

COMMUNAL ROOSTING AND FORAGING BEHAVIOR OF STAGING SANDHILL CRANES

DONALD W. SPARLING^{1,2} AND GARY L. KRAPU¹

ABSTRACT.—Each spring more than 300,000 Sandhill Cranes (*Grus canadensis*) roost communally at night in river channels in the Platte River Valley of Nebraska and disperse at dawn to forage in agricultural fields. Cranes with central roosts had activity ranges double the size of those with peripheral roosts; 42% of the birds changed activity ranges prior to the onset of migration. Minimum daily flight distance generally increased during the staging period. Cranes used native grassland and planted hayland more often than expected, relative to their percentage of occurrence, and fed longest there; cornfields were under-utilized. These differences probably reflect, in part, (1) limited distribution of grasslands and haylands resulting in a greater energy expenditure to acquire protein in the form of macroinvertebrates and (2) wider distribution of cornfields with adequate energy-rich foods but limited protein. Cranes probably forage more efficiently and conserve energy by following conspecifics from communal roosts to local feeding grounds, by settling in fields where foraging flocks are already present, and by establishing diurnal activity centers. Alert behavior varied with flock size but not as predicted from group size, presumably because predation of staging adult cranes is inconsequential. *Received 4 Jan. 1993, accepted 15 June 1993.*

Sandhill Cranes of the midcontinent population acquire nutrient reserves for migration and reproduction while on staging areas along the Platte and North Platte rivers in Nebraska (Krapu et al. 1985). Cranes roost communally at night in shallow waters of wide river channels or other wetlands and spend the days foraging in flocks on surrounding uplands (Krapu et al. 1984, Folk and Tacha 1990). Little is known concerning the specific functions of communal roosting and flocking to staging cranes beyond a probable advantage of reducing the risk of predation through increased predator detection (*sensu* Pulliam 1973, Caraco 1979) or evasive behaviors unique to groups. In some species of birds, communal roosts may serve as information centers, increasing foraging efficiency (Ward and Zahavi 1973; Waltz 1982, 1987; but see Bayer 1982; Stutchbury 1988 for contrary opinions). Foraging efficiency can also be increased through local enhancement (Hinde 1961) or use of alternative diurnal roosts (Caccamise and Morrisson 1986, 1988).

In the Platte River Valley, loss of communal roosting habitat has resulted in high densities of staging cranes (Krapu et al. 1984) prompting a need to evaluate spatiotemporal use of existing habitat and choice of foraging sites. In this paper, we examine (1) characteristics and use of

¹ Present address: U.S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, P.O. Box 2096, Jamestown, North Dakota 58402.

² U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, 11510 American Holly Dr., Laurel, Maryland 20708.

activity ranges relative to energy expenditure and food availability, (2) the role of communal roosts in foraging behavior, (3) habitat preferences, and (4) influence of group size and predation on foraging and other behaviors. We also discuss social factors as they pertain to staging behavior in Sandhill Cranes.

STUDY AREA AND METHODS

The study area encompassed 253-km² along the Platte River between Kearney and Shelton, Nebraska. Habitat composition within the study area was 49.8% cornfields, 17.3% native grassland, 10.8% planted hayland (primarily alfalfa and planted grasses), 11.6% riverine, and 10.5% other (roads, homesteads, plowed fields). Interstate 80 (I-80) is adjacent to the north channel of the Platte River. A more complete description is in Krapu et al. (1984).

Radiotelemetry.—During March and April 1978 and 1979, cranes were live-trapped with rocket and cannon-projected nets positioned near groups of mounted crane decoys in cropland and pastures. To minimize disturbance, nets were fired from blinds located several hundred m from decoys. Each captured bird was weighed, aged as juvenile or adult by head plumage (Lewis 1979), and banded. Battery-operated transmitters weighing approximately 40 g (<2% of body weight) were attached to 13 cranes in 1978 and 23 in 1979, using a neck and body loop and backpack harness. Ten birds in 1978 (8 adult, 2 juvenile) and 14 in 1979 (13 adult, one juvenile) were located frequently enough to permit statistically valid analyses of activity ranges and movements.

When feasible, each radio-equipped crane was located at hourly intervals during daylight and once each just after dusk and before dawn. Locations were determined by triangulation from ground vehicles to the nearest 100 m. Fixed-wing aircraft were used when birds could not be located from the ground. No individual was followed in more than one year.

Distances and angles between locations were calculated along straight lines. These distances represent minimal distances because cranes meandered between radio fixes. Birds that were located in the same habitat on two sequential observations were assumed to have remained in that habitat for the interval, and those located in different sites were assumed to have visited only those in which they were recorded.

Cranes center their activities within definable, undefended areas that may change in size and location through time. These "activity ranges" differ from conventional home ranges in that they are transient and occupied only for roosting and feeding. Areas of activity ranges were estimated with a harmonic means method (Dixon and Chapman 1980) including the 95% closest points. When cranes used two or more discrete (as determined by non-overlapping clusters of locations separated by at least 2 km) activity ranges, separate areas were calculated for each.

Time budgets.—Diurnal time budgets were developed within each of the habitats by recording activities of individual cranes at 12-sec intervals throughout the staging period. Time spent observing in each habitat was proportional to the percent of study area covered by that habitat. Individuals were selected arbitrarily by locating a group of cranes in a spotting scope's field of view and, after looking away and slightly moving the scope horizontally and vertically, observing the individual nearest to the intersection of the cross hairs. Observations on an individual lasted from a few sec to 5 min. Observations occurred from 06:00 to approximately 18:00 h CST. Behavioral categories included "resting" (sitting or standing still), "feeding", "alert", "calling", "courting", "aggression" (fighting or being attacked), "locomotion" (walking), and "comfort" (preening). An "unknown" category contained observations that could not be classified as one of the other behaviors.

Statistical analyses.—Unless otherwise stated, all values are means \pm SD. Statistical treatment of distances flown, either among habitats or within a day, were complicated both by missing cells in some cases and repeated observations from marked individuals. We used repeated-measures analysis of variance (Milliken and Johnson 1984) on these data. Angular statistics and correlations were conducted following Batschelet (1981). Behavioral frequencies based on counts were analyzed with *G*-tests (Sokal and Rohlf 1969). Sequential behaviors may not have been truly independent, but we believe that observations were adequately dispersed over birds, groups, and contexts to warrant this type of statistical treatment.

RESULTS

Characteristics and use of activity ranges.—Fifty-seven percent of the nocturnal roosts were centrally located within the activity ranges, 37% were at the periphery, and 6% had too few observations to determine type of activity range (Table 1, Fig. 1). Fourteen birds maintained one activity range, nine had two distinct activity ranges (crane 78–10 had two ranges but only one with enough observations for statistical purposes), and one had three ranges. Among cranes with peripheral roosts, 73% had activity ranges south of their nocturnal roosts.

We tested whether activity range size was dependent on type of roost, year, or interaction between type and year. Because accuracy of estimating activity range size is related to the number of observations for an activity range, we weighted the analysis by multiplying the squared residual for each observation by the square root of the number of observations within each range (SAS 1987). Size of activity range differed between roost types ($P = 0.049$). The weighted mean activity range area for individuals with central roosts ($39.6 \pm 64.3 \text{ km}^2$) exceeded that of peripheral roosts ($17.4 \pm 29.0 \text{ km}^2$). The unweighted mean for central roosts was $38.7 \pm 17.1 \text{ km}^2$ and for peripheral roosts was $17.4 \pm 8.3 \text{ km}^2$. There were no differences between years or in interaction between roost type and year ($P > 0.11$).

To test whether the type of roost affected travel distances to foraging locations, we compared the means of distances for first flights in the morning from roosts to feeding locations between years and type of roost. If a crane had two activity ranges of the same type, a combined mean was obtained by weighting each separate mean by its sample size. Means of actual distances from roosts to initial feeding areas did not differ between activity ranges with peripheral roosts ($1285 \pm 388 \text{ m}$) and those with central roosts ($1408 \pm 407 \text{ m}$) nor between years or interaction between years and roost type ($P > 0.40$).

We also examined changes in activity range size and in daily travel distance through the staging period. Activity range types were pooled to assure adequate sample size. No differences were noted between years, among weeks, or in the interaction of the two terms ($P > 0.26$).

TABLE 1
NUMBER, TYPE, AND SIZE (KM²) OF ACTIVITY RANGES OF SANDHILL CRANES DURING
STAGING AT THE PLATTE RIVER, NEBRASKA

Year	Bird	Number of ranges	Activity range size (days observed)		
			Central	Peripheral	
1978	1	1	15.3 (16)		
	3	2	30.3 (8), 23.0 (12)		
	4	2	47.1 (18)	8.9 (8)	
	5	1		15.9 (19)	
	6	1		23.6 (3)	
	10	2 ^a		15.8 (4)	
	12	1	15.3 (16)		
	13	1 ^b			
	15	1		17.6 (20)	
	16	1		11.8 (20)	
	1979	2	1	30.5 (35)	
		3	2	70.5 (26), 5.9 (9)	
		4	1	37.4 (29)	
5		1	61.4 (30)		
10		1	44.2 (25)		
11		2		2.5 (2), 6.0 (6)	
12		2	44.6 (21), 34.5 (8)		
13		3	25.3 (3)	10.2 (8), 12.6 (21)	
14		2	32.1 (13)	23.5 (2)	
15		2	49.6 (9)	17.5 (6)	
16		1	80.3 (27)		
17		1	41.1 (18)		
18		1		37.4 (22)	
19	2	21.2 (22), 4.9 (6)			

^a Only one activity range had sufficient observations to estimate size and determine type.

^b Insufficient observations to estimate size or type.

Minimum daily flight distance varied among weeks ($P = 0.019$). In 1978, flight distances increased from the first to the third week and then declined. In 1979, the increase lasted through the fourth week (Fig. 2). Minimum daily distance was also greater in 1979 (7858 ± 3950 m) than in 1978 (5705 ± 3577 m) ($P = 0.023$). None of the interactions between weeks, years, or roost type was significant ($P > 0.14$).

Information sharing and associations among roosting cranes.—We looked at two major sources of data to determine if cranes followed each other to specific foraging sites. First, we examined synchrony of departure from nocturnal roosts to feeding sites. Synchrony could mean that birds follow each other or that they use a common extrinsic stimulus such as

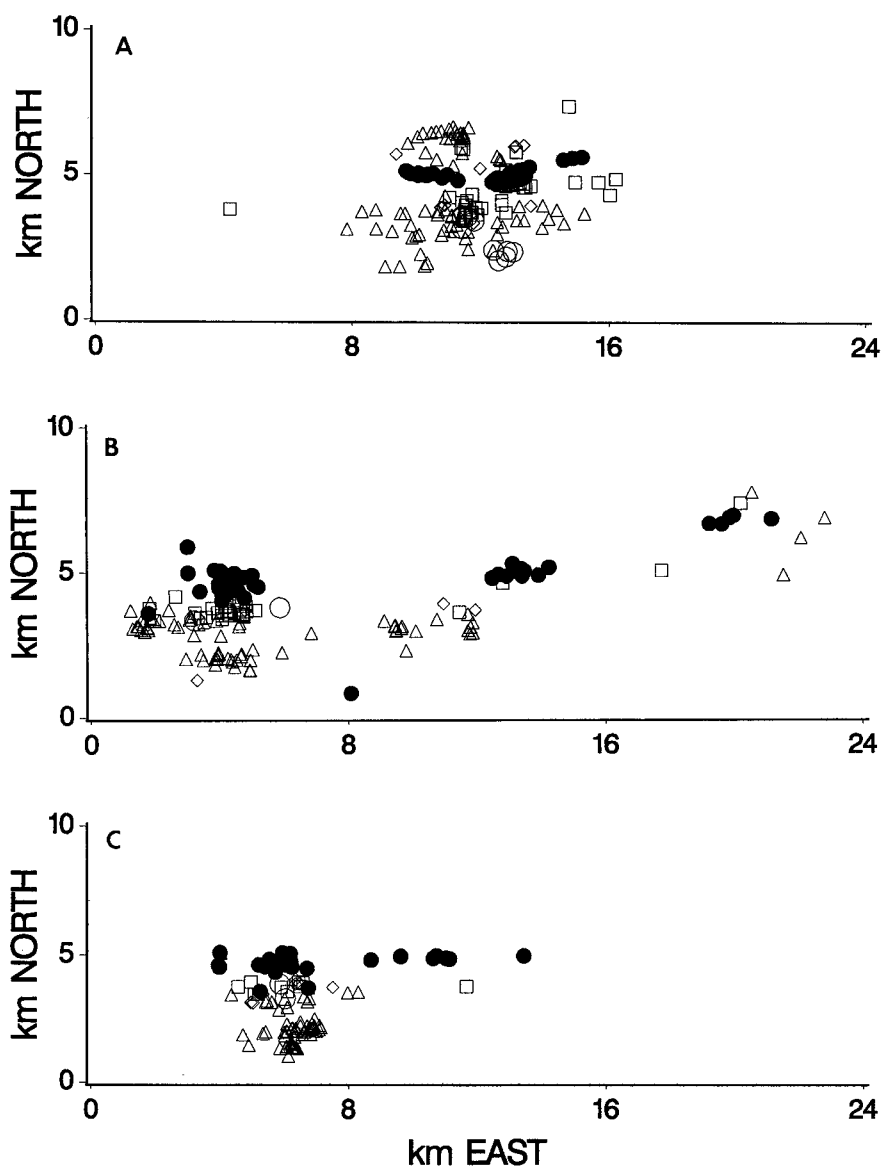


FIG. 1. Examples of activity ranges and habitat locations for staging Sandhill Cranes. A. Bird 79-2 with a centrally located roost, B. Bird 79-13 with three discrete activity ranges, two of which have peripheral roosts, C. Bird 79-18 with a peripheral roost. Habitat types are riparian—closed circles; native grassland—squares; planted hayland—diamonds; cornfields—triangles; other—open circles. Coordinates are based on a common meridian in the universal transverse mercator system. Approximately 33% of all observations were randomly deleted to improve clarity of figures.

sunrise to time departures. We used a χ^2 goodness-of-fit test to compare data presented by Lewis (1974) on crane departures to a Poisson distribution (Fig. 3). Lewis' data indicated that crane departures were more clustered than would be expected by chance ($P < 0.0001$).

Second, we noted that most telemetry locations occurred south of the roosts, suggesting a tendency for roost mates to flock together. For example, five of seven cranes in 1978 with sufficient observations and 12 of 13 in 1979 left roosts in a southern direction. Seventy-five percent of 3102 telemetry locations were south of the communal roosts. The frequency of telemetry locations to the south was higher for peripheral roosts (90.3%) than for central roosts (66.2%) ($P = 0.0035$), for 1979 (78.1%) than for 1978 (70.4%) ($P < 0.0001$), and for interaction between year and type of roost ($P < 0.0001$) (PROC CATMOD, SAS 1987). In 1979, peripheral roosts had a higher percentage of locations south of the communal roosts relative to central roosts than in 1978.

To address further whether cranes from the same roost flew to identical feeding areas, we correlated the angles of morning departures from roosts among all birds. In 1978, only three of 16 possible correlations proved significant ($P < 0.05$). In 1979, relationships were even weaker with three of 69 possible correlations significant ($P < 0.05$). The number of significant correlations in 1979 was not greater than would be expected by chance based on our accepted value for significance.

Habitat preferences.—Usage relative to availability gives some indication of preferred habitats. We characterized activity ranges used by six cranes in 1978 and 14 in 1979. Average habitat composition of these ranges was 44.3% cornfields (range 35.7–51.0%), 19.7% native grassland (12.6–25.8%), 9.6% planted haylands (7.1–14.2%), 17.9% riverine (7.6–29.2%), and 8.5% other (3.4–20.3%). We used the method of Byers et al. (1984) to compare number of locations within each habitat with availability based on overall habitat composition in the study area (Table 2). There was a highly significant difference ($P < 0.0001$) between use and availability. Sandhill Cranes used riverine habitats, native grasslands, and planted haylands more often than expected and cornfields and other habitats less than expected.

Habitat usage varied throughout the day. Before 08:00 h and after 20:00 h 53.1% of the telemetry locations occurred in riverine habitats. Between 08:00–18:00 h cranes primarily used cornfields (51.6% of all locations during this period), native grasslands (28.0%) and planted haylands (16.3%). Use of native grasslands (35.6%) and planted haylands (17.5%) increased from 10:00–16:00 h as cranes gathered in traditional resting areas; cornfield use (43.7%) declined during this period. Use of cornfields increased late in the afternoon (56.2%) before cranes returned to nocturnal roosts.

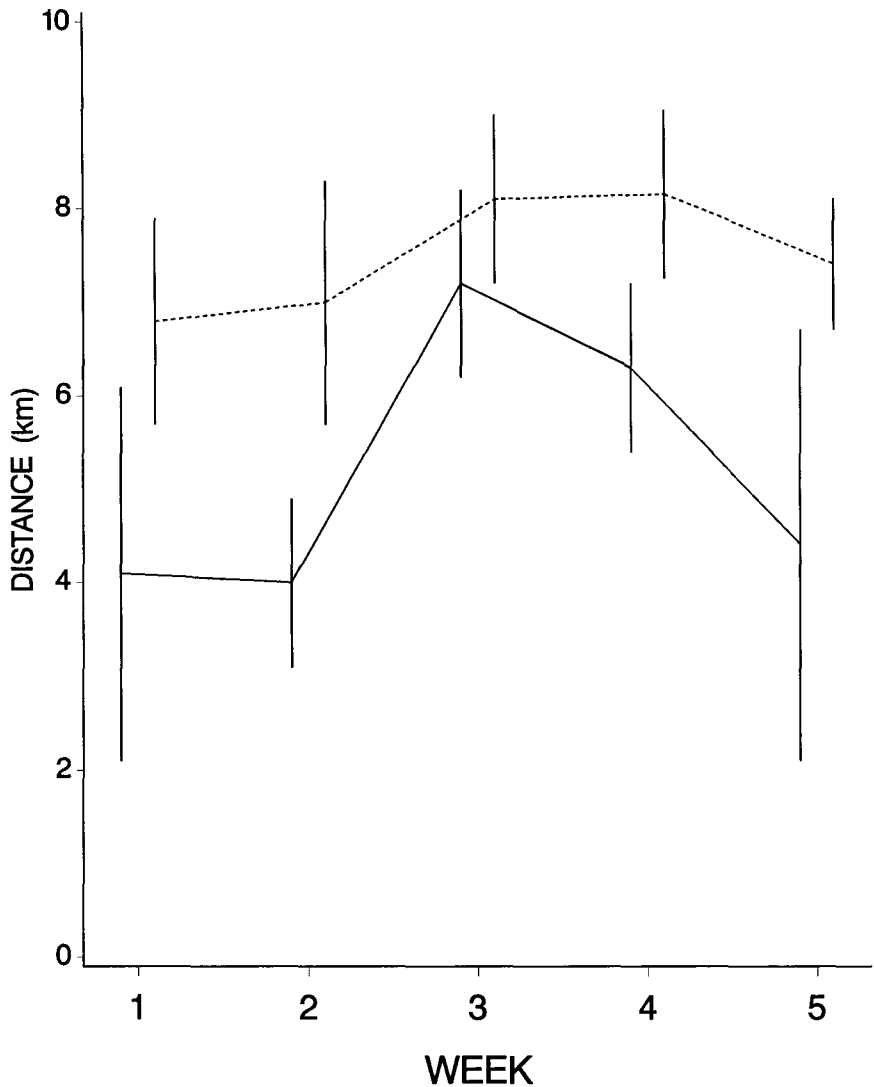


FIG. 2. Minimum daily flight distance through the Sandhill Crane staging periods of 1978 (solid line) and 1979 (dashed line). Birds with peripheral and central roosts are combined within each year. Bars represent $\bar{x} \pm 2$ SE.

We tested whether average flight distance differed among habitats, years, or interaction between year and habitat. To simplify interpretation, we included only cranes that had flown to all five habitats at least once ($N = 19$) and ignored any effect due to type of activity range. Flight distance

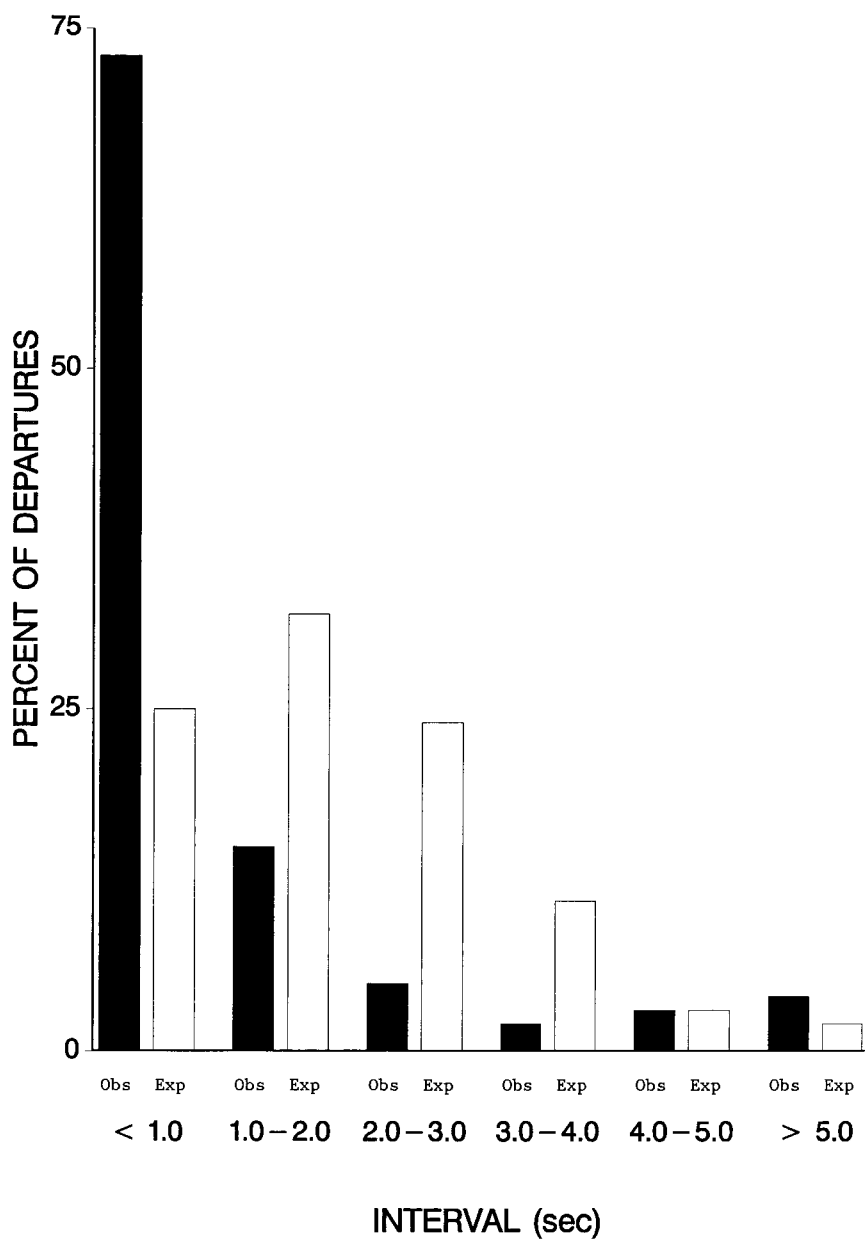


FIG. 3. Observed (filled) frequencies for departure intervals of Sandhill Cranes leaving roost sites compared to expected (open) based on a Poisson distribution of observed values. Data are from Lewis (1974), $N = 5850$ observations.

TABLE 2
PROPORTION OF SANDHILL CRANE VISITS AND MEAN FLIGHT DISTANCES (M) TO DIFFERENT HABITATS DURING STAGING IN NEBRASKA^a

Habitat	Percentage of locations		Bonferonni intervals ^b	Flight distance (SD)	
	Observed	Expected		1978	1979
Riverine	26.4	11.6	23.4–29.8	1839 (1137)	2053 (1467)
Native grassland	24.3	17.3	21.0–27.6	1162 (901)	1645 (1321)
Planted hayland	14.8	10.8	12.1–17.5	976 (893)	1440 (1268)
Cornfield	31.7	49.8	30.5–32.9	916 (800)	1589 (1251)
Other	2.8	10.5	2.4–3.2	712 (620)	1286 (755)

^a A total of 1506 observations were used in the analysis; χ^2 for overall analysis = 531, $df = 4$, $P < 0.0001$.

^b If expected values fall outside of Bonferonni interval, the difference between observed and expected is significant at $P \leq 0.05$ (Byers et al. 1984).

depended upon destination ($P < 0.0001$) (Table 2) and year ($P = 0.003$) but not on the interaction between year and habitat ($P > 0.38$). Flight distances between habitats were greater in 1979 (1741 ± 1354 m) than in 1978 (1156 ± 974 m). In both years, flight distances to riparian roost sites were the longest, followed by those to native grassland. Distances to planted hayland and cornfield were intermediate, and distances to other habitats were shortest.

During the day, cranes fed primarily in native grassland (pasture), hayland, and cornfield (Table 3). Locomotion, which may reflect food searching behavior, was greatest in native grasslands and haylands. Resting occurred primarily in native grasslands and cornfields. Cranes were least often alert in plowed fields (Table 3). Courtship, although rare, was most common in native grasslands and haylands.

Group size and activities.—Frequencies of behaviors during the day varied with flock size (Table 4). Groups of 1–5 and 100–199 individuals fed most, rested least, and were alert most often. Cranes in flocks > 200 tended to rest and engage in comfort behaviors such as preening more frequently than those in flocks of other sizes.

DISCUSSION

Spatial relationships.—Sandhill Crane activity ranges in the Platte River Valley were smaller and distances of flights from roosts to feeding grounds were shorter than those reported during fall in North Dakota (Melvin and Temple 1983). These differences may reflect greater abundance of high-energy foods in close proximity to roosts and absence of

TABLE 3
DIURNAL ACTIVITY BUDGETS (% OF TIME) OF STAGING SANDHILL CRANES BY TYPE OF
HABITAT ALONG THE PLATTE RIVER, NEBRASKA

Behavior	Habitat ^a					Total	G ^b	P
	NG	PHAY	CORN	CULT	PLOW			
Resting	39.4	23.2	36.6	0.7	0.0	19.6	1253	0.001
Feeding	29.9	43.9	20.3	5.6	0.3	42.0	87	0.001
Alert	35.2	41.1	18.3	5.0	0.4	14.4	246	0.001
Calling	34.3	40.0	14.3	11.4	0.0	0.1	4	ns
Courting	26.9	62.7	2.9	7.5	0.0	0.2	32	0.001
Aggression	31.1	42.6	23.0	3.3	0.0	0.2	0	ns
Locomotion	28.7	34.9	28.0	7.5	0.9	11.6	362	0.001
Comfort	47.5	29.2	17.8	4.6	0.9	11.1	503	0.001
Unknown	48.0	24.6	23.5	3.5	0.4	0.8	33	0.001
N	11,934	12,698	8258	1610	136	34,636		
Total %	34.4	36.7	23.8	4.6	0.5			

^a NG = native grassland; PHAY = planted hayland; CULT = cultivated other than corn; PLOW = plowed land.

^b $G_{\text{heterogeneity}} = 1580$, $df = 32$, $P < 0.001$.

hunting in Nebraska. Waste corn was sufficiently abundant within a radius of a few km of roosts to support energy requirements of thousands of cranes, even where feeding was focused south of the river. Crane densities on the study area ranged up to 12,500 cranes per km of river channel (U.S. Fish and Wildl. Serv. 1981). In the North Platte River Valley, spring staging cranes also acquire dietary needs in close proximity to their roosts (Iverson et al. 1987).

Human disturbance from traffic on I-80 probably was the principal cause of reduced use of habitat north of riverine roosting sites and for the high percentage of peripheral roosts. All nocturnal roosts were within 3 km of I-80. Krapu (pers. obs.) observed that low-flying cranes which flew north from roosts frequently hesitated, turned back, or gained altitude when trying to cross the highway. Birds with central roosts could be expected to travel less and conserve more energy than those with peripheral roosts (Wittenberger and Dollinger 1984), but we found no difference in travel distance between roost types. For cranes, waste corn was highly available during spring, 1978 and 1979, (Reinecke and Krapu 1986), and may have reduced the importance of roost type on foraging efficiency.

Foraging as a factor of crane staging.—We observed that cranes which roosted near each other typically departed in the morning in the same general direction but did not go to the same feeding sites as observed among Common Terns (*Sterna hirundo*) and Ospreys (*Pandion haliaetus*)

TABLE 4
DIURNAL ACTIVITY BUDGETS (% OF TIME) FOR SANDHILL CRANES STAGING ALONG THE
PLATTE RIVER, NEBRASKA, BY FLOCK SIZE

Behavior	Flock size					Total	G ^a	P
	1-5	6-9	10-99	100-199	200+			
Resting	1.4	27.3	23.7	8.1	19.2	19.6	875.1	0.001
Feeding	54.6	43.4	38.6	55.4	40.0	42.1	241.8	0.001
Alert	16.5	13.2	13.3	17.8	14.5	14.4	45.6	0.001
Calling	0.2	0.0	0.2	0.4	0.1	0.1	28.8	0.001
Courtship	0.3	0.0	0.3	0.5	0.2	0.2	29.5	0.001
Aggression	0.2	0.2	0.1	0.2	0.2	0.2	5.9	ns
Locomotion	22.0	9.2	10.9	11.6	11.8	11.6	111.9	0.001
Comfort	3.5	6.1	12.4	5.4	13.0	11.0	368.0	0.001
Unknown	1.4	0.4	0.3	0.5	1.0	0.8		
N	1250	2877	12,362	3848	14,231	34,568		

^a $G_{\text{Total}} = 1762$, $df = 35$, $P < 0.001$; $G_{\text{Heterogeneity}} = 1760$, $df = 31$, $P < 0.001$.

(Waltz 1987, Hagan and Walters 1990). Rather, flocks of cranes upon reaching the feeding grounds, tended to join existing groups of cranes already on the ground. As a result, large foraging aggregations of cranes became common by mid-morning through local enhancement (Hinde 1961, Wittenberger and Hunt 1985). Use of occupied fields probably increases the foraging efficiency of inexperienced birds because density of waste corn varies much more among fields, depending on post-harvest land use (Baldassarre and Bolen 1984, Reinecke and Krapu 1986) than within a field (Frederick et al. 1984). As a result, cranes that settle into occupied fields are likely to be more successful foragers.

Norling et al. (1991) showed that the variability in duration of departures from nocturnal roosts to foraging sites and percent of cranes leaving roosts after sunrise increased with date and population buildup. Cranes also left roosts later during fog or precipitation. These responses suggest that cranes rely heavily on visual cues to find food. The increased percentage of delayed departures as the number of cranes increased and food availability declined is consistent with our premise of the importance of local enhancement to enhance foraging efficiency. New migrants into the staging area and cranes that have recently switched activity ranges are likely to benefit most by using conspecifics to locate suitable foraging sites.

The availability of macroinvertebrates to cranes is much less predictable and distribution more clumped than that of corn and depend on soil temperature, escape mechanisms of the organisms, and local abundances

(Richter 1958, Edwards and Lofty 1977). Foraging efficiency among cranes seeking macroinvertebrates is more likely to be enhanced by cranes flying or walking to specific sites where concentrated foraging activity is in progress or signs of recent foraging activity are present. Intense probing by Sandhill Cranes in areas with high concentrations of soil invertebrates disturbs the soil surface (G. Krapu, pers. obs.) and may provide visual cues to other cranes seeking animal foods even after the initial foragers have departed. Cranes spent as much time foraging to obtain the 3% of the diet comprised of invertebrates as the 97% formed by corn (Reinecke and Krapu 1986), reflecting the disparate rates of foraging success on invertebrates and corn.

Cranes probably improve their foraging efficiency and reduce energy costs by remaining in the vicinity of their feeding grounds throughout the day. Only 1.7% of the locations of radio-marked cranes between 08:00 and 18:00 h were at communal roosts; most diurnal use of communal roosts occurred during periods when cranes failed to depart at dawn because visibility was poor. Some species are thought to establish centrally located diurnal activity centers (DAC) from which they base their foraging expeditions (Caccamise and Morrison, 1986, 1988; Caccamise 1993). These DACs are proximal to feeding sites and reduce energy spent in flying to different areas. Congregations of cranes in native grasslands and planted haylands near water and feeding grounds during mid-day are suggestive of DACs. Among the activity ranges that we followed, 29 had data that could be inspected for the presence of a DAC. Twelve had sites with concentrated observations on two or more days which are consistent with a DAC, 10 had possible sites but inadequate data, and seven showed no evidence for a DAC. Among European Starlings (*Sturnus vulgaris*), communal roost location is determined primarily by food distribution, and birds are more faithful to their feeding sites than to communal roosts (Morrison and Caccamise 1985), leading Caccamise (1991) to suggest that the information center hypothesis did not adequately explain starling behavior. Crane distribution, however, is determined primarily by availability of suitable communal roosting habitat (Krapu et al. 1984) which is more restricted than is food availability (Krapu et al. 1985). Cranes frequently change communal roosts and foraging sites and both communal roosts and DACs serve as information exchange centers for improving foraging efficiency. The theories of information centers and DACs are not mutually exclusive (Tye 1993), and further research should be conducted to determine the contributions each makes to foraging efficiency in Sandhill Cranes.

Differences in flight distances to specific habitats can indicate the importance of these habitats, presuming that birds will spend greater energy

traveling to more important sites. The higher than expected use of native grasslands and planted haylands relative to their availability reflects the limited distribution of these habitats, together with their importance in supplying macroinvertebrates. Consumption of animal foods high in protein compensates for the low protein content of corn (Reinecke and Krapu 1986). Biomass of macroinvertebrates is relatively low, particularly in wet meadows (Davis 1991), presumably adding to the search time cranes require to satisfy dietary needs.

Influence of predation and behavior on group size.—Models of flocking behavior and predation predict that the proportion of time spent watching for predators should decline with group size and reach an asymptote when the likelihood of spotting a predator no longer increases with group size. We found that cranes spent little time in alert behavior and that the proportion of time spent alert or feeding did not vary consistently with flock size. Similarly, Tacha (1988) did not find a relation between percentage of time in feeding or in alert with flock size and reported that only 0.5% of 1619 alert responses with known causes were in response to predators. The fact that alert did not vary with flock size as predicted also suggests limited vulnerability of cranes to predators that currently exist in the Platte River Valley. Raptors may kill a few cranes (Lewis 1974, Lingle and Krapu 1986), but most data are circumstantial. Only two of 170 Sandhill Cranes (1%) examined by Windingstad (1988) were apparently killed by predators during the nonbreeding season.

At night, cranes roost in riparian sites and semipermanent wetlands (Krapu et al. 1984, Folk and Tacha 1990), where they are protected by a water barrier and open canopy from most predators. Cranes spent less time in alert at night than during the day (8.6% versus 14.4%, G. Krapu, unpubl. data).

Other influences.—Mate finding and behavioral synchronization also have been identified as benefits of communal roosting and flocking (Moynihan 1968). Courtship was rare in our study compared with other behaviors, but it occurs most frequently in spring (Tacha 1988). Pair-bonds in young cranes are typically ephemeral, and several pairings may occur before mates are finally chosen (Nesbitt and Shapiro-Wenner 1987). Staging could facilitate mate selection by attracting numerous birds.

Epizootics have been reported frequently in staging waterfowl (Wobeser 1981). However, disease was not an observed problem in our study, and epizootics have not been reported in Sandhill Cranes. Reported occurrences of botulism, avian tuberculosis, *Salmonella* (Lewis 1974), and of avian cholera (Krapu and Pearson 1981, Kauffeld 1987, Windingstad 1988) are infrequent.

Conservation concerns.—Our findings indicate that staging behavior of

Sandhill Cranes is strongly influenced by the massive anthropogenic alterations that have taken place in the Platte River Valley. To date, habitat loss has caused a major redistribution of cranes (Krapu et al. 1982), but sufficient remaining roosting and foraging habitat continues to attract and support most of the midcontinent population for several weeks each spring. So far, cranes have successfully avoided the energetic consequences and associated displacement that would have resulted from massive habitat loss had an abundant supply of high energy waste corn and adequate sources of protein in native grassland not been available. The status of this important Sandhill Crane staging area remains precarious, however, because of continuing degradation and loss of open river channels and native pastures (Sidle et al. 1989). With continuing habitat loss, crowding will increase and available food supplies may prove inadequate. Human presence in the Platte River Valley has risen dramatically over the past decade due to increased public awareness of cranes (Lingle 1991). The effects of this increased activity on foraging behavior and activity range characteristics have not been measured.

ACKNOWLEDGMENTS

We thank B. Bowen, L. Oring, K. Reinecke, D. Caccamise, G. Lingle, R. Erwin, and an anonymous reviewer for critically reviewing this manuscript; W. Newton, T. Shaffer, G. Pendleton, and D. Smith for statistical assistance; L. Mechlin and C. Shaiffer for their assistance in capturing Sandhill Cranes for telemetry studies; and E. Fritzell, M. Hay, D. Jorde, and W. Norling for assistance in collecting telemetry and time budget data. Appreciation is expressed to U.S. Fish and Wildlife Service personnel in Nebraska who aided our study. In particular, we thank C. Frith, former supervisor of the Ecological Services Office at Grand Island, and his staff. We are grateful to Platte River Valley landowners for allowing us access to their properties. We thank the National Audubon Society and, in particular, R. Wicht, former manager of the Lillian Annette Rowe Sanctuary near Gibbon, Nebraska, for assistance.

LITERATURE CITED

- BALDASSARRE, G. A. AND E. G. BOLEN. 1984. Field-feeding ecology of waterfowl wintering on the southern high plains of Texas. *J. Wildl. Manage.* 48:63-71.
- BATSCHLET, E. 1981. Circular statistics in biology. Academic Press, New York, New York.
- BAYER, R. D. 1982. How important are colonies as information centers? *Auk* 99:31-40.
- BYERS, C. R., R. K. STEINHORST, AND P. R. KRAUSMAN. 1984. Clarification of a technique for analysis of utilization-availability data. *J. Wildl. Manage.* 48:1050-1053.
- CACCAMISE, D. F. 1991. European Starling fidelity to diurnal activity centers: role of foraging substrate quality. *Wilson Bull.* 103:13-24.
- . 1993. The "patch-sitting hypothesis": a parsimonious view of communal roosting behavior. *Wilson Bull.* 105:372-378.
- AND D. W. MORRISON. 1986. Avian communal roosting: implications of "diurnal activity centers." *Am. Nat.* 128:191-198.

- AND ———. 1988. Avian communal roosting: a test of the "patch sitting" hypothesis. *Condor* 90:453–458.
- CARACO, T. 1979. Time budgeting and group size: a theory. *Ecology* 60:611–617.
- DAVIS, C. A. 1991. Ecology of macro-invertebrates inhabiting native grasslands and their role in the feeding ecology of Sandhill Cranes. M.S. thesis, Iowa State University, Ames, Iowa.
- DIXON, K. R. AND J. A. CHAPMAN. 1980. Harmonic mean measure of animal activity areas. *Ecology* 61:1040–1044.
- EDWARDS, C. A. AND J. R. LOFTY. 1977. *Biology of earthworms*. John Wiley & Sons, New York, New York.
- FOLK, M. J. AND T. C. TACHA. 1990. Sandhill Crane roost site characteristics in the North Platte River Valley. *J. Wildl. Manage.* 54:480–486.
- FREDERICK, R. B., E. E. KLAAS, G. A. BALDASSARRE, AND K. J. REINECKE. 1984. A method for sampling waste corn. *J. Wildl. Manage.* 48:298–303.
- HAGAN, J. M. III AND J. R. WALTERS. 1990. Foraging behavior, reproductive success, and colonial nesting in Ospreys. *Auk* 107:506–521.
- HINDE, R. A. 1961. *Behavior*. Pp.373–411 in *Biology and comparative physiology of birds* (A. J. Marshall, ed.). Academic Press, London, England.
- IVERSON, G. C., P. A. VOHS, AND T. C. TACHA. 1987. Habitat use by mid-continent Sandhill Cranes during spring migration. *J. Wildl. Manage.* 51:448–458.
- KAUFFELD, J. D. 1987. An avian cholera epizootic among Sandhill Cranes in Colorado. Pp. 145–148 in *Proc. 1985 Crane Workshop* (J. C. Lewis, ed.). Platte River Whooping Crane Maintenance Trust, Grand Island, Nebraska.
- KRAPU, G. L., D. E. FACEY, E. K. FRITZELL, AND D. H. JOHNSON. 1984. Habitat use by migrant Sandhill Cranes in Nebraska. *J. Wildl. Manage.* 48:407–417.
- , G. C. IVERSON, K. J. REINECKE, AND C. M. BOISE. 1985. Fat deposition and usage by Arctic-nesting Sandhill Cranes during spring. *Auk* 102:362–368.
- AND G. L. PEARSON. 1981. Susceptibility of the midcontinent population of Sandhill Cranes to avian cholera in Nebraska—a preliminary report. Pp.7–12 in *Proc. 1981 Crane Workshop* (J. C. Lewis, ed.). Natl. Audubon Soc., Tavernier, Florida.
- , K. J. REINECKE, AND C. R. FRITH. 1982. Sandhill Cranes and the Platte River. *Trans. N. Am. Wildl. Nat. Resour. Conf.* 47:542–552.
- LEWIS, J. C. 1974. Ecology of the Sandhill Crane in the southeastern Central Flyway. Ph.D. diss., Oklahoma State Univ., Stillwater, Oklahoma.
- . 1979. Field identification of juvenile Sandhill Cranes. *J. Wildl. Manage.* 43:211–214.
- LINGLE, G. R. 1991. History and economic impact of crane-watching in central Nebraska. *Proc. North Am. Crane Workshop* 6:33–35.
- AND G. L. KRAPU. 1986. Winter ecology of Bald Eagles in southcentral Nebraska. *Prairie Nat.* 18:65–78.
- MELVIN, S. M. AND S. A. TEMPLE. 1983. Fall migration and mortality of Interlake, Manitoba, Sandhill Cranes in North Dakota. *J. Wildl. Manage.* 47:805–817.
- MILLIKEN, G. A. AND D. E. JOHNSON. 1984. *Analysis of messy data*. Vol. 1. Designed experiments. Lifetime Learning Publ., London, England.
- MORRISON, D. W. AND D. F. CACCAMISE. 1985. Ephemeral roosts and stable patches? A radiotelemetry study of communally roosting starlings. *Auk* 102:793–804.
- MOYNIHAN, M. 1968. Social mimicry: character convergence versus character displacement. *Evolution* 22:315–331.
- NESBITT, S. A. AND A. SHAPIRO-WENNER. 1987. Pair formation and mate fidelity in Sandhill

- Cranes. Pp. 117–122 in Proc. 1985 Crane Workshop (J. C. Lewis, ed.). Platte River Whooping Crane Maintenance Trust, Grand Island, Nebraska.
- NORLING, B. S., S. H. ANDERSON, AND W. A. HUBERT. 1991. Temporal patterns of Sandhill Crane roost site use in the Platte River. Proc. North Am. Crane Workshop 6:106–113.
- PULLIAM, H. R. 1973. On the advantages of flocking. J. Theor. Biol. 38:419–422.
- REINECKE, K. J. AND G. L. KRAPU. 1986. Feeding ecology of Sandhill Cranes during spring migration in Nebraska. J. Wildl. Manage. 50:71–79.
- RICHTER, P. O. 1958. Biology of Scarabaeidae. Ann. Rev. Entomol. 3:311–334.
- SAS INSTITUTE, INC. 1987. SAS/STAT guide for personal computers, version 6 ed. SAS Institute, Cary, North Carolina.
- SIDLE, J. G., E. D. MILLER, AND P. J. CURRIER. 1989. Changing habitats in the Platte River Valley in Nebraska. Prairie Nat. 21:91–104.
- SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry. W. H. Freeman Co., San Francisco, California.
- STUTCHBURY, B. J. 1988. Evidence that Bank Swallow colonies do not function as information centers. Condor 90:953–955.
- TACHA, T. C. 1988. Social organization of Sandhill Cranes from midcontinental North America. Wildl. Monogr. 99.
- TYE, A. 1993. “Diurnal activity centers” and “information centers”: a need for more critical study. Wilson Bull. 105:368–372.
- U.S. FISH AND WILDLIFE SERVICE. 1981. The Platte River ecology study. U.S. Fish Wildl. Serv. Spec. Res. Rep., Jamestown, North Dakota.
- WALTZ, E. C. 1982. Resource characteristics and the evolution of information centers. Am. Nat. 119:73–90.
- . 1987. A test of the information-centre hypothesis in two colonies of Common Terns, *Sterna hirundo*. Anim. Behav. 35:48–59.
- WARD, P. AND A. ZAHAVI. 1973. The importance of certain assemblages of birds as “information-centres” for food-finding. Ibis 115:517–534.
- WINDINGSTAD, R. M. 1988. Non-hunting mortality in Sandhill Cranes. J. Wildl. Manage. 52:260–263.
- WITTENBERGER, J. F. AND M. B. DOLLINGER. 1984. The effect of acentric colony location on the energetics of avian coloniality. Am. Nat. 124:189–204.
- AND G. L. HUNT, JR. 1985. The adaptive significance of coloniality in birds. Pp. 1–78 in Avian Biology, Vol. 8 (D. S. Farner, J. R. King, and K. C. Parkes, eds.). Academic Press, Orlando, Florida.
- WOBESER, G. 1981. Diseases of wild waterfowl. Plenum Press, New York, New York.