), reduced colony size of least terns (Burger et al. 1995), and reduced hatching success in herring gulls (*Larus argentatus*; Hunt 1972). Human activities can lead to increased visitation by predators attracted to refuse left behind (Hunt 1972, Burger 1981), but some mammalian predators (e.g., fox; *Vulpes* spp.) appear to avoid sites were humans have been (MacIvor et al. 1990).

The objective of this study was to examine anthropogenic impacts on reproductive success for least terns at SPNWR (Utych 1993, Koenen 1995, Winton 1997). If the terns were impacted by the human activity at SPNWR refuge, I predicted higher rates of predation and nest abandonment and lower nest success for nests located near the crystal dig site compared with a reference site with no human activity. I also expected nest placement to change relative to distance from the dig unit open to the public.

STUDY AREA and METHODS

This study was conducted at the SPNWR in Alfalfa County, Oklahoma, during summers 1991–1998. Nest monitoring was initiated in mid-May and continued through mid-August of each year. Nest monitoring was conducted by R. B. Utych in 1991-1992, M. T. Koenen in 1993-1994, B. R. Winton in 1995-1996, and J. B. Whittier in 1997-1998. Standarized methods were used among investigators. Least tern nests were located by a systematic search of defended territories within 2.5 km of the crystal dig units and at a reference site in the northeastern region of the salt flats, which was closed to the public (Fig. 1).

Nests were marked with a numbered dowel protruding 25 cm and placed ≥10 m away from the nest cup in a random direction to discourage habituation by predators. Nest distribution around the crystal dig units was determined using a grid system of stakes placed every 100 m that was established before least terns arrived. Distance to the corresponding active dig unit and to the center of dig unit C (Fig. 1) were measured for all nests found in 1991–1994 and 1997–1998. Nests were monitored every 3-10 days until hatching or failure. Because researcher disturbance could decrease reproductive success (Burger 1981, Carney and Sydeman 1999), I followed suggestions proposed by Fetterolf (1981) to reduce researcher impact by limiting the time spent in colonies and only visiting colonies when temperatures were <30°C.

During each visit, clutch size, presence of chicks or adults, and condition of nest, eggs, and chicks were recorded. Nest and egg condition and nest outcome were characterized using the protocol described by Koenen (1996a). Chick condition was categorized as alive or dead. Nests containing small fecal material or ≥1 juvenile were considered successful.

Although the Mayfield technique (Mayfield 1961, 1975) generally is considered a better estimator of nest success, I calculated apparent nest success as the proportion of nests that hatched ≥1 chick because the breeding habits of least terns violate the assumptions of the Mayfield technique (Johnson and Shaffer 1990). The Mayfield technique was developed for species whose nests were difficult to locate, did not experience synchronous failure, and generally were not found at nest initiation. The semi-colonial breeding habits of least terns make them conspicuous, and the close proximity of nests can lead to sudden colony failure due to events such as flooding and predation (Jenks-Jay 1980, Winton et al. 2000).

Logistic regression (Johnson 1998) was used to determine if nest outcome was influenced by human activity in the crystal dig complex. Nest outcome (successful, abandoned, depredated, flooded) was the dependent factor with reference and public access sites as a binary independent factor. Because nest outcome could be influenced by year, the main effect of year was included in each model. Regression diagnostics were used to evaluate model fit (Johnson 1998). Total number of eggs per nest and number of chicks hatched per successful nest at each location did not meet assumptions for parametric tests, such as equal variances, and were influenced by a year effect, so those variables were ranked and blocked by year in an ANOVA test (Conover and Iman 1981). Stepwise logistic regression was used to evaluate the influence of environmental variables on nest success at each site. Nest success was the binary dependent factor with environmental variables as the independent factors. Rainfall and temperature data were obtained for each year of the study from a weather station in Cherokee, Oklahoma, located about 8 km west of SPNWR.

Nest distribution around the crystal dig units was evaluated to determine if 1) nest outcome was a function of distance from human activity, 2) terns moved up- and downstream when human activity was closer to the ephemeral creek that ran along the north end of the public access area (Fig. 2), and 3) nest outcome differed for specific sites around the dig units. The first question was tested by measuring the distance from each nest to the center of the corresponding active dig unit. Nest outcome was calculated for each 500-m radius with a maximum distance of 2,000 m. Nest outcome was regressed against an ordinal arrangement of dig units (unit C to unit F).

The second question was assessed using trigonometric functions. The center of the dig unit C was selected as a fixed point from which to evaluate changes in nest distribution. The direct distance to the nest from the center of dig unit C, the distance, y, along the north-south orientation through the center of C, and the distance, x, along the east-west orientation were measured (Fig. 2). The angle formed by the direct distance and the north-south orientation determined an angle θ (Fig. 2). The sine of θ was computed by x divided by direct distance. Sine measurements of larger magnitude indicated an east-west orientation of nests from the fixed point. Nests to the east would have a positive sine and nests to the west would have a negative sine value. The absolute value of sine θ was used to obtain a measure of lateral placement. Because the sine measurement indicated lateral placement but not distance from the dig units, direct distance was incorporated into the analysis. An increase in both measurements indicated a shift in nest position farther up- and downstream. Changes in trigonometric measurements were tested using MANOVA (Johnson 1998) with absolute sine θ and direct distance as dependent factors and unit as the independent factor (Fig. 2). A linear response of absolute sine θ and direct distance with distance of human activity from the stream was assessed using a linear contrast.

The third question was modeled using stepwise logistic regression with sine θ, cosine θ, direct distance, all squared main factors, and interactions. Cosine of θ was computed by y divided by direct distance. Squared main factors were included to account for non-linear functions. The addition of cosine θ provided information on the north-south orientation. Negative cosine values indicated nests located south of the fixed point in dig unit C. Significance level for variables to stay in the model was set at $\alpha = 0.10$. Nest outcome was the binary dependent factor and the trigonometric measurements were independent factors. Because sine and cosine functions only provide a general orientation, direct distance was included as a factor in each model to refine the description of specific sites.

Significance for all tests, except the logistic regression using stepwise selection, was set at $\alpha = 0.05$. All statistical analyses were conducted with SAS computer software (SAS Institute Inc. 1996).

RESULTS

Nest Outcome

Mean nest success was <40% at both the crystal dig and reference site, with flooding accounting for the majority of nest failures (Table 1). Probability of nest success differed among years and between the crystal dig and reference sites (log likelihood χ^2 = 13.821, df = 2, P = 0.001). Nests at the dig site were more likely to hatch than those at the reference site (odds ratio = 1.458, df = 1, P = 0.04). However, the Hosmer and Lemeshow Goodness-of-fit Test suggested that the model did not fit the data well (Goodness-of-fit Statistic = 42.078, df = 8, $P < 0.001$), and concordance also was low (55%). Likelihood of nest predation was a function of year and site (log likelihood χ^2 = 10.203, df = 2, P = 0.006). Predation was less likely to occur at the dig site (odds ratio = 0.542, df = 1, P = 0.010). The Hosmer and Lemeshow Goodness-of-fit Test suggested that the model did fit the data well (Goodness-of-fit Statistic = 3.515, df = 7, P = 0.834) and concordance was 57%. Nest abandonment was related to year but not site (log likelihood χ^2 = 13.167, df = 2, P = 0.001; odds ratio for site = 0.831, P = 0.600). The Hosmer and Lemeshow Goodness-of-fit Test suggested that the model did not fit the data well (Goodness-of-fit Statistic = 20.166, df = 8, P = 0.010) and concordance was 61%. Likelihood of a nest flooding was not related to year or site (log likelihood χ^2 = 0.014, df = 2, P = 0.993). The Hosmer and Lemeshow Goodness-of-fit Test suggested that the model did not fit the data well (Goodness-of-fit Statistic = 55.858, df =7, P = 0.001) and concordance was 35%. Number of eggs per nest did not differ between locations (F = 0.40, df = 1, 549, $P = 0.526$). Number of chicks per successful nest differed between the crystal dig and reference sites ($F = 4.11$, df = 1, 549, $P = 0.043$) with more hatched chicks at the dig site.

Visitors occasionally wandered outside the boundaries of active dig units, disregarding signs mandating that visitors remain within the fenced unit. However, only 1 nest was stepped on by visitors walking outside the crystal dig boundaries during this study (Koenen 1995). Despite the high number of visitors to the crystal dig units ($\bar{x} = 25{,}000$/nesting season), nest success showed a weak positive trend with number of visitors ($r = 0.59$, $P = 0.125$). Average rainfall during the nesting season showed a weak negative trend with nest success around the crystal dig units ($r = -0.41$, $P = 0.316$) and number of visitors ($r = -0.47$, $P = 0.245$) suggesting that both were reduced by rainfall.

Nest success around the crystal dig units was related positively to the number of days with temperatures >32°C, maximum temperature, and number of days with >0.25 cm precipitation and negatively to total precipitation (log likelihood $\chi^2 = 27.290$, df = 3, $P < 0.001$; Table 2). The Hosmer and Lemeshow Goodness-of-fit Test suggested that the model did not fit the data well (Goodness-of-fit Statistic = 40.393, df = 8, $P < 0.001$), but concordance was 67%. Nest success at the reference site was found to be a function of the same variables (log likelihood $\chi^2 = 37.721$, df = 3, $P < 0.001$). The Hosmer and Lemeshow Goodness-of-fit Test suggested that the model did fit the data well (Goodness-of-fit Statistic = 10.882, df = 7, $P = 0.144$), and concordance was 80%.

Nest Distribution

To examine the relationship between nest outcome and distance from human activity, nests were grouped in 500-m radii from the center of active dig units. Nests only occurred within 500 m of an active dig on 7 occasions (Table 3). No relationships existed for nest outcome, total clutch size, or number of chicks hatched per successful nest compared with distance from human activity.

Distribution of nests determined by direct distance, and absolute sine θ differed among units (MANOVA Wilks' Lambda $P = 0.001$), and individually the variables direct distance and absolute sine θ differed among dig units (ANOVA $P < 0.02$ for both; Table 4). However, nest distribution was not linearly related to the direct distance or absolute sine θ ($P > 0.05$).

Model selection techniques for the nest success model yielded a prediction model with direct distance, direct distance squared, and cosine (log likelihood $\chi^2 = 9.211$, df = 3, $P = 0.027$). The Hosmer and Lemeshow test indicated a good fit for the model (Goodness-of-fit Statistic = 6.607, df = 8, $P = 0.580$), and concordance was 60%. Nests located north of the dig units (cosine 45 - 315) and between 500 - 1500 m away had the highest nest success (Table 5). Model selection techniques for the predation model yielded a prediction model with direct distance and absolute sine factor (log likelihood $\chi^2 = 16.356$, df = 2, $P = 0.001$). The predation model was not a good fit to the data (Hosmer and Lemeshow test; Goodness-of-fit Statistic = 13.928, df = 8, $P = 0.08$), but concordance was 70%. Predation appeared highest for nests located west of the dig units (cosine 225 - 315; Table 6). Model selection techniques for the abandonment model yielded a prediction model with direct distance, cosine and cosine squared (log likelihood $\chi^2 = 16.776$, df = 3, $P = 0.001$). The whole model fit the data well (Hosmer and Lemeshow test; Goodness-of-fit Statistic = 3.853, df = 8, $P = 0.870$). Abandonment was highest for nests located closer to and due east or due west of the dig units (cosine 90 and 270; Table 7). Model selection techniques for the flooding model yielded a prediction model with direct distance, cosine, cosine squared, and the interaction term absolute sine times direct distance (log likelihood $\chi^2 = 20.565$, df = 4, $P < 0.001$). The whole model fit the data well (Hosmer and Lemeshow test; Goodness-of-fit Statistic = 8.201, df = 8, $P = 0.414$). Flooding was highest for nests located east of the dig units and for those located directly to the north about 500 m away (cosine 45 - 90 and 360, Table 8).

DISCUSSION

Nest Outcome

Human activity near nesting grounds of colonial nesters such as least terns has the potential to increase predation rates and reduce reproductive success directly through trampling of nests and indirectly through disturbance (Burger 1981). At SPNWR, direct destruction of nests was minimal. During the 8 years of this study, a visitor who walked into a colony destroyed only 1 nest (Koenen 1995). Most people complied with the signs mandating that visitors stay within the boundary of each dig unit.

Nest success and predation rates differed between the public and reference sites; success was higher and predation rates were lower around the public access site compared with the reference site. Nest abandonment and flooding rates were the same for each site. Because the only logistic model that fit nest outcome data was for predation, results from the other models should be treated cautiously. Biologically, the difference between sites for flooding and abandonment was 1% while nest success was 8% higher at the public access site (equivalent to the difference observed for predation). Although the number of eggs per nest were the same for each site, the number of chicks that hatched per successful nest was higher around the public access site. None of the environmental factors examined adequately explained differences in nest success between each site.

Proximity to vegetation may explain the differences observed for these 2 sites. Koenen et al. (1996b) found that at SPNWR, coyotes *(Canis latrans)* were the primary mammalian predator on least tern nests and that artificial nests adjacent to vegetation were more likely to be depredated by coyotes than nests located >500 m from vegetation. Higher predation rates for artificial nests close to habitat edges have been documented repeatedly (Laudenslayer 1986, Andren and Angelstam 1988, Yahner and Scott 1988). The reference site paralleled a permanent creek that was vegetated on the opposite bank (~300 m away); whereas most nests around the public access site were >1 km from vegetation. Higher predation disturbance also may explain the disparity between sites of number for chicks per successful nest. When disturbed, herring gull (*L. argentatus*) chicks will run farther from nests (Hunt 1972). As with herring gulls, least tern eggs hatch asynchronously, and tern chicks are mobile shortly after hatching. So, it may be possible that frequent predator disturbance could cause chicks to leave their nest prior to all eggs hatching. It also is possible that fewer predators are using the public access area because of the presence of people (MacIvor et al. 1990).

Nest Distribution

Studies of flush distance for least terns have shown disparity among individuals in their tolerance to human approach (90-500 m; Erwin 1989, Koenen 1995, Rodgers and Smith 1995). At SPNWR, there were no gradients in nest outcome or reproductive parameters relative to distance from human activity. However, only 7 least tern pairs nested <500 m of an active dig unit and none <300 m. Although least terns tend to nest close to water sources (Faanes 1983), terns nests at SPNWR were not displaced farther upstream and downstream when the active dig unit was closest to the creek at the north end of the dig units (Fig. 2).

Nest productivity was higher at the public access site than the reference site, but the most productive region around the public access site was north of the dig units presumably as a result of lower flooding and abandonment rates. Nests located west of the public access site appeared to have higher rates of predation. These predation rates may be a result of vegetation encroachment facilitating predator access (Koenen et al. 1996b).

MANAGEMENT IMPLICATIONS

Merging the objectives of conservation and recreation requires a thorough understanding of the sensitivity of the species impacted by the recreation (Boyle and Sampson 1985). Even when intentions are well-meaning (e.g., photographers and bird-watchers), the effect can be detrimental (Boyle and Sampson 1985). At SPNWR, direct and indirect adverse impacts to nesting least terns likely have been avoided by limiting recreational activities to a small part of the available habitat and opening the dig units to public access prior to arrival of terns. Public visitation to the dig units has provided the refuge with an opportunity for public education via informational displays, and the public has a chance to see these endangered birds. The combination of seeing and learning about an endangered species can be a powerful tool toward promoting public support for conservation (Whiteman 1996).

Unfortunately, nest success at SPNWR tends toward the lower end of nest success estimates from throughout the range of interior least terns (Kirsch 1996, Table 23; Grover and Knopf 1982, Dinsmore et al. 1993, Kirsch and Lingle 1993, Lingle 1993, Mayer 1993, Kirsch 1996) despite the willingness of refuge personnel to implement various management plans to improve least tern productivity (Koenen 1995). Flooding is the primary cause of nest loss at SPNWR and has been impossible to prevent because terns that nest at SPNWR rarely use raised structures designed to avoid flooding (Koenen 1995, Koenen Koenen et al. 1996a). The second most common cause of nest failure is from predation. Koenen et al. (1996b) demonstrated that predation rates at SPNWR were greater for artificial tern nests near a vegetation edge and that vegetation has been encroaching onto the salt flats since 1941. Much of the recent encroachment in the reference site and northwest of the dig units has been from tamarisk (*Tamarix parviflora*; Whittier pers. obs.). Reducing nest loss from flooding has not been very effective but predation rates might be reduced by controlling tamarisk. Future research at SPNWR should address the relationship between vegetation encroachment and facilitation of predator access to nests on the salt flats. The presence of this population on a national wildlife refuge warrants aggressive recovery activities because many other breeding populations of interior least terns nest in unprotected habitat along interior waterways.

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Table 1. Nest outcome and reproductive parameters for least tern nests at a site adjacent to human activity (Dig) and at a reference (Ref) site at Salt Plains National Wildlife Refuge, Oklahoma, 1991 - 1998.

	1991		1992		1993		1994		1995		1996		1977		1998		All years	
	Dig	Ref	Dig	Ref	Dig	Ref	Dig	Ref	Dig	Ref	Dig	Ref	Dig	Ref	Dig	Ref	Dig	Ref
Number of nests	34	11	59	9	99	50	60	59	36	34	35	42	76	20	36	9	435	234
% success	50	27	32	0	24	18	52	51	50	12	17	36	39	20	72	78	39	31
% flooded	18	0	31	33	46	46	8	3	36	41	26	29	37	55	11	22	30	29
% depredated	18	45	17	33	9	12	9	15	0	24	26	17	8	10	8	0	11	17
% abandoned	6	0	12	12	6	6	13	17	6	9	3	0	0	0	0	0	6	7
% unknown	9	27	8	22	15	18	18	14	8	24	28	18	16	15	9	0	14	20
Eggs/nest	1.9	2.1	1.8	1.7	2.1	1.9	2.2	2.2	2.2	2.2	2.0	2.1	2.2	2.4	2.2	2.3	2.1	2.1
Chicks/successful nest	1.8	2.0	1.7	0	2.0	1.7	1.9	1.8	2.0	1.5	2.0	1.5	1.7	2.0	2.0	2.1	1.9	1.8

Table 2. Results of stepwise logistic regression to assess the influence of climatic variables on nest success at two sites (crystal dig and reference) at Salt Plains National Wildlife Refuge, Oklahoma, 1991 - 1998. The site adjacent to human activity (crystal-dig model) and reference site (reference-site model) were analyzed separately to examine causes for differences in reproductive parameters for the sites.

Model	Coefficient	*SE*	Wald X^2	*P*
Crystal-dig model				
Intercept	-9.505	3.328	8.156	0.004
Days >32°C	0.032	0.014	5.213	0.022
Maximum temperature	0.093	0.033	8.149	0.004
Total precipitation	-1.073	0.276	15.118	0.001
Reference-site model				
Intercept	-11.977	4.183	8.198	0.004
Days >32°C	0.062	0.017	12.783	0.001
Maximum temperature	0.100	0.040	6.249	0.012
Total precipitation	-0.792	0.216	13.461	0.001

Table 3. Fate of least tern nests located around a site of human activity at Salt Plains National Wildlife Refuge, 1991 - 1998. Nests were tallied by distance to center of the active dig unit; no least terns nested <300 m of human activity.

	300-501 m	501-1,000 m	1,001-1,500 m	1,500-2,000 m
Number of nests	7	93	154	32
% Successful	43	44	45	22
% Flooded	29	38	25	47
% Depredated	14	8	31	9
% Abandoned	0	11	6	0
Eggs/nest	1.7	2.0	2.1	2.1
Chicks/ successful nest	1.3	1.8	2.0	1.8

Table 4. Trigonometric measurements describing distribution of nest locations for least terns relative to the public access site at Salt Plains National Wildlife Refuge, Oklahoma. Dig units are listed in order of proximity to the closest creek (Fig. 2). Measurements were taken from the center of dig unit C to provide a fixed reference point to assess changes in nest distribution among active dig units. Direct distance refers to the straight-line distance between nests and the fixed reference point at the center of dig unit C. Absolute sine was calculated from the bearing to each nest. I hypothesized that least terns would place nests farther up- and downstream in response to decreasing distance between active dig units and the creek. Both trigonometric measurements would increase as distance between active digs and the creek decreased. Distance and absolute sine differed among units, however did not exhibit a linear response.

Dig unit	Direct distance (m)	Absolute sine
C	993	0.790
D	897	0.591
E	786	0.720
F	966	0.823

Table 5. Predicted probability of nest success for least terns based on a logistic equation* derived from data collected at Salt Plains National Wildlife Refuge, 1991 - 1998.

	Direct distance			
Cosine (nest angle)	500 m	1,000 m	1,500 m	2,000 m
Cosine (45)	0.46	0.57	0.47	0.20
Cosine (90)	0.35	0.46	0.37	0.14
Cosine (135)	0.27	0.36	0.28	0.10
Cosine (180)	0.23	0.32	0.24	0.09
Cosine (225)	0.27	0.36	0.28	0.10
Cosine (270)	0.35	0.46	0.37	0.14
Cosine (315)	0.45	0.57	0.47	0.20
Cosine (360)	0.50	0.61	0.51	0.23

* Nest success = -1.896 + (0.003*direct distance) - (1.69 X 10^{-6} *direct distance^2) + (1.591*cosine)

Table 6. Predicted probability of nest predation for least terns based on a logistic equation* derived from data collected at Salt Plains National Wildlife Refuge, 1991 - 1998.

	Direct distance			
Absolute sine (nest angle)	500 m	1,000 m	1,500 m	2,000 m
Absolute sine (45)	0.17	0.27	0.39	0.52
Absolute sine (90)	0.08	0.14	0.22	0.33
Absolute sine (135)	0.17	0.27	0.39	0.52
Absolute sine (180)	0.60	0.72	0.82	0.89
Absolute sine (225)	0.92	0.95	0.97	0.98
Absolute sine (270)	0.96	0.98	0.99	0.99
Absolute sine (315)	0.92	0.95	0.97	0.98
Absolute sine (360)	0.60	0.72	0.82	0.89

*Nest depredation = -0.1459 + (0.00111*direct distance) - (2.8014*absolute sine)

Table 7. Predicted probability of nest abandonment for least terns based on a logistic equation* derived from data collected at Salt Plains National Wildlife Refuge, 1991 - 1998.

	Direct distance			
Cosine (nest angle)	500 m	1,000 m	1,500 m	2,000 m
Cosine (45)	0.08	0.03	0.01	0
Cosine (90)	0.38	0.12	0.03	0.01
Cosine (135)	0.11	0.03	0.01	0
Cosine (180)	0.02	0.01	0	0
Cosine (225)	0.11	0.03	0.01	0
Cosine (270)	0.38	0.12	0.03	0.01
Cosine (315)	0.07	0.02	0	0
Cosine (360)	0.01	0	0	0

* Nest abandonment = 0.9939 - (0.00252*direct distance) - (0.3702*cosine) - (3.7405*cosine^2)

Table 8. Predicted probability of nest flooding for least terns based on a logistic equation* derived from data collected at Salt Plains National Wildlife Refuge, 1991 - 1998.

		Direct distance			
Cosine (nest angle)	Absolute sine (nest angle)	500 m	1,000 m	1,500 m	2,000 m
Cosine (45)	Absolute sine (45)	0.87	0.80	0.71	0.60
Cosine (90)	Absolute sine (90)	0.51	0.67	0.80	0.89
Cosine (135)	Absolute sine (135)	0.74	0.64	0.51	0.39
Cosine (180)	Absolute sine (180)	0.66	0.06	0	0
Cosine (225)	Absolute sine (225)	0.01	0	0	0
Cosine (270)	Absolute sine (270)	0	0	0	0
Cosine (315)	Absolute sine (315)	0.02	0	0	0
Cosine (360)	Absolute sine (360)	0.87	0.18	0	0

*Nest flooding = -0.648 - (0.00675*direct distance) + (0.6019*cosine) + (5.2903*cosine^2) + (0.00812*absolute sine*direct distance)

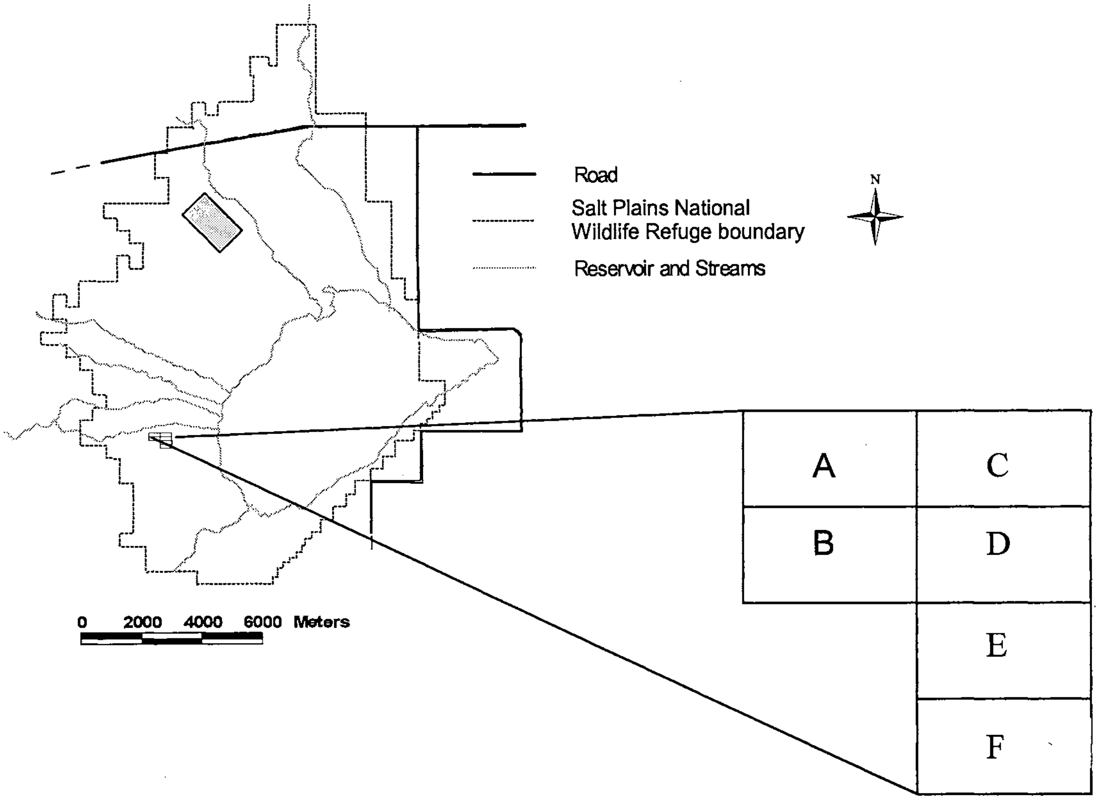

Fig. 1. Salt Plains National Wildlife Refuge showing the location of the reference site (shaded box) and of the crystal dig site that is open to the public. Magnified part is a diagram of the dig units (A - F) within the crystal-dig site.

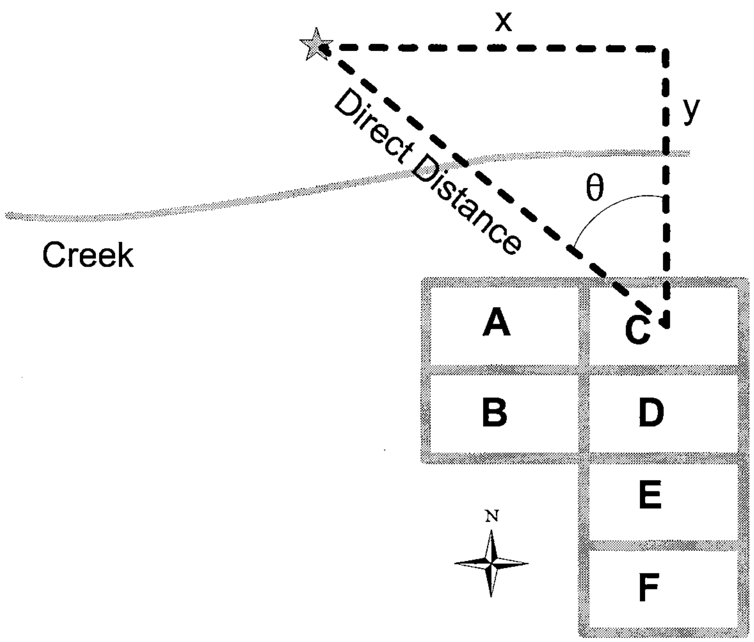

Fig. 2. Depiction of distance measurements used to assess nest placement of Least Terns relative to the public access area (dig units A - F) at Salt Plains National Wildlife Refuge. The shaded star represents a hypothetical least tern nest. Nests placed up- (west) and downstream (east) would have higher measurements for direct distance and sine θ and lower measurements for cosine θ than nests located closer to the midline through dig unit C.

CHAPTER III

POPULATION STABILITY OF A LONG-LIVED SPECIES WITH HIGH ADULT SURVIVAL AND ANNUAL NEST FAILURE

ABSTRACT.— It has been hypothesized that adult longevity coupled with occasionally high recruitment may offset generally low levels of reproduction. This question was assessed using a deterministic model with data from long-term monitoring programs of endangered Interior Least Terns (*Sterna antillarum athalassos*) nesting at Salt Plains National Wildlife Refuge (SPNWR) in Oklahoma, Quivira National Wildlife Refuge in Kansas, and along the Missouri River in South Dakota. Because chick survival was not measured at SPNWR during the long-term monitoring, the SPNWR population was modeled with a range of estimates for chick survival. This population also was modeled using a high and low estimate of survival from fledging to two years old. At the lower estimate of survival from fledging to two years of age, the model projected nearly stable to positive growth rates for all but the lowest measures of chick survival (0.10 and 0.26). Sensitivity of the model to equivalent increases (10%) in chick survival and survival from fledging to two years of age revealed that both productivity measurements exhibited a similar influence on population growth (48% and 52% increase in instantaneous growth rate, respectively). To compare the South Dakota and Kansas sites to the Oklahoma site, productivity measurements had to be converted from fledglings per pair to fledglings per nest. The Kansas and Oklahoma sites had similar measurements for fledglings per nest (0.33 and 0.36, respectively) with at least one year exceeding twice the

average measurement. The South Dakota site average of 0.25 fledglings/nest fell well below averages for Kansas and Oklahoma without any peak in productivity. The model projected an increase in Least Terns for the Kansas site and a decline in Least Terns at the South Dakota site. It appears that adult longevity can offset some levels of low productivity but will depend on level of productivity, magnitude of productivity peaks, and frequency of peaks. Population growth was influenced equally by chick survival and survival from fledging to two years of age. However, because it is impractical to increase survival during migration, management strategies should focus on factors influencing chick survival to improve productivity.

Long-lived species present unique challenges when assessing impacts of changing demography on population stability. Longevity of adults may mask detrimental impacts on population numbers (Thompson et al. 1997). For example, if recruitment is poor and the majority of individuals are in older age groups, the total population may appear to be stable until those older age groups die off. Conversely, adult longevity may nullify negative impacts of a generally low fecundity when productivity peaks occasionally (Caswell 1982, Boyd 1993). Management strategies and goals often rely on projection models to estimate viability of populations. Those projection models frequently take into account life span of individuals, but use productivity measurements randomly selected from a normally distributed range of productivity values.

Least Terns are a long-lived species with the oldest documented individual being >24 years old (Klimkiewicz and Futcher 1989). There are three breeding populations within the United States: California, Interior, and Eastern (Thompson et al. 1997). In the past century, the number of Least Terns has fluctuated widely. During the late 1800s, Least Terns declined in numbers due to harvesting for the millinery trade (Bent 1963). After the Migratory Bird Treaty Act was passed in 1916, tern numbers increased until the mid-1900s when alterations in normal flood regimes and urban and industrial development of shorelines led to further population declines (Thompson et al. 1997). These declines prompted the listing of California and Interior Least Terns as federally endangered (United States Fish and Wildlife Service 1980, 1985). I limited comparisons of population trend to sites within the range of the Interior Least Tern to reduce extraneous variance from modeling breeding populations using different habitats (interior versus coastal).

Interior Least Terns nest on open shorelines and islands throughout the Mississippi and Missouri river drainages (Thompson et al. 1997). They typically lay two to three eggs per nest and may renest if their nest is destroyed (Lingle 1993, Kirsch 1996). Least Terns raise a single brood per year and continue to feed offspring for several weeks after fledging (Thompson et al. 1997). Chick survival is difficult to estimate for these semi-precocial birds. Estimates of chick survival usually are based on the presence of fledglings at staging areas but may be biased by movement of fledglings between staging areas (Thompson and Slack 1984). Chick survival varies substantially between sites and years. Annual adult survival has been estimated at 85% (Renken and Smith 1995).

Deterministic models use life-table information on fecundity and survival to project trends in population growth given a fixed set of conditions (Hannon and

Ruth 1994). These models are static, representing the result of a particular set of conditions (Hannon and Ruth 1994). Deterministic models are considered most appropriate when the population being modeled has discrete birth-pulse type reproduction such as found in Least Terns (Caughley 1977). Data from a population or group of populations are combined to develop a base-line model. Sensitivity analysis conducted with the baseline model is used to evaluate parameters that most strongly influence persistence of the population (Boyce 1992). When fecundity does not offset adult mortality, the population is considered a sink and will not persist without immigration (Pulliam 1988). Population sources (fecundity rate exceeds adult mortality) either increase in size or export excess individuals (Pulliam 1988).

Two studies have modeled population dynamics of Least Terns. Both studies used deterministic models and found that change in adult survival was the most influential life stage in estimates of population stability (Thompson 1982, Kirsch 1996). Another important factor was maximum age; an increase in maximum age from 16 to 20 years resulted in a four-fold increase in population growth rate (Thompson 1982). Kirsch (1996) calculated that the population along the lower Platte River, Nebraska, was not self-sustaining and that 0.51 fledglings/pair was required to sustain a stable population. Kirsch (1996) suggested that the long life span of this species might offset low annual fecundity.

Long-term monitoring programs at Salt Plains National Wildlife Refuge (8 years; SPNWR) in Oklahoma, Quivira National Wildlife Refuge (11 years; QNWR) in Kansas (Boyd 1993), and along the Missouri River (7 years; MR) in South Dakota (Kruse 1993; Fig. 1) provided us with the opportunity to use empirical data to address whether occasionally high production could offset generally low reproductive output in a long-lived species. Annual reproductive estimates for the breeding population at SPNWR tended toward the low end of observed estimates for other sites throughout the range of Interior Least Terns (Table 1, 2). Although few estimates of chick survival have been conducted for the SPNWR breeding population, they tend to be low (<50%). These data suggest a tendency toward low chick survival at SPNWR. Average productivity for QNWR was slightly lower than at SPNWR but increased to twice the average in 20% of the studied years compared with 13% at SPNWR. Productivity at MR was lower than for SPNWR and QNWR and never doubled over the average. The influence of changes in chick survival and survival from fledging to two years of age was assessed for the SPNWR population.

METHODS

A model was developed to estimate population viability of a long-lived species that typically experienced poor annual reproductive success with occasional years of high success. A projection model (Hannon and Ruth 1994) was constructed using a Leslie matrix (Wilson 1975). Separate projections were conducted for each long-term monitoring site (SPNWR, QNWR, and MR). Instead of using an average fecundity in every year of a simulation, the model used fecundity estimates for each year of the monitoring periods. For example, Least Terns at SPNWR were monitored from 1991 to 1998. Year one of the model used fecundity estimates at SPNWR for 1991. For year two, the model used fecundity estimates for 1992 and so forth until year eight, when the end of the monitoring period was reached. Year nine of the model started over with data from 1991. The SPNWR data were repeated 25 times for a total of 200 years. Because monitoring periods at MR (7 years) and QNWR (11 years) differed from SPNWR, the models using the MR and QNWR data were repeated 29 and 19 times respectively until a minimum of 200 years was reached.

The estimate for chicks per nest rather than chicks per pair was used because population estimates were not available for SPNWR. Because Least Terns have the potential to renest within a breeding season, this would lower productivity estimates resulting in a decreased intrinsic growth rate. The components of the model consisted of annual fecundity and survival. Fecundity (F) for the Leslie matrix was calculated (Swartzman and Kaluzny 1987) as:

$$F = c_i * s * a * b_j * f$$

where:

c_i = average number of chicks per nest for each year i,

s = probability of chick surviving to fledging, held constant in each model run using the values 0.10, 0.26, 0.45, 0.50, 0.56, 0.80 (selection of values explained below),

a = probability of surviving first year (set at a constant of 1.0),

b_j = proportion of adults breeding for each age class j, and

f = probability of a chick being female (set at a constant of 0.5).

Because chick survival at SPNWR was estimated for only three of the eight years, a range of chick survival estimates was selected based on values reported for Interior Least Terns (Table 1). The values 0.10 and 0.80 were used as minimum and maximum because 90% of reported values fell within this range. The midpoint (0.45) was used for baseline comparisons. The values 0.26 and 0.56 were high and low estimates of chick survival at SPNWR that fell within the 90% confidence interval of reported values (Table 1). Average chick survival for QNWR and MR came from reported values at each site. The value of 0.50 represented a 10% increase in chick survival over the midpoint (0.45). The 10% increase was used to test sensitivity of the model to change in chick survival.

I assumed that first-year survival post-fledging was 100%. Although that assumption artificially boosted population estimates for yearling terns, excess yearlings did not contribute to production of chicks. Excess yearlings were removed from the population prior to breeding via estimates of survival from fledging to two years of age. Two estimates of survival to two years of age (Table 3) were used to incorporate low and high estimates reported by Thompson (1982) and Massey et al. (1992).

Only 33% of Interior Least Terns breed at two years of age (Lingle unpubl. data as reported by Kirsch 1996). All adults over two years of age were assumed to nest each year until death (Least Terns have been found nesting at 20 years old; Thompson et al. 1997). There is limited information on age-structured fecundity in terns. Studies of Roseate Terns (*S. dougallii*) and Sandwich Terns (*S. sandvicensis*) found increased hatch and fledging rates from younger to older birds, but results were not consistent across species (Veen 1977, Burger et al. 1996). No empirical data on age-structured fecundity were located for Interior Least Terns; therefore, fecundity was assumed to be constant for all ages. This is possibly an erroneous assumption; however, given that

Least Terns have been found nesting at 20 years old and adult survival is high after three years, it is likely that the majority of the breeding population consists of experienced nesters. Individuals entering the population were restricted to females by the final multiplier in the above equation. Fixed estimates of demographic parameters are shown in Table 3. It was assumed that reproductive and survival parameters did not vary between sexes and that sex ratio of chicks was 1:1.

The 10 age classes used in this model were based on age-structured survival rates reported in literature (Thompson 1982, Massey et al. 1992, Renken and Smith 1995; Table 3). An age class spanned the time from the start of one breeding season to the next. Chicks hatched during a breeding season were considered one year old at the start of the following breeding season; the first nine age classes represented ages 0 – 8 years, respectively. Because only two to three individuals were used to estimate age-structured survival for age classes >10 years (Massey et al. 1992), the tenth age class was composed of ages 9+. With the tenth age class set at a survival rate of 79%, the probability of survival to 20 years was 3% and <1% to age 25. Therefore, to simplify the model, no maximum age was incorporated.

Initial population size was set at 100 females. The model used repetitions of the monitoring data to estimate population size after 200 years. Intrinsic rate of population growth was calculated from the slope of the line after the trajectory became steady. Sensitivity of the model to changes in chick survival was assessed by increasing the midpoint for chick survival and the minimum fledging to two-year survival by 10%.

I selected two population viability indices designed to predict population stability based on reproductive measurements. One index used survival estimates to determine the number of female offspring per female per year required to maintain a stable population (Ricklefs 1972). The other was derived for Interior Least Terns. Kirsch (1996) estimated that a minimum of 0.51 fledglings/year would be required to maintain a Least Tern population. Those required recruitment indices were compared with recruitment measurements from each study population. Because those measurements were not available for the SPNWR population, they were calculated from observed number of chicks per nest and a range of chick survival estimates (Table 4). I hypothesized that if the indices of required recruitment predicted population declines when the model exhibited increasing growth rates, this would support the supposition of longevity compensating for low fecundity.

RESULTS

Only at the lowest levels of chick survival did the matrix model project negative intrinsic growth rates for the SPNWR population (Table 5). At the low estimate of survival to two years of age (0.60), chick survival at or above the baseline value (0.45) resulted in positive intrinsic rates of growth (Fig. 2a). Chick survival increments $\leq$26% produced population declines. Both a 10% increase in chick survival and a 10% increase in survival from fledging to two years of age resulted in nearly equal changes in intrinsic growth rates (48% and 52%, respectively; Fig. 3). A 10% increase in chick survival produced an initially greater response than a 10% survival to breeding increase. When survival from fledging to two years of age was held at 82%, chick survival estimates ≤26% still were insufficient to maintain population size, although 26% chick survival resulted in a nearly stable population size (Fig. 2b).

The estimate of recruitment required to maintain a stable population ranged from 0.19 to 2.08 female offspring/female/year (Table 4). At the lower levels of chick survival (0.10 and 0.26), both the model and the required recruitment index suggested that the population would decline. At chick survival of 45%, the required recruitment index indicated that the average number of female offspring/female/year used in the model should have resulted in a population decline, but the model predicted positive population growth. That appeared to indicate that longevity can offset generally low productivity.

Predictive indices for MR and QNWR populations indicated that those populations should be declining. Numbers of fledglings per pair for MR exceeded 0.51 (average determined by Kirsch [1996] as necessary to maintain a stable population of Least Terns) for only 29% of the years, but at QNWR, 36% were higher. Chick survival at the MR was 30% (Kruse 1993) giving required recruitment indices of 0.51 – 0.69 female offspring/female/year to maintain that population. Average fledglings/pair at the MR was below that range with only two of seven years exceeding 0.51. At QNWR, chick survival was 13% (Boyd 1993), producing a range of 1.17 – 1.60 female offspring/female/year required to sustain the population. Observed fledglings per pair averaged 0.42 with four years exceeding 0.51 and two years exceeding 1.00. However, modeling the QNWR and MR populations revealed a positive population trend at QNWR and a negative trend at MR (Fig. 4).

DISCUSSION

Previous models of Least Tern populations indicated that adult survival was critical to population stability (Thompson 1982, Kirsch 1996). These models support Caswell's (1982) contention that adult survival would impart the strongest influence on population stability for long-lived species, while fecundity would be more important for short-lived species. Thompson (1982) found that reduction of survival to breeding had a large impact on population growth rates of Least Terns. Modeling the separate components of survival to breeding revealed that changes in chick survival and survival from fledging to two years of age contributed equally to intrinsic growth rates. Based on these findings, the SPNWR breeding population was modeled using low and high estimates of chick survival and survival from fledging to two years of age taken from literature.

The average chick survival at SPNWR (41.8%; summarized by Schweitzer and Leslie [2000]) fell below the range of estimates required for a stable population (45 – 56%) based on Ricklefs index (1972) with 50% of the values below the minimal survival level. The SPNWR estimate of fledglings per successful nest (0.38) also was well below the level of 0.51 chicks/pair that Kirsch (1996) estimated as the minimum level required for population persistence. Although my estimate is not in the same units as the minimum value given by Kirsch (1996), the number of chicks per successful nest would be higher than the number of chicks per pair. Contrary to the above predictions, the matrix model indicated that the breeding population at SPNWR would persist despite persistently low productivity when chick survival was held at 0.45. Longevity coupled with occasionally high production offset the low fecundity exhibited by this breeding population.

The required recruitment indices also predicted population declines for QNWR. Despite a very low chick survival average (13%; Boyd 1993), the model produced a positive population trend. Number of fledglings per pair was very high (1.00 and 1.41) in two of the eleven years and these high measurements corresponded to relatively high chick survival and number of eggs hatched. Based on the growth curve produced from the population data from QNWR, colonies at this site could double every nine years. The required recruitment indices concurred with model results for the MR population. Longevity could not counteract low productivity at this site. This site differed from the other two in that the number of fledglings per pair never exceeded 0.65 although the average was >0.5.

SPNWR was designated as a critical site for recovery of Interior Least Terns because of the large number of terns that nested there each year (Sidle and Harrison 1990). Because adult longevity appears to offset the annual low production at SPNWR, this appears to be a stable if not increasing population. Improving chick survival would have a similar influence on population growth as increasing survival to two years of age; however, increasing chick survival is more realistic for this migratory bird. The main factor influencing nest success at SPNWR is flooding (see Chapter II, Koenen et al. 1996) and may be the primary factor reducing chick survival (Whittier unpubl. data). Because Least Tern chicks are mobile within a few days of hatching, it may not be practical to attempt to reduce the influence of flooding on chick survival. Attempts to improve nest success at SPNWR by providing raised structures were not particularly successful (Koenen et al. 1996). One flood prevention method that was not attempted at SPNWR is to physically move the nest contents onto a higher platform or to higher ground (Loftin and Thompson 1979). An intensive nest-moving management practice might increase the number of chicks hatched but would require very intensive monitoring and careful manipulation (Loftin and Thompson 1979). At the current level of productivity, the SPNWR population may be self-sustaining. Future research directions should include continued monitoring of chick survival to verify current estimates.

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Table 1. Reproductive indices for Interior Least Terns throughout their breeding range. Percentages given are for the number of years with values exceeding the given parameter.

Location	Chicks/nest		Chick survival[a]	Fledglings/pair		Source
	Range	% with ≥1 chick/nest	Range	Range	%≥ 0.51	
Missouri River	0.08-2.4	58				Woodrey and Szell 1998
Oklahoma	0.61-0.83	0				Wood 1994
Lower Mississippi River			0.57-0.82			Renken and Smith 1993
Texas				0.65-0.81	100	Thompson 1982
Nebraska			0.12-0.38	0.21-0.73	50	Kirsch 1996
South Dakota				0.59-0.86	50	Adolf 1998
South Dakota	0.30-1.27	29	0.19-0.51	0.20-0.64	29	Kruse 1993
Kansas	0.21-1.80	37	0.0-1.00	0.0-1.41	36	Boyd 1993
Lower Mississippi River			0.43-0.62	0.2-1.4		Dugger 19997, 2000
Oklahoma	0.33-1.45	25				This study[b]
Oklahoma	0.89	0	0.56	0.64	100	Boyd 1993[b]
Oklahoma			0.26			Whittier unpublished data[b]
Oklahoma				0.07	0	Hill and Talent 1985[b]
Oklahoma			19.2 - 68.6			Summarized by Schweitzer and Leslie 2000, Table 1

Table 1. Continued.

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[a] Proportion of hatched chicks surviving to fledge (except Whittier unpubl. data was Kaplan-Meier estimate and Dugger [2000] was a Jolly-Seber estimate).

[b] Data for Salt Plains National Wildlife Refuge, Alfalfa County, Oklahoma.

Table 2. A deterministic model of population persistence was constructed using repetitions of demographic measurements collected for a breeding population of Interior Least Terns at Salt Plains National Wildlife Refuge, Oklahoma.

Demographic parameters	1991	1992	1993	1994	1995	1996	1997	1998
Total nests	49	80	177	119	106	116	112	68
Nest success (%)	46	31	26	63	36	38	45	73
Chicks/nest	0.91	0.33	0.49	1.06	0.53	0.70	0.89	1.45

Table 3. Fixed demographic parameters used in the deterministic model to project population persistence for a breeding population of Interior Least Terns at Salt Plains National Wildlife Refuge, Oklahoma.

Parameter	Fixed level for model
Age at first reproduction	2[a]
Percent adults breeding at age 2	33[a]
Percent adults breeding at age 3+	100
Sex ratio at birth	1:1
Survival (%):[b]	
Years 0 – 1	100
Years 1 – 2	82, 60[c]
Years 2 – 3	80
Years 3 – 4	90
Years 4 – 5	92
Years 5 – 6	93
Years 6 – 7	87
Years 7 – 8	87
Years 8 – 9	92
Years 9+	79
Initial population size (females)	100

[a] Lingle unpubl. data as reported by Kirsch 1994.

[b] Survival estimates were based on age-specific survival reported by Thompson.

Table 3. Continued.

(1982) and Massey (1992).

[c] Two values were found in the literature for survival to two years of age. Because survival values were fairly different, I modeled at both levels rather than using an average.

Table 4. Estimated number of female offspring per female per year required to maintain a stable population (Ricklefs 1972). Adult survival was averaged across years 3^{+}.

	Chick Survival				
	0.10	0.26	0.45	0.56	0.80
Survival to breeding					
0.60	2.08	0.80	0.52	0.37	0.26
0.82	1.52	0.59	0.34	0.27	0.19
Estimated fledglings for SPNWR[a]	0.08	0.21	0.36	0.44	0.64

[a] Salt Plains National Wildlife Refuge, Oklahoma.

Table 5. Population growth for Interior Least Terns at Salt Plains National Wildlife Refuge in Oklahoma was modeled using a range of estimates for chick survival to fledging and low and high estimates of survival from fledging to two years of age. Initial population size was 100 females. With basal rates of survival to breeding as 0.60 and survival to fledging as 0.45, model sensitivity to changes in reproductive parameters was assessed by increasing chick survival and survival from fledging to two years of age by 10%. Basal rates also were compared with models of a population in Kansas and another South Dakota that experienced higher and lower rates of productivity peaks.

Survival to fledging	Intrinsic rate of increase	Final population size
Low survival to breeding (0.60)		
0.10	-0.1256	5
0.26	-0.0416	40
0.45	0.0228	195
0.56	0.0485	372
0.80	0.0999	1,437
High survival to breeding (0.82)		
0.10	-0.0090	87
0.26	-0.0055	91
0.45	0.0632	512
0.56	0.0935	856
0.80	0.1465	4,385
Sensitivity assessment		
Chick survival (0.39)	0.0338	259
Survival to breeding (0.66)	0.0348	259

Table 5. Continued.

Survival to fledging	Intrinsic rate of increase	Final population size
Comparison		
Kansas	0.0733	641
South Dakota	-0.0383	38

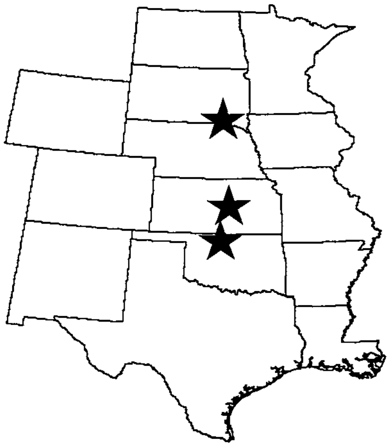

Fig. 1. Data used to model Least Tern populations came from three long-term monitoring programs. The most northerly population nested along the Missouri River in South Dakota (Kruse 1993). The Kansas population was at Quivira National Wildlife Refuge (Boyd 1993) and the Oklahoma population was at Salt Plains National Wildlife Refuge.

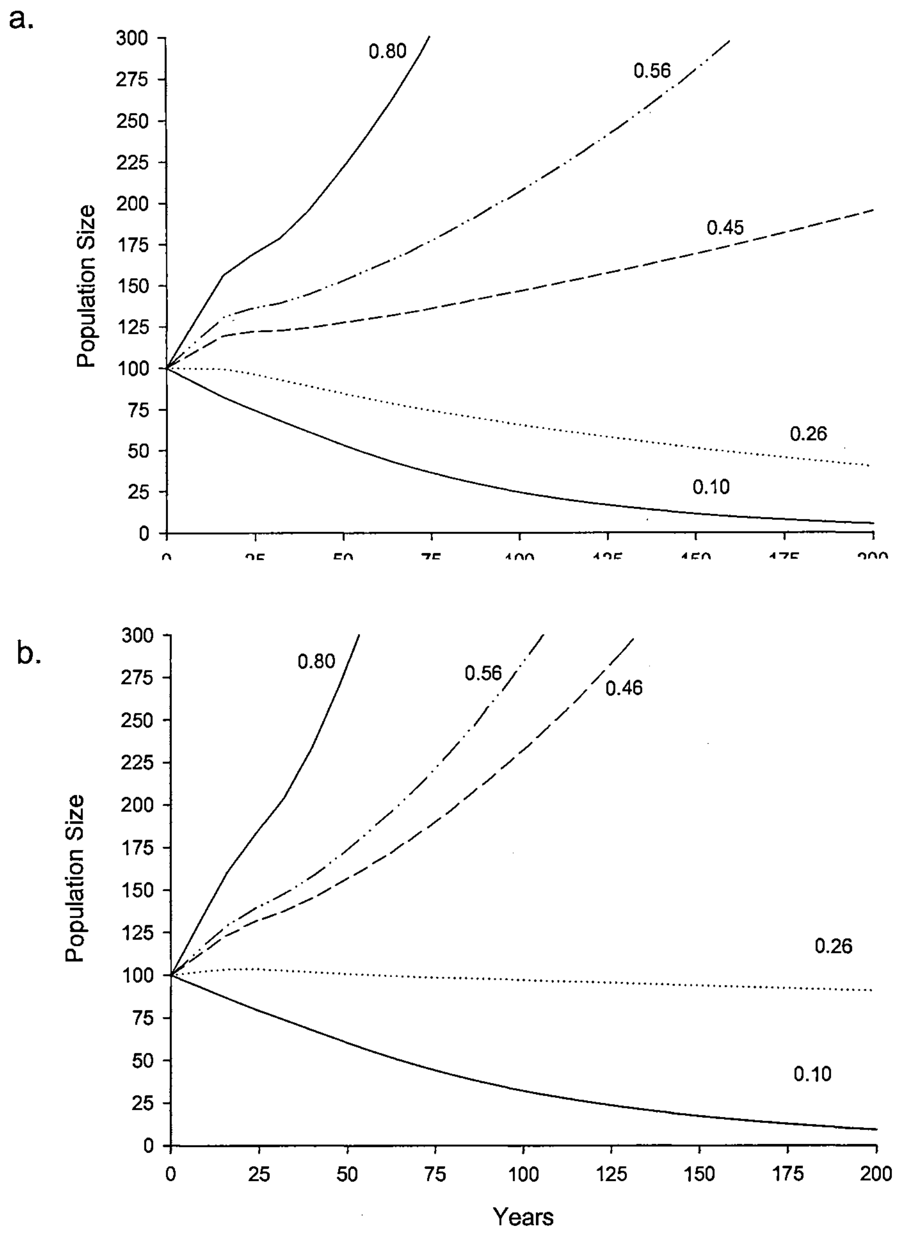

Fig. 2. Predicted population response to various estimates of chick survival to fledging (0.10 to 0.80) for a breeding population of Interior Least Terns. a) Survival to breeding was held at the lowest estimate found in literature (0.60; Thompson 1982). b) Survival to breeding was held at the highest estimate found in literature (0.82; Massey 1992).

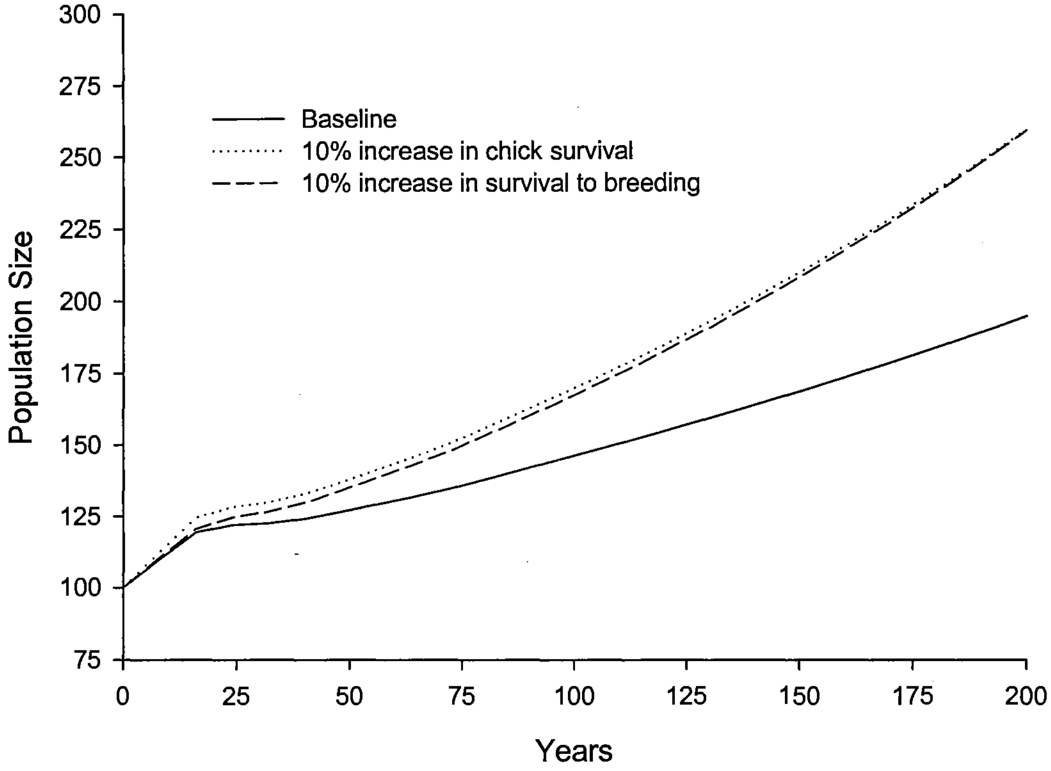

Fig. 3. Sensitivity of a population model for Interior Least Terns to a 10% increase in reproductive parameters. Plots indicate projected population response of each increase over baseline values. Baseline values were 0.45 chick survival with 0.60 survival from fledging to two years of age.

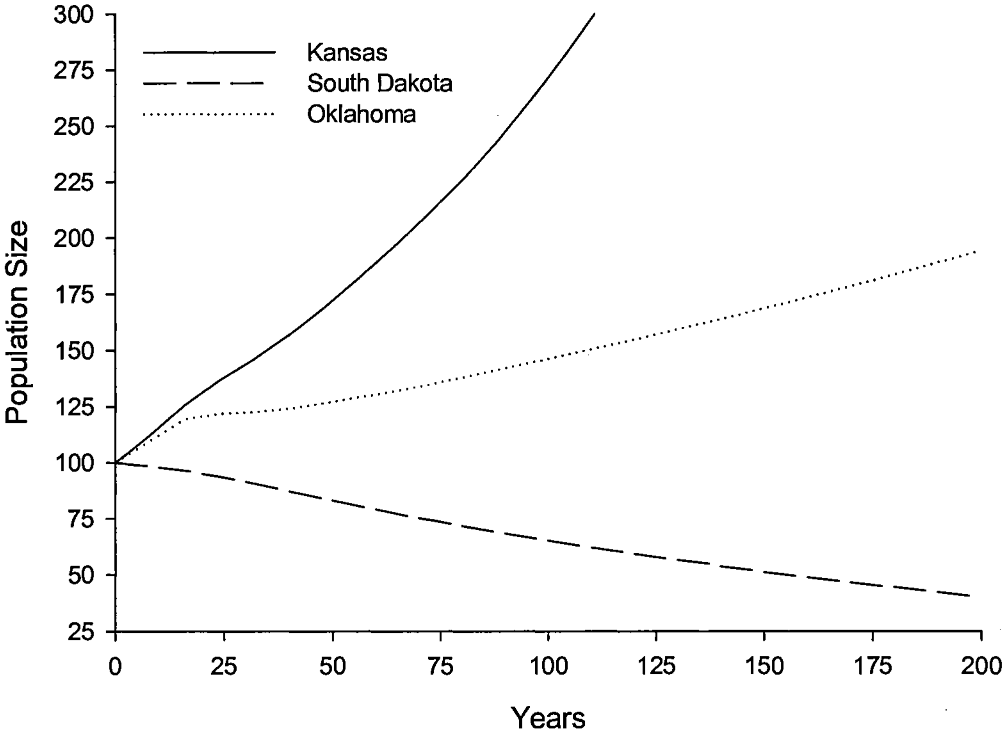

Fig. 4. Comparison of population trends for breeding populations of Least Terns at Salt Plains National Wildlife Refuge in Oklahoma, Quivara National Wildlife Refuge in Kansas, and along the Missouri River in South Dakota.

CHAPTER IV

RADIO TELEMETRY OF LEAST TERN CHICKS

ABSTRACT—Little is known about least tern (Sterna antillarum) chicks from the time they leave the nest to fledging because they are highly mobile and cryptically colored. My objective was to evaluate the efficacy of radio telemetry to monitor least tern chicks. In 1999, I attached radiotransmitters to 26 least tern chicks and tracked them for 2 - 19 days. No adults abandoned their chicks after transmitters were attached. Transmitters did not appear to alter growth rate of transmittered chicks ($P = 0.361$), prevent feather growth, or cause dermal irritation. However, without frequent reattachment, transmitters generally did not remain on chicks for >2 days because of feather growth. Although future assessments should investigate methods to improve retention of transmitters, presence of transmitters did not adversely affect chicks.

Survival of endangered least tern (Sterna antillarum) chicks from hatching to fledging is poorly understood. Survival estimates have been hindered because least tern chicks are semi-precocial, highly mobile, and cryptically colored. In addition, because least terns nest colonially in open habitats, undetected approach is difficult. Approaches within 250 m result in alarm calls from adults and at that distance, chicks are difficult to see (J. B. Whittier, pers. obs.). Accurate estimates of chick survivorship and factors influencing survivorship would be essential to determine management strategies for improving productivity of this endangered species.

Chick survivorship is an important for the development of population models (Kirsch, 1996). Most estimates of chick survival of least terns are based on ratios of observed number of fledged birds to number of successful nests (Kirsch, 1996; Woodrey, and Szell, in litt.) or estimated number of breeding pairs (Schwalbach, et al., 1993). Movement of fledglings to non-natal sites (Thompson and Slack, 1984) may bias estimates of chick survival. Dugger et al. (2000) successfully used a mark-recapture technique to estimate survival of interior least tern (S. a. athalassos) chicks nesting on islands. Because least tern chicks may move freely and randomly, mark-recapture techniques would be less useful in expansive habitats (e.g. salt flats) than restricted habitats (e.g. islands). In either case, neither method monitors factors affecting survival of individual chicks.

Advances in radio-telemetry equipment have facilitated monitoring small birds (Sykes et al., 1990; Yalden, 1991). Until recently, radio transmitters could be used only on mid- to large-sized animals because of excessive weight. Currently, transmitters can be obtained that are <1.0 g with a battery life of about 21 days. The life span of small transmitters limits their use for long-term monitoring of individuals, but least tern chicks fledge at about 20 days (Thompson et al. 1997), so transmitter life generally is long enough to confirm survival to fledging. My goal was to evaluate the response of least tern chicks to carrying a radio transmitter. I focused my efforts from hatching to fledging because I was concerned that transmitter weight might increase stress on young birds as they learned to forage and during migration and removal of transmitters from fledged birds was not feasible.

MATERIALS AND METHODS—Study Area--.This study was conducted from 1 June to 15 August 1999 at Salt Plains National Wildlife Refuge (SPNWR) in Alfalfa County, Oklahoma (98°15'N, 36°43'W). At this refuge, least terns nest on a salt flat of about 5,000 ha adjacent to the Great Salt Plains Reservoir (Koenen et al., 1996; Fig. 1). The nesting habitat is nearly level with little vegetative cover, making detection distance of transmitter signals nearly optimal. A study site was selected at the south end of the least tern nesting habitat (Fig. 1).

Nest Location—Nests were located by searching defended territories. To reduce disturbance, I initially located nests from outside defended areas by observing adults returning to nests. After a nest was located, it was marked with a numbered dowel placed about 10 m away from the nest cup. Dowels were placed in random directions to discourage habituation by predators. If the number of potential pairs present exceeded the number of nests, then a systematic search of the surrounding area was conducted to locate additional nests. Nests were monitored every 3 -10 days until hatching.

Radio-marked Chicks—All chicks in a nest were weighed and banded with United States Fish and Wildlife Service aluminum leg bands (band size 1A). Radiotransmitters were placed on the largest chick located at each nest at about 2 days of age. To increase sample size, transmitters were attached to 3 unmarked chicks located away from any nest. I followed the transmitter attachment technique used by Hill and Talent (1990) except for the type of glue used. Because cyanoacrylates have been linked with skin irritation and impaired skin functioning (Johnson et al., 1991), use of this class of glue might have been detrimental to chicks; thus I used a latex-based surgical glue. Transmitters were attached by first clipping down feathers of the interscapular region to expose the skin; then, surgical glue (Skin Bond, Smith and Nephew, London, United Kingdom) was brushed onto both the bare skin of the chick and the base of the transmitter. After the transmitter was in position, it was held in place for 1 min to seal the bond. When possible, surrounding feathers were glued over the top of the transmitter for camouflage, and to reduce the likelihood of the transmitter being removed. Processing time averaged 16 min ± 1.0 *SE*. Glue-on techniques have advantages over harnesses because 1) attachment is easier (Sykes et al., 1990) and 2) harnesses have been found to alter behavior and survival in birds (Kenward, 1987). I removed transmitters from chicks at 17 days of age because I did not want to hamper chicks during fledging.

Thirty transmitters were purchased from L.L. Electronics (model SMT-1-379-RS-T; Mahomet, Illinois) and Holohil Systems Ltd. (model LB – 2; Woodlawn, Ontario, Canada). Estimated life span of the transmitters was 2 - 3 weeks. L.L. Electronics transmitters averaged 0.8 g and measured 0.9 cm by 0.6 cm by 0.4 cm. Holohil transmitters averaged 0.6 g and measured 1.1 cm by 0.6 cm by 0.2 cm. At the time of attachment, transmitter weight was between 5 - 8% of the chicks' weights and by 6 days of age, transmitter weight was $\leq$3% of chick weight.

<u>Radio tracking</u>—The first three chicks to carry a transmitter were located once every 24 h. When a transmitter was found to be loose, it was reattached. Daily visits

proved to be too infrequent to prevent transmitter removal, as transmitter signals were lost or the transmitter removed after two days with no evidence of depredation. From those, I determined that daily visits were insufficient to detect loose transmitters before they were removed. Therefore, the remainder of chicks were located every 12 h.

Chicks were tracked during morning and evening hours when temperatures were <35°C and never during rainstorms. Each week, chicks were recaptured and weighed. If a chick exhibit potential indications of disease (e.g., feather loss, lethargy), any equipment that had come into contact with the ill bird, such as the weighing bag, was sterilized before being used again. When transmitters were removed, skin and feather condition were examined for damage.

A growth curve for transmittered chicks was calculated using weekly measurements. Because few chicks without transmitters could be relocated at SPNWR, growth rates of the transmittered chicks could not be compared with untransmittered chicks from the same location. Because I was unable to locate published data on growth rates of interior least tern chicks, growth data from California least tern chicks (S. a. browni; Massey, 1972) were used to estimate the impact of transmitters on growth of SPNWR chicks. The straight-line segment between day 4 and 16 of each growth curve and intercepts were compared using ANCOVA (SAS Institute Inc. 1996).

RESULTS—I attached radiotransmitters to 26 chicks. No chicks were deserted after transmitters were attached. For nests initiated in early June (*n* = 15), only 47% hatched at least one chick. Because of the poor nest success, transmitters were attached to only three chicks. Although those chicks were monitored daily, transmitter signals were lost for all three individuals after two days, possibly from removal of transmitters. All three of those transmitters were found to be loose at the first relocation and had to be reglued. During the second relocation, two transmitters signals were never detected and the third transmitter was found on the ground.

Terns began renesting in late June resulting in eggs hatching from mid-July to early August. Because transmitter retention appeared to be poor for the first set of chicks, the remainder of chicks were relocated every 12 h to reglue loose transmitters. When chicks were checked twice a day, only two of 23 transmitters were found on the ground. Loose transmitters continued to be a problem but retention improved as feathers developed (Fig. 2). Daily reattachment of transmitters was required for 50% for chicks up to 4 days of age. Transmitter retention improved to >80% for chicks over 4 days of age. Transmitters always were loosened from the posterior region next to the antennae, presumably by parents.

Growth of chicks at SPNWR was sigmoidal ($r^2 = 0.95$; Fig. 3) and averaged 2.2 g/day. Chicks at SPNWR weighed an average of 40.3 g at fledging. Based on weights taken from Texas and Nebraska adults (Thompson et al., 1997), SPNWR chicks fledge at 91% of the adult weight. A comparison of growth rates of transmittered chicks at SPNWR to untransmittered chicks in California (Massey, 1972) demonstrated that daily weights differed by an average of 1.8 g/day; however, variation was not consistently higher or lower (Fig. 3). Initial chick weight (ANCOVA; $F_{1,34} = 1.20$, $P = 0.241$) and average growth rate ($F_{1,34} = 0.86$, $P = 0.361$) did not differ between the SPNWR and California site.

I removed transmitters from chicks that died or were near fledging ($n = 9$); those individuals carried a transmitter for an average of 12 days. Only one chick exhibited slightly pink skin indicating mild irritation. Feather growth was not impaired on any of the chicks, and feathers were not visibly damaged. Feather growth under the transmitter shifted the position of the transmitter lower on the back.

DISCUSSION—The majority of avian telemetry studies are conducted on adult or fledged birds probably because of limitations related to transmitter weight and lack of need for altricial chicks. For this reason, little is known about the impact of the adhesive attachment technique on feather growth. Although Yalden (1991) glued transmitters to plover chicks, no mention was made of feather growth. My results indicated that surgical glue did not disrupt feather growth in least tern chicks and after the glue was removed using a mild solvent, feathers were not visibly damaged. Dermal irritation was observed on one chick and this individual had worn its transmitter for 17 days. The low level of dermal irritation observed in this study was consistent with findings of Sykes et al. (1990), who examined use of adhesives to attach transmitters to small passerines.

Feather growth resulted in transmitters being lifted from the skin and shifted posteriorly down the chicks' backs. Despite the transmitter's shift away from the center of gravity transmittered chicks appeared to be able to run normally (J. B. Whittier, pers. obs.). The tendency for feather growth to move the transmitter likely contributed to the poor retention of transmitters. Transmitter loss was heaviest during when chicks were under 4 days of age. Increased retention of transmitters appeared to coincide with the development of pinfeathers. Transmitters were loosened anteriorly, evidently from either parents or chick tugging on the antennae. Frequent (average 1.5 days) reattachment was required to prevent transmitter loss.

Ideally, the impact of carrying transmitters on growth rates should be assessed using a reference group within the same study area. However, chicks at SPNWR are difficult to relocate on the expansive salt flats. During this study, no previously banded chicks were relocated that were not either carrying transmitters or siblings of transmittered individuals. No published data was found on growth rates of interior least terns, so I used growth data from a California population (Massey, 1972). Although comparison of growth rates for geographically disjunct populations was not ideal, I found that transmitters did not impair growth rate of chicks at SPNWR. None of the adults abandoned chicks, and many returned to their chicks while I was within 100 m.

Survivorship and the factors impacting survival are difficult to determine for precocial and semi-precocial chicks because those chicks can be difficult to relocate. Advancements in transmitter technology has enabled production of smaller transmitters with weights that are reasonable for least tern chicks to carry. Those advancements have provided the opportunity to more accurately assess chick survivorship and examine the variables impacting survivorship for small semi-precocial chicks. Adhesives commonly are used for attaching radio transmitters to birds (Samuel and Fuller, 1994) and have the advantage of short handling times with minimal physical impairment to an individual's movement. Latex-surgical adhesive appear to be a safe method of attachment for least tern chicks because it did not irritate the skin, impair feather growth, or damage feathers. Chick growth and movement were not impaired by the presence of a transmitter. Accurate assessments of juvenile survival are important for understanding the demographics of any species, but particularly for assessing population viability of endangered species.

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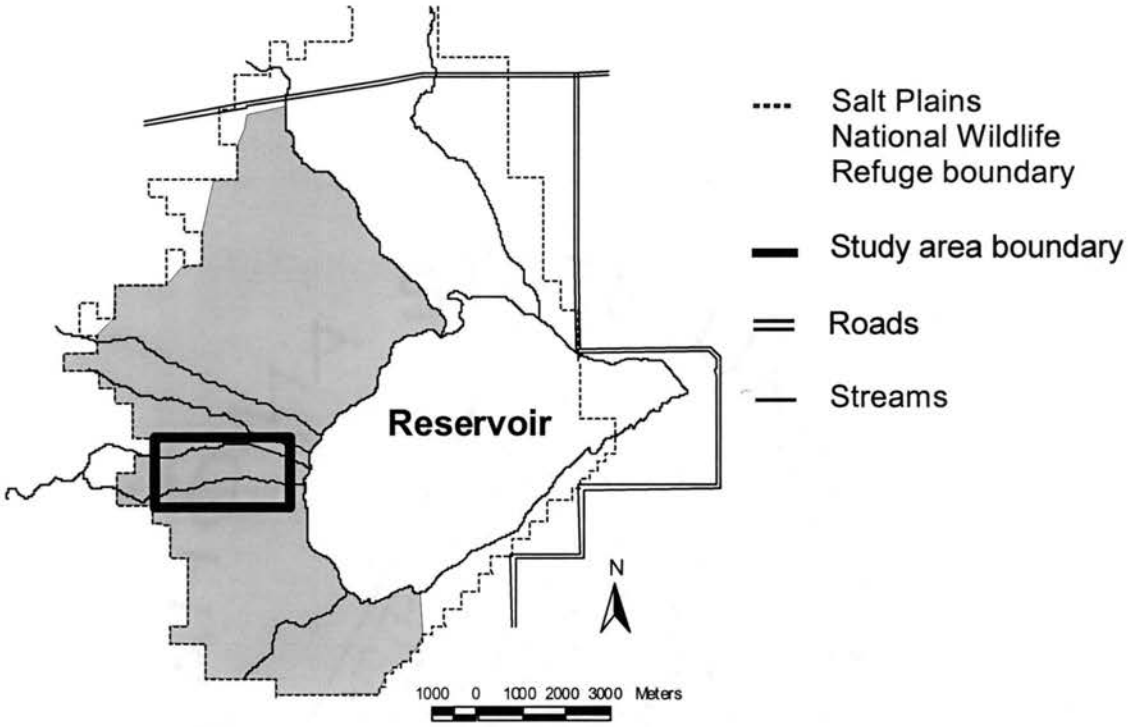

Fig. 1–Map of Salt Plains National Wildlife Refuge indicating least tern nesting habitat (shaded) and the study area (bold rectangle).

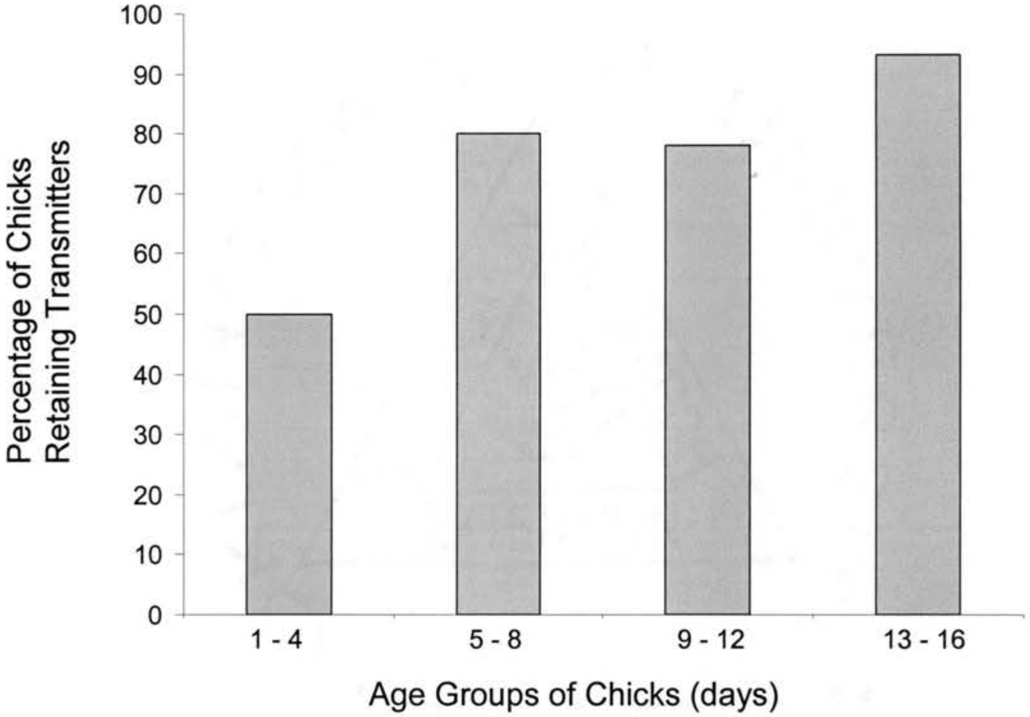

Fig. 2. Transmitter retention was calculated as the number of chicks without loose transmitters divided by total number of chicks with transmitters. These data were calculated by age of chick. Because of low sample size (n = 26), data were summarized into age groups.

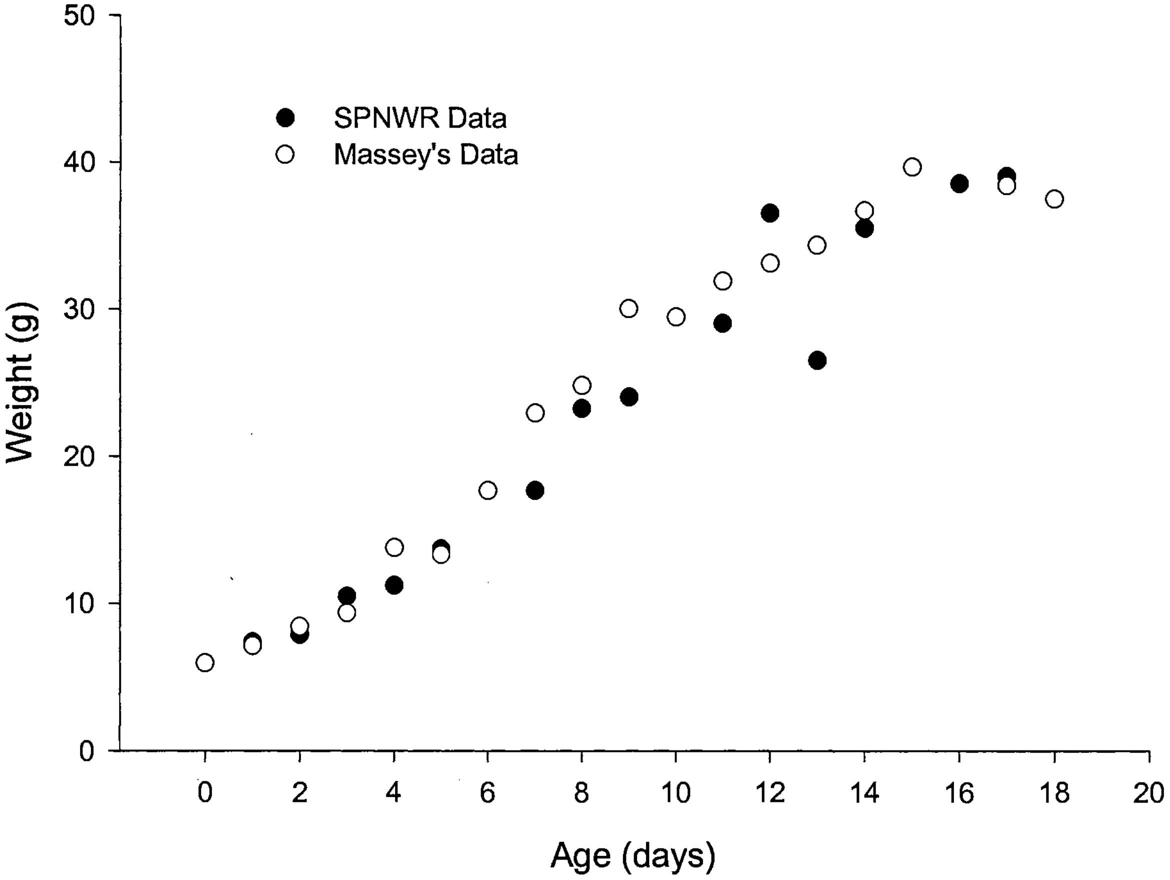

Fig. 3--Comparison of average weight (g) of least tern chicks from Salt Plains National Wildlife Refuge, Oklahoma, and Orange County, California (Massey, 1972).

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