BREEDING ECOLOGY OF INTERIOR LEAST TERNS ON THE UNREGULATED YELLOWSTONE RIVER, MONTANA

LYNN M. BACON AND JAY J. ROTELLA
Biology Department
Montana State University
Bozeman, Montana 59717 USA

Abstract.—We investigated the breeding ecology of Interior Least Terns (*Sterna antillarum athalassos*) on the unregulated Yellowstone River, Montana. In 1994–1996, we estimated hydrologic patterns, population size, habitat use, and breeding success along 200 km of river. We sampled habitat availability on 105 km of river during the 1995 breeding season. In 1994, river flows peaked early and were low throughout the breeding season. In 1995 and 1996, flows were more typical of the long-term-average hydrograph. Annual variation in estimates of the breeding population and the timing of nesting corresponded with annual variation in hydrology. We counted 40 adults (18 nests) in 1994, 21 adults (11 nests) in 1995, and 19 adults (6 nests) in 1996. Terns nested earlier in 1994 than in 1995 or 1996. During the peak period of nest initiation in 1995, the only nesting habitat available in 105 km of river was on eight vegetated channel bars. Almost all (32 of 35) nests were on bare cobble on the upstream portions of vegetated channel bars. Despite wide fluctuations in river flows, no nests were inundated. Nest success was 89% in 1994, 64% in 1995, and 100% in 1996. Annual variation in breeding numbers, clutch size, nest success, and chick survival caused large differences in annual estimates of recruitment (23 fledglings in 1994, 1 in 1995, and 4 in 1996). Although annual estimates of breeding numbers and nest-initiation dates varied according to yearly hydrologic patterns, annual variation in nest success and chick survival seemed unrelated to changes in river-flow rates. Poor recruitment in 1995 seemed to be most strongly influenced by weather events. Unlike on rivers with human-altered flows, predation and human disturbance did not appear to influence recruitment greatly.

ECOLOGÍA REPRODUCTIVA DE *STERNA ANTILLARUM ATHALASSOS* EN EL RÍO YELLOWSTONE NO REGULADO EN MONTANA

Sinopsis.—Investigamos la ecología reproductiva de *Sterna antillarum athalassos* en el Río Yellowstone no regulado en Montana. Entre 1994 y 1995, estimamos patrones hidrológicos, tamaño poblacional, uso del habitat, y éxito reproductivo a través de 200 km del río. Muestreamos la disponibilidad del habitat en 105 km del río durante la temporada reproductiva del 1995. Entre 1995 y 1996 los flujos fueron más típicos del promedio de largo tiempo del hidrógrafo. La variación anual en los estimados de la población reproductiva y en la temporada de anidaje correspondieron con variaciones anuales en hidrología. Contamos 40 adultos (18 nidos) en 1994, 21 adultos (11 nidos) en 1995, y 19 adultos (6 nidos) en 1996. Durante el período de mayor iniciación de nidos en 1995, el único habitat de anidaje disponible en los 105 km de río estaba en ocho barras de canal con vegetación. Casi todos (32 de 35) los nidos se hallaron en pedruzcos expuestos en las porciones de barras de canal con vegetación superiores. Ningún nido se nundó, a pesar de las amplias fluctuaciones en el flujo del río. El éxito de los nidos fué de 89% en 1994, de 64% en 1995, y del 100% en 1996. La variación anual en los números reproductivos, tamaños de las camadas, éxito de nido, y supervivencia de los pichones crearon grandes diferencias en los estimados anuales de reclutamiento (23 volantones en 1994, 1 en 1995, y 4 en 1996). Aunque los estimados anuales de numeros de aves reproduciéndose y las fechas de inicio de anidaje variaron de acuerdo a los patrones hidrológicos anuales, la variación anual en éxito de anidaje y en la supervivencia de pichones parecen no estar relacionados con cambios en las tasos de flujo del río. El pobre reclutamiento del 1995 pareció estar más altamente influenciado por eventos climáticos. A diferencia de ríos con flujos alterados por los humanos, la depredación y el disturbio humano no pareció influenciar el reclutamiento grandemente.

Historically, the interior population of Least Terns nested on sandbars throughout the Mississippi and Missouri river systems (Sidle et al. 1988). Changes in hydrology resulting from channelization, damming, and agricultural water diversions have reduced availability of sandbar habitat throughout most of this population's breeding range (U.S. Fish and Wildlife Service 1991, Whitman 1988). Loss of nesting habitat, less predictable flows, and untimely releases of water from dams combined with perceived declines and low productivity in Least Tern populations were the primary reasons the Interior Least Tern was listed as endangered in 1985 (U.S. Fish and Wildlife Service 1985, 1991).

Few colonies of Least Terns breed in free-flowing river systems because flows are altered and/or regulated on most interior rivers. Consequently, most information on use of breeding habitat is from birds using human-altered habitat. However, habitat choices in human-altered systems may be associated with low productivity (Kirsch 1996) and may misdirect management efforts to restore tern populations. It is important to study breeding ecology of Interior Least Terns in habitats that are less disturbed by humans (e.g., unregulated rivers; Kreil and Dryer 1987). Specifically, data are needed regarding habitat availability, habitat use, and breeding success of Least Terns nesting in river systems that undergo large, natural fluctuations in flow rates resulting from melting snow and local stormwater runoff.

We conducted this study along the Yellowstone River, an unregulated tributary of the Missouri River, which supports a small and previously undetermined number of Least Terns. The objectives of the study were to: (1) estimate the number of birds breeding on the area, (2) investigate habitat availability as a function of temporal variation in river flow, (3) characterize nesting habitat, and (4) evaluate breeding success.

STUDY AREA

The study area was the 200 river km (rkm) of the Yellowstone River occurring between Miles City (46°24′N, 105°39′W) and Crane (47°34′N, 104°16′W), Montana (Bacon 1996, Kellerhals et al. 1976). We delineated three strata within the study area. Each stratum had different characteristics and was approximately 66.5 rkm long. The river channel in stratum 1 (the upstream stratum) was sinuous to meandering with occasional channel bars. In stratum 3, the channel was sinuous to meandering with many islands (exposed land with mature trees and shrubs) and lateral channels (sloughs), and it had a higher frequency of mid-channel bars than stratum 1. Stratum 2 had intermediate characteristics.

Average historical mean-daily-discharge rate at Miles City was 357 m^3/s (Shields et al. 1994, 1995, 1996). The highest mean-monthly-discharge rate typically occurs in June (987 m^3/s) (Fig. 1). Mean annual rainfall on the study area averages 35 cm (5 cm/mo for May–August), and mean monthly high/low temperatures for May–August average 27/13 C (National Oceanic and Atmospheric Administration 1994).

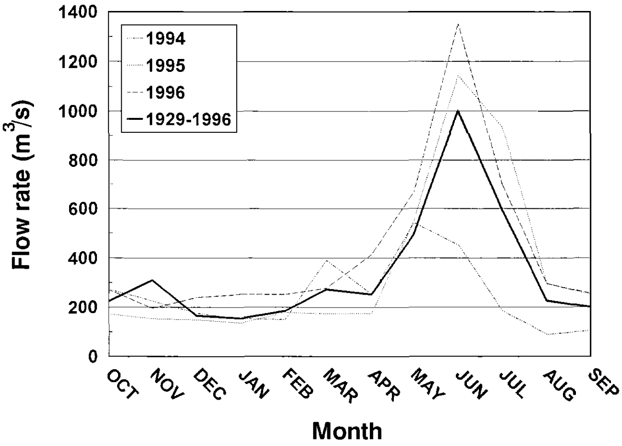

FIGURE 1. Annual variation in mean-monthly flow rates for the Yellowstone River at Miles City, Montana, 1929–1996.

METHODS

Hydrography.—Daily river-flow rates recorded at the Miles City hydrologic station (Shields et al. 1994, 1995, 1996) were used to depict historic data (1929–1996) on mean-monthly flow rates. We used historic data to calculate how often mean monthly flows such as those of 1994–1996 occurred during 1929–1993.

Breeding population.—In 1994–1996, we conducted surveys for Least Terns throughout the study area starting before nest-initiation (beginning in late May or early June) and continuing through early August to estimate the size of the breeding population. We surveyed the study area for terns at least once per week 9 Jun.–3 Aug. 1994, 26 May–4 Aug. 1995, and 12 Jun.–12 Aug. 1996. During surveys, we boated the entire study area and searched for terns except when high water flows prevented us from safely using boats. During high flows in mid-June 1995 and 1996, we surveyed nesting areas from the banks of the river.

Prior to nesting, terns often sat on exposed cobble or sand along the water's edge or flew (chasing other terns and usually vocalizing) above potential nesting areas. Therefore, during the first 1–3 surveys each year, we used binoculars and spotting scopes to scan all areas of bare cobble or sand in the river channel (including the river's banks) throughout the study area. Later in the season as terns became less visible, we walked all areas of exposed cobble (potential nesting habitat, see below) to locate terns and their nests. We assumed that all terns counted during surveys conducted before any nests hatched were adults and used the highest single-survey count in each year as an estimate of annual population size on the study area. Given our survey intensity and the small population size (see Results), we felt that we were able to census the population size with reasonable accuracy.

Available nesting habitat.—In 1995, we used a stratified sampling scheme to estimate the amount of available nesting habitat at three different times during the breeding season. We divided each river stratum into 19 3.5-rkm units, randomly selected 10 units/stratum, and sampled habitat availability in those units during: (1) pre-nesting (9–12 July; 1000–1100 m^3/s), (2) nesting (21–24 July; 800–850 m^3/s), and (3) chick-rearing (2–6 August; 400–500 m^3/s). Based on previous results (Kirsch 1996), we considered all exposed ground within the river channel that was greater than 30 m^2 and had less than 10% of its area covered by vegetation to be available nesting habitat. At each location with available nesting habitat, we recorded habitat type and habitat area. Habitat type was classified as vegetated or unvegetated mid-channel bar, slough bar (main river channel on one side and ephemeral channel on opposite side), or point bar (riverbank habitat) (Kellerhals et al. 1976). For vegetated bars, we only considered the portion of the bar that consisted of unvegetated cobble to be available nesting habitat for Least Terns. (We note that during our study annual vegetation growth never caused unvegetated areas to become vegetated to an extent that rendered them unsuitable for nesting.) We did not measure other habitat variables (e.g., landscape metrics) or measure habitat availability in other years because of logistical constraints.

Characteristics of nesting areas.—During the nesting season, we located nests by watching flying terns until they returned to their nests. For each bar used for nesting, we recorded habitat type, area of available nesting habitat (unvegetated cobble), location, vegetative cover, dominant plant species, and substrate characteristics. In 1995, we paced the dimensions of nesting bars to estimate the area (using appropriate formulae for calculating areas of ellipses or triangles) of the bar and the area of unvegetated cobble.

Productivity.—Each nest was marked with a small numbered stick (<0.5-m long and 1–2-m distant) and visited every 5–7 d. We estimated incubation stage of each nest based on egg flotation (Hays and LeCroy 1971, Schwalbach 1988). We estimated initiation date by subtracting the estimated number of incubation days and 1 d for each egg in the clutch. We considered nests with ≥1 pipped egg, egg fragments, or chick droppings in the nest bowl as successful. We calculated apparent nest success (number of successful nests/total number of nests) because detectability of Least Tern nests is high and mortality may occur catastrophically (e.g., flooding) rather than at a constant rate (Johnson and Shaffer 1990). We used the binomial estimator to estimate confidence intervals for nest success.

We visited nesting bars every 7 d through early August to estimate fledgling production for each colony. Because we did not individually mark young, we could not determine the number of young fledged by each nesting pair. Thus, we could calculate annual means but not variances for number fledged/nest. Consequently, we could not perform statistical comparisons of fledglings/nesting pair among years. However, because we had a virtual census of adults, nests, and fledglings each year, our

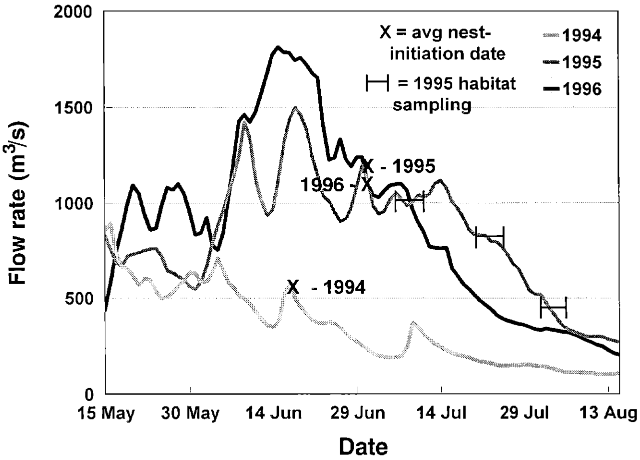

FIGURE 2. Spring and summer daily-mean flow rates for the Yellowstone River at Miles City, Montana, 1994–1996.

annual totals for fledgling production do indicate annual differences in total productivity.

We used ANOVA to compare annual means for clutch size, nest-initiation date, and the lag between timing of peak flows and nest initiation. If ANOVA results were significant, we used Tukey's test to conduct multiple comparisons (Steel and Torrie 1980). Given the small breeding population and resulting small sample sizes, we attempted to achieve a balance between Type I and Type II error rates by using 0.1 as a guideline for determining statistical significance of results.

RESULTS

Hydrography.—Annual hydrographs and the timing and magnitude of peak daily-discharge rates varied by year. In 1994, flows peaked early (16 May, 903 m^3/s) and were low throughout the season (Figs. 1 and 2). Mean monthly flow only peaked as early as the month of May in one other year from 1929–1993. Mean monthly flows as low as those of 1994 occurred in 10% of historic years. In contrast to 1994 data, hydrographs for 1995 and 1996 peaked later and were characterized by higher flows (Figs. 1 and 2). Flows peaked on 18 June in 1995 (1514 m^3/s) and 15 June in 1996 (1833 m^3/s). In 1995–1996, the timing and magnitudes of mean monthly flows were similar to flows in 50–67% of historic years.

Breeding population.—Estimates of numbers of adult terns and nesting pairs varied by year. We counted 40 adult terns and 18 nests (includes one renesting attempt) in 1994, 21 adults and 11 nests in 1995, and 19 adults and 6 nests in 1996. We were not able to determine when Least Terns returned to the study area in all years. In 1994 and 1996, birds had already arrived by the time surveys began on 9 and 12 June, respectively.

However, in 1995, surveys began on 26 May, and terns were not seen on the area until 10 June.

Timing of nesting.—Timing of nest initiation varied among years ($F_{2,31} = 13.9$, $P < 0.001$). In 1994, the mean nest-initiation date was 16 June ($n = 17$, SE = 2.3 d, range = 3 June–11 July), which was significantly earlier ($P < 0.008$) than the mean date in 1995 (30 June, $n = 11$, SE = 2.2 d, range = 20 June–15 July) or 1996 (1 July, $n = 6$, SE = 1.5 d, range = 26 June–5 July). Mean lag times between date of peak flow and nest-initiation date also varied by year ($F_{2,31} = 23.1$; $P < 0.001$). In 1994, the mean lag was 31 d (SE = 2.3), which was longer ($P < 0.008$) than the mean lag in 1995 (11 d, SE = 2.2) or 1996 (16 d, SE = 1.5). Lag times were not different in 1995 and 1996 ($P = 0.54$).

Available nesting habitat.—During the peak of nest initiation in 1995–1996, flows were approximately 1100 m^3/s (Fig. 2). During surveys conducted at 1000–1100 m^3/s, only a small amount of nesting habitat was available, all on vegetated channel bars ($n = 8$ in 105 rkm sampled; estimated 15.2 bars/200 rkm) with a Recent Alluvial Bar community type (Hansen et al. 1995). Each channel bar had an average of 2.38 ha ($n = 8$, SE = 1.14) of bar exposed above water and 0.13 ha (SE = 0.02) of unvegetated cobble (available nesting habitat) at its upstream end. At lower flow rates, all types of bars were exposed (Table 1). We estimated that 74 channel bars/200 rkm with available nesting habitat were exposed during the peak of nest initiation in 1994.

Characteristics of nesting areas.—Terns did not nest on all available bars in any year. We found nests on nine bars in 1994 (74 bars were estimated to be exposed in 200 rkm), six bars in 1994 (15 bars estimated to be exposed), and three (15 bars estimated to be exposed) in 1996. Terns nested on 11 different vegetated channel bars (nine in 1994, six in 1995, and three in 1996) and one point bar (1996). In 1995, terns re-occupied, five of the nine bars used in 1994. In 1996, terns re-occupied two previously used vegetated bars. Two channel bars were used in all three years. When terns were first seen on the study area in 1995–1996, two of the channel bars used for nesting in 1994 were submerged, and the other seven had <25 m^2 of available nesting habitat exposed per bar; on some of these seven bars, logs were the only exposed substrate. Prior to initiating nests in 1995–1996, terns loafed on the seven bars that had exposed substrate (either on cobble or logs). In 1995, one pair subsequently nested on a log that was the only exposed substrate during high flows.

Thirty-two of 35 nests were on bare cobble on the upstream portions of vegetated channel bars. Channel bars used for nesting were composed of recent sediment deposits and had a *Populus deltoides*/Recent Alluvial Bar community type (Hansen et al. 1995). Seedlings and saplings of *P. deltoides* (<13-cm diameter at breast height) dominated each bar. On the upstream portions of nesting bars, where nests were located, vegetative cover averaged 2.5% and primarily consisted of seedlings and saplings of plains cottonwood (*P. deltoides*) and sandbar willow (*Salix exigua*) <2.0 m in height. Ten of the 11 channel bars used for nesting remained sur-

TABLE 1. Amount of exposed bar habitat in 105 km of the Yellowstone River, Montana, at three flow rates in 1995. Unvegetated portions of vegetated bars and 100% of other bar habitat types were considered available habitat for Least Terns. Surveys were conducted 9–12 July (1000–1100 m^3/s), 21–24 July (800–850 m^3/s), and 2–6 August (400–450 m^3/s).

	Habitat amount (ha) in 105 km of river[a]											
	1000–1100 m^3/s				800–850 m^3/s				400–450 m^3/s			
Habitat type	*n*	Mean	SE	Total	*n*	Mean	SE	Total	*n*	Mean	SE	Total
Vegetated bar	8	2.38	1.13	19.0	20	5.10	0.89	102.0	35	7.30	0.82	486.7
unvegetated portion		0.13	0.02	2.0		0.31	0.05	11.8		0.68	0.06	23.8
Unvegetated bar	0				2	0.48	0.36	1.0	14	1.10	0.14	15.4
Point bar	0				3	1.17	0.51	6.7	19	2.49	0.56	90.1
Slough bar	0				6	1.56	0.51	17.8	3	2.78	0.29	72.3

[a] Data presented are the numbers of exposed bars for each habitat type (*n*), means and SEs for bar sizes, and totals for the amount (ha) of habitat exposed in each habitat type on 105 km of river.

rounded by flowing water throughout the breeding season. Channel bar locations were consistent among years.

In 1995, the average nesting bar found and measured when flows were 1000–1100 m^3/s had 2.0 ha of bar exposed above the water (n = 4, SE = 0.7, range = 0.6–3.2) and 0.4 ha of unvegetated cobble on its upstream end (SE = 0.2), which was more than the 0.1 ha (SE = 0.02) of cobble exposed on available bars (t_{10} = 1.94, P = 0.08). Two additional nesting bars that were found and measured when flows were 800–850 m^3/s had an average of 2.3 ha of exposed bar (SE = 0.4, range = 1.1–2.6) with 0.5 ha (SE = 0.2) of unvegetated cobble on their upstream ends. At flows of 800–850 m^3/s, the four bars found earlier in the season averaged 2.5 ha (SE = 0.8; 0.7 ha of unvegetated cobble, SE = 0.3). Amounts of exposed cobble on nesting bars ($\bar{x}$ = 0.6 ha, SE = 0.2) and available bars were not different ($\bar{x}$ = 0.4 ha, SE = 0.1) at flows of 800–850 m^3/s (t_{24} = 1.35, P = 0.19).

Productivity.—Clutch size varied by year ($F_{2,32}$ = 4.36, P = 0.02). Clutch size was higher (P = 0.05) in 1994 ($\bar{x}$ = 2.7, n = 18, SE = 0.1) than in 1995 ($\bar{x}$ = 2.1, n = 11, SE = 0.2). Clutch size in 1996 ($\bar{x}$ = 2.2, n = 6, SE = 0.8) did not differ from clutch size in other years ($P > 0.27$), but statistical power was low given the small sample size of nests in 1996. Nest success was 88.9% in 1994 (n = 18, 90% Cl = 76.7–100%), 63.6% in 1995 (n = 11, 90% Cl = 39.8–87.5%), and 100% in 1996 (n = 6). We estimated that 23 chicks fledged in 1994 (1.4 fledglings/nest), 1 fledged in 1995 (0.1 fledglings/nest), and 4 fledged in 1996 (0.7 fledglings/nest).

Although causes of most egg, nestling, and fledgling losses could not be determined with certainty, we found no evidence (e.g., presence of strand lines or water-borne debris) of nests being flooded in any year. Severe hailstorms occurred during the weeks in which four nests (three with eggs and one with nestlings) failed in 1995. We saw a toad (*Bufo woodhousii woodhousii*) ingesting a 1–2-day-old tern in 1995. In 1996, three chicks (<1-wk-old) hatched on a point bar may have died because of human disturbance: tire tracks were made approximately 20 m from the nest during the week in which the chicks died.

DISCUSSION

We hypothesize that the magnitude and timing of river flows influenced the number of breeding Least Terns on the Yellowstone River by affecting habitat availability early in the breeding season. In 1994, mean monthly flow rates peaked earlier than they have in 62 of the past 68 years, and average flow rates were unusually low. Thus, breeding habitat was available earlier and in greater abundance in 1994 than in more typical years (e.g., 1995 or 1996) and may have permitted more terns to nest. Accordingly, Least Terns were more numerous in 1994 (n = 40) than in 1995 (n = 21) or 1996 (n = 19).

Despite annual variation in the magnitude and timing of peak flow rates, all nests were initiated after flows had peaked each year, and no nests were inundated. We speculate that terns adjusted the timing of nest initiation in accordance with annual hydrologic patterns. During years with high spring flows, we saw terns loafing at previously used nesting bars and subsequently found nests on those bars when flows declined and nesting habitat was exposed. This suggests that the presence of exposed bare substrate may provide an important cue for adjusting the timing of nesting. However, in 1994 when much nesting habitat was exposed throughout the spring and summer, terns did nest earlier than in 1995–1996 but not as early as they might have based on availability of nesting habitat alone. Thus, we speculate that combinations of cues such as habitat availability and daylength may be used to adjust the timing of nesting. We also hypothesize that water clarity, water temperature, and the number of fish active near the water's surface may serve as proximate cues.

Reproductive success of Least Terns on the Yellowstone River varied greatly among years but was high on average. Our estimate of nest success was greater than point estimates from other studies of Interior Least Terms: 84.2% on the Yellowstone River (this study, years weighted equally) versus 51% on the Missouri River, 61% on the Platte River, and 60% on the Mississippi River (Kirsch 1996). Similarly, our mean annual estimate of fledglings/nesting pair ($\bar{x} = 0.73$, years weighted equally) was higher than average ratios for other populations nesting on rivers: 0.41 on the Missouri River, 0.38 on the Platte River, and 0.60 on the Mississippi River (Kirsch 1996).

Unlike results from studies of Interior Least Terns breeding in other areas (Kirsch 1996, Lingle 1993, Sidle et al. 1992, Smith and Renken 1993), predation and human disturbance apparently did not have strong negative effects on reproduction on the Yellowstone River. Hail, rain, and wind storms were likely the largest mortality sources during our study. The relative seclusion of the channel bars used for nesting (most had water flowing around them throughout the summer), the limited number of access sites to the river, and difficult navigation during mid-summer low flows likely decreased the probability of disturbance from humans. Habitat outside the riparian zone primarily consisted of large fields used for small-grain production and cattle grazing. Such land-use was not likely to contribute to predation or human disturbance along the river. (Cattle were rarely seen in the river except in sloughs where they were occasionally encountered late in the season when river flows declined.) Scouring ice and high flow rates each spring likely prevent the development of mature vegetation and associated predator communities.

Our results indicate that Least Terns can nest successfully despite variable river flow rates associated with a large unregulated river. In particular, nests were initiated after spring flows receded, and no nests were flooded during spring runoff. Usable nesting habitat was available in all years. Vegetated channel bars with early successional vegetation and the scouring flows necessary to maintain an early successional stage appear to be important to Least Terns on the Yellowstone River. The average breeding population was small ($n = 26.7$ adults). However, this small number represents 53.3% of the Montana Least Tern recovery objective of 50 adults breeding in Montana (U.S. Fish and Wildlife Service 1991). Although reproductive rates were, on average, quite high, fledgling production was extremely low in 1995. We suspect that random weather events were primarily responsible for losses.

The Yellowstone River provides a system for studying Least Terns under relatively natural conditions. However, because the Yellowstone River supports a relatively small number of nesting pairs, further investigation of factors influencing the timing of nesting and reproductive success should also be conducted on smaller, unregulated rivers less peripheral to the Missouri and Mississippi River drainages. In particular, rivers that have large populations of Least Terns should be chosen for study such that important hypotheses can be addressed with adequate statistical power.

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