

BREEDING ECOLOGY OF INTERIOR LEAST TERNS, SNOWY
PLOVERS, AND AMERICAN AVOCETS AT SALT PLAINS
NATIONAL WILDLIFE REFUGE, OKLAHOMA

By

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Bachelor of Science

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1980

Submitted to the Faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the Degree of
MASTER OF SCIENCE
December, 1985

Thesis
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ACKNOWLEDGMENTS

When I began my graduate program in Oklahoma I could not foresee the changes ahead. Tossed into an arena of cultural and political north-south/east-west dichotomies, I panicked, emotions bucking bronco-style. I am grateful to the many individuals who directly or indirectly encouraged me to hang on to the "bucking bull." They helped me regain a feeling of control over my destiny.

I sincerely thank my major professor, Larry Talent, for extended duty as critic, devil's advocate, philosopher, and idea mentor. Larry sometimes frustrated me, but frequently he broadened my perspectives. I appreciated his faith in my abilities on so many occasions, and his willingness to let me work without undue hassle.

Credit is due to Frank Schitoskey, Helen Miller, and Gene Maughan for service as committee members. Additionally, I acknowledge Gene for catalyzing a job search which ultimately led to my appointment with Ecological Services in Tulsa.

I appreciate the interest in my research expressed by biologists and educators outside of Oklahoma State University. I thank Jim Andreasson, Dana Base, Roger Boyd, Ken Frazer, Steve Hensley, Steve Hoffman, Steve Marlot, J. P. Myers, Charlie Scott, Bob Short, Dan Stinnett, Bruce Wagner, and Pete Wilkirson. Numerous faculty, staff, and graduate students at Oklahoma State University also assisted my research, particularly Alan Tipton, Judy Gray, Krista Peters, Mike Kemmerer, and Valerie Keener.

The cooperation of staff at Salt Plains National Wildlife Refuge was invaluable to my fieldwork. Gratitude is extended to refuge manager, Ron Sullivan, to assistant managers John Kirk and Billy Long, and to the rest of the crew, Otis Allen, Leroy Atchley, Jack Barnard, Phil Clover, and Harold Miller. Their hospitality, spiced with good-natured teasing, added to my enjoyment of summers on the refuge.

Many thanks are owed to the multitude of undergraduates in my biology labs who, with their barrage of questions, made me a better biologist. Teaching them also greatly heightened my confidence in public speaking.

Special thanks are due to fellow graduate students who at key times offered me moral support and insights to personal relations. I shall especially remember conversations shared with Alisa Shull, Jana Nelson, Pam Watt, and Chris Henry, who taught me much about individual commitments, purposes, and goals.

I offer my deepest appreciation and love to my closest friend, "Kimbies" Kim Brooks Gavigan, whose letters were a constant joy for me. Despite separation by distance, we continued to strengthen a friendship which originated some 22 years ago.

Lastly I thank my family, Dick, Ruth, Ross, and Karen Hill, for consistently providing love, encouragement, and comic relief throughout my graduate study. Thank you for thinking of me so often.

My research would not have been possible without funding and logistical support from many sources. A summer research stipend from the Payne County Audubon Society offset expenses during my first field season. Frank Schitoskey and Larry Talent were instrumental in securing funding from the U.S. Fish and Wildlife Service for my second field

season. Larry Talent and Gene Maughan renewed funding from the Fish and Wildlife Service for the third season and acquired nongame research monies from the Oklahoma Department of Wildlife Conservation for final stages of data analysis and manuscript preparation. I am indebted to the Oklahoma Cooperative Fish and Wildlife Research Unit for use of trailers, vehicles, and expendable supplies and equipment throughout my study. Salt Plains National Wildlife Refuge permitted me to camp on refuge land and to use office and shop facilities. Additionally, the refuge provided all-terrain-vehicles (ATV's) and fuel for the ATV's in 1984.

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CHAPTER I

INTRODUCTION

With the exception of the INTRODUCTION, chapters in this thesis are written in manuscript format suitable for submission to selected scientific journals. Each manuscript is complete without supporting materials. Chapter II follows the format of the Journal of Field Ornithology; chapters III and IV, the format of the Journal of Wildlife Management; and chapter V, the format of the Wilson Bulletin.

Three additional manuscripts resulting from this project were included in a final report submitted to the U.S. Fish and Wildlife Service and to the Oklahoma Department of Wildlife Conservation. These manuscripts cover results of: 1) a 1982-83 behavioral study (time budgets) of least terns, snowy plovers, and American avocets, 2) a 1984 pilot radio-telemetry study on habitat use, habitat preference, and brood survival of terns and plovers, and 3) a 1984 study of food availability for terns and plovers. Additionally, a fourth paper, not intended for publication, was written as a service to federal and state wildlife biologists who desire a concise summary of the project, emphasizing management implications and research needs. Individuals interested in obtaining copies of the final report should contact the Oklahoma Cooperative Fish and Wildlife Research Unit, Department of Zoology, Oklahoma State University, Stillwater, Oklahoma 74078 (Commercial phone, 405-624-6340; FTS phone, 728-4385).

CHAPTER II

CAPTURE, RADIO-MARKING, AND REPRODUCTIVE PERFORMANCE OF LEAST TERNS AND SNOWY PLOVERS

BY LAURA A. HILL, LARRY G. TALENT, AND O. EUGENE MAUGHAN

Capture and radio-marking of incubating birds is often necessary to study the breeding ecology, population dynamics, and behavior of marked individuals or populations. Although much information is available on radio application and trap design for ground-nesting birds (Godfrey 1970, Bray and Corner 1972, Dwyer 1972, Amstrup 1980, Day et al. 1980 and others), little information is available on species-specific response to radios and to the trap-handle-release sequence.

Species-specific effects of trapping and radio application need to be known by managers concerned about the well-being of populations and by researchers who must insure that the method does not affect the phenomenon studied. In particular, biologists working with threatened or endangered species must have efficient trapping and marking methods that have minimal effect on breeding success.

As part of a reproductive study on shorebirds in Oklahoma, we captured Interior Least Terns (Sterna antillarum athalassos) and Snowy Plovers (Charadrius alexandrinus) on their nests, banded all trapped individuals, and equipped a cohort of terns and plovers with experimental radios. The Interior Least Tern recently was listed as

endangered (Federal Register, 28 May 1985) whereas the Snowy Plover currently is a regional candidate for listing as endangered or threatened (U.S. Fish and Wildlife Service 1983). Hence, the well-being of our study populations was a concern. To further heighten that concern, previous workers reported that coastal subspecies of the Least Tern were trap-wary, did not tolerate handling well, and often deserted their nests if trapped during early or mid incubation (Brubeck et al. 1981, Massey and Atwood 1981). In addition, the effects of radio-marking Least Terns and Snowy Plovers had not been previously determined.

If trapping disturbance or radio application severely decreased the productivity of these study species, bias would have been introduced into our study of reproductive performance. Therefore, the objectives of our study were to develop a safe and efficient trapping technique applicable to both Least Terns and Snowy Plovers and to determine the effects of capture, handling, and radio transmitters on subsequent reproductive performance.

STUDY AREA

The study was conducted on a 4,050 ha salt flat located on the Salt Plains National Wildlife Refuge (NWR) in Alfalfa County, west northcentral Oklahoma. The salt flats border the western shore of the Great Salt Plains Reservoir. Tailwaters of the Salt Fork of the Arkansas River, West Salt Fork River, Cottonwood Creek and Clay Creek traverse that portion of the salt flats used by nesting Least Terns and Snowy Plovers. Strong southerly winds and average air temperatures exceeding 35° C combine in summer to produce a highly evaporative

environment. A 1-3 mm salt crust precipitates on the surface of the floodplain as water evaporates from brine drawn to the surface by capillary action. The salt flats are barren except for patches of salt cedar (Tamarix gallica), inland salt grass (Distichlis stricta), western sea purslane (Sesuvium verrucosum), and concentrations of driftwood and debris localized by flooding of streams and temporary rises in the reservoir level. The study area was described in more detail by Johnson (1972) and Grover and Knopf (1982).

MATERIALS AND METHODS

Nests were located during systematic searches of the salt flats from May-August 1983 and 1984. The incubation stage of each located nest was estimated by egg flotation (Hays and LeCroy 1971). Nests were given individual identification numbers, the location plotted on maps to facilitate relocation, and revisited at 1 to 3-day intervals to determine egg and nest survival. Colony locations were marked with numbered flagging tied to nearby objects, and individual nests were marked with numbered 15-cm stakes placed within 60 cm of the nest cup.

Trapping procedure.--Adult Least Terns and Snowy Plovers were captured on their nests with T-shaped traps (Fig.1). These traps minimized visual and physical obstruction of nests by providing birds with unrestricted aerial access and 180 ° of ground access to their nests. Each trap was constructed of a wooden frame, a U-shaped galvanized-wire bail (4 mm diameter wire), 2 springs from Victor rat traps, and 8-mm mesh stretch netting. To camouflage the traps on the white salt flats, frames were painted white and white netting was used on bails.

Traps were placed at nests with the stem of the "T" pointing downwind. The crossbar of the frame was placed 10-12 cm from the center of the nest and each trap was staked with 2 30-cm wires. To acclimate birds, traps were placed at nests about 2 hours before a 45-60 m trip line was attached and trapping operations begun. After attaching the trip line, the trapper sat on the ground at the free end of the line and watched the nest site with a 20X telescope. If the nesting bird hesitated to return to the nest or was not observed in the nesting area, the trapper entered a "blind," i.e., donned a white sheet for camouflage. When the bird returned to incubate or shade its eggs, the trip line was pulled, triggering the trap. The time from the onset of trapping until a bird returned to incubate/shade its eggs (return interval) was recorded to the nearest minute. To reduce heat stress to eggs at unattended nests, trapping attempts were discontinued if air temperature exceeded 31° C and birds failed to return to their nests within 30 minutes.

Handling procedure.--Nest-trapped terns and plovers were divided into 2 experimental groups that differed by the type of identification marker applied to birds and their stage of incubation. Captured birds from both groups were immediately removed from traps, and a black satin drawstring bag designed to mask the eyes but expose the beak was placed over the head of each bird. Subsequently, all birds were weighed and measured.

All terns and plovers in Group 1 were individually marked with a U.S. Fish and Wildlife Service band and most snowy plovers were also marked with 3 colored plastic bands to facilitate identification from a distance. Birds in Experimental Group 1 were banded throughout all

stages of incubation.

Birds in Group 2 were marked with a Fish and Wildlife Service band and equipped with a back-mounted radio transmitter during late incubation. The radio transmitters (164.425-164.700 MHz with 2 groups of pulse frequencies, 35 pulses/min and 60 pulses/min; Denver Wildlife Research Center, Denver, Co.) were approximately the size and shape of a kidney bean having a 12-15 cm antenna and weighing 2.0-2.6 g (6-7% of bird body weight) with potting. Before application the potted radios were painted with gray or tan enamel paint so they would blend with the spinal pterylae of Least Terns and Snowy Plovers, respectively. Painted radios were glued (cyanocrylate-base glue) on the flat of a bird's back, midway between the wings and rump. Glue was applied to the base of the radio and to the bird's skin. After bonding these 2 surfaces, surrounding feathers were glued over the radio.

Release procedure.--Prior to release, birds were placed alone inside a release box, a wooden box painted black inside with a vertically sliding door (Fig. 2). Total handling time (from when the bird was first picked up until placed in the release box) was noted. Birds were moved to a release site 90-100 m downwind from the nest, then freed once the trapper gathered equipment and entered a blind. The rationale for moving birds away from their nests before releasing them was that if a bird immediately returned to its nest, the bird would not be flushed from the area when the trapper left the blind.

Reproductive assessment.--To determine if trap presence affected nest depredation, traps were set and left overnight at 15 Least Tern and 20 Snowy Plover nests. The overall effects of trapping and equipping birds with radios were determined by comparing depredation rates, desertion

rates, daily nest survival, and daily egg survival of experimental groups with values of control groups that were not trapped, handled, or marked.

RESULTS

Thirty-two adult Least Terns on 25 nests and 84 adult Snowy Plovers on 81 nests were captured and banded and/or radio-marked during the study. Group 1 consisted of 12 Least Terns and 66 Snowy Plovers whereas Group 2 contained 20 radio-marked terns (13 females, 7 males) and 18 radio-marked plovers (11 females, 7 males) (Table 1). Additionally, we monitored reproductive performance at 104 Least Tern and 252 Snowy Plover nests where birds were not trapped, handled, or marked.

Trapping success.--We made 33 and 106 attempts to capture Least Terns and Snowy Plovers, respectively. Tern trapping success was high (91%) compared to plover trapping success (79%). Overall, tern trapping success was disproportionately higher than that of plovers because many terns were trapped during arid weather whereas many plovers were trapped during cloudy or rainy weather (Table 2). Hence, plover trapping success was low because we aborted many attempts to capture birds that did not readily return to their nests during the cool and damp weather of the early 1983 season. Both species tended to spend more time away from the nest during cool damp weather than during hot dry weather (Hill unpub. data).

Mean return intervals.--Mean return intervals of plovers and terns were not affected by stage of incubation (Table 3), but were affected by time of day (Table 4). Mean return interval for 32 Least Terns was 12.8 ± 3.3 min ($\bar{X} \pm SE$) with a range of 0-70 min. Sixty-nine percent

of all Least Terns trapped had return intervals less than 10 min. On average, 84 Snowy Plovers returned to their nests 14.1 ± 1.6 min after trap activation (range 0-79 min); however, 33% returned in 30+ minutes.

Handling times.--Average handling times for Group 1 and 2 terns and plovers were as follows: Group 1 terns, 8.4 ± 0.4 min; Group 1 plovers, 13.0 ± 0.6 min; Group 2 terns, 9.1 ± 0.4 min; and Group 2 plovers, 8.9 ± 0.5 min. About 84% of Group 1 plovers were trapped and processed by 1 individual during the 1983 field season. Therefore, mean handling times for Group 1 plovers were significantly greater than those for all other groups ($P < 0.001$). For all experimental groups, handling times decreased as trappers gained experience. Handling times less than 8 min were common late in the field season for all groups.

Behavioral response to trapping and marking.--Other precautions taken to reduce the stress of birds during handling included an attempt to reduce visual cues. The head of each bird was covered with a black fabric bag immediately after the bird was removed from the trap. While being removed from the trap, Least Terns sometimes screamed and frequently tried to bite. Defensive behavior subsided instantly after the eyes were masked. In contrast, captive Snowy Plovers rarely vocalized or bit when they were removed from traps and were docile while wearing masks.

To further reduce the effects of fright or temperature disturbance, birds were placed inside a dark box prior to release. Thus from almost the moment birds were trapped until they were released, their vision was restricted to a dark environment. Terns were quite sedate inside the release box. Plovers tended to be active in the box for the first 10-90 sec, but afterwards activity decreased. We kept birds inside the

box for a minimum of 4 min or until they became quiescent, i.e. until no noises came from the box. In general, the longer a bird was in the box, the longer the bird took to leave once the door was opened. Sometimes it was necessary to gently jostle the box to get birds to come out. When ready to leave the box, terns usually stepped out of the doorway and immediately took flight; plovers seldom flew directly from the box, but stepped out of the doorway then preened or ran.

Observation of Group 2 birds immediately upon release indicated that radios did not cause significant behavioral changes in birds. Several radioed terns and plovers immediately resumed incubation upon release. We never saw any radioed bird pull at the radio; however, some Group 1 plovers used their beaks to tug at their plastic legbands for several minutes after release. Detailed observations of terns immediately upon release were difficult to obtain because many flew away from the trapping site. Nevertheless, although we did not quantitatively measure effects of radios on diving and fishing abilities of terns, we observed radioed terns hovering and diving in an apparently normal manner.

Radio-life.--Glue bonds were not readily destroyed by submersion in salty water and exposure to ultraviolet rays because no Least Terns or Snowy Plovers lost their radios throughout the study. Most radios lost power before birds migrated; however, 6 of 16 fast pulse radios and 13 of 24 slow pulse radios were still transmitting when birds migrated from the study area. Most fast pulse radios operated about 1 month, but a few operated longer. Over half of the slow pulse radios transmitted for longer than 1 month and a few transmitted for over 2 months.

Nest depredation and desertion.--Coyotes (Canis latrans), raccoons (Procyon lotor), and striped skunks (Mephitis mephitis) were the most

common egg predators on the study area. Tracks of these mammals usually followed stream edges or the prairie-salt flat ecotone. Overnight trap sets did not increase the frequency of nest depredation at nests located in the center or at the edge of the salt flats. Nest mortality, defined by Mayfield (1961) as nest losses/days at risk to predation, for 15 tern nests with overnight trap sets was 0. Mortality (0.051) for 20 plover nests with overnight sets was not different from the 0.055 mortality of plover control nests ($\chi^2 = 1.113$, 1 df, $P > 0.25$).

Nest depredation and desertion due to trapping and/or equipping birds with radios was low. Only 1 of 25 tern and 3 of 81 plover nests were depredated or deserted within 2 days after the trapping and marking of adults. One pair of radioed terns returned to their nest on the day of trapping, but abandoned the nest 2 days later. Two plover nests were depredated and 1 nest surrounded by flood water was deserted when nests were checked the day following the trapping of 1 individual at each nest.

The incidence of nest desertion for both terns and plovers was not significantly different ($P > 0.05$) from the incidence of desertion among controls (Table 5). For both species, there was a highly significant difference ($P < 0.005$) between Group 1 depredation rates and control depredation rates; however, depredation rates of Group 1 birds were much lower than rates of control birds (Table 6).

Nest and egg survival rates.--We saw no evidence that colony or nest markers cued predators to nests. Daily nest and egg survival rates of Group 1 terns and plovers did not differ ($P > 0.90$) from survival rates of controls (Table 7). Radio-marked plovers had very high nest (1.000) and egg (0.9873) survival rates (Table 8). Although radio-marked terns

had slightly lower nest and egg survival rates than controls of the same incubation stage (Table 8), the differences were not significant ($P > 0.80$).

DISCUSSION

To facilitate trapping of shorebirds in mixed colonies, it is advantageous to have a single trap that is equally effective for capturing different species. Some ground-nesting shorebirds, such as the Snowy Plover, Piping Plover (C. melodus), American Avocet (Recurvirostra americana), and Common Tern (S. hirundo), return to their nest by walking to it whereas Least Terns, Arctic Terns (S. paradisaea), and many members of the subfamily Sterninae hover over their nest and alight directly on it (Wilcox 1959, McNicholl 1968, and personal observation). Therefore, a trap which does not allow a bird to alight directly on the nest, or run directly to it, probably is not the best design for capturing multiple species. The T-trap used in our study was effective for capturing terns and plovers that returned to their nests by wing or by foot.

Utility of trapping method.--Our trapping method was most efficient during sunny afternoons. Catch per unit effort was affected by weather and time of day, but not by incubation stage. Time required to catch a bird was shortest during the most thermally stressful period of the day, generally from 1200-1800 hours. Purdue (1978) concluded that nest attentiveness of Snowy Plovers on salt flats was reduced when ambient temperatures exceeded 41°C because plovers frequently left their nests to wet their breast feathers in nearby streams and pools, then returned to shade (stand over) their eggs. We observed Least Terns exhibiting

similar feather-wetting behavior but also noted that both species frequently left nests unattended for long intervals (15 min to over 1 hr) during early morning hours and on cool, cloudy days. Pairs foraged during this time and defended their nesting territories from conspecifics and predators. Nest relief episodes were thus frequent and of short duration during thermally stressful times. However, during cooler times nest relief periods were protracted, and often nests were left uncovered for long periods although pairs continued surveillance of the nesting territory. In actuality, the total time birds spent at the nest may have been greater during extremely hot weather than cool weather. Hence the probability of catching a bird during hot weather was high because birds were frequently returning to the nest. Although we had no problems with overheated eggs (induced addling) or heat-stressed adults, short return intervals and handling times are undoubtedly important during trapping sessions when heat stress to clutches and adults is possible. Further, trapping terns and plovers during the heat of the day may be lethal to their eggs if the nest substrate lacks evaporative cooling. Our study area is underlain by a high water table and may act like a large body of surface water in moderating thermal conditions of the nesting substrate (Purdue 1976).

In addition to having little effect on egg addling rates, our trapping operations apparently had little effect on nest desertion rates of Least Terns and Snowy Plovers. While trapping-induced desertion is known for Least Terns (Brubeck et al. 1981, Massey and Atwood 1981), Boyd (1972) reported no trap induced desertion among 45 Snowy Plovers captured with drop traps. In our study Snowy Plovers also tolerated trapping procedures. Plover nest desertion effected by capture with

T-traps was either as "high" as 3.7% or as low as 0%. This either/or dichotomy is used to avoid the post hoc fallacy of assuming that trapping caused desertion simply because trapping preceded desertion. The 3 deserted nests belonged to Experimental Group 1 plovers (trapped and banded) from the 1983 nesting season. We checked nests 1 day after trapping the adults and found these nests with completely or partially depredated clutches, or surrounded by water. Hence, contrary sequences of events were possible: 1) the birds initially returned to their nests but abandoned them when subsequently depredated or flooded, or 2) the birds initially abandoned their nests and subsequently they were depredated or flooded. Regardless of the true cause of desertion among the 3 Snowy Plover nests, we believe nest desertion of less than 4% is tolerable, especially for a species with the capacity to renest (Boyd 1972, Wilson 1980, Page et al. 1983).

Only 2 Least Terns (a pair from Experimental Group 2) deserted their nest after trapping (3.7% desertion among nests). The desertion occurred 2 days following trapping; the pair originally returned to their nest on the day of trapping. Brubeck et al. (1981) also had low nest desertion (7%) among 14 Least Terns banded after capture in walk-in funnel traps; however, all terns were trapped within 3 days of egg hatch. We trapped terns as early as 11 days pre hatch (mean nest age, 6.1 ± 0.5 days pre hatch), equipped 62% of the terns with radios, and still had low nest desertion. Brubeck et al. (1981) also found that desertion rates among trapped Least Terns varied widely between colony sites on the Texas coast. They suggested that terns habituated to pedestrian and vehicle traffic may be tolerant of trapping disturbances. Least Terns nesting on our study area may have habituated to the

presence of researchers during 3 consecutive field seasons; however, pedestrian and vehicle disturbance on the study area was minimal.

Necessity of masks and release boxes.--Low nest desertion in our study may be correlated with reducing the vision of experimental birds throughout the handling period; however, we did not empirically determine the effects of capturing and marking Least Terns and Snowy Plovers without masking birds or using release boxes. Poole (1981) placed hoods on trapped Osprey (Pandion haliaetus) because he thought masks reduced activity of Osprey during weighing, measuring, and banding. In our study, captive Least Terns ceased defensive behavior once masked, suggesting that the masks elicited docile behavior. Welty (1975:77) generalized that most birds gather more information about their environment from vision than other senses. Therefore, it seems plausible that avian stress during handling can be reduced via reduction of visual cues. We placed Least Terns and Snowy Plovers in a dark box as a prerelease precaution and made certain that trappers were camouflaged before birds were freed. The reluctance of some birds to leave the opened release box may reflect their "sedateness" in the box and/or be a result of ocular adjustment to sudden light.

Trapping precautions.--There was no direct evidence of immediate or delayed mortality of any Least Terns or Snowy Plovers that were trapped. However, on 2 occasions Snowy Plovers were knocked prostrate by the bail when it was released prematurely. These birds were unharmed, but the possibility of serious injury cannot be overlooked. Injury to birds can be avoided by not triggering the T-trap until a bird has sat on or stood over its eggs. Consistently the T-trap pinned birds 1 body length away from the nest (forward from the trap crossbar) if

birds were positioned directly over the nest when the bail was released.

In 3 of 84 captures, Snowy Plovers kicked at least 1 egg 1-8 cm from the nest. Egg rolling was not observed with Least Terns, possibly because the terns jumped upward into flight rather than ran forward when the bail was activated. We stress the importance of placing the trap crossbar 10-12 cm from the center of the nest. This distance was adequate to prevent egg damage if birds kicked eggs and adequate to prevent birds from being hit when bail rate (the rate at which a tripped bail flopped over the nest) was less than or equal to 0.75 sec.

Bail rates were critical to successful capture of birds and slowed as windblown salt and sand accumulated in springcoils. Bail rates greater than 0.75 sec enabled Least Terns and Snowy Plovers to escape the nest before the bail hit ground. The problem was remedied by periodically spraying springs with rust solvent.

Transmitter recommendations.--Observation of radio-equipped birds indicated no changes in behavior after placement of radio backpacks. No birds lost their radios and most radios transmitted over a 1 km distance for 1-2 months. Our method of radio application was quick, but necessitated that precautions be taken to avoid direct contact between glue, fingers, and feathers. In a hot environment, cyanocrylate-base glue bonds almost instantly. We recommend use of the handle of an artist's paint brush to smooth down feathers glued to the top of the radio.

SUMMARY

Effects of capture and marking on reproductive performance of Least

Terns and Snowy Plovers were studied at Salt Plains NWR, Oklahoma during 1983 and 1984. Disturbance to breeding populations was minimized by using T-shaped bail traps, release boxes, and masking captured birds. Trapping operations and equipping birds with radios did not significantly affect nest and egg survival of terns or plovers. Overnight trap sets did not increase the frequency of nest depredation. Nest depredation and desertion as a result of trapping and/or radio application was low. On average, terns and plovers returned to their nests 13-14 minutes after traps were activated; however, return intervals were shorter during torrid weather. Return intervals were not affected by incubation stages. Observation of radio-equipped birds indicated no aberrant behavior associated with radio backpacks. Most experimental radios transmitted over a 1 km distance for 1-2 months.

ACKNOWLEDGMENTS

This study was funded in part by the U.S. Fish and Wildlife Service, Region 2 (Contract 93510-1240-750), the Oklahoma Department of Wildlife Conservation (Nongame Research Project As-85-R-121), the Oklahoma Cooperative Fish and Wildlife Research Unit, and the Department of Zoology at Oklahoma State University. The Oklahoma Cooperative Fish and Wildlife Research Unit, Salt Plains NWR, Oklahoma State University, and Denver Wildlife Research Center provided technical assistance. Field work was aided by Valerie A. Keener.

We thank Helen C. Miller for reviewing the manuscript. Ronald S. Sullivan permitted us gratis camping on refuge lands and the entire refuge staff extended warm hospitality.

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TABLE 1. Distribution of Least Tern and Snowy Plover nests and individuals according to degree of handling and marking at Salt Plains NWR during 1983 and 1984.

Treatment	Least Tern		Snowy Plover	
	Nests	Individuals	Nests	Individuals
Control ^a	104	-- ^b	252	-- ^b
Experimental Group:				
1. Trap & band	10	12	66 ^c	66
2. Trap, band & radio	15	20	15	18

^a Controls were not trapped, handled, or marked.

^b Number of individuals in control groups is unknown. Doubling the number of nests would overestimate the number of individuals because renesting did occur.

^c Twenty-three of these nests were excluded from the comparison of nest and egg survival for experimental versus control groups because these nests were manipulated for a separate renesting study.

TABLE 2. Distribution of Least Terns and Snowy Plovers trapped during years of variable weather patterns at Salt Plains NWR.

	<u>May 1-31</u>		<u>June 1-30</u>		<u>July 1-31</u>		<u>Aug. 1-18</u>	
	'83	'84	'83	'84	'83	'84	'83	'84
% total trapping attempts:								
Least Terns	0	0	0	24.2	30.3	33.3	0	12.1
Snowy Plovers	0	10.4	36.8	23.6	20.7	8.5	0	0
Rainfall, ^a cm	10.5	2.7	13.0	3.3	0	0.8	3.2	3.0
Temperature, ° C ^b								
Ave. maximum	23.6	24.8	28.7	33.9	35.9	35.8	38.4	36.1
Ave. minimum	10.9	11.9	16.5	19.6	21.0	19.8	22.7	20.5
No. cool ^c and/or								
cloudy/rainy days	25	22	17	7	2	4	2	5

^a Rainfall on the salt flats was estimated by averaging precipitation records from 2 national weather stations located on the east shore of the lake and to the west of the salt flats (records from National Oceanic and Atmospheric Administration 1983, 1984).

^b Only the lake shore weather station recorded temperatures.

^c Days with highs less than 28 ° C were considered cool.

TABLE 3. Mean return intervals (min) for Least Terns and Snowy Plovers
at different incubation stages at Salt Plains NWR during
1983 and 1984.

Incubation stage	Least Terns ^a			Snowy Plovers ^a		
	n	\bar{X}	SE	n	\bar{X}	SE
Early (\leq 7 days)	0	-	-	20	15.6	2.9
Mid (8-14 days)	13	8.1	2.1	34	15.4	2.9
Late (\geq 15 days)	19	16.4	5.4	30	11.9	2.3
Total	32	12.8	3.3	84	14.1	1.6

^a There was no significant difference ($P > 0.05$) in mean return intervals for terns or plovers (unpaired t-tests).

TABLE 4. Distribution of Least Tern and Snowy Plover return intervals during different times of day at Salt Plains NWR in 1983 and 1984.

Time of day	Least Terns (min)				Snowy Plovers (min)			
	0-10	11-20	21-30	30+	0-10	11-20	21-30	30+ ^a
0600 - 0859	-	-	-	-	-	2	3	6
0900 - 1159	3	2	1	3	3	2	3	14
1200 - 1459	16	1	3	-	30	10	2	7
1500 - 1759	3	-	-	-	10	3	1	5
1800 - 2059	-	-	-	-	2	-	-	3
Total number:	22	3	4	3	45	17	9	35
Percent of total:	68.7	9.4	12.5	9.4	42.4	16.0	8.5	33.0

^a Twenty-two plovers having return intervals greater than 30 min were not trapped.

TABLE 5. Nest desertion rates of Least Terns and Snowy Plovers in Experimental Group 1
at Salt Plains NWR in 1983 and 1984.

Treatment	Least Tern nests						Snowy Plover nests					
	<u>Not deserted</u>		<u>Deserted</u>		χ^2	P <	<u>Not deserted</u>		<u>Deserted</u>		χ^2	P <
	n	%	n	%			n	%	n	%		
Control	220	87.3	32	12.7	3.39 ^a	NS ^b	94	90.4	10	9.6	1.21 ^a	NS ^b
Trap and band	63	95.5	3	4.5			12	100.0	0	0		

^a Chi-square test for goodness of fit, 1 df.

^b NS= not significantly different at the P = 0.05 level.

TABLE 6. Nest depredation rates of Least Terns and Snowy Plovers in Experimental Group 1
at Salt Plains NWR in 1983 and 1984.

Treatment	Least Tern nests						Snowy Plover nests					
	Not depredated		Depredated		χ^2	P <	Not depredated		Depredated		χ^2	P <
	n	%	n	%			n	%	n	%		
Control	165	65.5	87	34.5	25.89 ^a	0.001	62	59.6	42	40.4	8.96 ^a	0.005
Trap and band	64	97.0	2	3.0			12	100.0	0	0		

^a Chi-square test for goodness of fit, 1 df.

TABLE 7. Daily nest and egg survival rates of Least Tern and Snowy Plover cohorts that were trapped and banded versus cohorts that were not trapped or handled in 1983 and 1984 at Salt Plains NWR.

	^a Least Tern		^a Snowy Plover	
	Trapped & banded	Control ^b	Trapped & banded	Control ^b
Number of nests	10	10	43	43
Number of eggs	24	21	126	118
Daily nest survival (SE)	0.9735 (0.0131)	0.9503 (0.0242)	0.9730 (0.0063)	0.9655 (0.0078)
Daily egg survival (SE)	0.9654 (0.0098)	0.9529 (0.0145)	0.9581 (0.0046)	0.9668 (0.0046)

^a Nest and egg survival rates of trapped and banded cohorts did not differ from controls (Bart and Robson's (1982) 1-tailed Z-test, $P > 0.90$.)

^b Control nests were selected by stratified random sampling of nontrapped, nonhandled Least Tern and Snowy Plover pairs having nest initiation dates concurrent with those of trapped and banded birds.

TABLE 8. Daily nest and egg survival rates of Least Tern and Snowy Plover cohorts that were radio-marked versus cohorts that were not trapped, handled, or marked in 1983 and 1984 at Salt Plains NWR.

	^a Least Tern		^a Snowy Plover	
	^b Radio-marked	^c Control	^b Radio-marked	^c Control
Number of nests	15	15	15	15
Number of eggs	39	34	45	41
Daily nest survival (SE)	0.9543 (0.0223)	0.9912 (0.0088)	1.000 (0)	0.9874 (0.0125)
Daily egg survival (SE)	0.9442 (0.0164)	0.9801 (0.0088)	0.9873 (0.0073)	0.9815 (0.0092)

^a Nest and egg survival rates of radio-marked cohorts did not differ from controls (Bart and Robson's (1982) 1-tailed Z-test, $P > 0.80$.)

^b Exposure-days (Mayfield 1961) were counted from the day of radio application.

^c Control nests were of the same incubation stage as nests of radio-marked birds.

FIGURE 1. T-trap used to capture incubating Least Terns and Snowy Plovers.

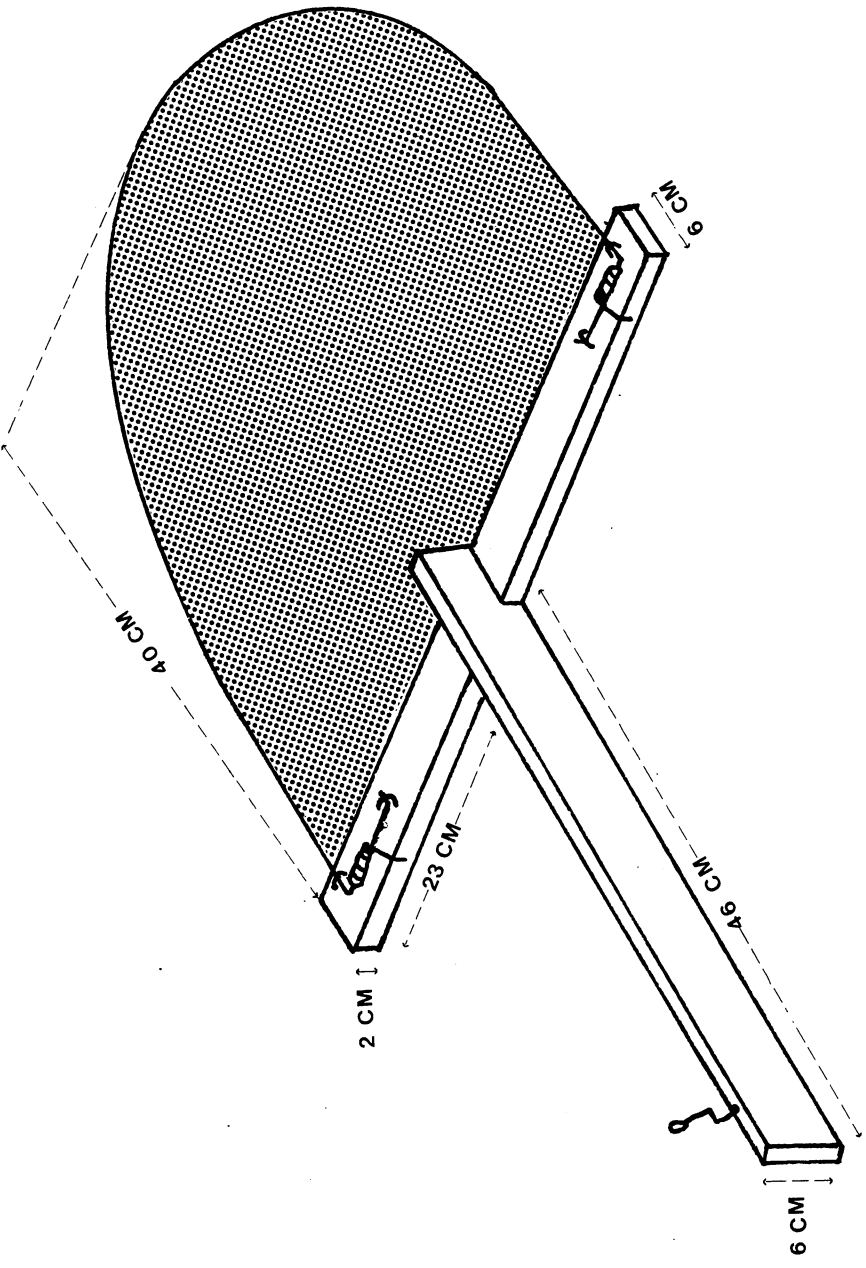
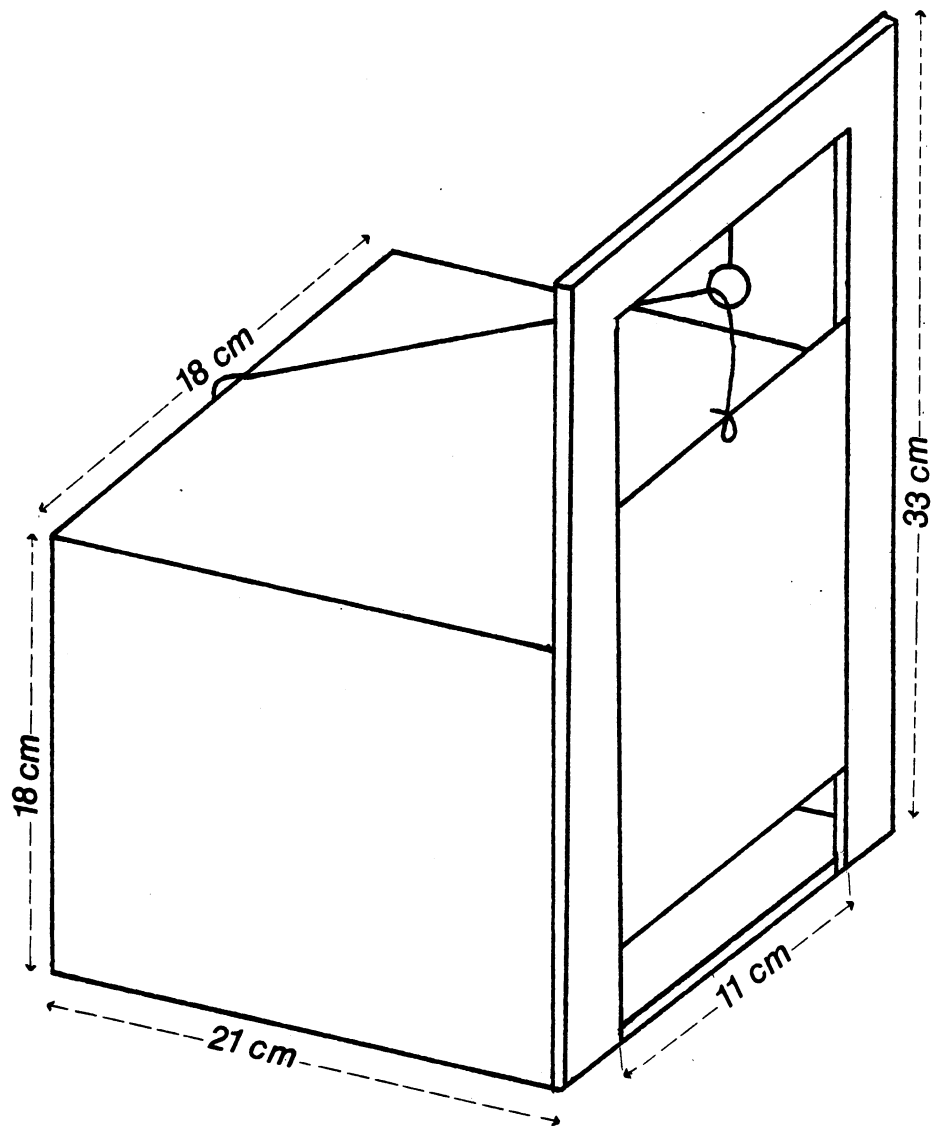


FIGURE 2. Wooden release box with a vertically sliding door.

Dimensions are tailored to Least Terns and Snowy Plovers.



CHAPTER III

DETERMINING INCUBATION STAGE OF INTERIOR LEAST TERN, SNOWY PLOVER, AND AMERICAN AVOCET CLUTCHES

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Researchers are often required to estimate the incubation stage of eggs during investigations of avian reproductive success. Accurate methods for estimating incubation are necessary before studies can be conducted on laying and hatching chronology and synchrony, intraclutch egg size variation, age-specific nest mortality, temporal clutch survival rates, and temporal changes in incubation behavior. If nests are located before clutches are complete, determining incubation stage is simple. However, complete clutches are often found when studying shorebirds because most species lay four or fewer eggs and the probability of finding incomplete clutches is directly related to the length of the laying period. An additional problem encountered when

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studying endangered species of shorebirds is that disturbance to nesting areas must be kept to a minimum and daily nest searches are often not justified. Therefore, there is a need for accurate models that predict the incubation stage or hatching date of complete clutches of eggs during any stage of incubation.

During studies on the reproductive biology of interior least terns (Sterna antillarum athalassos), snowy plovers (Charadrius alexandrinus), and American avocets (Recurvirostra americana) in Oklahoma, we frequently had to estimate the incubation stage of eggs. We did not visit each nesting colony on a daily basis to find newly initiated nests because both least terns and snowy plovers are endangered in parts of their range and unnecessary disturbance of nesting birds could not be justified. Therefore, complete clutches of eggs were usually found.

Several methods of predicting hatching dates or incubation stages of clutches were examined, but the egg flotation method (Hays and LeCroy 1971) appeared to be the most practical field tool. The flotation method uses changes in position of an egg in a water column to predict incubation stage. Eggs lose weight after laying and as the specific gravity of the egg decreases during incubation, the egg floats progressively higher in the water column. Egg flotation models are not available for shorebirds breeding in Oklahoma. Therefore, the purpose of this paper is to describe egg flotation models that fairly accurately predict the hatching date or incubation stage of eggs of interior least terns, snowy plovers, and American avocets that breed at a salt flat in west northcentral Oklahoma.

STUDY AREA AND METHODS

The study was conducted from May through August 1983 on a 4,050 ha

salt flat at Salt Plains National Wildlife Refuge (NWR) in Alfalfa County, Oklahoma. Climate is classified as dry subhumid to semiarid (Blair 1951). Prevailing southerly winds, averaging 34 km/hr, contribute to the highly evaporative environment. During the study, average maximum temperatures for May, June, July, and August were 24, 29, 36, and 38 °C, respectively (NOAA 1983). Johnson (1972) described the study area in more detail.

Shorebird nests were located by systematic searches of the salt flats in typical nesting habitat at Salt Plains NWR (Grover and Knopf 1982). All viable eggs in 20 known-age nests each of interior least terns, snowy plovers, and American avocets were measured at 3-5 day intervals throughout incubation. In the field, egg length (L) and breadth (B) were measured to the nearest 0.01 mm with a vernier caliper, and egg weight was measured to the nearest 0.2 g with a pesola spring scale. Individual eggs were placed in a translucent beaker of distilled water and the angle of flotation (Fig. 1) was estimated to the nearest 5 degrees with a protractor. The angle was recorded from 0 to 90° before eggs floated and 91 to 180° after flotation. If an egg floated, the flotation angle was recorded as 180° minus the observed angle, and the widest diameter of the shell protruding above the water surface (Fig. 1) was measured with a caliper to the nearest 0.1 mm. If some but not all eggs in a clutch floated, protrusion diameter was recorded as "0" for eggs not floating.

After field measurements were made, weight loss was determined by subtracting the weight of the egg at time of measurement from estimated fresh egg weight (W), where $W = (LB^2) \cdot 0.000563$ (Bergtold 1929, Romanoff and Romanoff 1949). The volume (V) of each egg was estimated using the

equation $V = (LB^2) \cdot 0.000507$ (after Hoyt 1979). Although these formulas do not use species-specific coefficients, and hence do not give absolute volume and specific gravity, the approximations are acceptable for comparisons between clutches within species (Runde and Barrett 1980). Specific gravity at each time of measurement was estimated by dividing calculated egg volume by egg weight. To correct for variation in egg size, additional variables were created by dividing specific gravity and weight loss by egg breadth, egg length, and Coulson's (1963) egg shape index ($B/L \times 100$).

Egg measurements were used to construct linear regression models to predict hatching dates (after Miles and Bizeau 1983). Variables were regressed against the number of days prior to hatch to determine the most accurate and simplest model to predict hatching dates.

RESULTS AND DISCUSSION

Regression models were based on observed mean incubation periods of 21 days for least terns ($N = 22$), 25 days for snowy plovers ($N = 31$), and 22 days for American avocets ($N = 12$). When prefloating and floating eggs were treated together, the best linear regression models constructed from Individual Egg Measurements (IEM) were fair to good indicators of hatching date (Table 1). For all 3 study species, flotation angle was the best predictor of hatching date (Y) of prefloating and floating eggs. However, 8 variables (Table 2) were needed to maximize the coefficient of determination (r^2) of the IEM model for terns ($r^2 = 0.87$), and 10 variables (Table 2) were needed to maximize the r^2 of the IEM model for plovers ($r^2 = 0.79$) and avocets ($r^2 = 0.84$).

Although the multiple regression models for both prefloating and

floating eggs were fairly accurate for the 3 study species, the models required that many measurements be made on each egg. The need for many variables decreased the utility of the models as field tools.

Therefore, we developed simple linear 1-variable models in order to reduce the amount of equipment and time needed to estimate incubation stages of nests in the field. The accuracy of predictive models was improved by converting individual egg measurement values to means for clutches. The 1-variable regression models based on the best predictor of hatching date, mean angle of flotation (X_a), were as follows: least terns, $Y = 23.93 - 0.12X_a$, $r^2 = 0.91$; snowy plovers, $Y = 28.18 - 0.15X_a$, $r^2 = 0.87$; and American avocets, $Y = 23.95 - 0.13X_a$, $r^2 = 0.89$. Using these models, mean prediction limits for estimating the number of days prior to hatching of tern, plover, and avocets eggs were developed (Table 3).

We noted variable incubation periods in our study populations (terns, 18-24 days; plovers, 23-28 days; avocets, 19-27 days), possibly caused by variation in egg-laying intervals, incubation attentiveness, brood patch development, and/or environmental pressures. The incubation periods of common and roseate terns (*S. hirundo* and *S. dougallii*) vary with age and experience of parents, and with environmental constraints (Nisbet and Cohen 1975). Courtney (1979) determined that nocturnal nest desertion in common terns occurred more frequently among early nesters than late nesters. Furthermore, brood patches of late nesting common terns were significantly more defeathered after birds laid the first egg than brood patches of early nesting terns at the same stage of laying. Hence, incubation periods of common terns decreased throughout the breeding season. In our study, the longest incubation periods of least

terns, snowy plovers, and American avocets also occurred early in the breeding season. Variability in incubation periods of avocets also may have been affected by degree of nest insulation. Avocets opportunistically lined their nests with nearby dried plant material. Poorly-lined avocet nests tended to have longer incubation periods than well-lined nests, particularly during the early breeding season when ambient temperatures were lowest.

Large intraspecific variation in incubation periods could greatly reduce the accuracy of models for predicting the number of days prior to hatching. However, prediction of hatching dates to within 2-3 days was usually possible in our study if mean values of clutch measurements were used rather than individual values of eggs. Manning (1977) advocated using whole clutches when high variation in intra-clutch measurements occurred. Therefore, we do not recommend restricting sampling to one egg in a clutch. Although it took more time to measure every egg in a clutch, disruptive effects of extended human disturbance at nest sites did not cause extensive nest desertion. Desertion rates were 3-5% on the study area in 1983, which were not significantly ($P < 0.05$) greater than the 1-4% desertion rates observed in 1982 when eggs were not handled.

Models presented in this paper were derived for inland populations of least terns, snowy plovers, and American avocets nesting in an extreme environment. Hence the models may require modification to fit other climates. Slight modification also may be justified due to visual bias among investigators in determining angle of flotation.

Acknowledgments.--We thank refuge staff at Salt Plains NWR for their cooperation and hospitality. This project was funded by the U.S. Fish

and Wildlife Service, Region 2 (Contract 93510-1240-750), the Oklahoma Department of Wildlife Conservation (Nongame Research Project As-85-R-121), the Oklahoma Cooperative Fish and Wildlife Research Unit, and the Department of Zoology at Oklahoma State University.

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Table 1. Linear regression of individual egg measurements on the number of days preceding hatching (Y) of interior least tern, snowy plover, and American avocet eggs.

Variable (X)	Least tern		Snowy plover		American avocet	
	Model ^{a,b}	r ²	Model ^{a,b}	r ²	Model ^{a,b}	r ²
Flotation angle, degrees	Y = 24.36 - 0.12X	0.82	Y = 26.66 - 0.12X	0.75	Y = 22.74 - 0.13X	0.77
Protrusion diameter, mm	Y = 13.85 - 0.49X	0.39	Y = 15.88 - 0.52X	0.26	Y = 10.81 - 0.30X	0.34
Egg weight, g	Y = -29.57 + 5.25X	0.52	Y = -38.85 + 6.44X	0.33	Y = -28.10 + 1.43X	0.52
Specific gravity (SG)	Y = 59.48 - 45.69X	0.43	Y = 89.97 - 74.00X	0.32	Y = 56.73 - 41.70X	0.33
Weight loss, g	Y = 19.25 - 6.11X	0.42	Y = 24.07 - 9.97X	0.28	Y = 19.35 - 1.49X	0.23
Weight loss divided by egg length, g/mm	Y = 19.47 - 191.85X	0.44	Y = 24.52 - 295.60X	0.31	Y = 55.81 - 2044.10X	0.43
Weight loss divided by egg breadth, g/mm	Y = 19.38 - 143.30X	0.43	Y = 24.28 - 211.44X	0.30	Y = 57.44 - 1442.90X	0.42
Weight loss divided by egg shape index, g	Y = 19.11 - 452.87X	0.41	Y = 23.75 - 634.33X	0.27	Y = 46.27 - 2201.96X	0.23
SG divided by egg length, mm ⁻¹	Y = 57.78 - 1340.17X	0.51	Y = 86.34 - 2208.74X	0.35	Y = 20.08 - 80.42X	0.28
SG divided by egg breadth, mm ⁻¹	Y = 59.84 - 1057.28X	0.46	Y = 81.81 - 1521.49X	0.34	Y = 20.04 - 54.59X	0.27
SG divided by egg shape index	Y = 48.25 - 2628.36X	0.28	Y = 59.87 - 3260.81X	0.20	Y = 19.13 - 98.87X	0.22

Table 2. Multiple linear regression (based on individual egg measurements) on the number of days preceding hatching (Y) of interior least tern, snowy plover, and American avocet eggs.

Species	"Best model" ^{a,b}	r ²	F-ratio ^c	P	df
Least tern	$Y = -5278.93 + 129.52X_2 - 0.12X_3 + 2793.74X_9 - 1.38X_{10}$ $+ 63435.17X_{12} - 69055.79X_{14} + 24980.19X_{15}$ $- 151104.75X_{16}$	0.87	10.01	0.0001	31
Snowy plover	$Y = -2096.44 + 27.82X_1 + 173.08X_2 - 0.10X_3 - 122.81X_5$ $- 1457.25X_7 - 101.01X_9 - 22.68X_{10} + 48517.96X_{11}$ $- 4536.70X_{15} + 12063.84X_{16}$	0.79	10.80	0.0001	39
American avocet	$Y = 140.56 - 0.10X_3 - 2.62X_5 - 2683.60X_7 + 492.48X_9$ $+ 136521.05X_{11} - 98540.48X_{12} + 191714.81X_{13}$ $- 23900.32X_{14} + 15773.82X_{15} - 32697.96X_{16}$	0.84	19.04	0.0001	47

^a Stepwise multiple regression analyses were performed using the SAS "STEPWISE/MAXR" procedure (Goodnight 1982). Variables were deleted from models if they did not maintain an F statistic at the $P < 0.1$ probability level.

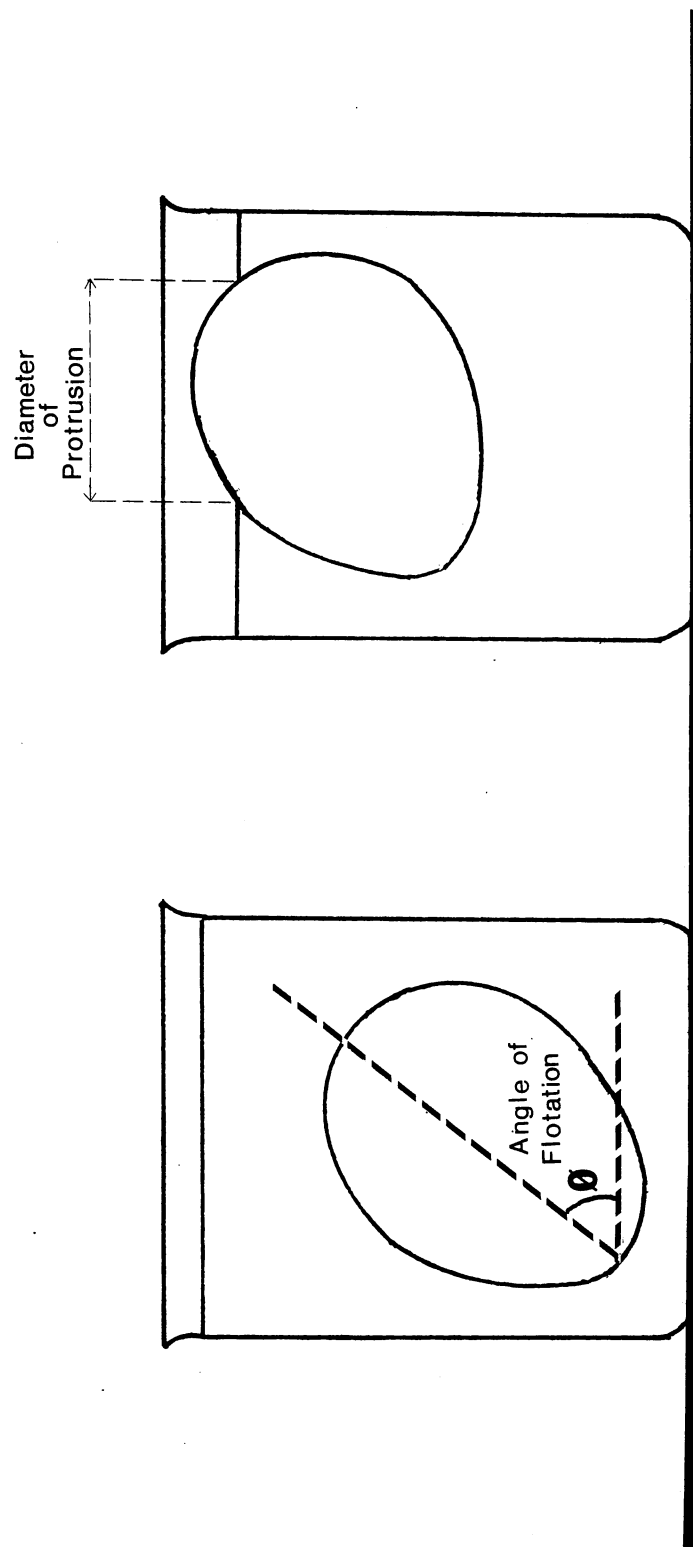
^b X_1 = egg length (mm), X_2 = egg breadth (mm), X_3 = flotation angle (degrees), X_5 = fresh egg weight (g), X_7 = specific gravity, X_9 = weight loss (g), X_{10} = egg shape index, X_{11} = specific gravity/length (mm^{-1}), X_{12} = specific gravity/breadth (mm^{-1}), X_{13} = specific gravity/shape index, X_{14} = weight loss/length (g/mm), X_{15} = weight loss/breadth (g/mm), and X_{16} = weight loss/shape index (g).

^c The F test is for the null hypothesis that all regression coefficients are zero.

Table 3. 95% confidence limits for estimating number of days prior to hatching of least tern, snowy plover, and American avocet eggs from mean flotation angle (degrees).

\bar{X} flotation angle	Predicted days before hatch		
	Least tern	Snowy plover	American avocet
0-30	20-21	24-25	19-22
31-50	18-20	21-24	17-19
51-70	15-18	17-20	14-17
71-90	13-15	14-17	12-14
91-110	11-13	11-14	9-12
111-130	8-11	8-11	6-9
131-150	6-8	5-8	4-6
151-170	3-6	2-5	1-4
171-180	0-3	0-2	0-1

Fig. 1. Measurement of the "angle of flotation" and the "diameter of protrusion" of an egg in a water column.



CHAPTER IV

THE EFFECTS OF NEST-SITE SELECTION ON BREEDING SUCCESS OF LEAST TERNS, SNOWY PLOVERS, AND AMERICAN AVOCETS IN NORTHCENTRAL OKLAHOMA

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Abstract: Nesting and hatching synchrony of interior least terns (Sterna antillarum athalassos), snowy plovers (Charadrius alexandrinus), and American avocets (Recurvirostra americana) at Salt Plains National Wildlife Refuge, Oklahoma was influenced by catastrophic weather during 1982-84. Nest success of terns, plovers, and avocets ranged from 25-60%, 17-65%, and 8-17%, respectively. Clutch survival was similar among nests located in the open, beside objects, or in/under objects; however, tern nests on sand/stone substrate and plover nests on clay substrate were less successful than nests on alkali. Avocets often nested on clay and lost 2-4 times more eggs to flooding than terns and plovers. During 1982, spacing between nests ranged from 7-180+ m.

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Colonial nesters had lower nest mortality than solitary nesters. Plovers and avocets nesting close to terns had lower nest mortality than congeners and may have benefitted from least tern nest defense. Annual fledging success of all 3 species was low during 1982-84 (< 0.5 fledglings/female).

There is a paucity of information on the reproductive success of interior least terns (*Sterna antillarum athalassos*), snowy plovers (*Charadrius alexandrinus*) and American avocets (*Recurvirostra americana*) throughout the midwest. Both least terns and snowy plovers are experiencing population declines, apparently as a result of nesting habitat loss and human disturbance. Least terns and snowy plovers are classified as threatened, endangered or of special status throughout much of their range in the United States and, recently, the interior least tern was listed as endangered (Federal Register of May 28, 1985). Therefore, information is critically needed on the reproductive status of interior least terns and snowy plovers throughout their range.

One of the largest breeding concentrations of interior least terns, snowy plovers, and American avocets in the Central Plains States occurs at Salt Plains National Wildlife Refuge (NWR), Oklahoma, where all 3 species nest primarily on barren salt flats. The refuge populations have not been well studied, although Grover and Knopf (1982) provided baseline information on the distribution and overall nest success of breeding birds. Little, however, is known about the specific factors affecting breeding success of least terns, snowy plovers, and American avocets nesting on salt flat habitat.

Considerable intra and interspecific variation occurs in nest-site selection and degree of coloniality of shorebirds at Salt Plains NWR (Grover and Knopf 1982). Other studies of colonial birds indicate that nest success often varies in relation to degree of coloniality (Goransson et al. 1975, Dyrce 1977, Dyrce et al. 1981), nesting phenology (Nelson 1970), location of a nest within a colony (Nelson 1970, Nettleship 1972, Siegel-Causey and Hunt 1981), colony topography (Nelson 1967, Nettleship 1972), nest substrate (Page et al. 1985), and nest cover (Page et al. 1985). Therefore, the purpose of our study was to examine nesting chronology and synchrony of interior least terns, snowy plovers and American avocets at Salt Plains NWR, and assess effects of weather, nest substrate, nest cover, nearest neighbors, and inter-nest distances on reproductive success.

This study was funded in part by the U.S. Fish and Wildlife Service, Region 2 (Contract # 93510-1240-750), the Oklahoma Department of Wildlife Conservation (Nongame Research Project As-85-R-121), the Oklahoma Cooperative Fish and Wildlife Research Unit, the Zoology Department at Oklahoma State University, and the Payne County Audubon Society. The Oklahoma Cooperative Fish and Wildlife Research Unit, Salt Plains NWR, Oklahoma State University, and Denver Wildlife Research Center provided technical assistance and/or logistical support. Field assistance was provided by V. A. Keener. We are grateful for the cooperation and hospitality of staff at Salt Plains NWR. R. S. Sullivan permitted us to use office and shop facilities and camp on refuge land. We thank H. C. Miller for critically reviewing an earlier draft of the manuscript.

STUDY AREA

The study was conducted at Salt Plains NWR, near Cherokee in Alfalfa County, Oklahoma. Climate in the area is typified by hot, dry summers with occasional thunderstorms, hail, and high winds.

Our study area was the entire salt flat within refuge boundaries and south of State Highway 11 (Fig.1). The salt flats occupy an area of about 4,050 ha on the west shore of Great Salt Plains Reservoir. The flats are barren except for debris localized by floodwaters, patches of sea purslane (Sesuvium verrucosum) on sandy outcroppings, and disjunct riparian zones of salt cedar (Tamarix gallica) and sedge (Carex sp.).

Four seasonally intermittent, dendritic streams traverse the salt flats in areas traditionally used by nesting birds. During drought, portions of these streams are reduced to isolated brine pools but during heavy rains numerous ephemeral streams are created. Due to the slight slope of the floodplain (0.75-1.50 m/km), these ephemeral streams change course often, creating pools that may last several weeks. Feeding and loafing migratory and breeding birds often congregate at the standing pools, flowing streams, and lakeshore. For a more detailed description of the study area, see Johnson (1972).

The study site was almost free of human disturbance except for activities associated with our research. The general public had authorized access to 2 sites on the perimeter of the salt flats; however, few birds nested in these areas. Unauthorized access by far-ranging recreationists on motorbikes occurred infrequently. Cattle from surrounding ranches sometimes ventured onto the salt flats for a day or 2 but were soon herded back to pasture.

METHODS

Chronology, Nest Site Characteristics, and Clutch Survival

Nests were located by systematically searching the salt flats. We searched for least tern and snowy plover nests during 1982, 1983 and 1984, but only searched for American avocet nests during 1982 and 1983.

Nests located were numbered serially and their locations plotted on study area maps. Whenever necessary, nests and colony locations were marked. In 1982 and 1983, locations were marked with orange or blue flagging tied to nearby objects. In 1984, almost all nests were marked with tongue depressor sticks placed within 60 cm of the nest.

At each nest, the distance and direction of the nearest reference point, substrate type, and relative distance to objects or vegetation was recorded. Nests within about 30 cm of an object were classified as "beside objects"; nests covered from above were classified as "under objects"; nests not scraped out of the earth but contained within a dry cow chip or other object were classified as "inside objects"; and all others were classified as "in the open". In 1982 after breeding birds deserted colonies, nest dispersion was quantified by measuring the distance from each nest to the nearest concurrent nest of the same and different species. Inter-nest distances exceeding 180 m were recorded as 180+ m.

Most nests were checked every 3-5 days until they hatched or failed. Nests were considered successful if at least one chick hatched. Hatching was indicated by sighting chicks and/or finding fecal droppings near tern nests, or tiny eggshell fragments inside plover and avocet nests. Nests were considered failed whenever a complete clutch disappeared well before the projected hatching date, or when egg remains

or predator signs were found at the nest cup.

Nest initiation dates, if unknown, were backcalculated from hatch dates or estimated via the egg flotation method of Hays and LeCroy (1971). Incubation periods of 21, 25 and 22 days, respectively, were assumed for least terns, snowy plovers and American avocets.

Nest and egg survival was analyzed using the Mayfield (1961, 1975) method. Johnson's (1982) test for equality of nest mortality rates between periods was used to quantify differences in nest mortality rates between laying and incubation, between early season (pre-median laying date) and late season (post-median laying date), and between nearest-neighbor nesting cohorts. Whenever temporal variation in nest mortality was evident, we estimated seasonal nest success by stratifying the sample (Klett and Johnson 1982). One-tailed Z-tests (Bart and Robson 1982) were used to detect differences in seasonal nest success.

Chi-square analyses were used to determine the significance of differences in observed nest success (successful nests/nests found) relative to nest substrate and nest placement near objects. We used Mayfield estimators to further examine differences noted from χ^2 analyses because observed hatching success generally is a biased estimate of true success (Mayfield 1961, 1975).

Population Status and Recruitment

Miller and Johnson's (1978) method of calculating nest "density" (number of nests initiated) from Mayfield (1961, 1975) hatch rates was modified to estimate number of breeding females. Calculations were done in 2 stages to correct for the effect of renesting. The correction for renesting was warranted because all 3 species renest (Fisk 1975, Page et al. 1983, and unpubl. data), and the formula uses nest success which

underestimates pair success. The correction involved dividing the breeding season into 2 parts (nests initiated prior to the median laying date and those initiated after the median laying date) and calculating nest density for both parts, under the following assumptions: 1) all adult least terns, snowy plovers, and American avocets attempted to nest prior to their respective median laying dates, and 2) all adult terns, plovers and avocets that failed in their initial nesting attempt, renested after the median laying date. Nest "density" of successful females during the early breeding season was added to nest "density" of renesters during the late breeding season to yield an estimate of total breeding females.

During 1982-84 and 1982-83, daily opportunistic observations of tern and plover, and avocet chicks, respectively, were made. Resightings of some broods were inferred on the basis of location data and chick size classes. Post-reproductive counts of juvenile shorebirds at staging areas augmented these rough estimates of chick survival. Additionally, survival of least tern and snowy plover broods was monitored in 1984 by radio-marking parents (15 tern and 15 plover broods) and tracking parental movements to relocate chicks; see Hill (1985) for detailed description of methods for trapping and application of radios. Chicks were considered dead if parental movements suddenly deviated from previous movements and chicks could not be located in areas where parents were radio-located. Estimates of fecundity/adult were calculated using a method similar to that used by Massey and Atwood (1981) for California least tern (S. a. brownii) populations.

RESULTS

Breeding Chronology and Synchrony

During 1982-84, snowy plovers arrived first on the study area (late March - early April), followed within a week by American avocets, and within 2-4 weeks by least terns. First clutches generally were laid 1-4 weeks after arrival on the breeding grounds. Despite disparate arrival times each year, interspecies nesting synchrony occurred during all years of the study (Fig. 2).

Within species, snowy plovers exhibited relatively higher nesting synchrony each year than least terns and American avocets. Consistently, 25% of plover nests were initiated in the first 20% of every nesting season (Fig. 2). Twenty-five percent of tern nests also were initiated in the first 20% of the 1984 season; however, only 3% and 6% of tern nests were initiated in the first 20% of the 1982 and 1983 seasons, respectively. Avocet nesting was synchronous during 1982 (30% of nests initiated in the first 20% of the season) but comparatively asynchronous during 1983 (10% of nests initiated in first 20% of the season).

Two distinct waves of hatching occurred in 1982; however, American avocets were not included in the second wave because they did not renest after a major flood on 8-9 July (Fig. 3). The peak of 1982 tern hatch occurred in early August when 70% of all successful tern nests hatched. Plovers had 2 equal peaks of hatching in 1982, with 25% of successful nests hatching prior to early July and another 25% (probably renests) hatching in early August. During 1983 avocets again exhibited only one major hatching peak (mid July) and all nesting attempts were terminated by 29 July. Plovers showed 2 hatching waves in 1983, each occurring

about one month ahead of respective 1982 waves. Tern hatching in 1983 began in mid June as in 1982, but the major late season hatching peak occurred about 10 days earlier than in 1982. During 1984, the hatching distribution of plovers and terns was protracted, asynchronous, and lacked well-defined peaks.

Nest Success

Variation in daily nest mortality between laying and incubation periods was constant or moderate ($P \geq 0.1$) during all years (Table 1). However, mortality rates sometimes differed ($P < 0.05$) between early and late season nesting attempts. Therefore, stratified samples (Klett and Johnson 1982) were used to estimate seasonal nest success when mortality rates varied temporally (Table 1). Seasonal nest success of least terns was 59.6% in 1984 and 25.3% in 1983. Nest success of snowy plovers ranged from 19.0% to 17.1 % in 1982 and 1983, respectively, but exceeded 60% in 1984. American avocets had the lowest nest success (8.4%) of all 3 species during 1982, but were as successful (17.1%) as terns and plovers during 1983 ($P < 0.05$).

Egg Loss

Egg success was 1-7% less than nest success due to partial loss of successful clutches (Table 2). Mammalian predators and inclement weather destroyed more than one third of all eggs laid by the 3 species in 1982 and 1983. During these 2 summers, total egg losses to predators were highest for snowy plovers and lowest for least terns, whereas total egg losses to flooding and hail were highest for American avocets. However, a hail storm on 5 June 1983 destroyed proportionately more plover (45%) than avocet (16%) and tern (13%) nests, and killed at least 17 adult snowy plovers. Although effects of predation and storms were

less severe in 1984 than in previous years, predation was still the greatest contributor to egg loss among terns and plovers. Collectively, thin-shelled eggs, fully incubated eggs that failed to hatch, and chick death during pipping, accounted consistently for 8-10% of tern egg loss but usually < 4% of plover and avocet egg loss. For all species, undetermined causes of egg disappearance (3-6%) and clutch desertion (4-5%) were greatest during 1983, but as a whole accounted for only 3-6% of egg loss during other years.

Nest Substrate and Clutch Fate

Most least tern and snowy plover nests were on alkaline substrate, whereas American avocet nests were almost equally distributed on alkaline (40.2%) and clay (38.5 %) substrates (Table 3). Fate of avocet nests did not differ ($P > 0.10$) among substrate types; however, fate of least tern and snowy plover nests differed significantly ($P < 0.05$) among substrate types (Table 3). Daily nest mortality rates (\underline{m}) were greater ($P < 0.01$) for cohorts of least terns nesting on sand/stone ($\underline{m} = 0.063$) than cohorts nesting on alkali ($\underline{m} = 0.029$), and greater ($P < 0.01$) for cohorts of snowy plovers nesting on clay ($\underline{m} = 0.082$) than cohorts nesting on alkali ($\underline{m} = 0.038$). Eighty-eight percent of least tern clutches ($\underline{N} = 33$) on sand/stone were lost to predation, while 70% of snowy plover clutches ($\underline{N} = 89$) on clay were lost to flooding or abandonment.

Nest Placement and Clutch Fate

All 3 species tended to select nests sites near cover; sixty-three percent ($\underline{N} = 554$) of all nests were beside debris or short vegetation (Table 4). Slightly more avocet (36.9%) and plover (32.5%) nests than tern (23.4%) nests were located in the open. A minority of tern and

plover nests were in or under objects, but no avocet nests were concealed in this way. Despite variation in nest-site selection, observed hatch rates for individual species did not differ ($P > 0.1$) among clutches located in the open, beside objects or in/under objects.

Nearest Neighbors and Clutch Fate

During 1982, 27.2 % of least terns, 34.0% of snowy plovers and 36.6% of American avocets nested in relative isolation, i.e., > 180 m from another active nest (Table 5). Remaining birds nested closer together and tended to place their nests nearer to active nests of conspecifics than to active nests of other species. In the most dense colonies, nests of conspecifics were usually < 100 m apart, whereas nests of different species tended to be > 100 m apart. On average, the nests of least terns and American avocets were farther apart than any other interspecific nearest-neighbor nesting cohort. Overall, however, no species nested significantly closer together or had significantly fewer isolated nests than any other species (Cramer-von Mises 2 sample tests, $P > 0.1$).

Daily nest mortality rates of least terns and snowy plovers increased linearly with increasing inter-nest distances, but daily nest mortality of avocets was not linearly related to inter-nest distance (Fig. 4). The nests of colonial and solitary avocets did not have significantly different mortality rates ($P > 0.1$), whereas colonial terns and colonial plovers had lower ($P < 0.05$) nest mortality rates than solitary cohorts (Table 6).

Least tern nest mortality rates were fairly constant irrespective of nearest neighbor identity. However, cohorts of plovers and avocets having a conspecific as nearest neighbor suffered slightly higher nest

mortality than cohorts having another species as nearest neighbor (Table 7). In particular, plovers and avocets with a tern as nearest neighbor had significantly ($P < 0.05$) higher nest survival than any other plover or avocet nearest-neighbor association.

Breeding Populations and Fledging Success

The estimated numbers of female birds breeding at Salt Plains NWR from 1982-84 ranged from lows of 48-67 least terns, 125-155 snowy plovers, and 31-41 American avocets to highs of 64-91 terns, 235-267 plovers, and 39-50 avocets (Table 8). Fledging success estimates were difficult to obtain because chicks were precocial and wandered away from nest sites within a few hours to a few days post-hatch. Many radio-marked terns and a few radio-marked plovers apparently left the study area a few days post-hatch when broods were lost (Hill unpubl. data). We documented a minimum of 52 and a maximum of 63 least tern fledglings over 3 breeding seasons. Over the 3 seasons approximately 98-118 snowy plovers fledged. Additionally, about 26-33 American avocets fledged during 1982-83. The number of chicks fledged represented only a fraction of the hypothetical maximum production (HMP) of young (Table 8). Annually, terns met 7-14% of HMP; plovers, 4-10%; and avocets, 7-10%. Fledging success was low for all species, never exceeding 0.5 fledglings/breeding female.

DISCUSSION

Breeding Chronology and Synchrony

The chronology of laying and hatching cycles of shorebirds from 1982-84 at Salt Plains NWR probably typified cycles during extremely wet conditions (1982), normal conditions (1983), and unusually dry conditions (1984). Nesting synchrony most likely was influenced primarily by

catastrophic weather rather than predation. In all years predation levels were fairly constant ($P > 0.1$) throughout the breeding season, contributing to a relatively steady rate of nest attrition and, therefore, were not responsible for successive waves of nesting attempts observed during some years.

Heavy rainfall and flooding caused waves of renesting in 1982 and 1983. Storms occurred regularly throughout May and early June 1982. Wet substrate conditions throughout much of this time probably delayed the onset of nesting. The first laying and hatching peak in early July 1982 (Fig. 3) was negated by a widespread flood on 8-9 July which inundated 90% of all active nests. Weather after the 1982 flood was hot and dry and 70% of successful least tern nests, and 25% of successful snowy plover nests occurred subsequent to the flood and most probably represented renesting attempts. During 1983, storms occurred less frequently and flooding was more localized on the study area, but waves of laying and hatching peaks still followed catastrophic weather. In the 1984 breeding season, a period with little rainfall and no flooding, no renesting waves were apparent and nest success was significantly higher ($P < 0.05$) than in 1982 or 1983. Therefore, our data suggest that flooding was the most important factor affecting nest and egg success of shorebirds at Salt Plains NWR.

Differential Mortality of Nests and Adults

Nest success was highly variable among species during 1982 but rather equitable during 1983 and 1984. The greater nest success of least terns compared to snowy plovers and American avocets in 1982 was a result of differential mortality of nests to floods. Faanes (1983) and Thompson and Slack (1982) stated that least terns tend to select slightly

elevated nesting sites. While this nest site selection may partially explain why least tern nests were less prone to flooding than other species at Salt Plains NWR, flooding severity and timing of nesting undoubtedly also influenced nest survival. Few nests of any species survived the 8-9 July 1982 flood which inundated almost the entire nesting area with water 0.1-1.0+ m deep. However, the majority of least terns were not nesting at the time of this flood and hence escaped the catastrophe.

Avocets lost significantly ($\chi^2 = 63.29$, 2 df, $P < 0.001$) more eggs to flooding than terns and plovers during 1982 and 1983. Only 8.1% of least tern nests were flooded during 1982, compared to 16.1% and 31.6% of plover and avocet nests, respectively. The large percentage of avocet nests on clay substrate suggests that they may select low lying nest sites more frequently than plovers and terns. Most clay substrates were close to major stream channels and probably were created by flood water deposition.

Differential losses to hail also were observed during this study. Hail destroyed more plover eggs than any other species during our study and killed at least 17 adult plovers at their nests in June 1983. The June storm was localized, sweeping over the middle third of the salt flats in the general area of Cottonwood and Clay Creeks. No adult avocets or terns were found dead after this storm or at any other time during the 3 breeding seasons studied. Grover and Knopf (1982) also reported mortality of snowy plovers following a hail storm at Salt Plains NWR in 1978, and also reported no least terns or American avocets killed. The fact that all dead snowy plovers in 1983 were found at their nests suggests that they may be susceptible to hail-stoning

because they have a tendency to sit tight on the nest during storms. All least tern and American avocet nests in the storm impact-zone suffered egg loss, suggesting that terns and avocets deserted their nests during the June 1983 storm.

Egg Loss

Potential egg predators on the salt flats included coyotes (Canis latrans), striped skunks (Mephitis mephitis), raccoons (Procyon lotor), American badgers (Taxidea taxus), thirteen-lined ground squirrels (Spermophiles tridecemlineatus), and bullsnakes (Pituophis melanoleucus). Coyote tracks were most often found at nests; however, in many instances the flats were firm and predators left no tracks. No sign of avian predation was ever found although all 3 species of shorebirds sometimes exhibited predator diversion displays toward Franklin's gulls (Larus pipixcan), ring-billed gulls (L. delawarensis), and turkey vultures (Cathartes aura).

Nearly twice as many tern as plover or avocet eggs failed to hatch despite full or nearly full incubation. It is likely that many of these eggs were nonviable because tern chicks usually remained at the nest 2-3 days post-hatch and all eggs in a clutch typically hatched within 1-2 days. Many least terns winter south of the U.S. border and are possibly exposed to numerous environmental toxicants. Therefore, the contaminant levels of terns and eggs at Salt Plains NWR need to be determined and related to reproductive success.

Nest Substrate

Page et al. (1985) found that snowy plover clutches on sand/gravel substrates in California were slightly less successful than those on alkali, and plovers selected sand/gravel substrates more frequently

early in the season than late. They related differential clutch survival to clutch conspicuousness, density-dependent factors, and temperature or humidity of the nest environment. At Salt Plains NWR, snowy plovers were equally successful on sand/gravel and alkali but less successful on clay. Most unsuccessful plover nests on clay were flooded or abandoned when eggs became stuck to the substrate during wet periods. "Egg-sticking" has also been reported to cause some egg loss in least tern nests on dredge spoils in Texas (Thompson and Slack 1982). Least terns at Salt Plains, however, did not have as high nest mortality due to egg-sticking as snowy plovers because terns tended to nest on clay later than plovers when substrate conditions were dryer. However, least terns did suffer higher nest mortality on sand/stone than plovers. Most terns that selected sand-stone nest sites nested along slightly elevated "roads" on the salt flats leading to an Army Corps of Engineers test impoundment. Only 2 of 31 least tern nests along these roads hatched; all others were depredated. Similarly, the few plover ($N = 15$) and avocet ($N = 5$) nests located along these roads were extremely unsuccessful. We suspect coyotes were important predators along roads because tracks indicated roads were heavily travelled by coyotes.

Nest Placement

Purdue (1976) postulated that small objects beside snowy plover nests at Salt Plains NWR conferred little protection from predators and weather. In addition, Page et al. (1985) found that snowy plover clutches beside objects at Mono Lake, California, were less successful than clutches in the open or beneath objects, and they implied that objects on their study area increased the likelihood of depredation by providing a search image for avian predators. In our study, objects

near nests had a neutral effect on nest and egg success perhaps because avian predation on eggs was rare or nonexistent on our study area. At Salt Plains NWR coyotes were most often implicated for nest loss. However, observations of coyotes on the study area indicated they did not usually actively search for eggs on the salt flats but opportunistically preyed on eggs if they found a nest as they travelled through the salt flats. In several instances the passage of a coyote near nesting shorebirds elicited no response from incubating birds. Page et al. (1985) observed similar behavior in snowy plovers in response to gulls and suggested that snowy plovers discriminated between actively-searching predators and those just passing through.

Nearest Neighbor

Nest and egg success was higher for colonial nesters than for solitary nesters at Salt Plains NWR. Lower nest mortality in colonies possibly was a result of communal mobbing of predators and/or aggressive nest defense by neighbors. Least terns and American avocets defended nests more aggressively than snowy plovers. Least terns swooped at potential mammalian and avian predators, uttered crys, sometimes struck predators with their feet, and nearly always defecated on predators. Terns frequently participated in group attacks, with 2 or more birds mobbing an intruder simultaneously. American avocets flew directly at human intruders, but sharply veered off when within 5 m of the target. Avocet response to other mammals generally involved flying in a loose circle about the predator, then landing, running in a crouched posture, and/or exhibiting wing-displays or incubation-like displays (see Sordahl 1980). Individuals or pairs of avocets harrassed other large birds by circling overhead and sometimes delivering swift kicks. In contrast,

plovers relied exclusively on subterfuge to thwart nest predators; plovers ran in a crouched posture away from the nest and either hid (lay prone in depression) or exhibited an injured bird display similar to the "mobile-lure" and "static-lure" displays described by Simmons (1951) for Kentish plovers (Leucopolis alexandrinus). In addition some snowy plovers effectively reduced nest and egg loss by nesting near least terns. Apparently, they benefitted from the aggressive nest defense of terns.

No data are available on the age structure of breeding shorebirds at Salt Plains NWR in relation to colonial versus solitary nesters. Nevertheless, many studies have shown that young inexperienced breeding birds often are less successful breeders than older experienced birds. Therefore, it is possible that many of the solitary nesters at Salt Plains NWR were young birds or less aggressive birds unable to secure prime nest sites.

Breeding Populations and Fledging Success

Grover and Knopf (1982) reported minimum breeding populations of 80-135 least tern pairs, 260-325 snowy plover pairs, and 46-53 American avocet pairs at Salt Plains NWR during 1977-78; fledging success was not determined. Overall, our population estimates of breeding females were lower than Grover and Knopf's estimates of breeding pairs. However, the difference may not be significant because breeding pair estimates double-count individuals that switch mates between renesting attempts. Mate switching, following nest failure, was observed in color-banded snowy plovers on our study area (Hill unpubl. data).

The extremely low fledging success of shorebirds we observed at Salt Plains NWR is cause for concern and may suggest that the refuge attracts

sizeable concentrations of breeding shorebirds but produces few recruits. Wilson (1980) reported low fledging success (0.2-0.4 fledglings/female) for snowy plovers on the Oregon coast, as did Page et al. (1983) for snowy plovers at Mono Lake, California (0.49-0.70 fledglings/female). Thompson (1982) reported good fledging success for least terns on the Texas coast (0.501-0.649 fledglings/adult, or about 1.0-1.3 fledglings/female assuming a 50:50 adult sex ratio). Page et al. (1983) and Thompson (1980), respectively, estimated 0.80 fledged young/female snowy plover and 0.500-0.667 fledged young/female least tern were required to maintain population stability. Assuming that these estimated maintenance requirements are reasonably accurate, it is apparent that < 0.5 fledglings/female produced at Salt Plains NWR during 1982-84 is inadequate to maintain a stable population. However, as noted by Page et al. (1983), the discrepancy may be overestimated if some females nest elsewhere either before or after their attempt at the study area.

There is documentation that some exchange of individuals occurs between populations of shorebirds in the Central Plains States. Snowy plovers banded at Quivera National Wildlife Refuge, Kansas, have been documented breeding at Salt Plains NWR (R. Boyd pers. comm.). In addition, at least 1 least tern banded as a juvenile on the Texas coast was found breeding at Quivira NWR (B. Thompson pers. comm.), and another least tern banded as a juvenile near Lookout, Oklahoma, was found 7 years later breeding at Salt Plains NWR (Hill unpubl. data). Therefore, the effects of emigration and immigration on the nesting population at Salt Plains NWR are unknown and our understanding of population trends is incomplete.

Causes of chick mortality at Salt Plains NWR merit further study. A few chicks apparently died from heat exposure due to the sparcity of cover on the salt flats; however, most chicks probably were depredated. The relative effects of mammalian and avian predation on chicks is unknown. However, it is possible that avian predation on chicks could increase. In addition to possible chick predation by gulls, chick loss to cattle egrets (Bubulcus ibis) may occur. During 1982 a mixed species colony of 2000+ herons and egrets began nesting on Ralston Island in Salt Plains Reservoir. Subsequently the heronry has increased in size and cattle egrets, the most abundant species, make regular trips across the salt flats on their early morning and evening flights between island and rangeland. Refuge personnel and local ranchers have observed cattle egrets killing bobwhite quail (Colinus virginianus) chicks on the refuge and surrounding areas (R. S. Sullivan pers. comm.). Hence it is possible that egrets also prey on shorebird chicks, particularly along streams traversing the salt flats and along the shoreline of Salt Plains Reservoir. Research is needed on food habits and habitat use patterns of herons and egrets breeding at Salt Plains NWR to evaluate their potential as predators on shorebird chicks.

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Table 1. Shorebird median laying dates and nest success at Salt Plains NWR during 1982-84.

	Least tern			Snowy plover			American avocet	
	1982	1983	1984	1982	1983	1984	1982	1983
Median laying date	3 July	18 June	12 June	14 June	4 June	15 May	15 June	15 June
Successful nests/total nests	42/81	33/77	44/59	54/153	92/215	93/122	11/41	16/41
Test for equality of nest mortality rates, P-value:								
Laying vs incubation	0.98	0.16	0.37	0.85	0.10	0.54	0.66	0.22
Early vs late season ^a	0.02 ^b	0.26	0.34	0.43	0.01 ^b	0.005 ^c	0.04 ^c	0.09
Seasonal nest success, % ^{d,e}	A36.6 ^C	A25.3	B59.6	A19.0 ^D	A17.1	B64.9	8.4 ^E	17.1
95% CL: lower limit	24.2	16.7	45.5	10.3	13.6	57.7	3.3	8.3
upper limit	53.1	38.2	77.7	26.6	25.4	75.2	19.0	34.3

^a Early season nests were initiated prior to the median laying date; late season nests, on or after the median laying date.

^b Early season mortality was significantly greater than late season mortality.

^c Late season mortality was significantly greater than early season mortality.

^d Nest success was calculated according to the methods of Mayfield (1961, 1975).

^e Values preceded or followed by different superscripts indicate significant differences ($P < 0.05$) in nest success among years within species, and among species within years, respectively.

Table 2. Egg losses of least terns (LT), snowy plovers (SP), and American avocets (AA) at Salt Plains NWR, 1982-84.

	1982			1983			1984	
	LT	SP	AA	LT	SP	AA	LT	SP
Successful eggs/total eggs	52/157	133/390	13/152	78/180	250/608	54/155	90/132	261/359
Seasonal egg success, % ^a	33.7	18.1	3.2	24.7	19.5	14.9	53.0	57.3
Percentage egg loss: ^b								
Mammalian predator	24.2	40.0	37.5	31.1	38.5	32.9	15.9	15.9
Heavy rain	8.1	16.1	31.6	6.0	4.9	18.1	0	2.5
Hail and rain	1.0	4.1	1.3	4.4	7.9	1.3	0	0
Crushed or dented (thin shell)	1.0	0.5	0	3.3	1.5	0.6	2.3	1.4
Incubated, did not hatch ^c	5.1	1.8	1.3	5.0	1.8	0.6	5.3	3.6
Died after pipping	2.5	0	2.0	1.1	0.8	1.3	2.3	0.8
Disappeared, unknown reason	2.0	1.8	0	6.1	2.6	4.5	1.5	3.1
Deserted, unknown reason	4.0	1.3	3.3 ^d	4.4	3.1 ^e	5.1 ^d	3.8 ^f	0.8

^a Egg success was calculated according to the methods of Mayfield (1961, 1975).

^b Classification was based on first determined cause of failure; e.g., if an egg was crushed prior to depredation, loss was classified "crushed".

^c Eggs may have been nonviable, or viable but deserted when parents and first-hatched chick(s) left nest before entire clutch hatched.

^d Desertion occurred very late in nesting season.

^e Desertion for 2.1% of these birds possibly was caused by trapping and banding.

^f Desertion occurred very late in nesting season and occurred a few days after application of radio transmitters to 3 adult terns (1 nesting pair, and 1 member of another pair).

Table 3. Distribution and observed success of shorebird nests at Salt Plains NWR according to substrate type during 1982-84.

Species (Sample size) ^a	Substrate	Percent occurrence	Nest fate		χ^2	P
			Fail	Hatch		
Least tern (<u>N</u> = 222)	Alkali	76.6	67	103		
	Sand/stone	14.9	21	12	6.7	0.03
	Clay	8.5	9	10		
Snowy plover (<u>N</u> = 495)	Alkali	61.8	150	156		
	Sand/stone	20.2	49	51	7.2	0.02
	Clay	18.0	58	31		
Am. avocet (<u>N</u> = 122)	Alkali	40.2	34	15		
	Sand/stone	21.3	21	5	1.8	0.40
	Clay	38.5	31	16		

^a Sample sizes are larger than those reported in Table 1 because we included nests of known fate that were visited only once but could not be used in Mayfield calculations of nest and egg success.

Table 4. Distribution and observed success of shorebird nests at Salt Plains NWR according to nest placement during 1982-84.

Species (Sample size) ^a	Nest placement	Percent occurrence	Nest fate		χ^2	P
			Fail	Hatch		
Least tern (<u>N</u> = 222)	Beside object	72.1	70	90		
	In the open	23.4	25	27	1.2	0.60
	In/under object	4.5	3	7		
Snowy plover (<u>N</u> = 495)	Beside object	59.2	142	151		
	In the open	32.5	94	67	4.1	0.14
	In/under object	8.3	21	20		
Am. avocet (<u>N</u> = 122)	Beside object	63.1	30	15		
	In the open	36.9	51	26	0.1	0.90

^a Samples include nests not used in Mayfield calculations of nest and egg success.

Table 5. Shorebird nest-spacing at Salt Plains NWR, 1982. Mean nest distances (X) are in meters.

Inter-nest distance ^a															
Least tern (LT)					Snowy plover (SP)					American avocet (AA)					
< 180 m					> 180 m					< 180 m					
N	X̄	SE	N	%	N	X̄	SE	N	%	N	X̄	SE	N	%	
Nearest LT nest	45	A85.7	6.3	36	44.4	43	A101.3	8.3	110	71.8	16	A109.4	13.0	25	61.0
Nearest SP nest	39	^{A,B} 100.2	8.2	42	51.8	85	B71.6	6.0	68	44.4	11	^{A,B} 80.4	22.5	30	73.2
Nearest AA nest	18	B120.8	11.2	63	77.8	32	A106.6	9.8	121	79.1	16	B78.3	12.9	25	61.0
Nearest nest, any species	59	^{A,C} 78.2	5.3	22	27.2	101	B70.0	5.4	52	34.0	26	B74.1	10.9	15	36.6

^a

Distances in a column preceded by different superscripts indicate significant differences ($P < 0.05$) in mean inter-nest distances among cohorts (Unpaired t-test).

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Table 6. Shorebird nest mortality in relation to nest density at Salt Plains NWR, 1982.

Nest density ^{a,b}	Daily nest mortality rate \pm SE					
	Least tern	(N)	Snowy plover	(N)	American avocet	(N)
Colonial	A0.032 \pm 0.008 ^C	(60)	A0.042 \pm 0.006 ^C	(100)	0.071 \pm 0.015 ^D	(27)
Solitary	B0.084 \pm 0.026	(21)	B0.088 \pm 0.013	(53)	0.114 \pm 0.034	(14)

^a

Birds nesting \geq 180 m from another bird are considered solitary; $<$ 180 m, colonial.

^b

Mortality rates in a column preceded by different superscripts, and mortality rates in a row followed by different superscripts, indicate significant differences ($P < 0.05$) in daily nest loss.

Table 7. Shorebird nest mortality in relation to nearest neighbor identity at Salt Plains NWR, 1982.

Nearest neighbor ^a	Daily nest mortality rate \pm SE					
	Least tern	(N)	Snowy plover	(N)	American avocet	(N)
Least tern	0.030 \pm 0.001 ^C	(38)	A0.013 \pm 0.006 ^D	(20)	0.060 \pm 0.033 ^{C,D}	(5)
Snowy plover	0.053 \pm 0.013 ^C	(37)	B0.062 \pm 0.007 ^C	(122)	0.113 \pm 0.027 ^D	(20)
American avocet	0.035 \pm 0.024 ^C	(6)	B0.048 \pm 0.017 ^C	(11)	0.133 \pm 0.036 ^D	(16)

^a Mortality rates in a column preceded by different superscripts, and mortality rates in a row followed by different superscripts, indicate significant differences ($P < 0.05$) in daily nest loss.

Table 8. Number of breeding female shorebirds and fledging success at Salt Plains NWR, 1982-84.

Species	Year	Number of breeding females	HMP ^a	Number of fledglings	Fledglings/breeding female ^b
Least tern	1982	54-79	177	12-18	0.15-0.33
	1983	64-91	204	19-24	0.21-0.37
	1984	48-67	150	21	0.31-0.44
Snowy plover	1982	190-220	627	23-24	0.10-0.13
	1983	235-267	761	30-39	0.11-0.16
	1984	125-155	442	45	0.29-0.36
Am. avocet	1982	31-41	155	11-15	0.27-0.48
	1983	39-50	189	15-18	0.30-0.46

^a HMP = hypothetical maximum production of young, calculated by multiplying maximum number of females by maximum observed mean annual clutch size (after Judge 1983).

^b Worst case was based on minimum number of fledglings/maximum number of breeding females (after Massey and Atwood 1981); best case, based on maximum number of fledglings/minimum number of breeding females.

Fig. 1. Map of the salt flats at Salt Plains NWR, Oklahoma. Nesting colonies used heavily by shorebirds during 1982-84 are shaded.

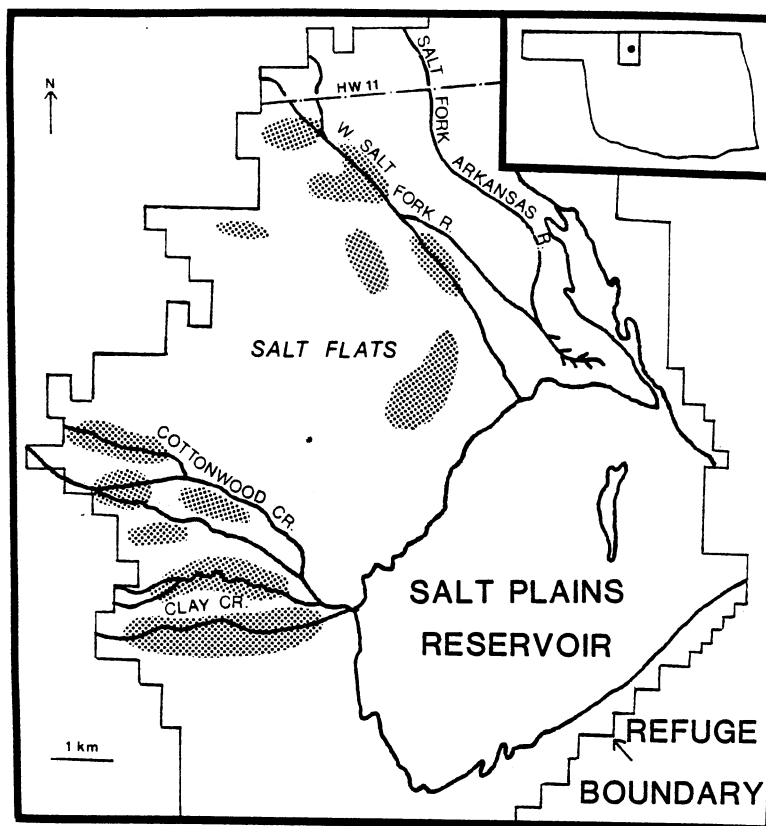


Fig. 2. Cumulative percent of least tern, snowy plover, and American avocet nests initiated at Salt Plains NWR throughout the 1982-84 breeding seasons. Graphs were drawn on probability paper for comparisons of nesting synchrony.

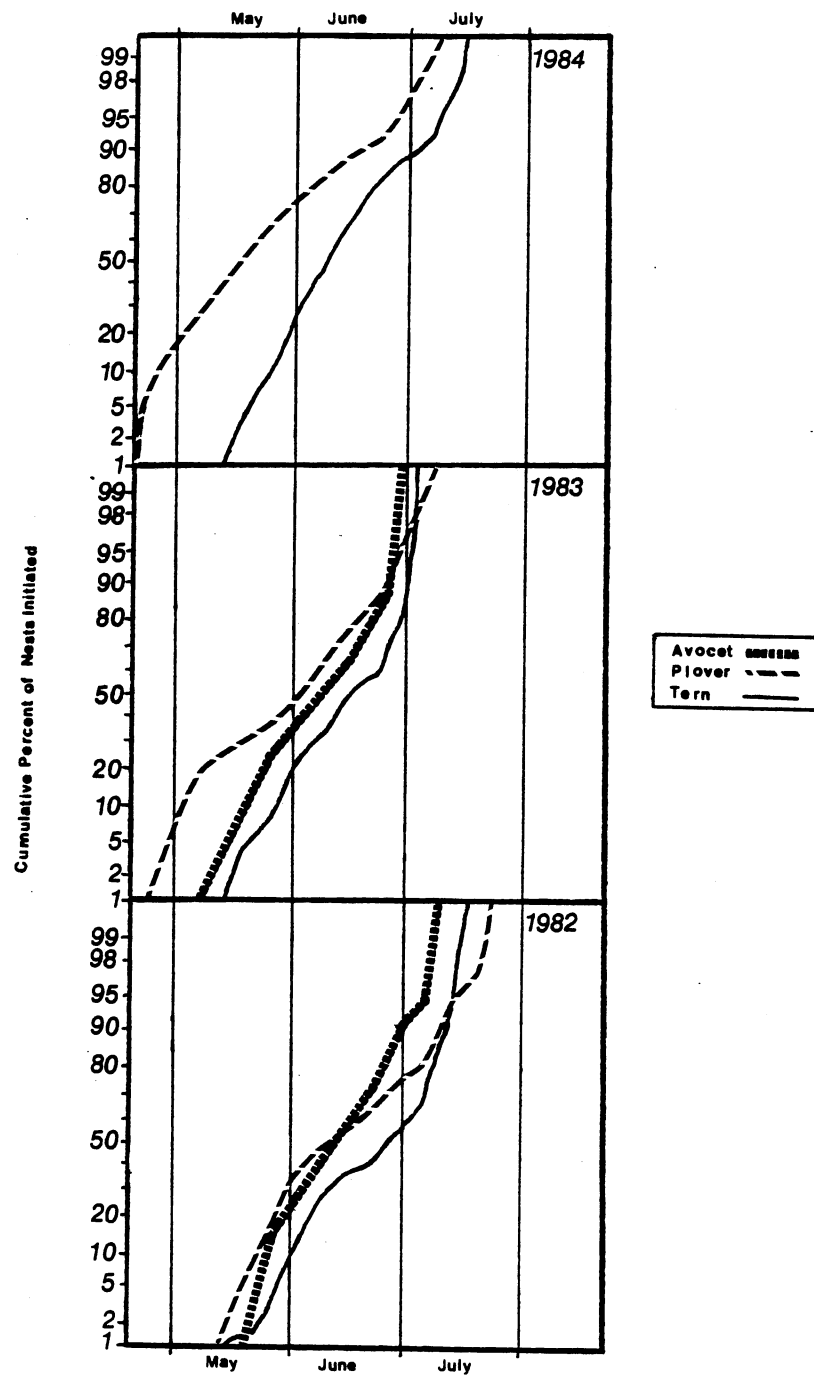


Fig. 3. Progression of hatching of least tern, snowy plover, and American avocet nests at Salt Plains NWR, 1982-84.

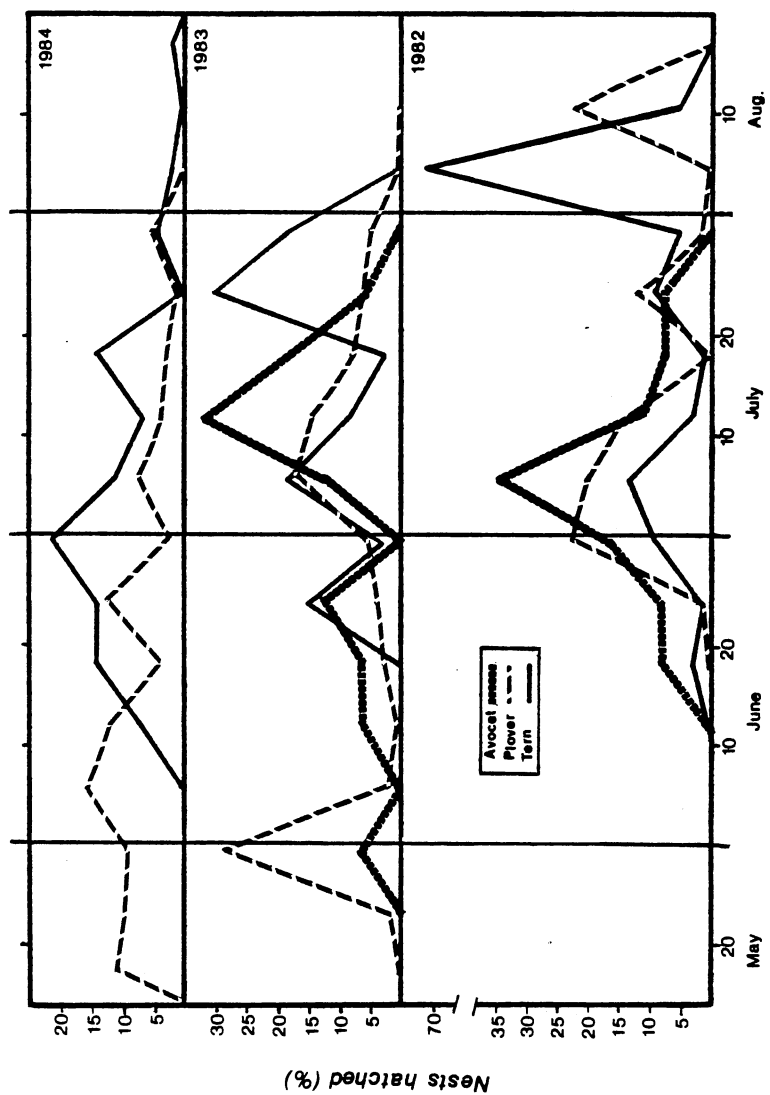
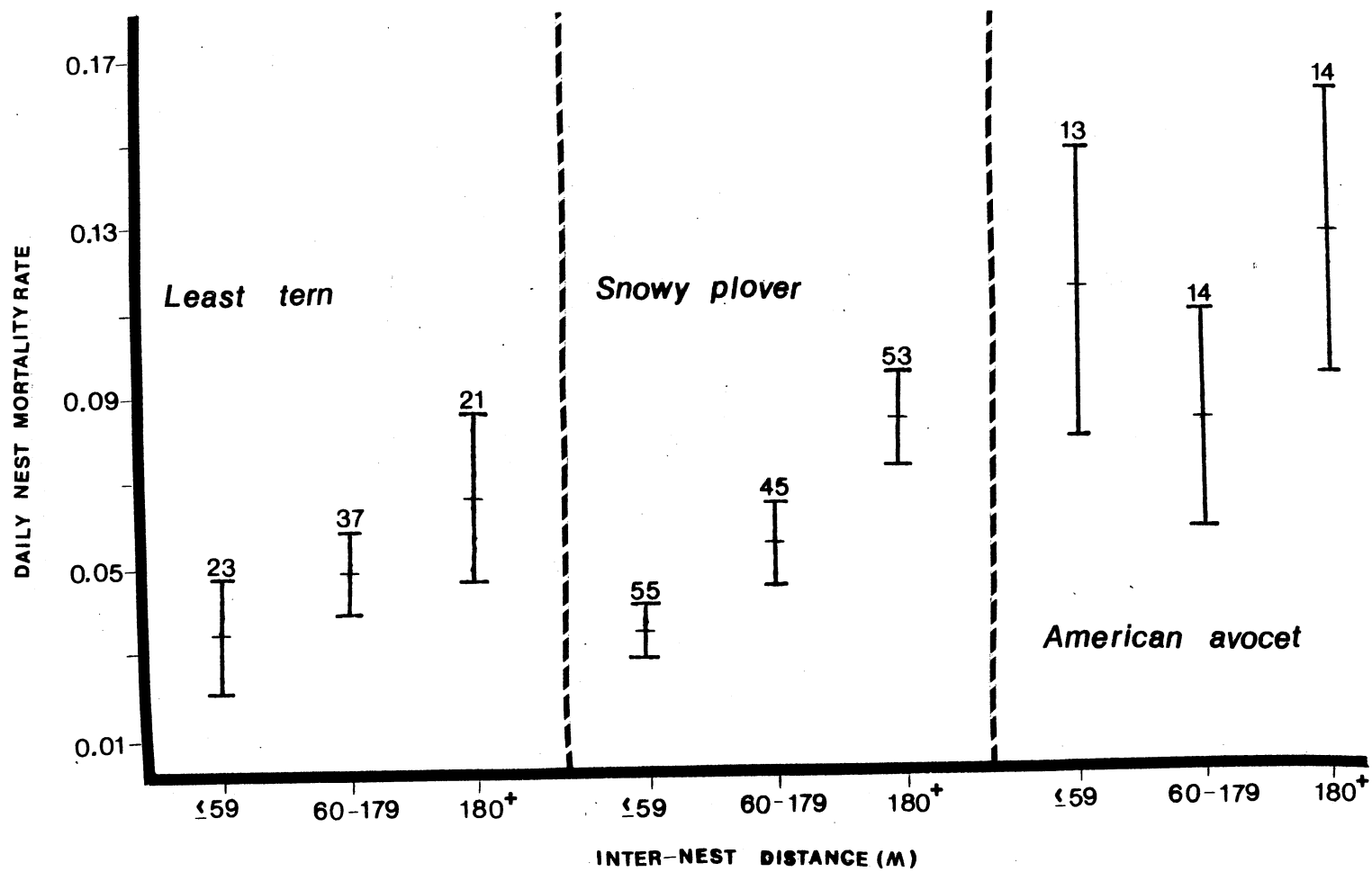


Fig 4. Daily mortality of shorebird nests in relation to nearest neighbor distances at Salt Plains NWR, 1982. The height of each vertical line represents 2 SE; the short horizontal line, the average daily mortality rate; and the numbers above bars, the sample size.



CHAPTER V

CLUTCH AND EGG SIZE CONSERVATISM

IN LEAST TERNS, SNOWY PLOVERS, AND AMERICAN AVOCETS

LAURA A. HILL, LARRY G. TALENT, AND O. EUGENE MAUGHAN

Hatching pattern, clutch size, and egg size vary in relation to environmental conditions and physiological condition of breeding birds. Birds that lay many eggs relative to the number of young they can normally feed are said to have adopted a "brood reduction strategy" that eliminates less competitive offspring during unfavorable environmental conditions. Brood reduction results via hatching asynchrony, a phenomenon that produces a size hierarchy within broods (Lack 1954, Hahn 1981, Mock 1982, Slagsvold 1982). Last-hatched chicks are smaller and less competitive than first-hatched chicks, and selective starvation may occur during times of poor food supply.

Clark and Wilson (1981) noted that in many passerine species egg size increases with laying order, an apparent contradiction to the brood reduction hypothesis because larger eggs generally produce larger, more competitive offspring. Because hatching asynchrony reduces the total time during which first-laid eggs are at risk to predators, Clark and Wilson (1981) argued that hatching asynchrony in altricial birds was an adaptation to minimize consequences of total nest failure from depredation. Richter (1982) disagreed, contending that Clark and Wilson's (1981) "brood survival" hypothesis was biologically implausible

for many species, but most likely applicable to species with little starvation.

In an attempt to further the understanding of avian egg-size variation, Slagsvold et al. (1984) conducted a comparative analysis of 67 bird species. They incorporated brood-reduction and brood-survival hypotheses into a 3-dimensional model based on the interplay between clutch size, egg size, and condition of breeders. The model predicts that birds adopting the brood reduction strategy lay a small final egg, whereas birds adopting the brood-survival strategy lay a relatively large final egg.

In this paper, we examined the Slagsvold et al. (1984) model in relation to Interior Least Terns (Sterna antillarum athalassos), Snowy Plovers (Charadrius alexandrinus) and American Avocets (Recurvirostra americana), all of which are precocial, ground-nesting shorebirds that nest on salt flats in west northcentral Oklahoma. There is a paucity of information on the breeding ecology of Interior Least Terns, Snowy Plovers, and American Avocets in the midwest. A comparison of egg and clutch size variation within and between these species is a necessary step toward understanding how they maximize reproductive fitness. Clues to survival strategies are essential to our understanding of population trends, particularly in light of apparent population declines of Least Terns and Snowy Plovers in the midwest (Downing 1980, Tate 1981).

STUDY AREA AND METHODS

Data were gathered at Salt Plains National Wildlife Refuge (NWR), west northcentral Oklahoma, during April - August 1982-84. Climate in the area is characterized by hot, dry summers with occasional

thunderstorms, hail, and high winds. During the study, precipitation patterns ranged from very wet (1982) to normal (1983) to very dry (1984).

Our study site was a 4,050 ha salt flat located on the west shore of Great Salt Plains Reservoir. The salt flat is barren except for debris localized by floodwaters, patches of sea purslane (Sesuvium verrucosum), and disjunct riparian zones of salt cedar (Tamarix gallica), salt grass (Distichlis stricta) and sedge (Carex sp.).

Four seasonally intermittent, braided streams traverse the salt flat in areas traditionally used by nesting shorebirds. During drought, portions of these streams are reduced to isolated brine pools but during heavy rains numerous ephemeral streams are created. Feeding and loafing migratory and breeding birds often congregate at the flowing streams, standing pools, and lakeshore. For a more detailed description of the study area see Johnson (1972).

Shorebird nests were located by systematically searching the salt flat for Least Tern and Snowy Plover nests during 1982, 1983 and 1984, and for American Avocet nests during 1982 and 1983. Located nests were numbered serially and their locations plotted on study area maps. Whenever necessary, nests and colony locations were marked with 15-cm stakes and flagging was tied to nearby objects.

Nests were usually located in the egg-laying or incubation stages and were rechecked every 3-5 days until we determined that they had hatched or failed. Only incubated complete clutches were included in analysis. Clutch size and egg success were recorded for all nests monitored during 1982-84. Additionally, during 1983, egg length (L) and breadth (B) were measured to the nearest 0.01 mm with vernier calipers.

Egg volume (ml) was estimated by means of the formula $0.00051 \cdot LB^2$ (after Hoyt 1979). Although this formula ignores asymmetry and biconeness (Preston 1974), and hence does not give absolute volume, the approximation is acceptable when comparing eggs from different clutches (Runde and Barrett 1980). Eggs also were individually marked with a felt-tip pen in 1983 to monitor hatching patterns. Eggs of known laying sequence were labeled a,b,c, ... in order of first-laid to last-laid egg, whereas eggs of unknown laying order were coded with a dot system.

Data on tern and plover adult body sizes were collected during 1983 and 1984. Terns and plovers were captured at their nests with T-shaped bail traps according to the methods described by Hill (1985). All captured birds were weighed, measured, and banded. We used body weight and flattened wing chord measurements to calculate condition indices of terns and plovers (Kalas and Byrkjedal 1984).

Unpaired t-tests, analysis of variance, Chi-square analyses, and Mann-Whitney tests were used to test hypotheses regarding egg variation. Differences were considered significant at the 0.05 probability level.

RESULTS

Clutch size.--Overall, modal clutch sizes were 2,3, and 4 eggs for Least Terns, Snowy Plovers, and American Avocets, respectively. Within seasons, modal clutch size of Least Terns was highly variable; 3-egg clutches were as common or more common than 2-egg clutches early in each season, whereas 2-egg clutches predominated late in each season (Table 1). Modal clutches of Snowy Plovers and American Avocets were more frequent than smaller clutches throughout early, mid, and late breeding seasons.

During 1982, 1983 and 1984, mean clutch size of terns decreased significantly ($P < 0.05$) from early to late season (Table 2). In contrast, 1982 mean clutch size of plovers peaked during mid season, but decreased significantly ($P < 0.05$) during late season. During 1983, mean clutch size of Snowy Plovers decreased significantly ($P < 0.05$) from early to mid season but returned in late season to a level not significantly ($P > 0.05$) different from that in the early season. Plover clutch sizes remained relatively constant throughout the 1984 breeding season. Mean clutch size of avocets was significantly smaller ($P < 0.05$) in mid season than in early or late season in 1982, but in 1983 there was no significant ($P > 0.05$) seasonal variation in clutch size.

Observed nest success and egg hatchability among clutch sizes.--

Observed nest success of 2-egg tern clutches was not significantly different ($X^2 = 0.034$, $df = 1$, $P > 0.5$) than observed nest success of 3-egg clutches (Table 3). However, plover 3-egg clutches were significantly more successful than 2-egg clutches ($X^2 = 3.910$, $df = 1$, $P < 0.05$). Avocet nests with 4-egg clutches also were more successful than nests with 3-egg clutches; however, the difference was not significant ($X^2 = 1.061$, $df = 1$, $P > 0.1$).

Egg success was higher in tern, plover, and avocet nests with definitive clutch sizes than in nests with fewer eggs (Table 3). The differences were not significant for terns ($X^2 = 0.106$, $df = 1$, $P > 0.5$), marginally significant for plovers ($X^2 = 3.724$, $df = 1$, $P = 0.054$), but highly significant for avocets ($X^2 = 6.298$, $df = 1$, $P < 0.025$).

Within successful nests of terns, plovers and avocets, there was no

significant ($P > 0.1$) difference in egg success of nests with definitive clutch sizes versus those with smaller clutch sizes (Table 4). Egg hatchability among successful tern nests was about 87% for both 2-egg and 3-egg clutches. Within successful plover nests, more eggs hatched in 2-egg clutches (95%) than in 3-egg clutches (82%); however, the difference was not significant ($\chi^2 = 0.478$, $df = 1$, $P > 0.1$). Egg hatchability of successful avocet nests also varied with clutch size (67-83%); however, sample size was small for 3-egg clutches and the difference in hatchability between 3- and 4-egg clutches was not significant ($\chi^2 = 0.074$, $df = 1$, $P > 0.5$).

Egg size within seasons.--During 1983, 73-78% of the variation observed in egg dimensions of Least Terns, Snowy Plovers, and American Avocets occurred between clutches rather than within clutches. Differences among eggs within clutches accounted for < 10% of the observed variation and little variation (2-5%) in egg size existed among eggs of different laying order. Most of the remaining variation (about 20%) occurred between early, mid, and late seasons.

Mean length and volume of Least Tern eggs increased significantly ($P < 0.05$) between early season and late, whereas egg breadth varied little across the 1983 breeding season (Table 5). Mean length of Snowy Plover eggs decreased significantly ($P < 0.05$) between early and mid season 1983, while average egg breadth and volume remained fairly constant all season. Among avocets, mean egg length, breadth and volume increased significantly ($P < 0.05$) between early and late season 1983.

Coefficients of variation for the 3 study species ranged from 3-4% for egg length, 2-3% for egg breadth, and 5-7% for egg volume (Table 5).

Egg volume in relation to intraclutch egg sequence.--There was no

significant difference in mean volume of first-laid and last-laid eggs of terns (2 tailed \underline{t} -test, $\underline{t} = 0.347$, $df = 91$, $P > 0.5$), plovers (same test, $\underline{t} = 0.172$, $df = 85$, $P > 0.5$), or avocets (same test, $\underline{t} = 0.750$, $df = 33$, $P > 0.4$). Two-tailed Mann-Whitney tests indicated further there was no significant difference in the probability that final eggs laid by terns ($T = 287$, $P > 0.25$), plovers ($T = 1357$, $P > 0.5$), and avocets ($T = 258$, $P > 0.1$) were larger or smaller than preceding eggs laid in the same clutch (Fig. 1). However, there was a weak trend for last-laid eggs of terns and plovers to be slightly more (0.4-1.4%) voluminous than the average volume of eggs within a clutch (Table 6). In contrast, last-laid eggs of avocets tended to be 1% less voluminous than the mean volume of eggs within the same 4-egg clutch.

Egg volume in relation to clutch size.--Although there was no significant difference in mean volume of eggs in relation to intraclutch egg sequence for any of the species studied, the volume of the smallest egg in 3-egg clutches of terns was significantly less (1-tailed \underline{t} -test, $\underline{t} = 2.118$, $df = 71$, $P < 0.025$) than that of the smallest egg in 2-egg clutches (Table 7). A similar trend existed among avocets; the volume of the smallest egg in 4-egg clutches was significantly less ($\underline{t} = 2.450$, $df = 32$, $P < 0.01$) than that of the smallest egg in 3-egg clutches. For Snowy Plovers, however, there was no significant difference ($\underline{t} = 0.159$, $df = 111$, $P > 0.25$) in volume of the smallest egg in relation to clutch size.

Egg sequence, volume, and hatchability.--Observed egg hatchability was independent of egg sequence in terns ($X^2 = 1.204$, $df = 2$, $P > 0.5$), plovers ($X^2 = 1.420$, $df = 2$, $P > 0.1$), and avocets ($X^2 = 0.988$, $df = 3$, $P > 0.5$). Addled eggs of terns, plovers, and avocets were not

significantly different in volume than eggs that did hatch (2-tailed t -tests: terns, $t = 0.702$, $df = 70$, $P > 0.4$; plovers, $t = 0.912$, $df = 80$, $P > 0.2$; avocets, $t = 0.558$, $df = 56$, $P > 0.5$). However, 92 % of all addled eggs were longer and/or wider than other eggs in the same clutch.

Clutch volume and condition indices.--Condition indices of 22 terns and 79 plovers in 1983 and 1984 were significantly greater during early season than late (Mann-Whitney test: terns, $T = 111.5$, $P < 0.005$; plovers, $T = 1063.5$, $P < 0.007$). Condition indices of terns with 2-egg clutches were significantly less than those of terns with 3-egg clutches (Mann-Whitney test, $T = 119$, $P < 0.0005$). Comparisons between plovers with 2-egg and 3-egg clutches were not made because only 1 condition index was known for plovers with 2-egg clutches.

DISCUSSION

The Slagsvold et al. (1984) model predicts 3 breeding strategies among birds. In general, species adopting the brood reduction strategy are expected to: 1) be relatively large birds invulnerable to predators, 2) lay small eggs relative to body size, 3) produce a large clutch relative to the number of young they can feed, and 4) lay a relatively small final egg. In contrast, birds adopting the brood survival strategy are expected to: 1) be relatively small birds vulnerable to predators, 2) lay large eggs relative to body size, 3) produce a small clutch relative to the number of young they can feed, and 4) lay a relatively large final egg. The third breeding strategy lies somewhere between these 2 extremes.

Based upon data from our study, classification of Least Terns, Snowy

Plovers, and American Avocets into one of these 3 strategies is not clearcut; however, the third strategy most closely resembles the strategy of the 3 species. All 3 species showed a relatively conservative reproductive pattern, reflecting relatively equal investment in each offspring. Most of the variation in clutch volume was due to between-clutch variation, suggesting a strong genetic component. However, seasonal variation in egg volume and clutch sizes probably indicates that food resources place constraints on egg production.

Least Terns.--Mean D-values of 0.44 and 0.59 for 3-egg and 2-egg clutches (Table 6) indicate that, on average, final eggs were only slightly larger than the mean size of eggs in the clutch. Whether or not this slight increase in provisioning of the final egg is sufficient to enhance the competitive position of the chick most disadvantaged by hatching asynchrony is unknown. If food is limiting during the time when chicks are reared, (particularly in late season), survival of last-hatched chicks is likely to be low because older, bigger siblings are more competitive.

Production of a large number of 3-egg clutches early in the breeding season may be a "bet-hedging tactic" (Stearns 1976) by which Least Terns increase production during times of abundant food resources. Because abundance of prey (minnows) decreases seasonally in streams on the salt flats (Hill unpub. data), early breeding terns (possibly older experienced birds) should be able to maintain a high condition index and produce larger clutches than late breeders.

The shift toward smaller clutches late in the season may reflect a high percentage of young birds nesting late and/or older birds

renesting. However, concurrent with a decrease in clutch size was a significant increase in mean egg volume from early to late season. For many species, renesters often produce larger but fewer eggs. Investment of energy reserves into fewer but larger eggs at the end of the breeding season may be an adaptation to increase the likelihood of success (production of fledglings) during a time when food resources are likely to be limiting.

Our data suggest that few terns on the study area successfully raised more than one chick to fledging during 1982-84. The number of fledglings/breeding female never exceeded 0.5 during the study. We believe chicks were lost to predators, weather, and/or starvation but further study is needed to document the extent of various mortality factors.

Snowy Plovers.--Snowy Plovers had a more conservative reproduction pattern than Least Terns and only minor variations in clutch and egg size were noted. The insignificant variation in egg dimensions within the 1983 season indicates Snowy Plovers made equal investment in individual offspring and suggests no age-related differences in egg production. Rittinghous (cited by Vaisanen et al. 1972:40) reported that eggs of yearling female Snowy Plovers were as large as eggs of older individuals. The constancy of Snowy Plover egg parameters suggests that they have adopted a strategy midway between brood reduction and brood survival. However, a related species, the Piping Plover (C. melodus), may be a brood survivalist; Piping Plovers tend to lay large final eggs (Wilcox 1959).

American Avocets.--Modal and mean clutch sizes of American Avocets were fairly constant in 1982 and 1983. The definitive clutch size of 4

eggs was recorded most frequently in mid-to-late season in both 1982 and 1983. No 5-egg clutches were observed on the study area; however, Shipley (1984) found that augmented nests (5 eggs) of American Avocets produced significantly more chicks/clutch than control (4 eggs) or depleted (3 eggs) nests. He suggested that the 4-egg limit in southern breeding populations evolved under great thermal constraints during incubation. Miller (1979) argued that extensive surface contact among shorebird eggs was an adaptation for conservation of heat during times when eggs are uncovered. If Miller (1979) is correct, it would be highly advantageous for early breeders to lay 4-egg clutches because temperatures are lowest during this part of the breeding season. However, under less than ideal food conditions, the 4-egg limit may not be achieved.

Egg size variation in 1983 possibly was related to food supply and feeding efficiency. Overall, egg dimensions of avocets increased significantly between early and late season 1983. During all years of the study, the avocet's principal insect prey (Corixids) was noticeably more abundant in streams on the salt flats in June and July than earlier (Hill pers. obs.). Observation of several avocets successfully foraging for minnows in May 1983, indicates that some avocets are opportunistic predators, able to modify feeding patterns on the study area during times of Corixid scarcity.

The weak trend toward laying small final eggs may indicate female avocets experience a drain on body reserves and/or adoption of a breeding strategy approaching brood reduction. However, we have no data on brood size dependent mortality or energy constraints of laying.

SUMMARY

The Slagsvold et al. (1984) model of avian breeding strategies was applied to inland populations of Least Terns, Snowy Plovers, and American Avocets. All 3 species showed relatively conservative reproduction patterns. Small seasonal variations in egg and clutch sizes most likely reflected constraints of food resources on egg production. A strong genetic component probably accounted for most of the observed variation in egg volume. None of the 3 species clearly fit into the "brood reduction" or "brood survival" strategies defined by Slagsvold et al. (1984); rather the species lie somewhere between these 2 extremes.

ACKNOWLEDGMENTS

We thank the staff at Salt Plains NWR for their cooperation, V. A. Keener for field assistance during 1984, and H. C. Miller for critically reviewing the manuscript. Logistical support was provided by the Oklahoma Cooperative Fish and Wildlife Research Unit, Salt Plains NWR, and Oklahoma State University. Project funding originated from a multitude of sources: the U.S. Fish and Wildlife Service (Contract 93510-1240-750), the Oklahoma Department of Wildlife Conservation (Nongame Research Project As-85-R-121), the Oklahoma Cooperative Fish and Wildlife Research Unit, the Zoology Department at Oklahoma State University, and the Payne County Audubon Society.

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TABLE 1.

SEASONAL AND ANNUAL FREQUENCY OF DIFFERENT CLUTCH SIZES OF
LEAST TERNS, SNOWY PLOVERS, AND AMERICAN AVOCETS
AT SALT PLAINS NWR, 1982-84.

Clutch size	1982					1983					1984				
	Early	Mid	Late	Total		Early	Mid	Late	Total		Early	Mid	Late	Total	
				N	%				N	%				N	%
Least Tern:															
2 eggs	9	8	21	38	53.5	6	22	16	44	60.3	9	8	13	30	56.6
3 eggs	16	3	14	33	46.5	13	13	3	29	39.7	10	10	3	23	43.4
Snowy Plover:															
2 eggs	8	8	13	29	19.6	5	22	5	32	13.1	5	3	4	12	10.0
3 eggs	21	58	40	119	80.4	81	97	34	212	86.9	38	32	38	108	90.0
Am. Avocet:															
3 eggs	0	5	0	5	13.9	4	1	1	6	16.2	-	-	-	-	-
4 eggs	5	11	15	31	86.1	10	13	8	31	83.8	-	-	-	-	-

TABLE 2.
SEASONAL AND ANNUAL MEAN CLUTCH SIZES OF LEAST TERNS, SNOWY PLOVERS,
AND AMERICAN AVOCETS AT SALT PLAINS NWR, 1982-84.

	Clutch size ^a								
	Early season			Mid season			Late season		
	<u>N</u>	<u>X̄</u>	SE	<u>N</u>	<u>X̄</u>	SE	<u>N</u>	<u>X̄</u>	SE
Least Tern:									
1982	25	^A 2.64	0.098	11	^B 2.27	0.140	35	^B 2.40	0.084
1983	19	^A 2.68	0.110	35	^B 2.37	0.083	19	^B 2.16	0.086
1984	19	^A 2.53	0.118	18	^A 2.53	0.120	16	^B 2.19	0.101
Total	63	^A 2.62	0.062	64	^B 2.41	0.062	70	^B 2.28	0.054
Snowy Plover:									
1982	29	^A 2.72	0.084	66	^B 2.88	0.040	53	^A 2.75	0.060
1983	86	^A 2.94	0.025	119	^B 2.82	0.036	39	^{A,B} 2.87	0.054
1984	43	2.88	0.050	35	2.91	0.048	42	2.90	0.046
Total	158	^{A,B} 2.89	0.025	220	^A 2.85	0.024	134	^B 2.80	0.032
Am. Avocet:									
1982	5	^A 4.00	0	16	^B 3.69	0.120	15	^A 4.00	0
1983	14	3.71	0.125	14	3.93	0.071	9	3.89	0.111
Total	19	^A 3.79	0.096	30	^A 3.80	0.074	24	^B 3.96	0.042

^a Means in a row preceded by different superscripts are significantly different ($P < 0.05$, 1-tailed t-tests).

TABLE 3.
PERCENT NEST AND EGG SUCCESS AMONG DIFFERENT CLUTCH SIZES OF LEAST TERNS,
SNOWY PLOVERS, AND AMERICAN AVOCETS AT SALT PLAINS NWR, 1982-84.

	Clutch size					
	Least Terns		Snowy Plovers		American Avocets	
	2 eggs	3 eggs	2 eggs	3 eggs	3 eggs	4 eggs
<u>N</u> of nests	112	85	73	439	11	62
% of nests	56.9	43.1	14.3	85.7	15.1	84.9
% nest success ^a	59.8	62.3	28.2	48.1	9.1	38.7
% egg success	51.8	54.5	27.4	39.2	6.1	32.3

^a A successful nest was one in which at least one egg hatched.

TABLE 4.

PERCENT EGG SUCCESS AMONG DIFFERENT CLUTCH SIZES OF SUCCESSFUL NESTS^a

OF LEAST TERNS, SNOWY PLOVERS, AND AMERICAN AVOCETS

AT SALT PLAINS NWR, 1982-84.

	Clutch size					
	Least Terns		Snowy Plovers		American Avocets	
	2 eggs	3 eggs	2 eggs	3 eggs	3 eggs	4 eggs
<u>N</u> of nests	67	53	21	211	1	24
% of nests	55.8	44.2	9.1	90.9	4.0	96.0
% egg success	86.6	87.4	95.2	81.5	66.7	83.3

^a Nests were considered successful if at least one egg hatched.

TABLE 5.
SEASONAL CHANGES IN MEAN LENGTH (MM), BREADTH (MM), AND CALCULATED
VOLUME (ML) OF LEAST TERN, SNOWY PLOVER, AND AMERICAN AVOCET
EGGS AT SALT PLAINS NWR, 1983.

	Early season		Mid season		Late season		Total Season			
	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	Range	SE	CV ^c
Least Tern ^a :	(N=59)		(N=94)		(N=35)					
Length	A30.33	0.137	A30.44	0.091	B31.02	0.183	30.52	27.88-33.54	0.073	3.26
Breadth	22.97	0.076	23.04	0.049	23.16	0.096	23.03	20.78-24.04	0.039	2.29
Volume ^b	A8.16	0.057	A8.25	0.043	B8.49	0.090	8.89	6.97-9.80	0.033	5.46
Snowy Plover ^a :	(N=112)		(N=168)		(N=58)					
Length	A31.56	0.094	B31.27	0.078	A,B31.22	0.132	31.36	28.44-36.40	0.055	3.24
Breadth	22.97	0.050	23.02	0.045	23.05	0.082	23.01	21.08-25.46	0.031	2.48
Volume ^b	8.50	0.047	8.46	0.042	8.47	0.078	8.48	6.70-10.19	0.029	6.33
Am. Avocet ^a :	(N=36)		(N=75)		(N=36)					
Length	A49.26	0.034	A49.52	0.220	B50.88	0.267	49.79	45.50-54.48	0.158	3.84
Breadth	A33.97	0.106	A,B33.99	0.136	B34.34	0.165	34.06	31.94-36.94	0.085	3.02
Volume ^b	A29.00	0.272	A29.22	0.282	B30.63	0.351	29.58	24.78-36.22	0.181	7.40

^a Means in a row preceded by different superscripts are significantly different ($P < 0.05$; 1-tailed t-tests).

^b Calculated volume = $0.00051 \times \text{Length} \times \text{Breadth}^2$ (after Hoyt 1979).

^c Coefficient of variation (CV) = $\text{SD}/\bar{X} \times 100$ and expresses amount of variation about different sample means.

TABLE 6.

PERCENTAGE DEVIATION IN VOLUME (D) OF LAST EGG FROM CLUTCH MEAN FOR
CLUTCH SIZES OF X AND X+1, WHERE X = 2 FOR LEAST TERNS AND
SNOWY PLOVERS, AND X = 3 FOR AMERICAN AVOCETS.

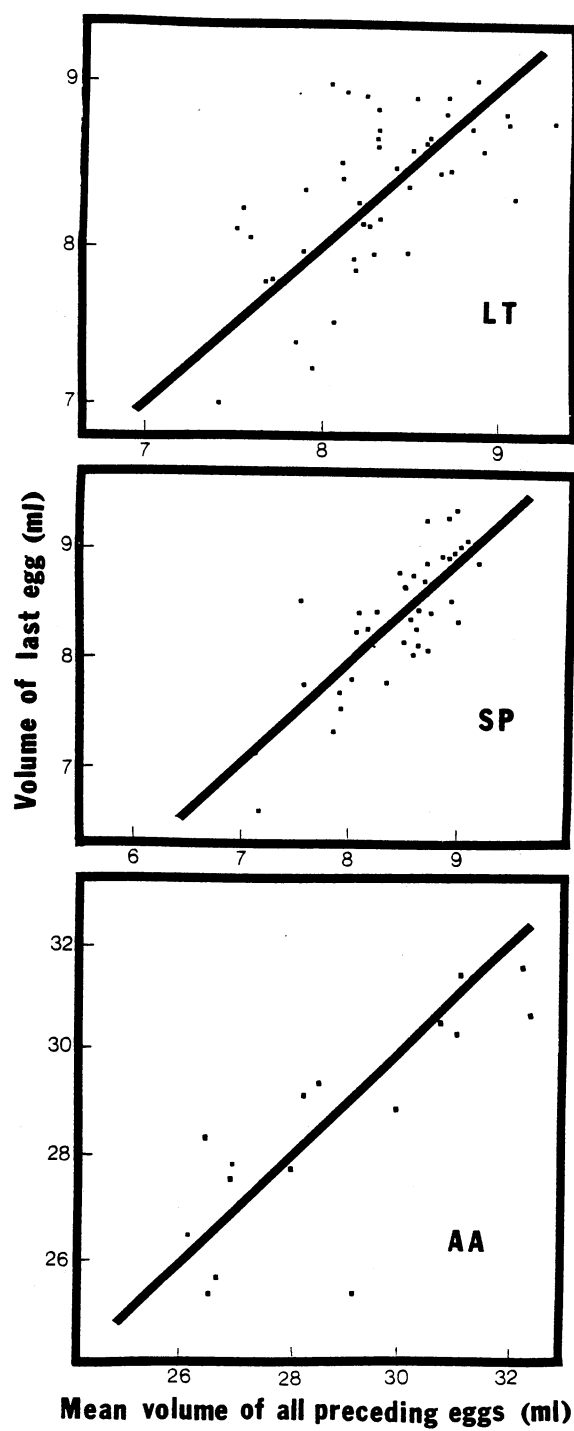
Species	Average D_x	(N)	Average D_{x+1}^a	(N)
Least Tern	+ 0.59	33	+ 0.44	14
Snowy Plover	+ 1.43	5	+ 0.27	37
American Avocet	- 4.09	1	- 0.97	17

^a
 D_{x+1} is definitive clutch size.

TABLE 7.
EGG VOLUME (ML) OF THE SMALLEST EGG IN RELATION TO CLUTCH SIZE
FOR LEAST TERNS, SNOWY PLOVERS, AND AMERICAN AVOCETS
AT SALT PLAINS NWR, 1983.

	Clutch size					
	Least Terns		Snowy Plovers		American Avocets	
	2 eggs	3 eggs	2 eggs	3 eggs	3 eggs	4 eggs
Mean	8.17	7.94	8.19	8.22	29.85	27.83
Standard Error	0.073	0.067	0.161	0.052	0.547	0.413

FIG 1. Volume of the final egg in a clutch versus the mean volume of all preceding eggs in the same clutch. The $y = x$ lines are drawn for Least Terns (LT), Snowy Plovers (SP), and American Avocets (AA).



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