Local populations of the endangered interior least tern *(Sterna antillarum)* nest within riverine and alkaline flat habitats of the central United States. We summarized estimates of survival for egg, chick, fledgling, subadult (<2 y), and adult (> 2 y) developmental stages of least terns nesting at Salt Plains National Wildlife Refuge from past and present research. We also recorded causes of mortality, physical condition, and morphological measurements of captured or dead least terns. Eggs had the lowest mean survival rate of all stages on the alkaline flat. Data on survival from fledgling to subadult stages were scant. Adult terns were in good condition at the time of death. Mortality of eggs and chicks was attributed primarily to mammalian predation and to flooding. Additional research is needed to discern the fate of the fledgling to subadult stages, protect eggs on the alkaline flat, and enhance recovery objectives.

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INTRODUCTION

Because of a decline in the interior population of the least tern *(Sterna antillarum)*, the U.S. Fish and Wildlife Service (USFWS) listed it as endangered by in 1985 (1). This population decline has been attributed primarily to loss of breeding habitat along inland riverine systems and alkaline flats (2). Various life-history traits of the least tern population nesting at Salt Plains National Wildlife Refuge, Oklahoma, have been studied intermittently since 1977. However, no unified effort summarizes the life-history traits gathered by previous and current researchers on this local population.

Interacting demographic, genetic, environmental, and catastrophic processes determine a population’s vulnerability to extinction (3). Increasingly, biologists are using simulation models to explore the dynamics of small (generally, \( n < 500 \)) populations (3-5). Some of the most powerful of these mathematical methods are based on stage-structured models (6). We summarized extant data to obtain estimates of stage-specific survival rates, to identify primary causes of mortality at each stage, and to distinguish the most sensitive stage(s) for least terns. We also recorded measurements characterizing the physical conditions of least terns in different developmental stages during the 1992 and 1993 breeding seasons.

STUDY AREA and METHODS

Least terns nest on an alkaline flat at Salt Plains NWR in northcentral Oklahoma from late May to August (7,8). Historically, the alkaline flat covered 11,137 ha (9). In 1941, 3,564 ha (32%) of the alkaline flat were flooded when the U.S. Army Corps of Engineers constructed a dam across the Salt Fork of the Arkansas River, creating the Great Salt Plains Reservoir (10). Since the dam was constructed, silt and other fine soils have accreted upstream, filling the reservoir, river, and intermittent streams west of the dam.
Increased flooding and soil deposition amenable to establishing various plants, including salt cedar (*Tamarix chinensis*), have reduced the area available for nesting least terns (11,12).

The alkaline flat is mostly barren and is seasonally encrusted with precipitated salt (13) from brine drawn to the surface by capillary action (7). The land is level to gently sloping and is bisected by stream flood plains (9), including those of the West Branch of the Salt Fork of the Arkansas River, Clay Creek, Cottonwood Creek, and intermittent streams. Frequent flooding occurs in spring and fall, and floodwaters may remain for days (14), carrying debris onto the flats (8). Hummocks of windblown sand anchored by vegetation occur near the margins of the alkaline flat.

Summers are long and usually hot (9). Average maximum daily air temperature in Cherokee (about 5 km west of the alkaline flat) is 36°C in July and August (14). Prevailing winds are from the south (9) and average about 21 km/h (14). Spring is the windiest season, during which gusty south-westerly winds of 48-72 km/h are common (14).

We defined the developmental stages of least terns as eggs, chicks (hatched, but unable to fly), fledglings (able to fly, but dependent on parents), subadults (<2 y, sexually immature and independent of parents), and adults (>2 y, sexually mature and independent). Delineation of stages was based on behavioral and physical development of the terns (15).

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

Our estimate of mean survival of eggs to hatching was based on published (7,8,16-20) estimates of egg success (number of eggs hatched/number of eggs monitored). We used previously reported (8,17-20) fledgling counts and number of eggs that successfully hatched and those recorded by us during 1992-1993 seasons to estimate the mean survival rate of chicks (number of fledglings/number of eggs hatched). Least terns rarely migrate to nesting sites until they are >2 y (21,22), and there are no reported sightings of banded least terns on wintering grounds in Central and South America; thus, the survival rate of the fledgling to subadult developmental stage is uncertain. We reviewed recapture rates of terns banded as chicks by Boyd (22) in Kansas and Oklahoma and data reported for other local populations (23-25) to estimate the survival of that developmental stage. Estimates of annual survival of breeding adults (>2 y) were summarized from returns of banded adults reported by Boyd (16,19), Kirsch (24), Massey and co-workers (25), and Renken and Smith (26).

The percentage of eggs lost to various factors on the alkaline flat was summarized from Grover and Knopf (7), Hill (8), Boyd (16-18), and Utych (19). During the 1992 and 1993 breeding seasons, coyote (*Canis latrans*) scat found in colony sites was collected and examined for egg shell fragments, feathers, bones, and keratin structures (e.g., bill, nails). All captured chicks were weighed and fitted with a USFWS aluminum band on the right tarsometatarsus, date of hatching was estimated, and chicks recaptured were weighed. Chicks and adults found dead were collected. Cause of death and physiological indexes (e.g., fat deposition, presence of parasites, histopathological abnormalities) of collected birds were determined by the National Wildlife Health Research Center, Madison, Wisconsin. Morphological features (culmen length, wing chord, tail length, tarsus length, and total length) were measured on all collected adult terns.

**RESULTS**

Survival rates of least tern eggs on the alkaline flat ranged from 12 to 64.3% in 12 y from 1977 to 1993 (Table 1). Overall mean (± SE) survival of eggs was 31.8 ± 4.8%. Overall mean survival of chicks was 41.8 ± 5.8% and ranged from 19.2 to 68.6% in 8 y from 1982 to 1993 (Table 1).

Boyd (22) banded 537 least tern chicks from 1980-1991 in Kansas and Oklahoma and recaptured seven as adults (1.3% re-
TABLE 1: Survival of least tern (Sterna antillarum) eggs (number hatched/number monitored) and chicks (number fledged/number hatched) and percentage of eggs lost (number lost/number monitored) to predation by mammals or flooding on the alkaline flat of Salt Plains National Wildlife Refuge, Oklahoma.

<table>
<thead>
<tr>
<th>Year</th>
<th>Eggs (%)</th>
<th>Chicks (%)</th>
<th>Predation (%)</th>
<th>Flooding (%)</th>
<th>Reference</th>
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</thead>
<tbody>
<tr>
<td>1977</td>
<td>64.3</td>
<td>—</td>
<td>57.7</td>
<td>42.3</td>
<td>Grover and Knopf (7)</td>
</tr>
<tr>
<td>1978</td>
<td>16.7</td>
<td>—</td>
<td>32.8</td>
<td>67.2</td>
<td>Grover and Knopf (7)</td>
</tr>
<tr>
<td>1982</td>
<td>33.7</td>
<td>27.4</td>
<td>24.2</td>
<td>8.1</td>
<td>Hill (8)</td>
</tr>
<tr>
<td>1983</td>
<td>24.7</td>
<td>47.3</td>
<td>31.1</td>
<td>6.0</td>
<td>Hill (8)</td>
</tr>
<tr>
<td>1984</td>
<td>53.0</td>
<td>29.3</td>
<td>15.9</td>
<td>0.0</td>
<td>Hill (8)</td>
</tr>
<tr>
<td>1986</td>
<td>38.0</td>
<td>—</td>
<td>5.0</td>
<td>15.0</td>
<td>Boyd (16)</td>
</tr>
<tr>
<td>1987</td>
<td>12.0</td>
<td>—</td>
<td>1.0</td>
<td>38.0</td>
<td>Boyd (16)</td>
</tr>
<tr>
<td>1989</td>
<td>37.0</td>
<td>39.8</td>
<td>10.4</td>
<td>23.7</td>
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</tr>
<tr>
<td>1990</td>
<td>46.0</td>
<td>56.2</td>
<td>12.3</td>
<td>23.3</td>
<td>Boyd (18)</td>
</tr>
<tr>
<td>1991</td>
<td>25.7</td>
<td>46.2</td>
<td>45.0</td>
<td>0.0</td>
<td>Utych (19)</td>
</tr>
<tr>
<td>1992</td>
<td>17.8</td>
<td>68.6</td>
<td>33.3</td>
<td>33.3</td>
<td>Utych (19)</td>
</tr>
<tr>
<td>1993</td>
<td>12.5</td>
<td>19.2</td>
<td>—</td>
<td>—</td>
<td>Koenen (20)</td>
</tr>
</tbody>
</table>

$x \pm SE$ 31.8 ± 4.8 41.8 ± 5.8 24.4 ± 5.3 23.4 ± 6.2

$^a$ No data available.

capture rate). Kirsch (24) used a postfledging survival rate of 85% in her population trend models of least terns nesting along the Platte River, Nebraska. A total of 5,425 least tern chicks from four colony sites in California was banded from 1973 to 1983, and 328 were recovered as adults (6.0% recapture rate; 23). Massey and coworkers (25) reported a mean recapture rate of 6.3 ± 1.1% for adult least terns banded as chicks at Venice Beach, California, from 1978 to 1986.

The recapture rate of adult least terns on the alkaline flat, based on banding studies from 1980 to 1991 (19), was 13.3% (14 recovered/105 banded adults). In the Kansas-Oklahoma region, the recapture rate was 33.6% (19). Renken and Smith (26) estimated an adult survival rate of 85 ± 5.7% for terns nesting along the Mississippi River adjacent to Missouri. Kirsch (24) used annual adult survival rates of 80, 85, and 90% in her deterministic population models of least terns nesting along the Platte River. Overall survival rate of adult least terns in California was 88% (25). The oldest ages of breeding least terns ranged from 10 (16) to 16 y (24).

Mammalian predation and flooding were the greatest threats to egg survival on the alkaline flat (Table 1). A $t$-test on ranked means (27) determined that the percentages of eggs lost to mammalian predation and flooding were not different ($t = -0.32, df = 20, P = 0.75$; Table 1). Seasonal egg survival and precipitation were correlated inversely ($r^2 = 0.52, P = 0.0188$), but precipitation alone did not explain the likelihood of eggs surviving to hatch. Addling (incubated, but did not hatch), abandonment by adults, hail storms, and cracked shells (presumably caused by abnormally thin shells) (8) also reduced egg survival. Chick survival was

<table>
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<tr>
<th>Date</th>
<th>Location</th>
<th>Sex</th>
<th>USFWS band number</th>
<th>Age (y)</th>
<th>Culmen length (mm)</th>
<th>Wing chord length (mm)</th>
<th>Tail length (mm)</th>
<th>Tarsus length (mm)</th>
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<td>74</td>
<td>17</td>
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</tr>
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<td>QNWR</td>
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<td>1411-24899</td>
<td>ū 3</td>
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<td>79</td>
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<td>none</td>
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<td>85</td>
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<td>205</td>
</tr>
<tr>
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<td>25</td>
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<td>76</td>
<td>15</td>
<td>199</td>
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<tr>
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<tr>
<td>10 Aug 93</td>
<td>SPNWR</td>
<td>female</td>
<td>none</td>
<td>unknown</td>
<td>25</td>
<td>169</td>
<td>73</td>
<td>14.5</td>
<td>167</td>
</tr>
<tr>
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</tbody>
</table>
SURVIVAL RATES OF ENDANGERED LEAST TERN

reduced by drowning (16,17), heat stress (8), and starvation (8), but most losses were likely because of predation (8). No authors reported causes of mortality for fledglings. Adult mortality was due to hail and predation (28). Egg shell fragments were found in 2 of the 14 coyote scats that we collected in colony sites; all other remains were of mammals, insects, or plant material.

We banded 102 least tern chicks during the 1992 and 1993 nesting seasons on the alkaline flat. Eleven were recaptured, and one was found dead. Weights of chicks increased linearly with age ($r^2 = 0.93, P = 0.0001$) and were similar to those of least tern chicks in Kansas (29) and California (15).

In June 1992, one adult at Salt Plains NWR and five adults at Quivira NWR, Kansas (150 km north of Salt Plains NWR) were killed by hail storms (Table 2). No parasites were found in any gastrointestinal tracts, and the terns appeared to be in good condition with visible amounts of subcutaneous, abdominal, and coronary fat.

Two adults (Table 2) and three chicks were found dead in 1993. One adult and two chicks were too decomposed to determine their causes of death or their physiological conditions. The second adult appeared to have died from trauma, possibly from avian predation. A puncture wound in the right pectoral muscle suggested it was attacked by a raptor. At the time of death, it was in good condition with adequate subcutaneous, abdominal, and coronary fat. The chick was in good body condition, but had wet lungs and may have died from drowning or hypothermia.

DISCUSSION

Our synthesis of extant records of stage-specific survival rates of the least tern provides important data for biologists working to recover this endangered population. Small populations are particularly vulnerable to extinction because of heightened stochasticity in processes such as mating, reproduction, migration, disease, and predation (3,5). Knowledge of stage-specific survival rates of a population allows using models to study population dynamics and to identify the life stages that most strongly influence population size over time.

Mean survival of eggs (31.8%) on the alkaline flat was notably lower than survival at riverine (41-65.5%, 24; 74-98%, 30) and coastal (79.2%, 15) sites. Mean survival from chick to fledgling stage on the alkaline flat (41.8%) was greater than that on the sand bars of the Platte River (11.8 to 31.2%, 31) and the California coast (10.7 to 33.3%, 15). However, chick survival on the Mississippi River (64-82%, 26) was greater than that on the alkaline flat. Risks to egg and to chick survival on the alkaline flat that have not been reported elsewhere were frequent sheet flooding and hail storms. Colony sites on alkaline flats are not protected from mammalian predators by water barriers as colony sites are on sandy islands in rivers. Salt cedar has replaced 3400 ha of the formerly barren alkaline flat at Salt Plains NWR (11) and has provided additional cover for predators, especially coyotes (12). California least terns have been managed intensively (e.g., fencing around colony sites, predator control, substrate supplementation) since the late 1970s (24), and consequently they have experienced slight increases in numbers.

Our estimate of survival of chicks to fledgling stage was calculated by using counts of fledglings present on the Great Salt Plains Reservoir shoreline (18). Accurate fledgling counts are difficult to obtain (30,32) and may be biased by arrival and staging of fledglings from other colony sites (31,33). This bias can not be removed unless individuals can be identified by unique marks such as numbered leg bands.

Better estimates of survival of the fledgling to subadult stage are needed. Accurate documentation of the wintering range of local least tern populations is sparse (24,25,34). There are no data available on mortality factors affecting terns during their first 6 months on their migratory route and wintering grounds (2). Existing data and modeling efforts (24) indicate that survival during this stage may exert the greatest influence on population trends.

Repeated observations of banded least terns are affected by fluctuating banding and resighting effort. The alkaline flat is expan-
sive, and colony site locations shift annually making banding and resighting or recapture efforts difficult. Recapture rates reported by Boyd (22) were lower than those recorded in Missouri (26), possibly an artifact of the difficulty of resighting and recapturing banded terns on alkaline flat habitats. More precise estimates of returns are probably obtained at riverine and coastal colony areas because colony sites are restricted to discrete areas (e.g., sand islands and bars, linear beaches).

The physiological conditions of least terns have not been reported by others, thus we have no comparative data for our findings that adult terns from alkaline flats were in good condition at the time of death. Catastrophic events, such as hail storms and predation, were the only causes of mortality identified for adults. Morphological measurements of terns collected at Salt Plains NWR and Quivira NWR were similar to those of least terns from other regions (31,35).

Our summaries of stage-specific survival rates suggest that survival from fledgling to adult stages appears low, but additional data are needed to substantiate this contention. During the breeding season on the alkaline flat, egg survival was lower than survival of the other developmental stages. Management techniques such as enclosing colony sites with electric fences and providing elevated mounds or ridges for placement of nests have successfully decreased mammalian predation (18,32,36,37) and washing out of eggs from sheet flooding (21), but it would be difficult to protect eggs from catastrophic events such as hailstorms or to enclose enough of the extensive flats to increase nesting success appreciably (37).

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