Habitat Selection and Productivity of Least Terns on the Lower Platte River, Nebraska
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HABITAT SELECTION AND PRODUCTIVITY OF LEAST TERNS ON THE LOWER PLATTE RIVER, NEBRASKA

by

EILEEN M. KIRSCH

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FRONTISPIECE. **An adult least tern and nest containing 3 eggs on a sandbar in the Niobrara River in northern Nebraska (photo by John Farrar, Nebraska Game and Parks Commission, Lincoln).**

HABITAT SELECTION AND PRODUCTIVITY OF LEAST TERNS ON THE LOWER PLATTE RIVER, NEBRASKA

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Abstract: Least terns (*Sterna antillarum*) were studied on the lower Platte River, Nebraska, where this endangered population nests on natural sandbar habitat and on sandpit sites created by gravel dredging adjacent to the river. Theoretically terns should select habitats according to habitat suitability. However, the introduction of sandpits and conversion of tallgrass prairies along the river banks to agriculture, residential, and wooded areas may have affected terns' abilities to distinguish suitable habitat or the suitability of nesting habitats in general. I examined habitat selection and productivity of least terns to determine if terns selected habitat according to suitability (as indicated by productivity), what factors affected habitat selection and productivity, and if estimated productivity could support this population.

Available habitats of both types were characterized and quantified using aerial videography (1989–90), and habitat use was assessed from census data (1987–90). Productivity of adults and causes and correlates of egg and chick mortality were estimated (1987–90). Population trend was assessed with a deterministic model using my estimates of productivity and a range of survival estimates for Laridae reported in the literature.

Terns tended to use river sites with large midstream sandbars and a wide channel, and large sandpit sites with large surface areas of water relative to unused sites on both habitats. Number of sites and area of sand available were estimated using discriminant function analysis of variables quantified from video scenes of both habitats. Terns apparently did not use all potentially available sandbar and sandpit sites because discriminant function factor scores for used and unused sites overlapped broadly for both habitats. Terns did not prefer 1 habitat over the other. Although proportions of available sites used were greater on sandpits than on the river, proportions of available sand used did not differ between habitats. Proportion of terns using each habitat was similar to proportion of available sand on each habitat. The distribution of nest initiation dates and rates of colony-site turnover also were similar on both habitats.

Productivity did not differ between habitats but varied significantly among sites. Nest success, fledging success, and fledglings per pair averaged 0.54, 0.28, and 0.47, respectively. Key factor analysis revealed that chick survival had a greater influence on production of fledglings (on both sandbars and sandpits) than did failure to produce a maximum clutch size or egg mortality. Most egg mortality was caused by predation on sandpits and by flooding on sandbars. Predation was suspected as the major cause of loss for chicks on both habitats. Path analysis revealed no strong or consistent correlations among mortality, numbers of nests and chicks, track trails of intruders into colonies, and habitat variables at colonies on either habitat.

Theoretically, terns should not prefer a habitat when habitats are equally suitable if terns have had time to respond to habitat changes. Although sandbars and sandpits appeared equally suitable and terns did not prefer either habitat, local productivity will not support this population unless annual postfledging survival is higher than current estimates for the species. Population trend estimated with fledglings per pair = 0.50 was negative for all but the highest (ca 0.90) rates of annual postfledging survival. Furthermore, deterministic models like the one used in this study overestimate trend.

Productivity insufficient to support the local population, in spite of habitat use that reflects habitat suitability, could be due to increased predation caused by habitat alteration adjacent to the river that may have changed the predator community. Alternatively, terns in this area could persist in spite of prevailing low productivity because they are relatively long-lived birds, if highly productive years occasionally occur or if this population is augmented by immigrants from elsewhere.

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Key words: fledging success, habitat selection, least tern, manmade habitat, Nebraska, nest success, Platte River, population modeling, productivity, sandbar, *Sterna antillarum*.

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INTRODUCTION

Understanding the proximate and ultimate causes for habitat selection is essential to understanding patterns in the abundance and distribution of animals. In natural systems, we expect animals to have evolved to select habitats that optimize their individual fitness. In systems disturbed by humans, however, animals may not choose appropriate habitats. I studied habitat selection and productivity (as an indicator of habitat suitability) in least terns that nest along the lower Platte River, Nebraska, during 1987–90. My study was particularly important because this population of small colonial-nesting birds is endangered (U.S. Fish and Wildl. Serv. 1985) and individuals may not choose habitats appropriately in this human-altered system.

Habitat selection is the behavioral process that results in the distribution of animals among available habitats. Theoretically, animals respond to the potential for fitness differences in habitats (habitat suitabilities) and choose habitats to optimize individual fitness (Fretwell and Lucas 1970, Fretwell 1972). The ideas of ultimate and proximate causation are central to habitat selection theory (HildÉn 1965, Partridge 1978, Hutto 1985). Forces that affect the fitness of individuals in habitats constitute the ultimate causes for habitat selection. The cues that individuals use to select habitats constitute the proximate causes for habitat selection. Proximate and ultimate causes for habitat selection must be closely linked for animals to correctly assess habitat suitability and choose the appropriate habitat.

Studies of habitat selection have followed essentially 2 tracks—(1) associating habitat features with animal abundance and distribution, where habitat preference is inferred when animals either use 1 habitat more than expected based on proportionate availability of habitats or they occupy 1 habitat before alternative habitats (Partridge 1978), or (2) examining the response of individuals to habitat features in a laboratory setting. Results from studies in the first category indicate that some features of habitats are associated with animal abundance and distribution, and authors postulate these may be proximate cues for habitat selection (e.g., MacArthur et al. 1962, James 1971, Karr and Roth 1971, McCrimmon 1978, Rice et al. 1983, Giffin et al. 1987, Hines 1987, Vermeer and Devito 1987, Burger and Gochfeld 1988). Results of laboratory studies indicate that habitat selection in response to certain habitat features is innate (Wecker 1963, 1964; Klopfer and Hailman 1965; Wiens 1970, 1972; Partridge 1974). Most field studies of habitat selection have been descriptive (Morse 1985:153). Typically, factors that affect fitness in different habitats (and thus the ultimate reasons for habitat selection that is observed in the field or laboratory) are postulated but not investigated.

Animals may select habitats according to habitat suitability in habitats not altered by human development. However, this may not be true in disturbed habitats or in a source–sink habitat mosaic (Wiens and Rotenberry 1981, Pulliam 1988, Pulliam and Danielson 1991). Unfortunately, many systems have been severely altered by humans. Human-caused changes in habitats can change suitabilities of habitats as well as the proximate cues animals use to select habitats. Suitabilities of a few or all available habitats may change depending on the extent and type of habitat alteration. More importantly, proximate and ultimate causes for habitat selection may become uncoupled by habitat alterations that change only the proximate features of habitats or the relative fitness values of alternate habitats. Animal populations may decline because suitabilities of all habitats have decreased or because individuals can no longer choose the most suitable habitat.

To determine whether animal distributions reflect habitat suitabilities, we must quantify both habitat use and components of fitness as an indicator of habitat suitability (Van Horne 1983, Martin 1992). In natural systems where animals have adapted to spatial and temporal patterns in habitat suitabilities and proximate features of those habitats, we would expect animals to prefer the most suitable habitat, or show no preference for a habitat when habitat suitabilities are equal. In recently naturally-disturbed systems, animals may prefer a habitat less suitable than others or show no preference even though habitat suitabilities differ. Animals in natural systems also could prefer a particular habitat because of site fidelity, even though habitat suitabilities are equal. Human-caused disturbance may change proximate or ultimate causes, and animals may not be able to choose suitable habitats. Furthermore, populations may be declining because of reduced suitability of all potentially available habitats.

Colonial waterbirds provide good opportunities for studying proximate and ultimate causes of habitat selection. Individuals of these species usually nest in habitats that we can differentiate and that are relatively easy to describe. Because these birds nest in groups, investigators can locate nests, measure elements of productivity (e.g., clutch size, egg mass, nest success, fledging success, fledgling weight), and estimate adult survival more easily for colonial nesters than for solitary nesters. One also can sample disturbances, diets, competitive interactions, and predation more easily.

The Interior population of least terns (least terns other than those nesting in coastal areas), estimated to be 3,360 pairs (conversion factor 0.7 individuals for each pair; *see* Methods) in 1987 (U.S. Fish and Wildl. Serv. 1991), provided an opportunity to examine habitat use and productivity in a rare species whose numbers may be declining. As opposed to the California and East Coast populations of least terns (which nest on beaches and spoils near ocean shorelines), Interior least terns nest on bare, sandy areas along the Mississippi and Missouri river systems of the United States. Two factors apparently caused recent declines of the Interior population: (1) loss of nesting habitat due to commercial and agricultural development of river systems and (2) lower productivity caused by human disturbance and severe levels of predation (Whitman 1988, U.S. Fish and Wildl. Serv. 1991).

About 350–420 pairs of least terns nest on 2 different habitats along the Platte River, Nebraska (U.S. Fish and Wildl. Serv. 1991). Historically, least terns on the Platte River only nested in sandbar habitat (Fig. 1). Now, terns also nest on sand and gravel areas of sandpits created by gravel dredging operations near the river (Fig. 2). Sandbar habitat along the Platte River between North Platte and Grand Island has largely disappeared due to changes in flow regimes caused by impoundments and diversions upstream (Williams 1978, Ziewitz et al. 1992). However, sandbar habitat on the lower Platte River (below the mouth of the Loup River near Columbus) is more abundant. The unimpounded Loup and Elkhorn rivers feed the lower Platte (Fig. 3). Therefore, periodic high flows carrying

Fig. 1. Examples of sandbars on the lower Platte River, Nebraska (from Sidle and Kirsch 1993). Note contrast of bright white sand versus the water and vegetation on the sandbar near the lower left corner of the photo. To the right and left of the river are sandpits that have been developed with housing and are no longer suitable for least tern nesting.

Fig. 2. Example of sandpit habitat along the lower Platte River, Nebraska (from Sidle and Kirsch 1993). Note bright sand versus water and vegetated areas. Bare sandbars are present within the river banks in this photo.

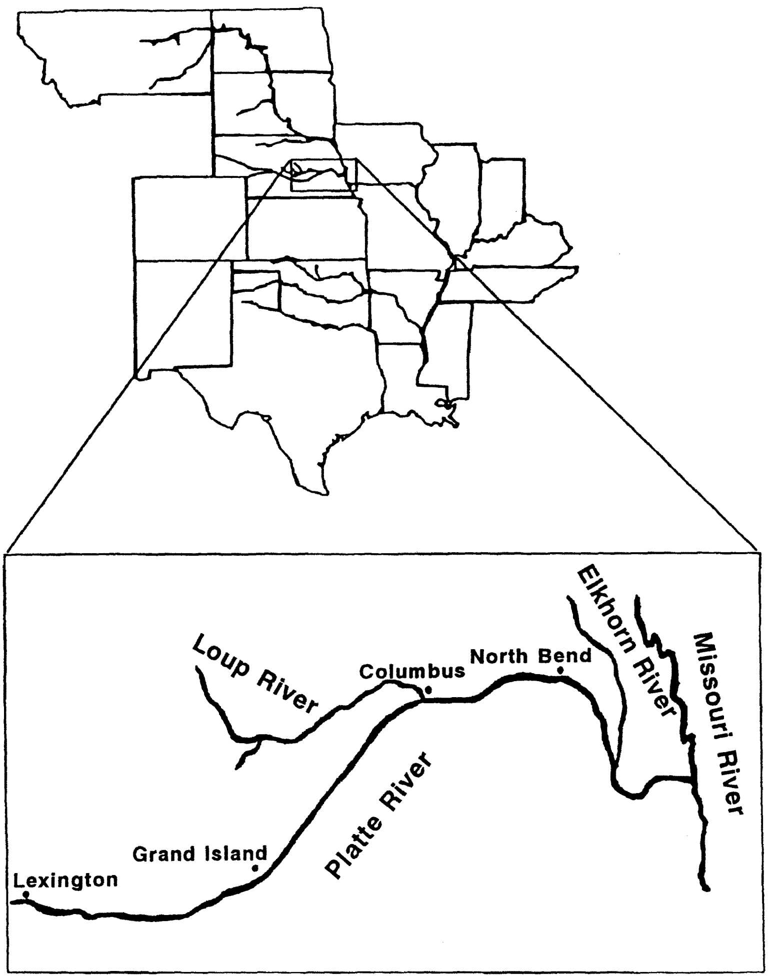

Fig. 3. Location of lower Platte River in relation to river systems of the central United States.

large amounts of sediment occur more often on the lower Platte, maintaining a broad channel with numerous bare sandbars (Bental 1982).

Thus, least terns historically used a relatively ephemeral habitat—i.e., sandbars that varied in location, size, and availability. In some years sandbars could remain submersed under high spring flow (the result of snow melt in the Rocky Mountains) for varying lengths of time after terns had returned to nest. Locations of the highest sandbars that became exposed first (as flows receded) probably were variable.

Other features of the system have changed drastically since Europeans settled along the Platte River valley in the mid-1980's. Habitats adjacent to the entire Platte River have been severely altered (e.g., Sidle et al. 1989). Tallgrass prairies and wetland meadows now are rare and have been replaced by cottonwood (*Populus deltoides*) woodlands, agricultural fields, sandpits, and residential areas. The suite of predators that potentially prey on terns has changed because of these habitat changes. Although predators probably disturbed terns on some sandbars in the past, sandpits are not isolated from the mainland and are easily accessed by terrestrial predators. Also, dredging operations disturb terns that nest on sandpits, and humans now recreate on both sandbars and sandpits. These changes could potentially affect tern habitat selection, productivity, and survival.

The objectives of this study were to (1) describe least tern distribution in sandbar and sandpit habitats throughout each breeding season and among years, (2) estimate productivity and disturbance in habitats and determine if potential differences between habitats reflect patterns of habitat use, and (3) estimate population trend for least terns on the lower Platte River.

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METHODS

This study was conducted along the lower Platte River in Nebraska between river kilometer 164.5 (river mile 102) near Columbus to the confluence of the Platte River with the Missouri River (river kilometer or mile 0) south of Omaha.

Several terms that I use in this paper must be defined to avoid confusion. A colony is an assemblage of breeding birds (≥1 pair) in a single location that interact socially with one other. Colonies then are groups of birds separated by distances sufficient that individuals from different colonies do not interact with each other except possibly when away from the colony site (Gochfeld 1980). A colony site is the place (riverine sandbar or sandpit) where ≥1 pair of terns nest and raise chicks to fledging. A colony area is that part of a colony site that terns actually use for nesting, brooding and feeding chicks, and loafing.

Habitat Use

I quantified habitat use with aerial videography (1989–90) and census data (1987–90). I measured 5 criteria to evaluate preference: (1) the ratio of used to available sites, (2) the ratio of used to available area of sand, (3) numbers of nests, (4) timing of nesting, and (5) rate of colony-site turnover between pairs of consecutive years.

All least tern colony sites were located each year during simultaneous surveys of river and sandpit habitat in early June 1987–90. Nebraska Game and Parks Commission and U.S. Fish and Wildlife Service personnel and I checked for nesting terns at all sandpit areas not developed with housing and located all nesting terns on the river from an airboat. We visited each colony site during this survey and recorded all nests and adults present during that single visit. Results from these censuses and similar censuses from 1984 to 1986 (J. J. Dinan, Platte River interior least tern and piping plover nesting survey, Unpubl. reports to Nebr. Game and Parks Comm., Lincoln, 1984, 1985, 1986) were used to determine the number of nests in each habitat. Nebraska Game and Parks Commission numbers were reported as individuals. I converted numbers of individuals to numbers of pairs by multiplying the number of individuals by 0.7. This conversion factor is based on the average of numbers of nests divided by average numbers of individuals seen on colony sites on the same date during early June surveys of the lower Platte River, 1988–90 (Nebr. Game and Parks Comm., Lincoln, unpubl. data, 1988–90). Sandpits and sandbars that were not occupied by terns during the initial survey were periodically checked (1–3-week intervals) to determine if any terns had initiated nesting on these sites later in the season.

Habitat variables were quantified using aerial videography (Sidle and Ziewitz 1990, Ziewitz et al. 1992). A video camera (10.5-mm focal-length lens) with a strobe shutter was mounted above a fuselage port in the baggage compartment of a Cessna 172, which was flown at an altitude of 1,370 m (5,000 feet) above ground. A wings-level attitude was maintained during filming to avoid image distortion (Sidle and Ziewitz 1990). In 1989 and 1990, videos were taken of river habitat during the initial nesting (3 Jun 1989, 11 Jun 1990) and renesting peaks (29 Jun 1989, 4 Jul 1990). A single video was taken of sandpits in each year during the breeding season (4 Jul 1989 and 17 Jun 1990) because sandpit habitat changes little during the breeding season. To compare river and sandpit habitat during the initial and renesting peaks, I created 2 sets of data from each sandpit video each year to compare to data sets corresponding to river videos. To create these 2 data sets from a sandpit video for each year, I categorized sandpit sites as used or unused based on whether terns were nesting or were not nesting at each site on the same dates that river sites were categorized as used or unused (within 10 days of when river videos were taken) by visiting all river and sandpit sites. Dates of these surveys were 9–13 and 20–22 June 1989, and 12–14 June and 2–3 July 1990. All variables in the 2 sandpit data sets for a year were the same except the use categorization. Video images were processed and habitat variables quantified using Map and Image Processing System (MIPS) (MicroImages, Lincoln, Nebr.).

The river was sampled systematically to characterize river habitat. Thirty-four images were analyzed from each river video. Each image was a 402-m (quarter-mile) segment centered on every third 1.6 km of river (river mile), from river kilometer 3.2 (river mile 2) to river kilometer 162 (river mile 101). All river sites used by terns also were characterized from images of 402-m segments centered on each colony site from each river video. All river images only included areas within the stabilized banks of the river and did not include upland areas. Occasionally colony sites coincided with sample sites; this information was used in use-availability analysis (described below). Potentially-usable nesting substrate—areas of dry sand with <25% vegetative cover within the stabilized banks of the river (Ziewitz et al. 1992)—was identified and quantified on used and sample sites. Numbers and mean size of these sand areas, total area of sand in the image, channel width, percentage of the image covered by permanent vegetation, and location of most of the sand (≥75% of the sand in the image) in relation to river banks were quantified from river videos. Sand was identified by selecting pixel shades that corresponded to bare, dry sand. Computer processing selected all other pixels in the image with those shades and calculated mean size of sand areas as well as total amount of sand. Although determining which pixel shades depict bare, dry sand is subjective, I am confident that my interpretations are consistent and relatively accurate because I had been to all sites at least once during the June surveys and I visited my study sites numerous times during each season. I drew polygons around areas of perennial vegetation (woody and herbaceous), and MIPS calculated the percent of the image covered by perennial vegetation. All unclassified areas in the image were water or mud. Mean channel width was calculated as the image size (m^2) divided by 402 m. The location of sand was classified as bank, midstream, or side stream. The bank classification was assigned to images where >75% of the sand in the image was connected to the river bank. The other 2 classifications were assigned if >75% of the sand in the image was completely surrounded by water. The midstream classification was assigned when the closest shoreline of the largest amount of sand was >25% of the channel width from the river bank. The sidestream classification was assigned when the closest shoreline of the largest amount of sand was <25% of the channel width from the river bank. I did not attempt to define a sandbar because size and connectivity of sand areas change greatly with different river flows. Therefore, sand areas were not necessarily synonymous with sandbars but were areas of sandbars that were relatively bare and dry. I refer to river sites or river habitat when speaking of habitat analyses; however, I refer to sandbars or sandbar habitat when referring to breeding biology of terns later in the paper.

Because sandpits are not connected linearly to one another, I developed a different scheme to characterize sandpit habitat. I defined a sandpit site as any portion of an area mined for sand and gravel that lay within a quarter of a section (804-m by 804-m square) where each section is a 1.6-km by 1.6-km (1 mile by 1 mile) square defined by county township–range–section maps. Hereafter I refer to these 804-m by 804-m square areas as sections. Many sand-mining operation areas fell entirely within a single section and were classified as a single sandpit site. Some sand-mining operations were large and fell into 2–6 sections; these sandpit areas were classified as more than 1 site.

Aerial videos were taken of all sandpit sites that had areas of sand and gravel with <25% vegetative cover and no housing development. Sandpit sites with nests were classified as used. Potentially-usable (i.e., available) nesting substrate—areas of sand or gravel with <25% vegetative cover and not disturbed by sandpit operations (roads, areas of slurry run-off)—was identified and quantified at used and unused sandpit sites. Along with this area of usable sand, the area of unusable sand (frequently disturbed by equipment and humans or covered by slurry run-off), area of water, area of vegetation (portions of some sandpit sites were covered with perennial vegetation), and size of the sandpit site were quantified from videos. Sand and vegetation were quantified in the same way as for river videos, and the area of water was identified the same way as vegetation. All unclassified areas in sandpit images were covered with oil, asphalt, mud, or rock piles.

Differences in variables between used and unused sites on both habitats (unused sample sites for the river and unused sandpit sites) were tested using multivariate analysis of variance (MANOVA) (Johnson and Wichern 1988:252–258). For each survey date, if differences were detected, then each variable was tested with univariate analysis of variance.

Discriminant function analysis (Sokal and Rohlf 1981:683–685) was run on variables estimated from each video to separate available (potentially usable) from unavailable sites. Sites that terns used and unused sites that discriminant function analysis classified as used were defined as available. Two types of error were estimated for each discriminant function: the overall classification error of the original discriminant function and cross-validation classification error (PROC DISCRIM, SAS Inst., Inc. 1990). The overall classification error is the number of used sites classified as unused and the number of unused sites classified as used, divided by the total number of sites. In the cross-validation procedure, each site is classified by a discriminant function calculated excluding that site and the error count is calculated as above. Two variables (total amount of sand on river sites and size of the sandpit site) were not used in discriminant function analysis because they were highly correlated with other variables. River flow also was not a variable used in analysis because it was represented by a single value of mean daily flow calculated from the gauge at North Bend, Nebraska, for the date of each river video. Although flow differs from site to site along the river, staff gauges and flow meters were not set up at every colony and sample site to record this information. It is important to mention flow because it contributed to differences in variable loadings and the amount of habitat available on the river among the 4 sample periods.

For the river, the total number of available sites and the ratio of used sites to available sites were estimated as follows. The number of available sample sites was the number of available, unused sample sites plus the number of used sample sites. The proportion of river sites available was estimated from the sample sites as the number of available sample sites divided by the total number of sample sites. The estimated total number of available river sites was the proportion of river sites available times 408, because 408 402-m segments occurred along the lower Platte. Therefore, the ratio of sites used to sites available for the river was the actual number of used sites divided by the estimated total number of river sites available.

The number of sandpit sites available was the number of used sites plus the number of available unused sites. The ratio of used to available sites was the number of used sites divided by the total number of available sites.

The area of sand available on the river and the ratio of used to available area were estimated as follows. The area of sand on the river was estimated as the area of sand on all sample sites divided by 0.083, because 0.083 was the proportion of the river sampled. The area of available sand on the river was the area of sand on the river times the proportion of river sites available (estimated above). The ratio of used to available sand on the river was the area of sand on all used river sites divided by area of available sand on the river. The ratio of used to available sand on sandpit sites was the area of sand on used sandpit sites divided by the area of sand on available (used and unused, as above) sandpit sites.

To compare the timing of nesting in both habitats, initiation dates of nests at study colonies were conservatively estimated by subtracting 21 days from the date the first chick hatched (range for the Interior population = 17–28 days) (Moser 1940, Hardy 1957, Faanes 1983, Schwalbach 1988). Although all eggs in all nests (1988–90) were floated to estimate incubation stage (Hays and LeCroy 1971, Schwalbach 1988), this information was used to estimate nest initiation dates only for nests that were destroyed before hatching. Two-sample Kolmogorov–Smirnov tests (Sokal and Rohlf 1981:440–445) were used to test for differences in the distributions of nest initiation dates in both habitats each year.

Proportions of colony sites abandoned and available sites colonized between consecutive years (rates of colony-site turnover) were calculated for both habitats from

$$\text{colony-site turnover rate} = [0.5[(S_1 \div N_1) + (S_2 \div N_2)],$$

where

S_1 = number of sites occupied only the first year,
N_1 = total number of sites occupied the first year,
S_2 = number of sites occupied only the second year, and
N_2 = total number of sites occupied the second year

(Erwin 1978, Erwin et al. 1981, Burger 1984). These rates reflected abandonment and colonization of apparently available sites only because I used sites that had exposed sand and <25% vegetative cover both years in N_1 and N_2. Differences in colony-site turnover rates between the river and sandpits were tested with chi-square tests with the null hypothesis of equal proportions (Sokal and Rohlf 1981:700–702).

Productivity and Mortality

Field Methods.—I measured productivity, causes of mortality, and variables possibly associated with productivity (evidence of disturbance and certain features of colony sites) during 4 breeding seasons (1987-90). I sampled colonies in each habitat based on the number of nests found during the simultaneous survey of both habitats in early June of each year. The average number of nests per colony was calculated each year for each habitat. I randomly chose from those colonies with an average number of nests, and I chose the largest colony in each habitat. Two, 3, 5, and 5 average-sized sandbar colonies were chosen in 1987 through 1990; and 4, 2, 5, and 6 sandpit colonies were chosen in 1987 through 1990. The colonies with an average number of nests were chosen to represent average colonies, and the largest colony was chosen to increase the portion of the population monitored. Small colonies were not studied because I chose to monitor as large a portion of the population as possible. All nests were marked 1 m to the north with a surveyor's flag rolled up and pushed into the ground leaving 4–5 cm of flag exposed. Nest number, contents, and date found were recorded on each flag.

Colonies were visited every 2–3 days throughout the breeding season. Numbers of adults, chicks, and fledglings; nest contents (e.g., numbers of eggs or chicks, shell fragments) and outcome (e.g., hatched, abandoned, depredated) of each nest; and track trails of intruders into the colony site were noted on each visit. Although I did not attempt to individually identify each egg in nests, the outcome of eggs in each nest were noted (e.g., 2 hatched, 1 abandoned). Adults, nests, fledglings, and chicks were counted from a distance (20–200 m) using 20–45× spotting scopes for at least 1 hour at each site before entering and after leaving sites, and when weather or flooding precluded entering sites. The maximum number of fledglings counted on any single day was considered to be the minimum number of fledglings produced by respective colonies. Other chicks known to have fledged more than 10 days previous and chicks know to have fledged after that day were added to the maximum number, assuming that fledglings leave colony sites within 10 days after fledging. Hardy (1957) observed that least terns on the Ohio River departed colony sites when they were capable of sustained flight. This estimate also seemed reasonable because I observed fledglings near colony sites more than 10 days after the last possible chick had fledged on only 5% of the visits that I saw fledglings (8 of 166 visits).

Statistical Methods—Productivity.—Components of productivity (clutch size, nest success, fledging success, and fledglings per pair) were calculated for each colony. I defined fledging success as the proportion of all chicks hatched in a colony that fledged. Nest success was not adjusted for exposure days as discussed by Mayfield (1975). Apparent nest success better represents true nest success in this study, because least tern nests were highly detectable, were visited often, and losses tended to be catastrophic (Johnson and Shaffer 1990). Average clutch size, nest and fledging success, and fledglings per pair were calculated for each habitat each year. As well, overall clutch size, nest and fledging success, and fledglings per pair were calculated by pooling information from all colonies for all years and over both habitats.

To estimate the number of fledgling per pair for each colony, the number of nesting pairs for each colony was estimated as the largest number of active nests and broods of chicks present at a colony site on the same day. This assumed that renesting pairs remained at their original colony site or the number of pairs immigrating to sites balanced the number of pairs emigrating from sites. Because few adults were individually banded, actual movements of adults could not be monitored. Two-way ANOVA (unweighted least squares, Sokal and Rohlf 1981:321–344) was used to test for differences among years and between habitats in clutch size, nest and fledging success, and fledglings per pair.

Statistical Methods—Mortality.—Instantaneous per capita mortality rates were derived and analyzed for 3 periods—egg laying, egg life stage, and chick life stage (e.g., Begon and Mortimer 1986:179). Mortality rates in both habitats were compared using Student's t tests. I also performed a "key factor analysis" of the mortality rates. In a key factor analysis, the life stage that contributes the most to overall mortality is discovered by regressing overall mortality on mortality rates for each life stage. The rate with the highest r^2 explains the most variation in overall mortality (Morris 1959, Varley and Gradwell 1960, Podoler and Rogers 1975, Begon and Mortimer 1986:179) and, hence, is termed the "key factor." Instantaneous per capita mortality rates across a life stage were calculated as follows:

$$\ln(\text{numbers at the beginning of the stage} + 1) - \ln(\text{numbers at the end of the stage} + 1).$$

One was added because ln 0, as occurred when no eggs or chicks survived, is undefined, and $\ln 1 = 0$ provides an intuitive result when no individuals reach the next life stage. Four rates were calculated as follows:

1. The reduction in per nest production due to not laying the typical maximum clutch for this population of 3 eggs (laying mortality) is

   $$\ln[3(\text{number of nests}) + 1] - \ln(\text{number of eggs laid} + 1).$$

   This "mortality rate" assumes that all females can lay 3 egg clutches and measures the portion of "mortality" due to reduced female output as a result of renesting and differences among females in age and experience.
2. Egg mortality is

   $$\ln(\text{number of eggs laid} + 1) - \ln(\text{number of chicks hatched} + 1).$$

3. Chick mortality is

   $$\ln(\text{number of chicks hatched} + 1) - \ln(\text{number of fledglings} + 1).$$

4. Per capita instantaneous mortality over the nesting period (or overall mortality) is laying mortality plus egg mortality plus chick mortality.

   Per capita productivity then is

   $$\ln(\text{number of fledglings} + 1) = \ln[3(\text{number of nests} + 1)] \cdot (1 - e^{\text{overall mortality}}).$$

Rates were transformed (ln[1 + mortality rate]) to normalize the data for statistical analyses. This analysis was performed for all nests initiated during the season (total), for nests initiated before 15 June (early), and for nests initiated on or after 15 June (late). I chose 15 June as the cutoff date because the first nests typically hatched by about that date.

I tested for differences between habitats in proportions of eggs lost due to different causes each year with chi-square tests of probabilities (Conover 1980:153–157). If the tests were significant, I tested for differences between habitats within each cause of loss (using chi-square tests) with the null hypothesis that equal proportions of eggs in both habitats were lost due to each cause. Although individual eggs in each nest do not have independent probabilities of loss, this is true in both habitats; therefore, tests between habitats within each cause of loss should not be biased.

Correlates of Productivity and Mortality.—Track trails of intruders to colony sites that would have provoked defensive behavior (evidence of disturbance) were tallied from nest initiation through fledging of the last chick during each visit to a colony site. Track trails were not obliterated by sweeping the perimeter of each colony area on each visit. This would have required a great deal of time and would have caused more disturbance. However, it was easy to tell that new tracks were made between visits because the sand did not hold its shape very well. If anything, the number of tracks were underestimated if weather had obscured tracks made between visits making them appear older than they really were.

Track trails were indexed as the total number of track trails observed on all visits to a colony site divided by the number of visits to a colony site. In 1990, I searched unused but seemingly usable sandbars ($n = 3$) and sandpits ($n = 4$) for track trails to determine whether the number of track trails differed between used and unused sites.

Relationships among track trails, numbers of nests and chicks, causes of egg mortality, and proportions of chicks known alive were explored using Spearman rank correlation (Sokal and Rohlf 1981:607). Correlation coefficients were calculated between numbers of each type of track trail detected during the nesting period (initiation until 75% of nests became inactive), numbers of nests, and causes of egg loss. Correlations were calculated between numbers of each type of track trail detected on each visit to a site after the first chick hatched and proportions of chicks known alive on each visit. Correlations also were calculated between the number of chicks hatched at each site and track trails detected during the chick-rearing period (from the end of the nesting period to fledging of the last chick). Proportions of chicks known alive on each visit were calculated as number of chicks known alive due to subsequent sighting divided by number of chicks hatched <20 days previous. I assumed that chicks hatched 20 days prior to a count had fledged (Hardy 1957, Massey 1974).

Path analysis (Wright 1968; Li 1975; Sokal and Rohlf 1981:642–656; *see* Mitchell-Olds 1987; Crespi 1989, 1990; Wootton 1994) was used to examine relationships among mortality rates, habitat features, numbers of nests and chicks, and track trails in habitats. Path analysis is a technique for examining hypothesized relationships in a complex system where variables may be intercorrelated. A path diagram representing hypothesized causal relationships among variables is constructed based on an investigator's knowledge of variables and interactions in a system. Relationships among these variables are depicted in the diagram by either 1-headed arrows that indicate a direct effect of 1 variable on another, or 2-headed arrows that depict Pearson correlations (indirect effects) between variables. The magnitudes of the 1-way relationships are given by path coefficients (b'), the partial regression coefficient standardized by the ratio of the standard deviations of the independent and dependent variables. Path coefficients are standardized regression coefficients and, therefore, not constrained to lie between -1 and 1 as are correlation coefficients. The absolute value of a path coefficient can exceed 1 when alternate pathways (direct and indirect) of opposite sign exist to compensate. If $b' > 1$, or $b' < -1$, that path explains a large amount of the variance, and the relationship is important in the hypothesized path framework (Wright 1960).

I use the terms dependent and independent for convenience and continuity with statistical terminology for multiple regression analyses performed in path analysis and consistent with Wright (1968). Path diagrams that I constructed depict the presumed most-independent variables at the top and the most-dependent variable at the bottom as the "outcome" of the interactions of all the preceding variables. Variables between these 2 extremes are independent or predictor variables (at the origin of 1-headed arrows) for variables depicted below them in diagrams, yet they are dependent or response variables (with 1-headed arrows pointing to them) of the variables depicted above them in diagrams.

Path analysis was exploratory in this study. Given my knowledge of the system and possible causal relationships, the method was used to estimate the relative strengths of the direct and indirect relationships. Different or more complex path diagrams could be constructed and tested against each other as more becomes known about the system.

Path analysis was the most powerful analysis possible because of probable multicolliniarity among variables, but small sample sizes can make significance tests unreliable (T. Mitchell-Olds, Univ. Montana, Missoula, pers. commun.). Bonferroni probabilities also were calculated for Pearson correlations to adjust for multiple tests (Johnson and Wichern 1988:188–190).

Habitat variables that could be quantified at all sites and potentially could be related to mortality by predation, flooding, or disturbance (as indexed by track trails) were used in path analyses. For sandbars, these variables were (1) distance of the nesting sandbar to the nearest river bank and (2) percent of the colony area flooded during the highest flows of a season. For sandpits, they were (1) distance of colony area to abundant vegetation (vegetation cover >50% and height >30 cm) and (2) percent of the colony site bordered by water. Distance of a sandbar to the nearest river bank and the percent of a sandpit colony area surrounded by water were estimated from aerial videos in 1989–90 and visually at sites in 1987–88. Distance to abundant vegetation was measured from videos in 1989–90 using MIPS and estimated by pacing distances in 1987–88. Percent of a colony area flooded was estimated visually during a visit to the site during high flows. Numbers of nests and chicks at colonies were not normally distributed and were transformed before analysis. Numbers of nests and chicks and the track trail index were transformed as ln(number of nests or chicks) and ln(1 + track trail index). Track trail indices in habitats were compared using Student's t tests.

All analyses except chi-square and MANOVA were performed using the SYSTAT program (Wilkinson 1990). MANOVA and cross-validation of discriminant function classifications were performed using SAS (SAS Inst., Inc. 1990), and chi-square tests were calculated by hand. A significance level of $\alpha = 0.05$ was required to reject the statistical null for all tests. Power of 2-way and single-classification ANOVA tests was calculated by hand (Kirk 1982).

Population Trend

To assess whether current productivity is adequate for least terns to persist on the lower Platte River without immigration from other areas, I examined population trend (r, instantaneous rate of population change; e.g., Caughley 1977:52) using a deterministic computer model. The instantaneous rate of population change is

$$[\ln(N_t) - \ln(N_0)] \div t.$$

Where N_t is the number of terns at the end of a period with t units of time, N_0 is the number of terns at the beginning of a period. If $r > 0$, the population is growing; if $r < 0$, the population is decreasing; if $r = 0$, the population is stable.

Although the results of deterministic models should be used very cautiously, there are advantages to using deterministic models. The reliability of stochastic model output is not certain when estimates of variation for model parameters are not available (annual adult survival) or reliably estimated from only 4 years of data (productivity), or when data are limited for any life history parameter (*see* Shaffer 1981). Although stochastic models can yield estimates of the mean and standard error of r, the probability that r really falls within these limits is not known when characteristics of model parameters (mean, variance, and shape of variance distribution) are not well understood. Deterministic models that use point estimates of parameters give clear results. The strength of certain variables to influence model behavior (model sensitivity) is easy to see and interpret. Furthermore, because there is no variation, these models yield optimistic results, because they tend to overestimate trend slightly (Slade and Levenson 1982). These results can be used as a springboard to determine further data needs as well as to give insights to conservative management options and the behavior of more complex models (*see* Mertz 1971, Simons 1984, Lande 1988, Dobson and Lyles 1989, Eberhardt 1990, Noon and Biles 1990). Results from stochastic models that introduce variation in model parameters every cycle are less clear and less easy to interpret, unless the life history parameter estimates used in them are accurate and their variances are well understood. Introducing inaccurate point and variance estimates for parameters makes models less meaningful, although how much less meaningful will be difficult to determine unless deterministic modeling has been done first. For example, the distribution of survivorship in a single age class can strongly influence estimates of population growth (Slade and Levenson 1984).

In the model population, each pair produced fledglings, and a proportion of adults and fledglings survived to the next year. Certain assumptions are made in simple deterministic models such as equal sex ratio, no immigration or emigration, all adults breed, equal reproductive success among pairs, and no adult mortality during the breeding season. Virtually no information on least tern demography exists for the

Interior population, so the following 2 assumptions were best guesses:

1. I conservatively assumed maximum adult longevity of 16 years because approximately 92% of all band recoveries of known-age terns, current through August 1990, were of birds <16 years of age (Kirsch 1992:106).
2. I also assumed that one-third of the 2-year-olds breed because, of the terns banded as chicks that return and breed on the central Platte River, one-third return when they are 2 years old (G. R. Lingle, Platte River Whooping Crane Habitat Maintenance Trust, Inc., Grand Island, Nebr., unpubl. data).

I ran the model for 100 simulated years, and I estimated r after a stable age distribution was reached (after 20 simulated yrs). Sensitivity of the model was evaluated by varying a single parameter while holding the others constant. The model was most sensitive to the parameter that yielded the steepest slope of r plotted against values of that parameter.

Estimates of annual juvenile (fledging to first breeding at 2 or 3 years old) and adult (2 or 3 yrs old or older) survival were required to estimate trend. Survival estimates of approximately 0.85 have been derived from band returns for least terns from the California (Massey et al. 1992) and Interior (Renken and Smith 1995) populations. Renken and Smith (1995) estimated annual adult survival of 0.85 (95% confidence interval 0.73–0.95) for Interior least terns on the lower Mississippi River, and Massey et al. (1992) estimated adult survival of 0.88 for California least terns. I estimated r using a range of annual adult and juvenile survival rates based on these and other values reported in the literature for other Laridae (Table 1) and the estimate of overall fledglings per pair derived from this study. The relationship between mean annual adult survival and mean number of reproductive years has not been investigated for least terns. I assume here that adult least terns can breed until their last year. This is generally assumed to be the case with birds like terns. I also assume

Table 1. Reported values of annual adult (birds old enough to breed) survival for larid species estimated from mark–recapture, mark–resighting, or band returns.

Species	Mean annual survival	Method[a]	Source
Swallow-tailed gull (*Creagrus furcatus*)	0.94	MR	Harris 1979
Herring gull (*Larus argentatus*)	0.91–0.93	BR	Kadlec and Drury 1968
Red-billed gull (*L. novaehollandiae scopulinus*)	0.89 females, 0.84 males	MR	Mills 1990
Western gull (*L. occidentalis*)	0.81 females, 0.84 males	MR	Spear et al. 1987
Common black-headed gull (*L. ridibundus*)	0.80 adults, 0.40 first yr	BR	Isenmann et al. 1990
	0.82	JS	Clobert et al. 1987
Black-legged kittiwake (*Rissa tridactyla*)	0.81–0.86	MR	Coulson and Wooller 1976
Least tern (*Sterna antillarum*)	0.83–0.85	BR	Thompson 1982, Kirsch 1992
	0.88	JS	Massey et al. 1992
	0.85	JS	Renken and Smith 1995
Caspian tern (*S. caspia*)	0.89	BR	Gill and Mewaldt 1983
Roseate tern (*S. dougallii*)	0.74–0.75	JS	Spendelow and Nichols 1989
Common tern (*S. hirundo*)	0.92	MR	DiCostanzo 1980
Arctic tern (*S. paradisaea*)	0.87–0.88	MR	Coulson and Horobin 1976

[a] BR = calculated from band-return data; JS = calculated from mark–recapture or mark–resighting data and analyzed using a Jolly–Seber-type model (Pollock et al. 1990); MR = calculated from mark–recapture or mark–resighting data and analysis other than a Jolly–Seber-type model.

that reproductive output (number of eggs laid) is constant with age, although the effect of age on reproductive output has not been documented in least terns.

RESULTS

Habitat Use

Terns tended to use river sites with a relatively wide channel and large mid-stream sandbars (Table 2). Used and unused river sites differed in more than 1 variable for 3 dates (MANOVA—3 Jun 1989: $F = 3.34$; 3, 61 df; $P = 0.025$; 11 Jun 1990: $F = 4.12$; 3, 45 df; $P = 0.011$; 4 Jul 1990: $F = 6.29$; 3, 48 df; $P = 0.001$). River sites that were used had greater total area of sand, greater mean size of sand areas, and greater channel width than unused sample sites. The univariate differences were significant in 7 of 9 comparisons.

Terns tended to use relatively large sandpit sites with large surface areas of water (Table 3). Used and unused sandpit sites differed in greater than 1 variable for 3 dates (MANOVA—29 Jun 1989: $F = 5.02$; 4, 30 df; $P = 0.003$; 11 Jun 1990: $F = 3.92$; 4, 30 df; $P = 0.011$; 4 Jul 1990: $F = 4.61$; 4, 30 df; $P = 0.005$). Used sandpit sites had greater areas of water and were larger than unused sandpit sites. The univariate differences were significant in 5 of 12 comparisons. Although differences were not significant, the mean area of usable sand was consistently larger at used sites than at unused sites.

Discriminant function analysis correctly classified a greater proportion of the used sites on the river than on sandpits (Table 4). Classifications for the river also were better during high flows (29 Jun 1989 and 11 Jun 1990) than during lower flows (3 Jun 1989 and 4 Jul 1990) (Table 4). During these higher flows, fewer river sites had exposed sand and terns used a greater portion of those sites. For the river, mean size of sand areas and location of sand areas with respect to the river bank were important in discriminating used and unused sites during low flows (Table 5). Location of most of the sand with respect to the

Table 2. Summary statistics for habitat variables derived from aerial videos of river habitat along the lower Platte River, Nebraska, 1989–90. Pairs of values from used and unused sites that differ significantly (ANOVA) are indicated with asterisks.

						Habitat variables					
						Channel width (m)		Mean size sand areas (m^2)		Total area of sand (m^2)	
Nesting period and year	Date of video	Date of site-use survey	River flow m^3/sec[a]	Type of site	n	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Initial 1989	3 Jun	9–13 Jun	69.3	Used	35	424	21	71*	8	12,348**	152
				Unused	30	394	168	45	6	7,070	839
Renesting 1989	29 Jun	20–22 Jun	328.3	Used	16	452	19	48	10	1,553	553
				Unused	33	394	14	32	9	785	250
Initial 1990	11 Jun	12–14 Jun	145.5	Used	16	474	17	538*	274	3,484**	599
				Unused	33	445	15	33	9	1,363	457
Renesting 1990	4 Jul	2–3 Jul	57.2	Used	22	489**	12	510*	91	25,477	3,468
				Unused	29	428	16	308	54	1,100	1,759

[a] Mean daily flow in cubic meters per second at the North Bend gauge river kilometer 116.8 (river mile 72.4) (Boohar et al. 1989, 1990).
* Differences between used and unused within nesting periods, $P < 0.05$.
** Differences between used and unused within nesting periods, $P < 0.01$.

Table 3. Summary statistics for habitat variables (1,000 m²) derived from aerial videos of sandpit sites along the lower Platte River, Nebraska, 1989–90. Pairs of values from used and unused sites that differ significantly (ANOVA) are indicated with asterisks.

Nesting period and year	Date of video[a]	Date of site-use survey	Type of site	n	Area of usable sand[b] $\bar{x}$	Area of usable sand[b] SE	Area of unusable sand[c] $\bar{x}$	Area of unusable sand[c] SE	Area of water $\bar{x}$	Area of water SE	Area of sandpit site $\bar{x}$	Area of sandpit site SE
Initial 1989	4 Jul	9–13 Jun	Used	6	23.4**	6.1	14.7	6.4	87.6	35.2	158.3	57.2
			Unused	33	11.9	1.4	6.7	1.5	51.1	11.2	89.2	14.2
Renesting 1989	4 Jul	20–22 Jun	Used	7	17.9	4.7	7.3	1.9	104.9*	44.0	145.4	48.9
			Unused	32	12.8	1.7	8.1	2.0	46.2	8.9	89.9	14.8
Initial 1990	17 Jun	12–14 Jun	Used	12	31.4	4.5	3.6	12.4	135.8*	25.5	243.3**	26.9
			Unused	23	22.1	7.7	22.7	4.8	66.5	13.8	131.2	19.7
Renesting 1990	17 Jun	2–3 Jul	Used	12	31.5	4.6	28.9	9.0	125.7	26.1	229.9*	24.8
			Unused	23	22.1	7.7	26.7	6.6	71.8	14.5	138.2	21.9

[a] A single video was actually taken of sandpits in each year because sandpit habitat changes little during the breeding season.
[b] Sand that was not disturbed by equipment or humans or covered with slurry run-off.
[c] Sand that was frequently disturbed by equipment and humans or covered by slurry run-off.
* Differences between used and unused within nesting periods, $P < 0.05$.
** Differences between used and unused within nesting periods, $P < 0.01$.

river bank was the only important variable for discriminating used and unused sites during high flows. For sandpits, area of water was important in discriminating used from unused sites for both dates in 1990 and for 29 June 1989; area of usable sand and area of unusable sand were important for 3 June 1989.

Many river sites with exposed sand were not used, especially during low flows when most of the river had exposed sand (Fig. 4). Terns potentially could have used most sandpits because factor scores for used and unused sites overlapped broadly (Fig. 5). Therefore, number of sites and amounts of habitat available referenced below are minimum estimates.

The proportion of available habitat on both the river and sandpits varied between years (Tables 6, 7). Proportions of river habitat available also varied within years due to differences in flows. Proportions of sandpit habitat available did not vary within years because terns tended to use the same sandpits throughout the season and sandpits change little within a season.

Four of the 5 criteria for judging habitat preference suggested that terns did not prefer 1 habitat over the other. With regard to the first criterion for judging habitat preference, the number of sandpit sites used was greater than that expected, based on the availability of both habitats; that is, the ratio of used sites to available sites was about twice as large on sandpits (54–70%) as on the river (16–35%) (Tables 6, 7). In contrast, in regard to the second criterion for preference, the ratios of the areas of sand used to sand available were similar on both habitats (36–66% on sandbars and 45–58% on sandpits; Tables 8, 9). For the river, this ratio of area of sand used to sand available was almost twice as large as the ratio of sites used to sites available (16–35%).

Regarding the third criterion for preference, more birds nested on the river than on sandpits except in 1984 when the river was flooded the entire breeding season (Table 10). They also occupied more river than sandpit sites. However, 71 and 49% percent of the mean area of all available

Table 4. Classification of river and sandpit sites based on bird use and discriminant function analysis (DFA) of variables obtained from aerial videos[a] along the lower Platte River, Nebraska, 1989–90. River and sandpit sites that terns actually used or did not use are depicted under "observed," and sites that DFA predicted terns would use or not use are depicted under "predicted."

Habitat	Nesting period and year[b]	Predicted class	Observed class		Error count estimate of redistribution classification[c]	Error count estimated of cross-validation classification[d]
			Used	Unused		
River	Initial 1989	Used	24	9	0.31	0.34
		Unused	11	21		
	Renesting 1989	Used	15	7	0.16	0.14
		Unused	1	26		
	Initial 1990	Used	16	3	0.06	0.08
		Unused	0	30		
	Renesting 1990	Used	18	6	0.19	0.23
		Unused	4	24		
Sandpits						
	Initial 1989	Used	4	5	0.18	0.23
		Unused	2	28		
	Renesting 1989	Used	4	5	0.20	0.26
		Unused	3	27		
	Initial 1990	Used	7	6	0.31	0.49
		Unused	5	17		
	Renesting 1990	Used	8	5	0.26	0.34
		Unused	4	18		

[a] Variables used in DFA for the river were channel width, number of sand areas, mean size of sand areas, percent of 402-m segment covered with permanent vegetation, and location of most (≥75%) of the sand in relation to river bank; variables for sandpits were area of usable sand, area of unusable sand, area of water, and area of vegetation.

[b] *See* Tables 2 and 3 for dates sites were surveyed for terns and classified as used or unused and for dates of videos.

[c] Error count estimate of the reclassification of sites based on classification criterion of the discriminant function.

[d] Error count estimate of the redistribution results of cross-validation classifications.

sand on both habitats occurred on the river in 1989 and 1990, respectively, and 77 and 54% of all the birds nested on the river in 1989 and 1990, respectively. Therefore, the numbers of birds nesting in both habitats may have reflected relative habitat availability.

Distributions of nest initiation dates did not differ between river and sandpit habitats (Table 11). However, terns tended to

Table 5. Loadings for habitat variables estimated from discriminant function analysis of used and unused river and sandpit sites along the lower Platte River, Nebraska, 1989–90.

Habitat and variable	Nesting period, year, and river flow[a]			
	Initial 1989 69.3 m³/sec	Renesting 1989 328.3 m³/sec	Initial 1990 145.5 m³/sec	Renesting 1990 57.2 m³/sec
River				
Channel width	0.299	0.306	−0.156	0.410
Number sand areas	−0.015	0.249	0.238	0.385
Mean size sand areas	0.518	0.142	0.182	0.561
Percent vegetation[b]	−0.395	−0.189	−0.222	−0.432
Location of sand[c]	0.539	0.940	0.973	0.642
Sandpits				
Area of usable sand	0.835	0.366	0.190	0.450
Area of unusable sand	0.782	−0.053	0.005	−0.123
Area of water	−0.129	0.655	0.930	0.921
Area of vegetation	0.618	−0.309	0.182	−0.422

[a] *See* Tables 2 and 3 for dates sites were surveyed for terns and classified as used or unused and for dates of videos. Flows were determined for the same day that river videos were taken (mean daily flow, North Bend gauge river kilometer 116.8 [river mile 72.4] [Boohar et al. 1989, 1990]).

[b] The percentage of the 402-m segment with permanent vegetation.

[c] The position of most (≥75%) of the sand in the 402-m segment in relation to river bank.

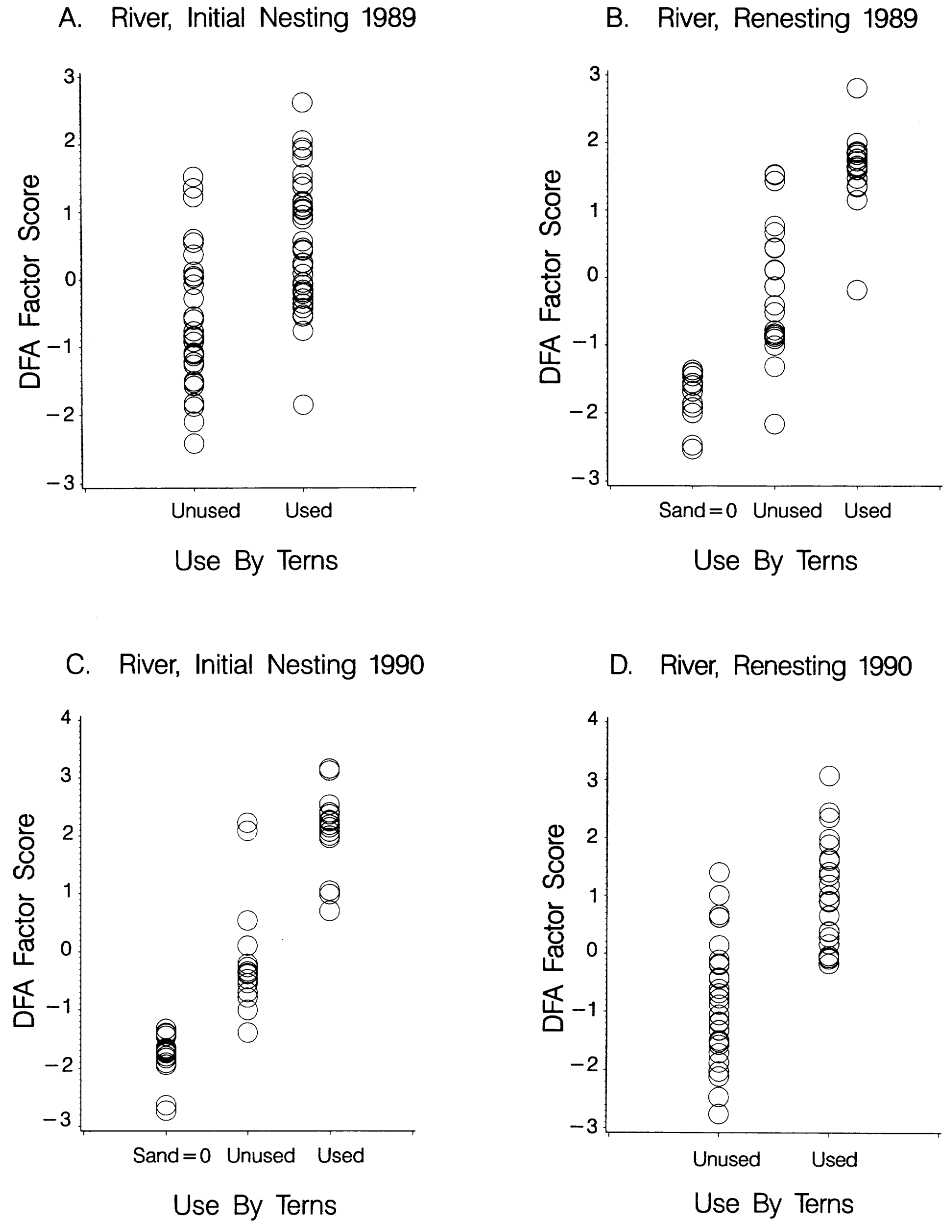

Fig. 4 Plots of discriminant function analysis (DFA) factor scores for river sites along the lower Platte River that were used by least terns, unused sites with sand, and unused sites with no sand (no sand, B and C only) during 4 sampling periods. B and C depict periods of high flow. *See* Table 2 for dates sites were surveyed for terns and classified as used or unused and for dates of videos.

initiate more late nests and renests on river habitat than on sandpits. High flows in 1989 (28 Jun) and 1990 (14–19 Jun) destroyed many nests and chicks on the river, and median nest-initiation dates were later on the river because more renests occurred on river habitat than on sandpits.

Least terns abandoned former colony

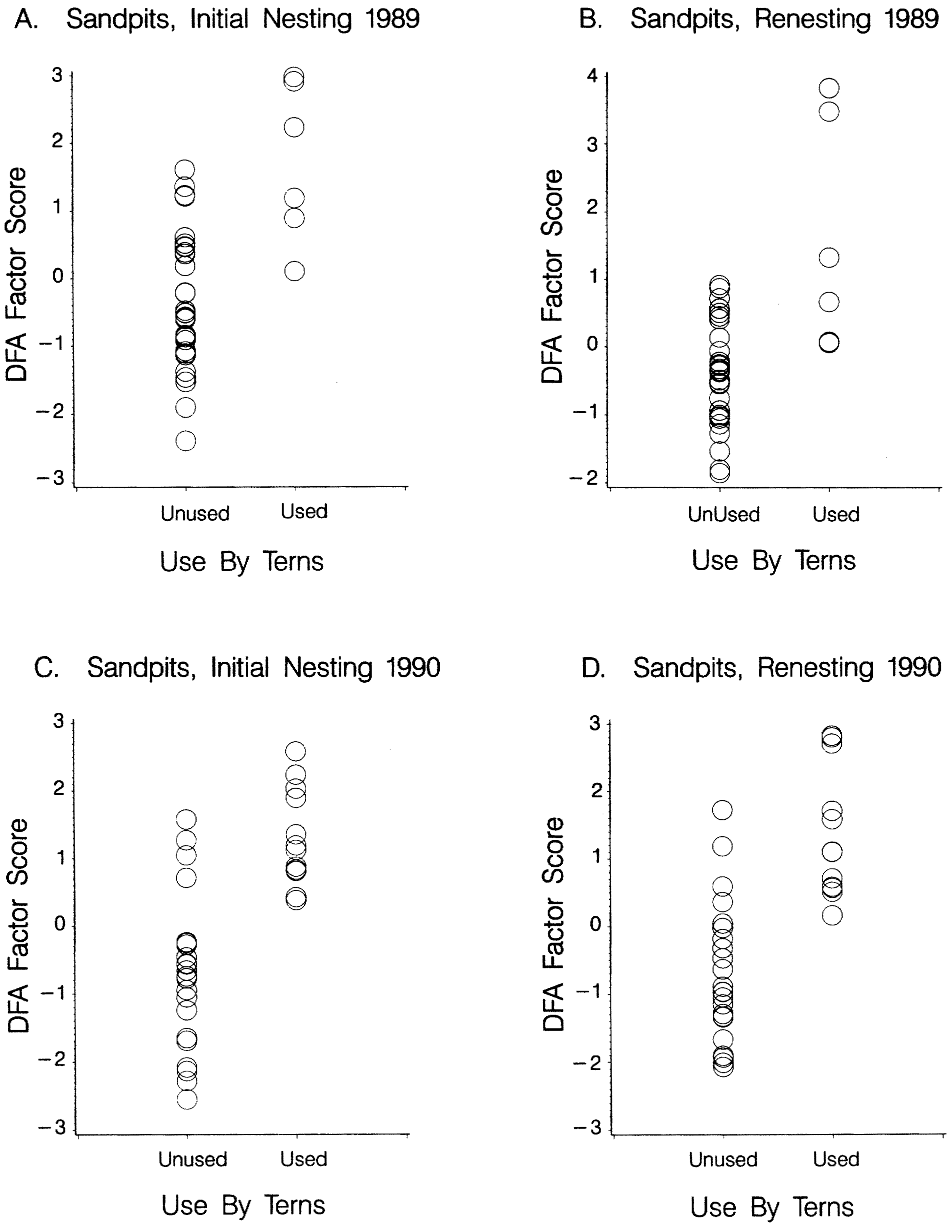

Fig. 5. Plots of discriminant function analysis (DFA) factor scores for sandpit sites along the lower Platte River that were used by least terns, and unused sites during 4 sampling periods. *See* Table 3 for dates sites were surveyed for terns and classified as used or unused and for dates of videos.

sites and colonized new sites in both habitats at approximately the same rate (Table 12). Rates of colony-site turnover were low and did not differ among years or between habitats. Rates of colony-site turnover also did not differ among years within both habitats (chi-square—river, $P > 0.5$; sandpits, $P > 0.1$).

Table 6. Estimated proportions of river sites available as determined by discriminant function analysis (DFA) and ratios of river sites used to sites available on the lower Platte River, Nebraska, 1989–90.

Nesting period and year[a]	River flow[b]	No. of river sample sites available[c]		Proportion of sample sites available[e]	Number of river sites			Ratio of river sites used ÷ available
		Used by terns	DFA[d] as used		Total	Available[f]	Used	
Initial 1989	Low	4	9	0.38	408	155	35	0.22
Renesting 1989	High	1	7	0.24	408	98	16	0.16
Initial 1990	High	1	3	0.12	408	49	17	0.35
Renesting 1990	Low	4	6	0.29	408	118	23	0.19

[a] *See* Table 2 for dates sites were surveyed for terns and classified as used or unused and for dates of videos.

[b] Qualitative river flow for each date (*see* Table 2).

[c] Available sites are defined as sites that terns actually used and, in addition, unused sites that DFA classified as used.

[d] Error of discriminant functions are given in Table 4.

[e] The total number of available sample sites (columns 3 and 4) divided by 34 (the total number of sample sites for each river date).

[f] Values in this column were calculated as 408 times the proportion of sample sites available (column 5 in this table), where 408 is the number of 402-m segments of river in the study area.

Table 7. Estimated proportions of sandpit sites available and ratios of sandpit sites used to sites available on the lower Platte River, Nebraska, 1989–90.

Nesting period and year[a]	Total no. of sandpit sites	No. of sandpit sites available[b]		Ratio of sites used ÷ available
		Used by terns	DFA[c] as used	
Initial 1989	39	6	5	0.54
Renesting 1989	39	7	5	0.58
Initial 1990	35	12	6	0.67
Renesting 1990	35	12	5	0.70

[a] *See* Table 3 for dates sites were surveyed for terns and classified as used or unused and for dates of videos.

[b] Available sites are defined as sites that terns actually used and, in addition, unused sites that discriminant function analysis (DFA) classified as used.

[c] Error of discriminant function classifications are given in Table 4.

Table 8. Estimated area of available sand (ha) on river sites and ratios of sand used to available on the lower Platte River, Nebraska, 1989–90.

Nesting period and year[a]	Total area of sand				Ratio of area of sand used ÷ available
	Sample sites	Total river[b]	Available river sites[c]	Used river sites	
Initial 1989	25.3	304.6	115.7	41.7	0.36
Renesting 1989	2.7	32.7	7.5	2.8	0.37
Initial 1990	6.0	72.0	8.5	5.6	0.66
Renesting 1990	34.5	416.0	120.6	54.6	0.45

[a] *See* Table 2 for dates sites were surveyed for terns and classified as used or unused and for dates of videos.

[b] Values in this column were calculated as the area of sand on sample sites divided by 0.083 (where 0.083 is the proportion of the river sampled).

[c] Values in this column were calculated as the area of sand on the river times the proportion of sample sites available from Table 6 (where the proportion of the sample sites available was used to approximate the proportion of the river available).

Table 9. Estimated areas of available sand (ha) on sandpit sites and ratios of the area of sand used to available on sandpits along the lower Platte River, Nebraska, 1989–90.

Nesting period and year[a]	Area of sand on available sites[b]			Ratio of area of sand used ÷ available
	Used by terns	DFA[c] defined as used	Total available	
Initial 1989	11.8	12.1	23.9	0.49
Renesting 1989	11.6	14.1	25.7	0.45
Initial 1990	39.3	29.6	68.9	0.57
Renesting 1990	37.8	27.9	65.7	0.58

[a] *See* Table 3 for dates sites were surveyed for terns and classified as used or unused and for dates of videos.

[b] Available sites are defined as sites that terns actually used and, in addition, unused sites that discriminant function analysis (DFA) classified as used.

[c] Error of discriminant function classifications are given in Table 4.

Table 10. Numbers of nesting sites and numbers of least terns counted on river and sandpit habitats between river kilometers 164.5 and 0 (river miles 102 and 0) of the lower Platte River, Nebraska, 1984–90. Data for 1984–86 were obtained from Nebraska Game and Parks Commission (unpubl. data[a]). Data for 1987–90 include Game and Parks Commission data as well as those collected in the present study.

Year	River		Sandpits	
	No. sites	No. pairs terns	No. sites	No. pairs terns
1984	0	0	10	137–144
1985	12	77	7	35
1986	6	150	8	77
1987	27	214	15	105
1988	24	256	11	118
1989	38	240	10	64
1990 early[b]	17	155	9	122
1990 renest[b]	23	144	11	74

[a] J. J. Dinan, Platte River interior least tern and piping plover nesting survey, Unpubl. reports to Nebr. Game and Parks Comm., Lincoln, 1984, 1985, 1986.

[b] Flooding inundated all sandbars during 14–19 June (Boohar et al. 1990). These 2 rows indicate the numbers counted before the flood and about 10 days after the flood had receded (20 Jun) when terns had begun to renest.

Table 11. Distribution of dates of nest initiation for least terns on river and sandpit colonies along the lower Platte River, Nebraska, 1987-90.

	Range of nest initiation dates		Median nest initiation date		No. of nests in analysis			
Year	River	Sandpits	River	Sandpits	River	Sandpits	Test statistic[a]	P
1987	21 May-30 Jun	28 May-3 Jul	4 Jun	5 Jun	36	41	0.100	>0.98
1988	21 May-25 Jun	23 May-18 Jun	5 Jun	31 May	61	44	0.250	>0.18
1989	20 May-11 Jul	21 May-10 Jul	7 Jun	1 Jun	74	46	0.250	>0.08
1990	31 May-7 Jul	24 May-14 Jul	11 Jun	6 Jun	104	95	0.135	>0.78

[a] Kolmogorov-Smirnov test statistic of maximum distance.

Productivity and Mortality

Productivity.—Terns were studied at 40 colonies located on 26 different sites (Appendix A). Clutch size, nest success, fledging success, and fledglings per pair averaged 2.40, 0.54, 0.28, and 0.48 over both habitats for all 4 years. Overall clutch size, nest success, fledging success, and fledglings per pair were 2.39, 0.60, 0.25, and 0.50. Interaction between habitat and year was not significant for any of these variables (2-way ANOVA—clutch size, P = 0.90; nest success, P = 0.76; fledging success, P = 0.60; fledglings per pair, P = 0.22). Clutch size did not differ between habitats or among years (ANOVA—habitat, P = 0.85; year P = 0.16). Nest success varied widely among sites in both habitats each year (Table 13), but did not differ significantly between habitats or among years (ANOVA—habitat, P = 0.42; year, P = 0.29; Appendixes B, C). Fledging success and fledglings per pair also varied widely among sites in both habitats (Table 13; Appendixes B, C) and did not differ consistently between habitats or among years (ANOVA—fledging success, habitat, P = 0.19; year, P = 0.56; fledglings per pair, habitat, P = 0.61; year, P = 0.14). The power of these tests, however, was weak (0.3–0.4) because of high variability of the data and small sample size.

Mortality.—Sample sizes for chick mortality were smaller than those for laying and egg mortality because all eggs were destroyed before hatching at 3 sites (2 sandpits and 1 sandbar). Instantaneous rates of laying, egg, and chick mortality did not differ between habitats (Table 14). These mortality rates differed even less between sandbar sites that were not flooded and sandpits.

Overall mortality, and thus productivity, was most influenced by chick mortality in both habitats (Table 15). Egg mortality also was important for terns nesting on sandbars and was more important than chick mortality on sandbars that were not flooded and sandbars early in the season. Chick mortality most influenced productivity in both habitats late in the season

Table 12. Rates of turnover of least tern colony sites along the lower Platte River, Nebraska, 1986–90. Colony-site turnover for sites between 1989 and 1990 before the 1990 flood (14–19 Jun) are indicated as 1989–90 early, and turnover rates for sites within 1990 are indicated as 1990 early-renest. Data for 1986 were derived from Nebraska Game and Parks Commission (unpubl. data[a]).

	Turnover rate			χ^2 between habitats	
Year	River	Sandpits	Overall	χ^2	P
1986–87	0.17	0.23	0.16	0.07	>0.75
1987–88	0.12	0.13	0.13	0.03	>0.75
1988–89	0.07	0.14	0.09	0.001	>0.90
1989–90 early	0.09	0.07	0.08	0.11	>0.50
1990 early-renest	0.18	0.05	0.12	1.45	>0.25

[a] J. J. Dinan, Platte River interior least tern and piping plover nesting survey, Unpubl. rep. to Nebr. Game and Parks Comm., Lincoln, 1986.

Table 13. Nest and fledging success, and fledglings per pair for least terns on sandbars and sandpits along the lower Platte River, Nebraska, 1987–90.

Year	No. of study colonies		Nest success				Fledging success				Fledglings per pair			
			Sandbars		Sandpits		Sandbars		Sandpits		Sandbars		Sandpits	
	Sandbars	Sandpits	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
1987	3	5	0.49	0.25	0.46	0.18	0.14	0.04	0.37	0.21	0.21	0.12	0.28	0.08
1988	4	3	0.72	0.14	0.72	0.12	0.27	0.02	0.24	0.13	0.73	0.15	0.55	0.23
1989	6	6	0.41	0.08	0.54	0.06	0.35	0.10	0.38	0.11	0.57	0.17	0.50	0.06
1990	6	7	0.44	0.05	0.64	0.12	0.12	0.08	0.33	0.05	0.25	0.16	0.64	0.14

(sites with only late nests, or sites with renests). All early nests on sandbars in 1990 were destroyed during the 14–19 June high flows just after we had begun monitoring colonies; therefore, nests on sandbar study sites in 1990 were renests and were not included in the early sandbar data set. The importance of chick mortality in contributing to overall mortality of tern young on sandbars was strongly influenced by 4 sites in 1990 where flooding during 25–26 July killed all chicks.

Causes of Egg and Chick Mortality.—Predation or flooding of nests at 1 or 2 study sites each year caused substantial variation in nest success within habitats. Each year, proportions of eggs lost due to different causes differed between habitats (1987: $\chi^2 = 19.97$, 4 df, $P < 0.005$; 1988: $\chi^2 = 10.58$, 4 df, $P < 0.05$; 1989: $\chi^2 = 54.4$, 4 df, $P < 0.001$; 1990: $\chi^2 = 178.9$, 4 df, $P < 0.001$). Flooding caused most egg mortality on sandbars, but did not occur on sandpits (Table 16). Predation and abandonment (of fertile and infertile eggs) accounted for most of the egg loss on sandpits. Predation was significantly greater on sandpits than on sandbars in 1987, 1988, and 1990. Abandonment was significantly greater on sandpits than on sandbars in 1989 and 1990. Human-caused losses were significantly greater on sandpits than on sandbars in 1990, although the actual difference in proportions lost was very small. Predation and abandonment also accounted for much egg loss on sandbars. The "other" causes of loss were greater on sandpits than sandbars in 1987 and greater on sandbars than sandpits in 1989.

Six hundred eighty of the 906 chicks hatched did not fledge. Most of these chicks (554 chicks, 81%) were missing, although intensive searches were made to find carcasses. I rarely found direct evidence of predation such as body parts or carcasses. I found remains of 6 chicks killed by predators, and I saw a black-crowned night-heron (*Nycticorax nycticorax*) eat 1 chick. I also found remains of 7 chicks that died during cold, wet weather, 2 chicks that were run over or stepped on by humans, and 12 chicks that died from undeter-

Table 14. Comparisons between sandbars and sandpits of instantaneous rates of laying, egg, and chick mortality for least tern young along the lower Platte River, Nebraska, 1987–90.

	Habitat								
	Sandbar			Sandpit					
Mortality rate	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	Student's *t*	df	*P*
Laying	19	0.216	0.017	21	0.207	0.024	0.320	38	0.751
Egg	19	0.548	0.083	21	0.471	0.082	0.661	38	0.513
Chick	18	0.873	0.077	19	0.722	0.076	1.394	35	0.174
Overall	19	1.225	0.066	21	1.082	0.048	1.785	38	0.087

mined causes. Ninety-eight chicks (14% of all chicks and 24% of the 412 chicks on sandbars) died during flooding in 1989 and 1990.

Evidence of Disturbance.—Track trails of dogs, coyotes (*Canis latrans*), red fox (*Vulpes vulpes*), mink (*Mustela vison*), striped skunk (*Mephitis mephitis*), great horned owl (*Bubo virginianus*), black-crowned night-heron, gopher snake (*Pituophis melanoleucus*), beaver (*Castor canadensis*), woodchuck (*Marmota monax*), smooth softshell turtle (*Trionyx muticus*), Canada goose (*Branta canadensis*), mallard (*Anas platyrhynchos*), great blue heron (*Ardea herodias*), humans, and vehicles were identified and new track trails counted during each visit to a colony site. Terns would leave nests and mob these intruders on or near the colony area (pers. observ.)

Track trail indices did not differ between habitats (chi-square—$P = 0.884$). These indices did not differ between nesting and chick rearing periods for either sandbars or sandpits (Table 17; chi-square—sandbars, $P = 0.562$; sandpits, $P = 0.126$).

During 177.5 hours of observations at colonies, I noted several instances that terns were disturbed, but the perpetrator did not leave tracks in the sand and, therefore, would not have been represented in track trail counts. These disturbances were passing airboats and fly overs by turkey vultures (*Cathartes aura*), American kestrels (*Falco sparverius*), red-tailed hawks (*Buteo jamaicensis*), Franklin's gulls (*Larus pipixcan*), great egrets (*Casmerodius albus*), and great blue herons.

Limited data on unused sites for 1990 suggested that track trail indices were greater on unused than used sites in both habitats (Table 17; sandbars, $t = -3.158$, 20 df, $P = 0.005$; sandpits, $t = -3.897$, 23 df, $P = 0.001$). However, track trail indices on some used sites of both habitats were as high as those on unused sites.

Track trail indices for the nesting period were not correlated with numbers of aban-

Table 15. Contributions of instantaneous rates of laying, egg, and chick mortality to total instantaneous mortality (Key Factor Analysis) of least tern young on the lower Platte River, Nebraska, 1987–90. Values are coefficients of determination (r^2) of overall instantaneous mortality regressed upon instantaneous mortality for each life stage. Rate with the highest r^2 explained the most variation in overall mortality. Slopes of regressions that are significantly different from zero are indicated by asterisks.

	Sandbars			Sandpits			Sandbars not flooded		
Mortality rate	Early	Late	Total season	Early	Late	Total season	Early	Late	Total season
Laying	0.378**	0.006	0.001	0.081	0.276	0.063	0.356	0.154	0.071
Egg	0.575***	0.017	0.262*	0.083	0.333*	0.008	0.539*	0.196	0.332*
Chick	0.365*	0.577**	0.614**	0.353**	0.557**	0.427**	0.312	0.249	0.291

* Significant regression, $P < 0.05$.
** Significant regression, $P < 0.01$.
*** Significant regression, $P < 0.001$.

Table 16. Causes of egg loss for least tern colonies along the lower Platte River, Nebraska, 1987–90.

Egg variables	Year and habitat											
	1987			1988			1989			1990		
	Sandbar		Sandpit	Sandbar		Sandpit	Sandbar		Sandpit	Sandbar		Sandpit
Number of eggs	171		188	197		143	185		145	247		298
Porportion of eggs												
Abandoned	0.09		0.11	0.09		0.04	0.10	***	0.15	0.02	***	0.10
Depredated	0.19	*	0.24	0.12	***	0.17	0.15		0.10	0.02	***	0.14
Human destroyed	0.01		0.00	0.02		0.02	0.02		0.04	0.00	***	0.02
Flooded	0.05	***	0.00	0.04	*	0.00	0.28	***	0.00	0.53[a]	***	0.00
Other losses[b]	0.00	**	0.04	0.03		0.01	0.02	*	0.10	0.00		0.00
Unknown outcome	0.06		0.05	0.04		0.08	0.00		0.02	0.01		0.04

[a] In 1990, all early eggs were lost (approx 122 eggs as calculated from no. of pairs renesting and the average clutch size before the flood: (53 nests) × (2.3 eggs/nest). Only 7 eggs from renests were flooded.

[b] Includes severe weather and disturbance by nonpredatory animals.

* Chi-square differences between sandbars and sandpits each year, $P < 0.05$.

** Chi-square differences between sandbars and sandpits each year, $P < 0.01$.

*** Chi-square differences between sandbars and sandpits each year, $P < 0.001$.

doned or depredated eggs or numbers of nests in either habitat (Table 18). Numbers of nests were positively correlated with numbers of abandoned eggs in both habitats. On sandbars, track trails of terrestrial predators correlated with numbers of depredated eggs. On sandpits, track trails of heavy equipment correlated with abandoned and depredated eggs, and track trails of terrestrial predators correlated negatively with numbers of abandoned eggs.

Frequency of track trails for all intruders combined was positively correlated with the number of chicks on sandpits but was not correlated with proportions of chicks known alive in both habitats (Table 19). Track trails of great horned owls and ATV's on sandbars and humans on foot on sandpits correlated positively with numbers of chicks. Track trails of ATV's correlated negatively with proportions of chicks known alive on sandbars, and track trails of terrestrial predators correlated negatively with proportions of chicks known alive on sandpits.

Path Analysis.—The 3 sites where no eggs hatched were excluded from this analysis. Three strong relationships emerged in both habitats (Figs. 6, 7; Appendixes D, E). Number of nests influenced egg mortality. Egg mortality influenced the number of chicks hatched. Finally, chick mortality influenced overall mortality. On sandpits, egg mortality also correlated negatively with chick mortality (Pearson correlation, $P = 0.002$; Bonferroni, $P = 0.08$), and numbers of nests correlated positively with numbers of chicks (Pearson correlation, $P = 0.0001$; Bonferroni, $P = 0.001$). I examined paths for early and late season but found no other consistent relationships.

Causes for apparent density dependence of egg mortality in both habitats were not clear. In both habitats, the number of abandoned eggs (but not the number of depredated eggs) were correlated with numbers of nests (*see* Table 18). No significant relationships other than those mentioned above were found (Appendixes D, E).

The track trail index and habitat vari-

Table 17. Mean frequencies of track trails at least tern colony sites on sandbars and sandpits on the lower Platte River, Nebraska, 1987–90. The nesting period ran from nest initiation to when 75% of the nests became inactive (hatched or destroyed). The chick rearing period followed the nesting period and ended when the last chick fledged.

			Total season		Nesting		Chick rearing		Unused sites[a]	
Habitat	Year	n	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Sandbar	1987	3	0.76	0.19	0.82	0.22	0.44	0.10		
	1988	4	0.68	0.16	0.88	0.23	0.30	0.06		
	1989	6	0.66	0.28	0.71	0.34	0.74	0.46		
	1990	6	1.34	0.38	0.57	0.26	2.08	1.10	2.50	0.50
Sandpit	1987	5	0.39	0.04	0.46	0.14	0.32	0.12		
	1988	3	0.47	0.07	0.37	0.03	0.70	0.25		
	1989	6	0.87	0.22	0.62	0.23	1.03	0.36		
	1990	7	1.66	0.40	1.45	0.54	1.73	0.37	3.04	0.87

[a] Data from unused sites were collected in 1990 from 3 sandbar and 4 sandpit sites.

Table 18. Correlations among number of nests, numbers of eggs lost due to predation and abandonment, and frequency of different types of track trails for least tern colonies along the lower Platte River, Nebraska, 1987–90. Correlations between track trail types and other variables were Spearman rank, and all other correlations were Pearson product-moment.

		No. eggs lost to		Frequency of track trails					
Habitat	Number	Predation	Abandonment	Terrestrial predator	Human	Owl	ATV[a]	Heavy equipment	All trails
Sandbars	Nests	0.317	0.574**	0.107	0.303	0.233	0.113		0.316
	Depredated eggs		0.288	0.494**	0.170	0.399	−0.144		0.565
	Abandoned eggs			0.039	0.143	−0.027	−0.024		−0.037
Sandpits	Nests	0.049	0.631**	−0.306	0.286	0.182	0.013	0.220	−0.185
	Depredated eggs		0.148	−0.357	−0.018	0.284	−0.392	0.433*	0.235
	Abandoned eggs			−0.529*	0.459	0.247	−0.324	0.433*	−0.308

[a] All-terrain vehicle.
* Significant correlation, $P < 0.05$.
** Significant correlation, $P < 0.01$.

Table 19. Spearman rank correlations of proportions of least tern chicks known alive on each visit and numbers of chicks hatched at a colony, with frequency of different types of track trails on sandbar and sandpit colony sites on the lower Platte River, Nebraska, 1987–90.

		Frequency of track trails					
Habitat	Chick variables	Terrestrial predators	Humans on foot	Owl	ATV[a]	Heavy equipment	All track trails
Sandbars	Proportion of chicks alive (n = 156 visits)	−0.002	−0.010	0.007	−0.223*		−0.117
	Number of chicks hatched (n = 18 sites)	0.242	0.497	0.306*	0.561*		0.569
Sandpits	Proportion of chicks alive (n = 223 visits)	−0.234**	−0.023	−0.106	−0.093	0.016	−0.172
	Number of chicks hatched (n = 18 sites)	0.222	0.567*	0.226	0.386	0.030	0.413*

[a] All-terrain vehicle.
* Significant correlation, $P < 0.05$.
** Significant correlation, $P < 0.01$.

ables (Tables 20, 21) were not strongly related to mortality or numbers of nests and chicks in both habitats. Relationships between numbers of nests or chicks and chick mortality also were weak. However, the correlation between number of chicks and chick mortality was positive and relatively strong on sandpits ($b' = 0.40$, Appendix E).

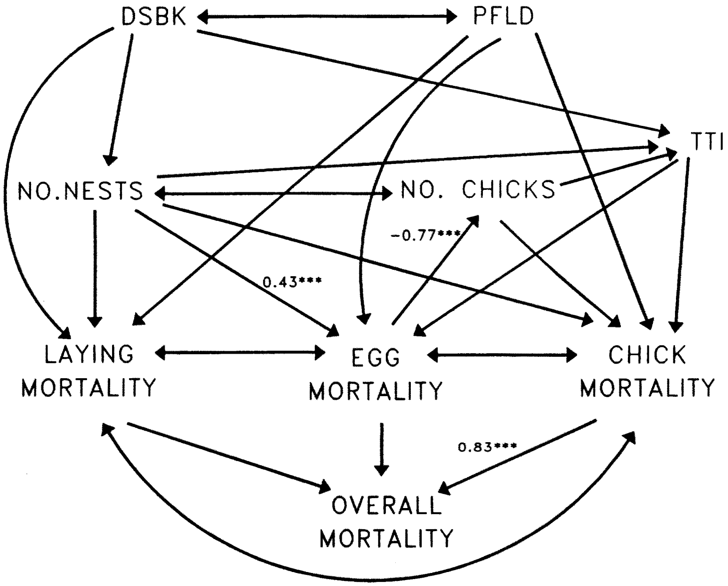

Fig. 6. Path diagram depicting relationships among habitat and disturbance variables, numbers of nests and chicks, and mortality rates for least terns on sandbar colonies along the lower Platte River, 1987–90. One-headed arrows indicate paths for which standardized partial regression coefficients (*b′*) were calculated. Two-headed arrows indicate paths for which Pearson correlation coefficients were calculated. The values for *b′* or Pearson correlation coefficients are presented next to arrows only if they were significant (*** = $P < 0.001$). Variables used in the analysis were distance of the sandbar from the nearest river bank (DSBK), percent of the bar flooded (PFLD), track trail index (TTI), numbers of nests and chicks, and instantaneous mortality rates.

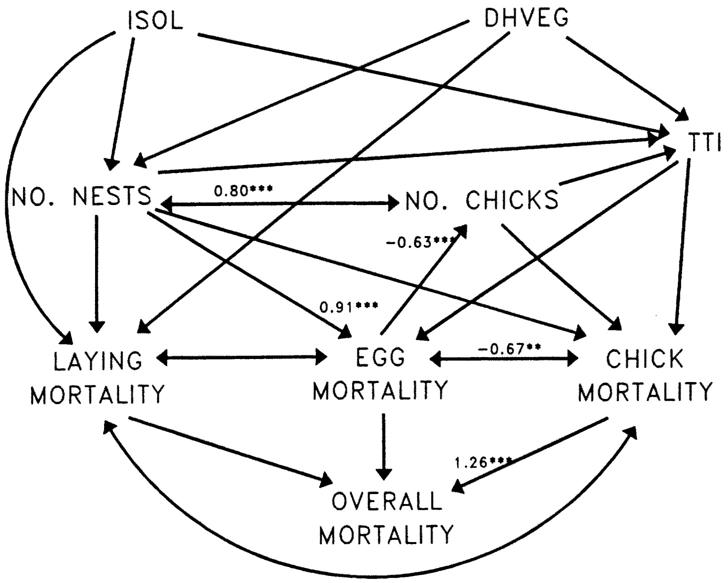

Fig. 7. Path diagram depicting relationships among habitat and disturbance variables, numbers of nests and chicks, and mortality rates for least terns on sandpit colonies along the lower Platte River, 1987–90. One-headed arrows indicate paths for which standardized partial regression coefficients (*b′*) were calculated. Two-headed arrows indicate paths for which Pearson correlation coefficients were calculated. The values for *b′* or Pearson correlation coefficients are presented next to arrows only if they were significant (** = $P < 0.01$, *** = $P < 0.001$). Variables used in the analysis were distance to abundant vegetation (vegetation cover >50% and height >30 cm) (DHVEG), the percent of the colony site perimeter bordered by water (ISOL), track trail index (TTI), numbers of nests and chicks, and instantaneous mortality rates.

Table 20. Summary of habitat variables at least tern colony sites on sandbars along the lower Platte River, Nebraska, 1987–90.

Year	No. sites	Distance to bank (m)	% of colony area[a] flooded
1987	3	5–25	0–5
1988	4	25–120	0–10
1989	6	85–165	80–95
1990	6	0–190	0–100

[a] That part of a nesting site that terns actually used for nesting, brooding and feeding chicks, and loafing.

Table 21. Summary of habitat variables at least tern colony sites on sandpits along the lower Platte River, Nebraska, 1987–90.

Year	No. sites	% of colony area[a] perimeter bordered by water	Distance to abundant vegetation[b] (m)
1987	5	25–75	5–200
1988	3	25–75	40–200
1989	6	25–75	10–200
1990	7	25–75	25–400

[a] That part of a colony site that terns actually used for nesting, brooding and feeding chicks, and loafing.
[b] Abundant vegetation = >50% cover and >30 cm tall.

Population Trend

The model was most sensitive to changes in adult survival, followed by juvenile survival, and then chick survival (Kirsch 1992). Population trend (instantaneous rate of change, r) was positive only for very high levels of juvenile and adult survival (Table 22). Estimated population trends when both juvenile and adult survival were 0.85 and 0.88 were $r = -0.003$ and $r = 0.031$, respectively.

DISCUSSION

Least terns on the lower Platte River (a disturbed system) used habitats as predicted by theory for natural systems. Furthermore, habitat preference should be detected more easily at low population densities (Fretwell 1972), and terns used few of the available sites in both habitats. Terns may not perceive sandbars and sandpits as different because they evolved to use unstable or ephemeral habitats for nesting and may simply use the area of bare sand and proximity to other resources to choose colony sites. Productivity in terms of fledglings per pair was poor and varied a great deal among sites, but was similar in both habitats. Therefore, there may be no selective pressure to distinguish habitats, to prefer 1 habitat over the other, or to abandon usable colony sites.

Productivity and habitat selection are rarely estimated at the same time. Where this has been done, theoretical predictions are supported in relatively natural or undisturbed situations, but not always in human-disturbed situations. On relatively undisturbed habitats on Great Gull Island, Newfoundland, Atlantic puffins (*Fratercula arctica*) and herring gulls (*Larus argentatus*) in preferred habitat fledge more chicks than birds in less preferred habitat (Nettleship 1972, Pierotti 1982). In an experimental situation (nest boxes provided), Alatalo et al. (1985) found pied flycatchers (*Ficedula hypoleuca*) preferred deciduous over coniferous forest. Although females were equally successful in both habitats, a larger portion of the males were bigamous in deciduous versus coniferous forest resulting in males in deciduous forests producing more fledglings. Mallards in dis-

Table 22. Estimated population trend (r) for model least tern populations with 0.50 fledglings per pair, 6 levels of survival from fledging to 2 years of age, and 6 levels of annual adult survival.

Adult survival	Survival from fledging to 2 yrs 0.30	0.40	0.50	0.65	0.70	0.80
0.70	−0.260	−0.225	−0.191	−0.166	−0.143	−0.120
0.75	−0.209	−0.175	−0.142	−0.119	−0.096	−0.074
0.80	−0.161	−0.128	−0.096	−0.074	−0.052	−0.031
0.85	−0.116	−0.083	−0.053	−0.031	−0.010	0.010
0.90	−0.072	−0.041	−0.011	0.010	0.030	0.050
0.95	−0.003	0.000	0.029	0.049	0.069	0.088

turbed habitats such as farmed prairies and parklands of North America (Cowardin et al. 1985, Greenwood et al. 1987) and reed warblers (*Acrocephalus scirpaceus*) in disturbed *Phragmites* marsh–grasslands in central England (Catchpole 1974) did not prefer the most suitable habitat. However, dickcissels (*Spiza americana*) in Kansas preferred old fields to prairie habitats and overall success was greater in old fields (Zimmerman 1982).

Although least terns on the lower Platte River used habitats as predicted by theory, this population may not be sustained by local recruitment. Estimated fledglings per pair would not support the population at current levels or allow it to grow unless postfledging survival is extremely high. Furthermore, the instantaneous rates of change (r) of -0.003 or 0.031, as estimated with reasonable rates of annual adult survival of 0.85 or 0.88 (Thompson 1982, Kirsch 1992, Massey et al. 1992, Renken and Smith 1995) are optimistic. These survival estimates also were used for juvenile survival, but survival from fledging to first breeding is likely to be lower than 0.85 or 0.88 (Massey et al. 1992). Furthermore, any variation in parameters of the model lowers r (Kirsch 1992).

Habitat Use

Least terns did not strongly select sites with distinct sets of features of either habitat, and they did not occupy most of the apparently available habitat of either type. They tended to use river sites with a wide channel and with large midstream sandbars and large sandpit sites with large surface areas of water. Discriminant function scores of used and unused river sites with sand, and used and unused sandpit sites overlapped, indicating that many unused sites were potentially usable. However, because factor loadings for these variables fluctuated, site selection within each habitat was not strongly based on the set of variables I was able to measure. These results further suggest that bare sand and proximity to other resources may be enough for terns to colonize a site.

Because least terns typically use ephemeral or unstable habitats such as sandbars and beaches, they are thought to have low site fidelity and high group adherence (McNicholl 1975). Site fidelity in least terns is relatively high in California where only a few sites are available for nesting (Atwood and Massey 1988), but is relatively low in some East Coast areas (Burger 1984). The occurrence and degree of group adherence in least terns have been reported in only a few instances (Massey and Fancher 1989, Boyd 1993). These behavioral traits may cause terns to continue to use sites even though they are not suitable, and group adherence likely contributes to groups of birds rather than single pairs colonizing new sites quickly. I would expect least terns to have chosen colony sites on sandbars opportunistically before the advent of the more stable sandpit habitat. However, site fidelity and group adherence may have made it difficult to determine physical habitat features that relate to site selection within habitats and ultimately selection between habitats.

None-the-less it appeared that terns occupied little of either habitat: a maximum of 20–33% of the available river sites and 50–66% of the available sandpit sites. Ratios of the number of sites used divided by those available were greater on sandpits than on the river, but ratios of the area of sand used divided by that available were similar in both habitats. This occurred because terns tended to use available river sites with the greatest areas of sand. Although differences were not significant, used river sites consistently had more sand (12–64% more) and larger mean sandbar size (4–95% larger) than available sites (Kirsch 1992). As opposed to river habitat, on sandpit habitat, proportions of sand used divided by sand available were similar to proportions of sites used divided by sites available. This occurred because areas of sand on used sites were similar to areas of sand on available sites on sandpit habitat. River sites with large areas of sand and sandpits may be primary habitat, and the remaining available river sites secondary habitat.

I measured horizontal, 2-dimensional variables from video images to estimate habitat availability, but other variables such as elevation, substrate composition, and disturbance could have been important and resulted in broadly-overlapping discriminant-function-analysis factor scores. These variables may not have differed between used and unused sites, however. Although used sandbars were higher than unused ones on the lower Mississippi River (Smith and Renken 1991), mean and maximum elevations did not differ between used and unused sandbars on the lower Platte (Ziewitz et al. 1992). Elevations of tern nests on sandpits ranged from 0.1 to 9.0 m above water level (Nebr. Game and Parks Comm., Lincoln, unpubl. data; author, unpubl. data), and these elevations occurred on most sandpit sites. Water level at pits close to the river was about the same as the water level of the river. What is important at sandpits is that a wide range of elevations were present at most sandpits and that terns nested at a wide range of elevations, indicating that elevation may not have been important in selecting sandpit sites. Substrate was similar on used and unused sandpits (Kirsch 1992), and on used and unused sandbars (author, pers. observ.). Terns may avoid disturbed sites (Gochfeld 1983); although I measured disturbance, I could not measure it at enough sites to say with any confidence that disturbance played a role in tern site and habitat selection. Other evidence that least terns showed no preference for either river or sandpit habitat included (1) the proportion of terns that nested in both habitats approximated the proportional availability of habitats, (2) nest initiation dates did not differ, and (3) turnover rates of colony sites did not differ.

Because least terns on the lower Platte River did not use much of either habitat that was apparently available and did not prefer 1 habitat over the other, the amount of usable habitat does not seem to limit this population. Least terns may be limited by habitat in other regions. Although habitat preference and habitat availability have not been investigated in California and East Coast least tern populations, these terns use a variety of natural and manmade habitats (such as dredge spoil areas and rooftops). Least terns in California, New York, and New Jersey cannot use most areas of natural habitat because of extensive recreational use and development (Calif. Least Tern Recovery Plan 1980, Gochfeld 1983, Safina et al. 1989), but they readily nest on manmade habitats throughout their range (Fisk 1978, Jernigan et al. 1978, Calif. Least Tern Recovery Plan 1980, Thompson and Slack 1982, Jackson and Jackson 1985, Burger and Gochfeld 1990).

Habitat preferences of colonial waterbirds on a small scale (single or closely spaced colonies) or habitat availability and habitat preference on a large scale (barrier island chain, river system, etc.) have been infrequently investigated. Nettleship (1972) and Pierotti (1982) demonstrated that Atlantic puffins and herring gulls prefer a specific subset of habitats available at Great Island, Newfoundland. On larger scales, Burger and Lesser (1978*a,b*) demonstrated that, although common terns (*Sterna hirundo*) used most of the available islands in New Jersey, herring gulls used little of the available habitat; and Vermeer and Devito (1987) demonstrated that nesting mew gulls (*Larus canus*) select lakes and islands with certain features on Vancouver Island, British Columbia. Recent advances in remote sensing techniques should make habitat investigations easier to conduct.

The paucity of research investigating habitat preference of colonial waterbirds in natural and artificial habitats, or on small or large scales, allows no general conclusions concerning the prevalence of habitat preference nor the degree of acceptance of manmade habitats. Any animal should prefer less-disturbed habitats if disturbance reduces productivity or adult survival. Colonial waterbirds that typically use unstable or ephemeral habitats often use manmade habitats (e.g., Buckley 1978, Fisk 1978, Jernigan et al. 1978, Jackson and Jackson 1985, Vermeer et al. 1988). Colonial waterbirds may accept manmade areas that resemble natural habitats and occur close to other resources. These birds may readily colonize new habitats and continue to use suitable habitats because they accept habitats with certain general features and because they display group adherence (McNicholl 1975) and social attraction (Burger 1988). Fidelity to natal and former breeding sites in new habitats may reinforce use of these habitats.

Productivity and Mortality

Mortality of young and productivity did not differ between sandbars and sandpits, but varied tremendously among colonies within both habitats. This variation and the small number of sites studied would make it difficult to detect a small difference in productivity between habitats. I was unable to measure fledgling weights or chick growth rates. One habitat could contribute more recruits to the next generation if these variables differed between habitats and influenced survival of juveniles.

Productivity (nest success and fledglings per pair) also varies greatly among colonies in other least tern populations (Massey and Atwood 1981, Thompson 1982, Burger 1984). My estimates from the lower Platte are comparable with others from the Interior population (Table 23).

Chick mortality was a more important determinant of number of fledglings than egg mortality or failure to lay 3 egg clutches in both habitats, but especially so on sandpits. Predators may have killed most chicks on sandpits and many chicks on sandbars, although in most cases I could not find physical evidence for this.

Chick mortality also was slightly density dependent on sandpits; reasons for this relationship remain unclear because there were no strong, consistent correlations between number of chicks, disturbance by predators or humans, and chick mortality. On sandpits, track trails of humans on foot and all track trails combined correlated with numbers of chicks, and, although track trails of terrestrial predators were positively correlated with chick disappearance (leading to my suspicion that predators took most chicks), they were not correlated with number of chicks.

Relationships among numbers of chicks, chick disappearance, and track trails also were not straightforward on sandbars. Disturbances by great horned owls and ATV's (as indexed by trail counts) were positively correlated with numbers of chicks. Activity caused by larger numbers of chicks may have attracted great horned owls, but track trails of great horned owls did not correlate with chick disappearance. The correlation between numbers of chicks hatched and ATV disturbance may be coincidental (sites attractive to ATV users also were attractive to terns and relatively safe from sources of egg mortality), because I doubt that greater numbers of chicks attracted ATV users. The weak negative correlation between ATV disturbance and proportions of chicks known alive on sandbars may indicate that ATV use affected chick survival. Chick mortality may not have been density dependent on sandbars because flooding, a density-independent cause of mortality, claimed many chicks in 1990. Habitat variables also were not clearly related to disturbance or mortality.

Overall, egg mortality was not as important as chick mortality in determining fledglings produced. However, for early nests on sandbars (most of the nests in any year) and on sandbars that were not flooded, egg mortality was the most important determinant of number of fledglings produced. Predation and flooding caused most egg mortality on sandbars, and predation caused most egg mortality on sandpits. Many eggs also were abandoned in both habitats. Egg mortality seemed density dependent in both habitats but reasons for density dependence of egg mortality remain unclear because correlations among number of nests, egg mortality due to predation or abandonment, and disturbance by predators were not consistent.

Disturbance can reduce productivity in least terns and many colonial waterbirds (Ellison and Cleary 1978, DesGranges and Reed 1981, Goodrich 1982, Jackson and Jackson 1985, Flemming et al. 1988, Goldin et al. 1989). I may not have been able

Table 23. Summary of productivity estimates for least terns in the Great Plains.

Location	Years	Nest success	Fledglings per pair	Frequency of visits to sites	No. pairs monitored	Source
Missouri River, N.D.	1988	0.62	0.42[a]	7–10 days	42	Mayer and Dryer 1989
	1989	0.56	0.21	7–19 days	52	
Missouri River, S.D.	1986		0.20	3–5 times/season	102	Schwalbach 1988
	1987		0.64		146	
	1988	0.36	0.44[b]	7–10 days	148	Dirks 1990
	1989	0.51	0.55	7–10 days	121	
Lower Platte River, Nebr.	1987–90	0.60	0.50	2–3 days	291	This study
Central Platte River, Nebr.	1986	0.62	0.26[c,d,e]	2–3 days	68[f]	Lingle 1993*a*
	1987	0.72	0.11[c,d,e]		75[f]	
	1988	0.52	0.33–0.46[c,d]		94[f]	
	1989	0.57	0.44–1.44[c,d,e]		84[f]	
	1990	0.60	0.19[c,d,e]		68[f]	
Mississippi River, Mo.	1986	0.65[g]	0.40	variable	381[g]	Smith and Renken 1993
	1987	0.69	0.6		397	
	1988	0.59	1.2		455	
	1989	0.45	0.2		912	
Cimmeron River, Kans.	1980		1.19	>3 times/season	46	Schulenberg and Ptacek 1984
	1981		1.08		41	
	1982		0.56		36	
Salt Plains NWR, Okla.	1977	0.64		1–3 days	28	Grover and Knopf 1982
	1978	0.38			42	
	1987	0.12			100–105	
	1987	0.44–0.33	0.44–0.15	1–3 days		Hill 1985
	1990	0.46	0.64	variable	120	Boyd 1990
Quivera NWR, Okla.	1980–90	0.10–0.57[h]	0.00–1.00[h]	variable	15–34	Boyd 1990
Optima Reservoir, Okla.	1986	0.60	1.00	variable	26	Boyd 1987
	1987	0.59	1.07		30	

[a] Chicks seen at 12 days of age or older were assumed to fledge.
[b] Chicks seen at 15 days of age or older were assumed to fledge.
[c] Estimates for number of nests, not pairs.
[d] Cursory estimate.
[e] Fledglings per nest.
[f] Number of nests monitored.
[g] Mayfield weighted average.
[h] Values are a range for the years of study.

to relate disturbance to density dependence of egg and chick mortality because I could not always detect disturbances. Aerial predators probably rarely left evidence that I could detect, and weather and substrate types may have affected my ability to detect terrestrial intruders. Wind and rain quickly obscure tracks in fine sand, and small predators may not leave tracks on small areas of gravel and hardened mud.

Although egg and chick mortality seemed density dependent on sandpits, pits are important in years when high flows continually submerge sandbars (e.g., 1983–84); such flows occur about every 6 years (Sidle et al. 1992:135). Terns would produce no fledglings those years if sandpits were not available. However, because of the greater degree of density dependence on sandpits, fledglings per pair could be low when large numbers of terns use sandpits during flood years.

Relationships hypothesized here (among variables on both habitats) should be considered a first estimation of the relative strengths of relationships. Alternative or more complex path diagrams could be constructed and tested against each other to determine which hypothesized set of relationships is most likely correct (*see* Wootton 1994). These types of analyses potentially provide powerful insights into mechanisms operating in natural systems and their relative strengths (Wootton 1994).

Productivity of colonial waterbirds that nest in ephemeral habitats typically varies among colonies (Erwin and Smith 1985, Safina et al. 1989). However, productivity is rarely compared among different nesting habitats. Productivity of common terns did not differ between beaches and marshes in New Jersey, Maryland, Virginia (Erwin and Smith 1985), and New York (Safina et al. 1989). Productivity of least terns in Florida and South Carolina tends to be greater on manmade habitats (roof tops and dredge spoil islands) than on natural beaches (S. M. Roche, Relative reproductive success of least tern colonies in the Charleston, South Carolina area, Unpubl. rep. to the National Audubon Soc. Comm. on Grants, Apr 1978–Jan 1979, 42 pp; Gore and Kinnison 1991). Predation causes most egg and chick mortality in other least tern populations and other species of colonial birds that nest on beaches and in marshes (Calif. Least Tern Recovery Plan 1980, Burger 1984, Erwin and Smith 1985, Safina et al. 1989). Flooding also can cause severe egg and chick mortality (Burger and Lesser 1979, Burger and Shisler 1980, Erwin and Smith 1985, Sidle et al. 1992, Lingle 1993*a*).

Population Status

If demographic parameters can be adequately modeled (i.e., if there are good estimates of the mean, variance, and shape of the frequency distribution) it could indicate that terns can persist with $r = 0$. However, because the deterministic model for the productivity and mortality estimates that I used yielded r slightly <0 and because deterministic models are optimistic, the results indicated that this population may not be sustained by local recruitment. Further, the model indicated that r for least terns on the lower Platte River was negative for most feasible levels of adult and juvenile survival. Postfledging survival must be very high for observed levels of productivity to sustain this population. Even higher levels of survival than indicated here would be required, however, because random variation in model parameters lowers population trend (Kirsch 1992).

Estimates of annual postfledging (juvenile and adult) survival are the weakest link in our demographic data on Interior least terns because there are too few recoveries of known-age birds and birds banded as adults to reliably estimate postfledging survival (Brownie et al. 1985) for the entire population. Mark–recapture techniques have proven useful for least terns that nest in California and the lower Mississippi River Valley; however, estimates of survival from fledging to first breeding (juvenile survival) are still not available for either of these populations. If estimates of adult survival from California and the Mississippi River are applicable to terns on the Platte River and if juvenile survival also is this high, the population on the Platte River may be approximately stable. However, population trends in long-lived birds are extremely sensitive to postfledging survival rates. We need to assess the effects of variation in estimates of postfledging survival on population viability, as well as to obtain estimates of juvenile survival. Without adequate estimates for population models, we can only detect population trends by regularly censusing Interior least terns during the breeding season throughout their breeding range over a number of years. Even this information will not reveal causes for changes in numbers.

Population trends have been evaluated using modeling techniques for some nongame bird species (Thompson 1982, Simons 1984, Lande 1988, Isenmann et al. 1990, Noon and Biles 1990, Ryan et al. 1993). One needs accurate demographic data to reasonably estimate population trend, and postfledging survival data are probably weak for most migratory nongame species. However, reliable data on productivity can reveal useful information if trend is calculated for a range of postfledging survival rates (e.g., Eberhardt 1990). Buckley and Downer (1992) illustrate that models such as RAMAS metapopulation models (Akcakaya 1994) may prove useful in determining importance of local populations, or breeding areas such as the lower Platte, in maintaining the Interior population of least terns when adequate demographic and movement data become available.

A metapopulation modeling approach was not feasible here for several reasons. Survey methods and coverage vary within the Interior range making comparing numbers of terns difficult and fledging success estimates are not directly comparable because of differing methods and definitions (author and J. G. Sidle, U.S. For. Serv., Chadron, Nebr., unpubl. data). Furthermore, there are virtually no data on exchange among the Interior, East Coast, and California populations of least terns (only 1 citation, Boyd and Thompson 1985) and only scattered records of movements within the Interior range. Data on postfledging survival also is lacking for least tern populations on both coasts as well as the interior. Surveys and productivity monitoring need to be better coordinated, and more data on movements will be required to develop a meaningful metapopulation model for least terns. Data quantity and quality and a huge coordinated effort such as exists for the roseate tern (*Sterna dougallii*) on the East Coast (Spendelow et al. 1995) would make metapopulation modeling feasible.

Least tern populations in California and portions of the East Coast also are considered endangered by federal or state agencies. These other populations are stable or increasing (Calif. Least Tern Recovery Plan 1980, Engstrom et al. 1990) perhaps because of intensive management of habitats and control of human disturbance and predators. Least terns in California have been intensively studied and managed for more than 20 years (e.g., Massey 1974, Massey and Atwood 1981, Atwood and Massey 1988). Although region-wide trend for the East Coast population seems positive (Engstrom et al. 1990), numbers may be declining in New Jersey, New York, and Virginia, where disturbance and development are rendering typical least tern nesting habitat (mainland beaches) unsuitable (Gochfeld 1983, Beck et al. 1990). On the Gulf Coast, numbers of least terns (about 3,000 in Mississippi and up to 8,000 in Texas) seem stable (Thompson 1982, Jackson and Jackson 1985).

Conclusions and Proposed Scenarios

The results of this study reveal the danger of inferring habitat suitability and potential for population persistence from habitat use patterns and habitat features (Van Horne 1983, Kellner et al. 1992, Martin 1992). I could have concluded that this population should persist and grow because terns neither preferred nor fully used sandbar nor sandpit habitat. Unfortunately, proximate habitat features may not indicate habitat suitability, nor do they reveal the possible selective pressures that influence habitat selection in a system. One must measure components of fitness, determine factors that influence fitness, and relate fitness and factors influencing fitness to habitats or habitat features (Kellner et al. 1992).

Although the numbers of terns on the lower Platte fluctuated somewhat during the 4 years of the study, these data are not enough to demonstrate effects of habitat suitability on population trend in such a long-lived species, especially when immigration and emigration rates are unknown. The simulation model based on realistic parameter estimates indicated that productivity may not be high enough on the lower Platte to sustain the local population through local recruitment alone. This indicates that habitat suitability in general (on both sandbars and sandpits) is not quite adequate to support the population.

Population trends must be assessed as well as patterns of habitat use and suitability, especially in disturbed systems. Populations in disturbed systems may be declining despite appropriate habitat use. Patterns of habitat use that match habitat suitability may not lead to population persistence in the following 3 scenarios: (1) when habitat suitabilities have been reduced below that required for population maintenance because of human disturbance, (2) when habitat suitability is naturally low, and immigration from source areas maintains the population (Weins and Rotenberry 1981, Pulliam 1988, Pulliam and Danielson 1991), or (3) when post-fledging survival is poor during migration or on wintering grounds.

Historically, least terns were abundant along the Missouri and Mississippi drainages (Hardy 1957, U.S. Fish and Wildl., Serv. 1991). Although decline of least terns on the Platte River is not certain because no reliable population estimates are available prior to 1982, nesting habitat has been degraded along the central Platte (Ziewitz et al. 1992). Habitat changes adjacent to the Platte River probably have changed predator populations and may have increased predation rates on terns, thus reducing habitat suitability. Humans also influence egg and chick mortality by disturbing colonies. Recreationists and sandpit operators have crushed some nests and chicks every year since 1985, when monitoring started (Nebr. Game and Parks Comm., Lincoln, Platte River interior least tern and piping plover nesting survey, Unpubl. mimeogr. reports, 1985–90). When disturbed by humans or airboats, older chicks often ran into heavy vegetation near the nesting area and to shorelines on both habitats, and chicks on sandbars occasionally jumped or fell into the river (author, pers. observ.; J. G. Sidle, U.S. For. Serv., Chadron, Nebr., pers. commun.). Disturbed adults were noisy and also may have attracted predators.

This population may have been a "sink" before humans altered the system if overall habitat suitability has always been low, or this population may have recently become a sink if habitat changes and human influences have altered predation and mortality rates. Because there are little data on movement of Interior least terns among breeding areas or of productivity in these areas, it is impossible to determine which areas could provide immigrants to the Platte River. Terns that nest within 200 km of the lower Platte either produce few fledglings (central Platte—Lingle 1993*a*; Missouri River between Gavins Point Dam and Ponca, Nebr.—Schwalbach 1988, Dirks 1990) or their numbers are small (1–13 pairs, Elkhorn River—Dinan et al. 1993; 9–11 pairs, Council Bluffs, Ia.—Dinsmore et al. 1993). Twenty to 108 pairs of terns use the Loup River (which drains into the Platte) and 100 to 204 pairs of terns use the Niobrara River (approx 200 km to north), but productivity for these populations is unknown or only estimated for 1 year (1985, 0.96 fledglings/pair; G. Wingfield, Niobrara River interior least tern and piping plover nesting survey, Unpubl. rep. to Nebr. Game and Parks Comm., Lincoln, 13pp., 1985) (Dinan et al. 1993). Least terns can disperse to distant areas and wander widely (e.g., Boyd and Thompson 1985, Bardon 1992, Lingle 1993*b*); thus, the lower Platte River population may be supplemented by terns from distant areas.

If the lower Platte population is declining, high postfledging mortality during migration and on wintering grounds is unlikely the only cause. Productivity would need to be very high to sustain a population with annual postfledging mortality >15%. If observed productivity reflects historical productivity, this population would have gone extinct long ago without immigration from other areas.

Alternatively to these 3 scenarios, populations of long-lived animals could decline slowly over long periods and recover during relatively short and infrequent periods of high productivity (Mertz 1971, Caswell 1982). The population of least terns on the lower Platte may exhibit such a pattern. Many more years of census data or age-structure data would be required to test this scenario.

Most animals live in systems disturbed in some way by industrialized society. In disturbed systems, we must assess habitat availability and suitability and evaluate possible population trends to understand how to conserve species. Under the dominant paradigm of natural selection, habitat selection will adjust in response to selective pressures within the constraints of a species' behavioral plasticity and genetics. If change is rapid and suitabilities are severely reduced, animals cannot respond effectively to the change. Many habitats have changed slowly and insidiously. Animals may settle in habitats according to habitat suitabilities as predicted by theory, but habitat suitabilities may be unnaturally poor and the populations cannot persist.

MANAGEMENT IMPLICATIONS

No matter which of the 3 above scenarios applies to least terns on the Platte River, clearly the goal of management on the breeding grounds should be to increase chick survival. The Nebraska Game and Parks Commission, U.S. Fish and Wildlife Service, Platte River Whooping Crane Habitat Maintenance Trust, and Nebraska and Central Public Power districts currently use a variety of fences and nest exclosures at least tern and piping plover (*Charadrius melodus*) colonies on the Platte. These agencies also actively educate the public and post colonies with signs to discourage human disturbance. These efforts generally have been successful in protecting eggs from predators and humans in Nebraska and elsewhere (Minsky 1980, Rimmer and Deblinger 1992). However, I have demonstrated that chick survival is critical to fledgling production. Chicks wander widely and often are not adequately protected with measures currently used in Nebraska. Entire sandbars should be declared off limits to humans, and fencing needs to be designed to keep chicks in and predators out, perhaps by adding hardware cloth along the bottom of the fence. When terns nest on a sandpit peninsula, nests and chicks can be protected by placing electric fencing across the peninsula arm (Lackey 1994). However, most terns nest on sandbars or areas of sandpits that are not easy or economical to fence. Chick shelters (Jenks-Jay 1982) can be placed in areas used by chicks if owls and black-crowned night-herons are suspected predators. Further monitoring is needed to determine which predators take large numbers of chicks, and research is needed to determine how chicks (and nests) can be protected from different predators. Fencing cannot alleviate avian predation. Current management efforts should continue and their effectiveness should be monitored.

Nebraska Game and Parks Commission has found that visual fencing (signs and painted wooden laths with baling twine strung between) is usually effective in deterring human intrusion at colonies. Although Erwin (1989) recommends that signs be placed at least 100 m from the closest nest, and Rogers and Smith (1995) recommend about 200 m, this is often not possible on many sites, especially sandbars. Because colony-site turn-over rates are relatively low for least terns on the Platte, signs could be put up before birds arrive (Erwin 1989) at many recently used sites.

Managers will always run the risk of having the birds colonize outside of the posted area, not return to nest at the site (Britton 1982), or having chicks disperse to areas outside of the fencing. Such posting of colonies occasionally attracts attention, and vandalism has been a problem at some sites on the Platte River (Cooper and Fries 1993; G. R. Lingle, Platte River Whooping Crane Habitat Maintenance Trust, Inc., Grand Island, Nebr., pers. commun.; J. J. Dinan, Nebr. Game and Parks Comm., Lincoln, pers. commun.). However, if colonies are posted with signs informing that these birds are protected by the Endangered Species Act of 1973 (Public Law No. 93-205, 87 Statute 884), vandals and intruders can be more easily prosecuted (Cooper and Fries 1993).

How effective increasing chick survival is in ensuring population recovery will depend on levels of postfledging survival and population structure. Postfledging survival and immigration and emigration need to be estimated for the Platte River and other breeding areas. Interior least terns have been banded throughout their breeding range for several years. However, relocating and identifying banded terns is difficult in a large study area. More effort needs to be expended to recapture and resight banded terns to estimate survival and dispersal rates.

LITERATURE CITED

AKCAKAYA, H. R. 1994. RAMAS/metapop: viability analysis for stage-structured metapopulations (version 1.0). Applied Biomathematics, Setauket, N.Y. 185pp.

ALATALO, R. V., A. LUNDBERG, AND S. ULFSTRAND. 1985. Habitat selection in the pied flycatcher *Ficedula hypoleuca*. Pages 59–83 *in* M. L. Cody, ed. Habitat selection in birds. Academic Press, Inc., San Diego, Calif.

ATWOOD, J. L., AND B. W. MASSEY. 1988. Site fidelity of least terns in California. Condor 90:389–394.

BARDON, K. 1992. Least terns in Dakota County. Loon 64:222–223.

BECK, R. A., J. W. AKERS, J. W. VIA, AND B. WILLIAMS. 1990. Status and distribution of the least tern in Virginia—1975 to 1988. Va. J. Sci. 41: 404–418.

BEGON, M., AND M. MORTIMER. 1986. Population ecology—a unified study of plants and animals. Second ed. Blackwell Scientific Publ., Boston, Mass. 200pp.

BENTAL, R. 1982. Nebraska's Platte River, a graphical analysis of flows. Conserv. and Surv. Div., Univ. Nebr., Lincoln. Nebr. Water Surv. Pap. 53. 47pp.

BOOHAR, J. A., C. G. HOY, AND M. J. ELLIS. 1989. Page 165 *in* Water resources data—Nebraska—water year 1989. U.S.D.I. Geol. Surv. Water-Data Rep. NE-89-1.

———, ———, AND G. V. STEELE. 1990. Page 148 *in* Water resources data—Nebraska—water year 1990. U.S.D.I. Geol. Surv. Water-Data Rep. NE-90-1.

BOYD, R. L. 1987. Habitat management and population ecology studies of the least tern in Kansas and Oklahoma. Biol. Dep., Baker Univ., Baldwin City, Kans., Prepared for Nongame Wild. Progr., Kansas. Wildl. and Parks Comm., Topeka. 61pp.

———. 1990. Habitat management and population ecology studies of the least tern in Kansas and Oklahoma. Biol. Dep., Baker Univ., Baldwin City, Kans., Prepared for Nongame Wild. Prog., Kans. Wildl. and Parks Comm., Topeka. 49pp.

———. 1993. Site tenacity, philopatry, longevity, and population trends of least terns in Kansas and northwestern Oklahoma. Pages 196–205 *in* K. F. Higgins and M. R. Brashier, eds. Proc. Missouri River and its tributaries: piping plover and least tern symp. South Dakota State Univ., Brookings.

———, AND B. C. THOMPSON. 1985. Evidence for reproductive mixing of least tern populations. J. Field Ornithol. 56:405–406.

BRITTON, E. E. 1982. Least tern management by protection of nesting habitat. Trans. Northeast Sect. Wildl. Soc., Cherry Hill, N.J. 39:87–92.

BROWNIE, C., D. R. ANDERSON, K. P. BURNHAM, AND D. S. ROBSON. 1985. Statistical inference from band recovery data: a handbook. Second ed. U.S. Fish and Wildl. Serv., Res. Publ. 156. 305pp.

BUCKLEY, F. G. 1978. Colony site selection by colonial waterbirds in coastal New Jersey. Proc. Colonial Waterbird Group 1:17–26.

BUCKLEY, P. A., AND R. DOWNER. 1992. Modelling metapopulation dynamics for single species of seabirds. Pages 563–585 *in* D. R. McCullogh and R. H. Barrett, eds. Wildlife 2001: populations. Elsevier, London, U.K.

BURGER, J. 1984. Colony stability in least terns. Condor 86:61–67.

———. 1988. Social attraction in nesting least terns: effects of numbers, spacing, and pair bonds. Condor 90:575–582.

———, AND M. GOCHFELD. 1988. Nest-site and temporal patterns in habitat use of roseate and common terns. Auk 105:433–438.

———, AND ———. 1990. Nest site selection in least terns (*Sterna antillarum*) in New Jersey and New York. Colonial Waterbirds 13:31–40.

———, AND F. LESSER. 1978*a*. Selection of colony sites and nest sites by common terns *Sterna hi-*

rundo in Ocean County, New Jersey. Ibis 120: 433–449.

———, AND ———. 1978*b*. Nest site selection in an expanding population of herring gulls. J. Field Ornithol. 51:270–280.

———, AND ———. 1979. Breeding behavior and success in salt marsh common tern colonies. Bird-Banding 50:322–337.

———, AND J. SHISLER. 1980. Colony and nest-site selection in laughing gulls in response to tidal flooding. Condor 82:251–258.

CALIFORNIA LEAST TERN RECOVERY PLAN. 1980. U.S. Fish and Wildl. Serv., Reg. 1, Portland, Oreg. 58pp.

CASWELL, H. 1982. Life history theory and the equilibrium status of populations. Am. Nat. 120: 317–339.

CATCHPOLE, C. K. 1974. Habitat selection and breeding success in the reed warbler (*Acrocephalus scirpaceus*). J. Anim. Ecol. 43:363–380.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York, N.Y. 234pp.

CLOBERT, J., J. D. LEBRETON, AND D. ALLAINE. 1987. A general approach to survival rate estimation by recaptures or resightings of marked birds. Ardea 75:133–142.

CONOVER, W. J. 1980. Practical nonparametric statistics. Second ed. John Wiley and Sons, Inc., New York, N.Y. 494pp.

COOPER, J. L., AND D. E. FRIES. 1993. Law enforcement: how we can help protect least terns and piping plovers. Pages 15–19 *in* K. F. Higgins and M. R. Brashier, eds. Proc. Missouri River and its tributaries: piping plover and least tern symp. South Dakota State Univ., Brookings.

COULSON, J. C., AND J. HOROBIN. 1976. Influence of age on the breeding biology and survival of the arctic tern *Sterna paradisaea*. J. Zool. 178: 247–260.

———, AND R. D. WOOLLER. 1976. Differential survival rates among breeding kittiwake gulls *Rissa tridactyla* (L.). J. Anim. Ecol. 45:205–213.

COWARDIN, L. M., D. S. GILMER, AND C. W. SHAIFFER. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildl. Monogr. 92. 37pp.

CRESPI, B. J. 1989. Variable selection and size-related mating patterns in natural populations of *Elaphrothrips tuberculatus*: a path analysis. Am. Midl. Nat. 122:142–155.

———. 1990. Measuring the effect of natural selection on phenotypic interaction systems. Am. Nat. 135:32–47.

DESGRANGES, J., AND A. REED. 1981. Disturbance and control of selected colonies of double-crested cormorants in Quebec. Colonial Waterbirds 4:12–19.

DICOSTANZO, J. 1980. Population dynamics of a common tern colony. J. Field Ornithol. 51:229–243.

DINAN, J. J., G. A. WINGFIELD, AND J. G. SIDLE. 1993. Surveys of least terns and piping plovers in Nebraska. Pages 62–63 *in* K. F. Higgins and M. R. Brashier, eds. Proc. Missouri River and its tributaries: piping plover and least tern symp. South Dakota State Univ., Brookings.

DINSMORE, S. J., J. J. DINSMORE, AND D. L. HOWELL. 1993. Least terns nesting on fly-ash deposits. Pages 103–107 *in* K. F. Higgins and M. R. Brashier, eds. Proc. Missouri River and its tributaries: piping plover and least tern symp. South Dakota State Univ., Brookings.

DIRKS, B. J. 1990. Distribution and productivity of least terns and piping plovers along the Missouri and Cheyenne rivers in South Dakota. M.S. Thesis, South Dakota State Univ., Brookings. 64pp.

DOBSON, A. P., AND A. M. LYLES. 1989. The population dynamics and conservation of primate populations. Conserv. Biol. 4:362–380.

EBERHARDT, L. L. 1990. Survival rates required to sustain bear populations. J. Wildl. Manage. 54: 587–590.

ELLISON, L. N., AND L. CLEARY. 1978. Effects of human disturbance on breeding of double-crested cormorants. Auk 95:510–517.

ENGSTROM, R. T., G. S. BUTCHER, AND J. D. LOWE. 1990. Population trends in the least tern (*Sterna antillarum*) from Maine to Virginia: 1975–1986. Pages 130–138 *in* J. R. Sauer and S. Droege, eds. Survey designs and statistical methods for the estimation of avian population trends. U.S. Fish and Wildl. Serv. Biol. Rep. 90(1).

ERWIN, R. M. 1978. Population and colony site dynamics in selected Massachusetts waterbirds. Proc. Colonial Waterbird Group 1:19–25.

———. 1989. Responses to human intruders by birds nesting in colonies: experimental results and management guidelines. Colonial Waterbirds 12: 104–108.

———, J. GALLI, AND J. BURGER. 1981. Colony site dynamics and habitat use in Atlantic coast seabirds. Auk 98:550–561.

———, AND D. C. SMITH. 1985. Habitat comparisons and productivity in nesting common terns on the Mid-Atlantic coast. Colonial Waterbirds 8:155–165.

FAANES, C. A. 1983. Aspects of the nesting ecology of least terns and piping plovers in central Nebraska. Prairie Nat. 15:145–154.

FISK, E. J. 1978. Roof-nesting terns, skimmers, and plovers in Florida. Fla. Field Nat. 6:1–22.

FLEMMING, S. P., R. D. CHAISSON, P. C. SMITH, P. J. AUSTIN-SMITH, AND R. P. BANCROFT. 1988. Piping plover status in Nova Scotia related to its reproductive and behavioral responses to human disturbance. J. Field Ornithol. 59:321–330.

FRETWELL, S. D. 1972. Populations in a seasonal environment. Monogr. Popul. Biol. 5. 217pp.

———, AND H. L. LUCAS, JR. 1970. On territorial behavior and other factors influencing habitat distribution in birds: I. Theoretical development. Anim. Behav. 19:16–36.

GIFFIN, J. G., J. M. SCOTT, AND S. MOUNTAINSPRING. 1987. Habitat selection and management of the Hawaiian crow. J. Wildl. Manage. 51:485–494.

GILL, R. E., JR., AND L. R. MEWALDT. 1983. Pacific coast Caspian terns: dynamics of an expanding population. Auk 100:369–381.

GOCHFELD, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. Pages 207–270 *in* J. Burger, H. Winn, and B. Olla, eds. Behavior of marine animals. Vol. 4. Marine birds. Plenum Press, New York, N.Y.

———. 1983. Colony site selection by least terns: physical attributes of sites. Colonial Waterbirds 6:205–213.

GOLDIN, M., C. GRIFFIN, AND S. MELVIN. 1989. Reproductive and foraging ecology, human disturbance, and management of piping plovers at Breezy Point, Gateway National Recreation Area, New York. Natl. Park Serv. Coop. Res. Unit, Rutgers State Univ., New Brunswick, N.J. 58pp.

GOODRICH, L. J. 1982. The effects of disturbance on reproductive success of the least tern (*Sterna albifrons*). M.S. Thesis, Rutgers State Univ., New Brunswick, N.J. 100pp.

GORE, J. A., AND M. J. KINNISON. 1991. Hatching success in roof and ground colonies of least terns. Condor 93:750–762.

GREENWOOD, R. J., A. B. SARGEANT, D. H. JOHNSON, L. M. COWARDIN, AND T. L. SHAFFER. 1987. Mallard nest success and recruitment in prairie Canada. Trans. North Am. Wildl. and Nat. Resour. Conf. 52:298–310.

GROVER, P. B., AND F. L. KNOPF. 1982. Habitat requirements and breeding success of Charadriiform birds nesting at Salt Plains National Wildlife Refuge, Oklahoma. J. Field Ornithol. 53:139–148.

HARDY, J. W. 1957. The least tern in the Mississippi Valley. Mich. State Univ. Mus. Publ. Vol. 1(1). 60pp.

HARRIS, M. P. 1979. Survival and ages of first breeding of Galapagos seabirds. Bird-Banding 50:56–61.

HAYS, H., AND M. LECROY. 1971. Field criteria for determining incubation stage in eggs of common tern. Wilson Bull. 83:425–429.

HILDÉN, O. 1965. Habitat selection in birds: a review. Ann. Zool. Fenn. 2:53–75.

HILL, L. A. 1985. Breeding ecology of Interior least terns, snowy plovers, and American avocets at Salt Plains National Wildlife Refuge, Oklahoma. M.S. Thesis, Oklahoma State Univ., Stillwater. 106pp.

HINES, J. E. 1987. Winter habitat relationships of blue grouse on Hardwiche Island, British Columbia. J. Wildl. Manage. 51:426–435.

HUTTO, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. Pages 455-476 *in* M. L. Cody, ed. Habitat selection in birds. Academic Press, Inc., San Diego, Calif.

ISENMANN, P., J. D. LEBRETON, AND R. BRANDL. 1990. The black-headed gull in Europe. Acta. Congr. Int. Ornithol. 20:2384–2389.

JACKSON, J. A., AND B. J. S. JACKSON. 1985. Status, dispersion, and population changes of the least tern in coastal Mississippi. Colonial Waterbirds 8:54–62.

JAMES, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215–236.

JENKS-JAY, N. 1982. Chick shelters decrease avian predators in least tern colonies on Nantucket Island, Massachusetts. J. Field Ornithol. 53:58–60.

JERNIGAN, L. S., JR., R. F. SOOTS, JR., J. F. PARNELL, AND T. L. QUAY. 1978. Nesting habits and breeding populations of the least tern (*Sterna albifrons antillarum*) in North Carolina. Univ. North Carolina, Wilmington, NOAA Sea Grant Publ. UNC-SG-78-07. 39pp.

JOHNSON, D. H., AND T. L. SHAFFER. 1990. Estimating nest success: when Mayfield wins. Auk 107:595–600.

JOHNSON, R. A., AND D. W. WICHERN. 1988. Applied multivariate statistical analysis. Second ed. Prentice Hall, Englewood Cliffs, N.J. 607pp.

KADLEC, J. A., AND W. H. DRURY. 1968. Structure of the New England herring gull population. Ecology 49:644–676.

KARR, J. R., AND R. R. ROTH. 1971. Vegetation structure and avian diversity in several New World areas. Am. Nat. 105:423–435.

KELLNER, C. J., J. D. BRAWN, AND J. R. KARR. 1992. What is habitat suitability and how should it be measured? Pages 476–488 *in* D. R. McCullough and R. H. Barrett, eds. Wildlife 2001: populations. Elsevier, London, U.K.

KIRK, R. E. 1982. Experimental design: procedures for the behavioral sciences. Second ed. Brooks/Cole Publ. Co., Belmont, Calif. 911pp.

KIRSCH, E. M. 1992. Habitat selection and productivity of least terns (*Sterna antillarum*) on the lower Platte River, Nebraska. Ph.D. Thesis, Univ. Montana, Missoula. 119pp.

KLOPFER, P. H., AND R. H. HAILMAN. 1965. Habitat selection in birds. Adv. Study Behav. 1:279–303.

LACKEY, J. L. 1994. Planning strategies and recommendations for the protection of least terns and piping plovers at sand and gravel mines along the lower Platte and Loup rivers, Nebraska. M.S. Thesis, Univ. Nebraska, Lincoln. 78pp.

LANDE, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). Oecologia (Berlin) 75:601–607.

LI, C. C. 1975. Path analysis—a primer. Boxwood, Pacific Grove, Calif. 346pp.

LINGLE, G. R. 1993*a*. Causes of nest failure and mortality of least terns and piping plovers along the central Platte River. Pages 130–136 *in* K. F. Higgins and M. R. Brashier, eds. Proc. Missouri River and its tributaries: piping plover and least tern symp. South Dakota State Univ., Brookings.

———. 1993*b*. Site fidelity and movements of least terns and piping plovers along the Platte River, Nebraska. Pages 189–191 *in* K. F. Higgins and M. R. Brashier, eds. Proc. Missouri River and its tributaries: piping plover and least tern symp. South Dakota State Univ., Brookings.

MACARTHUR, R. H., J. W. MACARTHUR, AND J. PEER. 1962. On species diversity: II. Prediction of bird census from habitat measurements. Am. Nat. 96: 167–174.

MARTIN, T. E. 1992. Breeding productivity considerations: what are the appropriate features for management? Pages 455–473 *in* J. Hagan and D. W. Johnston, eds. Ecology and conservation of neotropical migrants. Smithsonian Institution Press, Washington, D.C.

MASSEY, B. W. 1974. Breeding biology of the California least tern. Proc. Linn. Soc. N.Y. 71:1–23.

———, AND J. L. ATWOOD. 1981. Second-wave nesting of the California least tern: age composition and reproductive success. Auk 98:596–605.

———, D. W. BRADLEY, AND J. L. ATWOOD. 1992. Demography of a California least tern colony including effects of the 1982–1983 El Niño. Condor 94:976–983.

———, AND J. M. FANCHER. 1989. Renesting by California least terns. J. Field Ornithol. 60:350–357.

MAYER, P. M., AND M. P. DRYER. 1989. Population biology of piping plovers and least terns on the Missouri River in North Dakota, 1989 field season. Div. Fish and Wildl. Enhancement, U.S. Fish and Wild. Serv., Bismark, N.D. 54pp.

MAYFIELD, H. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456–466.

MCCRIMMON, D. A. 1978. Nest site characteristics among five species of herons on the North Carolina coast. Auk 95:267–280.

MCNICHOLL, M. K. 1975. Larid site tenacity and group adherence in relation to habitat. Auk 92: 98–104.

MERTZ, D. B. 1971. Life history phenomena and increasing and decreasing populations. Pages 361–399 *in* G. P. Patil, E. C. Pielou, and W. E. Waters, eds. Statistical ecology. Vol. 2. Pennsylvania State Univ. Press, University Park.

MILLS, J. A. 1990. Lifetime production in the red-billed gull. Acta. Congr. Int. Ornithol. 20:1522–1527.

MINSKY, D. 1980. Preventing fox predation at a least tern colony with an electric fence. J. Field Ornithol. 51:180–181.

MITCHELL-OLDS, T. 1987. Analysis of local variation in plant size. Ecology 68:82–87.

MORRIS, R. F. 1959. Single-factor analysis in population dynamics. Ecology 40:580–588.

MORSE, D. H. 1985. Habitat selection by North American parulid warblers. Pages 131–157 *in* M. L. Cody, ed. Habitat selection in birds. Academic Press, Inc., San Diego, Calif.

MOSER, R. 1940. The piping plover and least tern in Omaha. Nebr. Bird Rev. 8:92–94.

NETTLESHIP, D. N. 1972. Breeding success of the common puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. Ecol. Monogr. 42:239–268.

NOON, B. R., AND C. M. BILES. 1990. Mathematical demography of spotted owls in the Pacific Northwest. J. Wildl. Manage. 54:18–27.

PARTRIDGE, L. 1974. Habitat selection in titmice. Nature 247:573–574.

———. 1978. Habitat selection. Pages 351–376 *in* J. R. Krebs and N. Davies, eds. Behavioral ecology: an evolutionary approach. Sinauer Assoc., Sunderland, Mass.

PIEROTTI, R. 1982. Habitat selection and its effect on reproductive output in the herring gull in Newfoundland. Ecology 63:854–868.

PODOLER, H., AND D. ROGERS. 1975. A new method for the identification of key factors from life-table data. J. Anim. Ecol. 44:85–114.

POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture–recapture experiments. Wildl. Monogr. 107. 97pp.

PULLIAM, H. R. 1988. Sources, sinks, and population regulation. Am. Nat. 132:652–661.

———, AND B. J. DANIELSON. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am. Nat. 137:S50–S66.

RENKEN, R. B., AND J. W. SMITH. 1995. Annual adult survival of Interior least terns. J. Field Ornithol. 66:112–116.

RICE, J., R. D. OHMART, AND B. W. ANDERSON. 1983. Habitat selection attributes of an avian community: a discriminant analysis investigation. Ecol. Monogr. 53:263–290.

RIMMER, D. W., AND R. D. DEBLINGER. 1992. Use of fencing to limit terrestrial predator movements into least tern colonies. Colonial Waterbirds 15:226–229.

ROGERS, J. A., AND H. T. SMITH. 1995. Set-back distances to protect nesting bird colonies from human disturbance in Florida. Conserv. Biol. 9:89–99.

RYAN, M. R., B. G. ROOT, AND P. M. MAYER. 1993. Status of piping plovers in the Great Plains of North America: a demographic simulation model. Conserv. Biol. 7:581–585.

SAFINA, C., D. WITTING, AND K. SMITH. 1989. Viability of salt marshes as nesting habitat for common terns in New York. Condor 91:571–584.

SAS INSTITUTE, INC. 1990. SAS/STAT user's guide, version 6. Fourth ed. SAS Inst., Cary, N.C. 943pp.

SCHULENBERG, J. H., AND M. B. PTACEK. 1984. Status of the Interior least tern in Kansas. Am. Birds 38:975–981.

SCHWALBACH, M. J. 1988. Conservation of least terns and piping plovers along the Missouri River and its major western tributaries in South Dakota. M.S. Thesis, South Dakota State Univ., Brookings. 93pp.

SHAFFER, M. L. 1981. Minimum population sizes for species conservation. BioScience 31:131–134.

SIDLE, J. G., D. E. CARLSON, E. M. KIRSCH, AND J. J. DINAN. 1992. Flooding: mortality and habitat renewal for least terns and piping plovers. Colonial Waterbirds 15:132–136.

———, AND E. M. KIRSCH. 1993. Least tern and piping plover nesting at sand pits in Nebraska. Colonial Waterbirds 16:139–148.

———, E. D. MILLER, AND P. J. CURRIER. 1989. Changing habitats in the Platte River valley of Nebraska. Prairie Nat. 21:91–104.

———, AND J. W. ZIEWITZ. 1990. Use of aerial videography in wildlife habitat studies. Wildl. Soc. Bull. 18:56–62.

SIMONS, T. R. 1984. A population model of the endangered Hawaiian dark-rumped petrel. J. Wildl. Manage. 48:1065–1076.

SLADE, N. A., AND H. LEVENSON. 1982. Estimating population growth rates from stochastic Leslie matrices. Theor. Popul. Biol. 22:299–308.

———, AND ———. 1984. Effect of skewed distributions of vital statistics on growth of age-structured populations. Theor. Popul. Biol. 26: 361–366.

SMITH, J. W., AND R. B. RENKEN. 1991. Least tern nesting habitat in the Mississippi River valley adjacent to Missouri. J. Field Ornithol. 62:497–504.

———, AND ———. 1993. Reproductive success of least terns in the Mississippi River valley. Colonial Waterbirds 16:35–44.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Second ed. W. H. Freeman & Co., New York, N.Y. 859pp.

SPEAR, L. B., T. M. PENNIMAN, J. F. PENNIMAN, H. R. CARTER, AND D. G. AINLEY. 1987. Survivorship and mortality factors in a population of western gulls. Stud. Avian Biol. 10:44–56.

SPENDELOW, J. A., AND J. D. NICHOLS. 1989. Annual survival rates of breeding adult roseate terns. Auk 106:367–374.

———, ———, I. C. T. NISBET, H. HAYS, G. D. CORMONS, J. BURGER, C. SAFINA, J. E. HINES, AND M. GOCHFELD. 1995. Estimating annual survival and movement rates of adults within a metapopulation of roseate terns. Ecology 76:In Press.

THOMPSON, B. C. 1982. Distribution, colony characteristics, and population status of least terns breeding on the Texas coast. Ph.D. Thesis, Texas A&M Univ., College Station. 123pp.

———, AND R. D. SLACK. 1982. Physical aspects of colony selection by least terns on the Texas coast. Colonial Waterbirds 5:161–168.

U.S. FISH AND WILDLIFE SERVICE. 1985. Endangered and threatened wildlife and plants: Interior population of the least tern determined to be endangered. Fed. Regist. 50:21784–21792.

———. 1991. Recovery plan of the Interior population of the least tern, *Sterna antillarum*. U.S. Fish and Wildl. Serv., Twin Cities, Minn. 90pp.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. J. Wildl. Manage. 47: 893–901.

VARLEY, G. C., AND G. R. GRADWELL. 1960. Key factors in population studies. J. Anim. Ecol. 29: 399–401.

VERMEER, K., AND K. DEVITO. 1987. Habitat and nest-site selection of mew and glaucous-winged gulls in coastal British Columbia. Stud. Avian Biol. 10:105–118.

———, D. POWER, AND G. E. J. SMITH. 1988. Habitat selection and nesting biology of roof-nesting glaucous-winged gulls. Colonial Waterbirds 11: 189–201.

WECKER, S. C. 1963. The role of early experience in habitat selection by the prairie deer mouse, *Peromyscus maniculatus bairdi*. Ecol. Monogr. 33:307–325.

———. 1964. Habitat selection. Sci. Am. 211:109–116.

WHITMAN, P. L. 1988. Biology and conservation of the endangered Interior least tern: a literature review. U.S. Fish and Wildl. Serv. Biol. Rep. 88(3). 22pp.

WIENS, J. A. 1970. Effects of early experience on substrate pattern selection in *Rana aurora* tadpoles. Copeia 1970:543–548.

———. 1972. Anuran habitat selection: early experience and substrate selection in *Rana cascadae* tadpoles. Anim. Behav. 20:218–220.

———, AND J. T. ROTENBERRY. 1981. Censusing and the evaluation of avian habitat occupancy. Stud. Avian Biol. 6:522–532.

WILKINSON, L. 1990. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Ill. 677pp.

WILLIAMS, G. P. 1978. The case of the shrinking channels—the North Platte and the Platte rivers in Nebraska. U.S. Geol. Surv. Circ. 781. 48pp.

WOOTTON, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology 75:151–165.

WRIGHT, S. 1960. Path coefficients and path regressions: alternative or complementary concepts? Biometrics 16:189–202.

———. 1968. Genetic and biometrical foundations. Vol. 1. Pages 299–372 *in* Evolution and genetics of populations. Univ. of Chicago Press, Chicago, Ill.

ZIEWITZ, J. W., J. G. SIDLE, AND J. J. DINAN. 1992. Characteristics and management of least tern and piping plover nesting habitat on the Platte River, Nebraska. Prairie Nat. 24:1–20.

ZIMMERMAN, J. L. 1982. Nesting success of dickcissels (*Spiza americana*) in preferred and less preferred habitats. Auk 99:292–298.

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APPENDIXES

Appendix A. Latitude–longitude locations of sandbar and sandpit study sites along the lower Platte River and numbers of pairs present at each during 1987–90.

Study sites	Latitude	Longitude	Years and no. of pairs monitored			
			1987	1988	1989	1990
Sandbar						
Loup Return	41°23′N	97°15′W		12		
Schuyler-Medinger	41°23′N	97°05′W				21
Skull Creek	41°28′N	96°52′W		16		
North Bend	41°27′N	96°47′W	14			
Morse Bluff	41°26′N	96°44′W			12	
Fremont Bridge	41°22′N	96°30′W			12	
Leshara	41°22′N	96°27′W				3
Two Rivers	41°11′N	96°19′W			9	
Willow Point	41°03′N	96°19′W	33	9		
I-80 Bridge	41°01′N	96°18′W				9
South Bend	41°01′N	96°15′W			7	
Hwy 50 Bridge	41°01′N	96°10′W				5
Cedar Creek West	41°04′N	96°08′W			6	
Cedar Creek	41°03′N	96°05′W		14		3
Lower Cullom	41°05′N	96°01′W			9	
Upper Cullom	41°03′N	96°03′W				12
Chris Lake	41°03′N	95°59′W	14			
Sandpit						
Columbus	41°25′N	97°22′W	21			
Bellwood Section 13	41°21′N	97°15′W	11	15	7	7
Arps	41°26′N	97°04′W				6
Wolf	41°26′N	96°44′W	9			
Hartford Fremont	41°27′N	96°32′W	12	16	5	9
Western Fremont	41°25′N	96°29′W				9
Ginger Cove	41°20′N	96°21′W			5	
Hartford Valley	41°17′N	96°19′W			11	27
Gretna	41°08′N	96°18′W			5	21
Western North	41°00′N	96°02′W	9	5	6	19

Appendix B. Numbers of pairs, nests, and eggs; nesting, hatching, and fledging success; and fledglings per pair at sandbar colonies on the lower Platte River, 1987–90. Plus signs indicate that the number of eggs in all nests had not been determined before certain nests were lost or destroyed.

Year and colony	No. pairs	No. nests	No. eggs	Nesting success	Hatching success	Fledging success	Fledglings/ pair
1987							
Willow Point	33	33	86	0.81	0.79	0.09	0.18
Chris Lake	14	22	52	0.67	0.65	0.18	0.43
North Bend	14	14	33	0.00	0.00		0.00
1988							
Loup Return	12	24	63	0.32	0.30	0.21	0.33
Skull Creek	16	19	50	0.89	0.78	0.28	0.69
Willow Point	9	12	29	0.82	0.86	0.32	0.89
Cedar Creek	14	22	55	0.86	0.84	0.30	1.00
1989							
Morse Bluff	11–12	20	34+	0.05	0.06	0.00	0.00
Fremont Bridge	12	17	39	0.47	0.44	0.53	0.75
Two Rivers	9	10	26	0.60	0.62	0.06	0.11
South Bend	7	16	33	0.38	0.52	0.41	1.00
Cedar Creek West	6	6	21	0.62	0.71	0.07	0.17
Lower Cullom	9	15	32	0.33	0.41	0.54	0.78
1990[a]							
Schuyler	21	22	49	0.95	0.90	0.38	0.81
LeShara	3	3	7	1.00	0.86	0.33	0.67
I-80 Bridge	9	9	17+	0.89	0.82	0.00	0.00
Louisville Bridge	5	5	13	1.00	1.00	0.00	0.00
Cedar Creek	3	3	6	1.00	1.00	0.00	0.00
Upper Cullom	12	12	31	0.58	0.58	0.00	0.00

[a] Numbers of nests and eggs for 1990 are from renest sites. All early nests and eggs were lost during flooding.

Appendix C. Numbers of pairs, nests, and eggs; nesting, hatching, and fledging success; and fledglings per pair at sandpit colonies on the lower Platte River, 1987–90. Numbers in parentheses indicate nests and eggs at a site for which outcomes were known. Plus signs indicate that the number of eggs in all nests had not been determined before certain nests were destroyed.

Year and colony	No. pairs	No. nests	No. eggs	Nesting success	Hatching success	Fledging success	Fledglings/ pair
1987							
Columbus	21	21	60	1.00	0.92	0.16	0.43
Bellwood	11	11	27	0.09	0.11	1.00	0.27
Morse Bluff	9	10	27	0.00	0.00		0.00
Hartford Fremont	12	18	38	0.64	0.62	0.24	0.50
Western North	9	16	34	0.56	0.65	0.09	0.22
1988							
Bellwood	15	29	72	0.60	0.55	0.10	0.27
Hartford Fremont	16	20	52	0.95	0.88	0.13	0.38
Western North	5	6	16	0.66	0.62	0.50	1.00
1989							
Bellwood	7	16	26	0.38	0.52	0.28	0.57
Hartford Fremont	5	8 (7)	20 (18)	0.43	0.44	0.38	0.60
Ginger Cove	5	6	14	0.67	0.78	0.18	0.40
Hartford Valley	11	17	38	0.70	0.74	0.32	0.82
Gretna	5	10	23 (22)	0.67	0.59	0.92	2.40
Western North	6	11	24+	0.36	0.46	0.20	0.33
1990							
Bellwood	7	13	30+	0.60	0.80	0.62	1.14
Arps	6	8	11+	0.00	0.00		0.00
Hartford Fremont	9	9 (8)	21 (18)	0.78	0.76	0.12	0.22
Western Fremont	9	10 (9)	25 (23)	0.70	0.67	0.47	0.89
Hartford Valley	27	36 (33)	83 (77)	0.64	0.65	0.37	0.74
Gretna	21	28 (27)	70 (67)	0.82	0.84	0.30	0.86
Western North	19	21 (20)	58 (55)	0.95	0.86	0.20	0.53

Appendix D. Path coefficients and Pearson correlation coefficients (indicated in parentheses) among mortality rates, numbers of nests and chicks, track trail index, and habitat variables for least tern colonies on sandbars along the lower Platte River, 1987–90. For path coefficients, independent variables are depicted at the head of arrows and dependent variables are depicted at the end of arrows in Figure 6.

	Dependent variables							
Independent variables	Overall mortality	Laying mortality	Egg mortality	Chick mortality	No. nests	No. chicks	Track trail index	Distance to bank
Laying mortality	−0.01		(0.05)	(0.28)				
Egg mortality	−0.16	(0.05)		(−0.44)		−0.77***		
Chick mortality	0.83***	(0.28)	(−0.44)					
No. nests		0.73	0.43***	0.07		(0.56)	−0.05	
No. chicks				−0.08	(0.56)		−0.55	
Track trail index			−0.19	0.20				
Distance to bank		0.32			−0.16		−0.50	
% colony flooded		0.39	0.23	0.37				(0.30)

*** Significant Pearson correlation or partial regression, $P < 0.001$.

Appendix E. Path coefficients and Pearson correlation coefficients (indicated in parentheses) among mortality rates, numbers of nests and chicks, track trail index, and habitat variables for east tern colonies on sandpits along the lower Platte River, 1987–90. For path coefficients, independent variables are depicted at the head of arrows and dependent variables are depicted at the end of arrows in Figure 7.

	Dependent variables						
Independent variables	Overall mortality	Laying mortality	Egg mortality	Chick mortality	No. nests	No. chicks	Track trail index
Laying mortality	−0.08		(0.33)	(−0.07)			
Egg mortality	−0.29	(0.33)		(−0.67)***		−0.63***	
Chick mortality	1.26***	(−0.07)					
No. nests		2.05	0.91***	0.13		(0.80)	−0.32
No. chicks				0.40			0.40
Track trail index			−0.02	0.03			
% area bounded by water		−0.08			0.09		−0.10
Distance to abundant vegetation		0.18			0.30		0.53

*** Significant Pearson correlation or partial regression, $P < 0.001$.