SPACE USE OF KILLDEER AT A GREAT BASIN BREEDING AREA

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Abstract: Wetland conservation efforts require knowledge of space use by a diversity of waterbirds. However, determining space use of animals requires intensive monitoring of individual organisms. Often, activity patterns during much of the annual cycle are neglected in analyses of home range and habitat use. From 1995–97, we monitored space use in a population of individually marked killdeer (*Charadrius vociferus*) that breed, and reside for a number of additional months each year, in the western Great Basin. We used linear distance measures and home range-area estimates, derived by fixed-kernel methods, to examine patterns of space use of adults prior to, during, and following nesting. Overall, killdeer used a local area of approximately 6 ha. Birds remained closer to nests while tending eggs than either before or after nesting, although extensive movements away from the nest were observed during all time periods. Females tended to move farther from nests than did males. Birds nesting farther from water bodies were generally observed at greater distances from nests than those nesting closer to shorelines during all time periods. Twenty-seven percent of individuals were observed greater than 1 km from nest locations, particularly during postnesting periods. During nesting periods, males were less likely to be observed at longer distances from nests than were females. There were no differences in home range size based upon sex, time period, or distance from water. We suggest that home range size may not always accurately measure differences in space use and that multiple measures, including distance from nests, should be considered. Understanding the sedentary nature of killdeer during much of the annual cycle and their intense use of local areas is important for making management decisions. Coupled with data on other shorebird species, this information also has broader implications for management of wetland systems by indicating large scale spatial and habitat requirements and the connectivity of geographically distinct habitat patches.

Key words: *Charadrius vociferus*, fixed kernel, Great Basin, home range, killdeer, shorebirds, space use, wetlands.

Studies of the demographic effects of habitat degradation and fragmentation on avian populations have focused on aspects of population size, reproductive success, and survival. Habitat alteration also results in shifts in space use and movement patterns among individuals that occupy the area, with subsequent effects on population viability and structure (May 1981, Bierregard and Lovejoy 1989, Hagan et al. 1996, Haig et al. 1998). Species that use North American wetlands are often considered priorities for conservation because of extensive loss of and anthropogenic threats to these habitats (Frayer et al. 1983, Dahl 1990, Catallo 1993). In the Great Basin region of the western United States, wetlands represent isolated habitat patches within the matrix of an otherwise arid environment. Numerous species of waterbirds are obligately associated with these wetlands for

part or most of their annual cycle, including 9 species of shorebird (Order: Charadriiformes) that regularly breed in the region. Of these, killdeer are the most widespread, although their population numbers throughout the western United States and Canada have declined substantially in recent years (Page and Gill 1994; Sauer et al. 1997; P. M. Sanzenbacher, Oregon State University, and S. M. Haig, U.S. Geological Survey, unpublished data).

Despite being a common and easily recognized species of shorebird, few studies of killdeer have been conducted and have focused almost exclusively on nesting and chick-rearing periods (Mace 1971; Schardien 1981; Mundahl 1982; Brunton 1988*a,b,c,* 1990). As with many shorebirds (Oring and Reed 1997; Warnock et al. 1998; Plissner et al. 1999, 2000), however, killdeer also are present in breeding areas prior to and following nesting, and may use feeding and resting sites other than those occupied dur-

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ing the nesting period. Therefore, we examined how space use and movements varied throughout the time that killdeer were present in the breeding area.

Home range analysis is the most common method for examining space use by individuals. Home range includes the area regularly used by an individual during a specified period of its life. Home range size is influenced by population density, habitat variation, environmental conditions, and energetic constraints (Burt 1943, Mace et al. 1984, Lucherini and Lovari 1996, Blackburn et al. 1997, Howell and Chapman 1997, Marzluff et al. 1997). Estimates of home range for shorebirds are rare and have focused on defended territories, often neglecting other areas regularly used by individuals during their life histories (Ryan and Renken 1987, Knopf and Rupert 1996, but see Warnock and Takekawa 1996). Therefore, we observed a population of killdeer over 3 years, throughout the extended time each year that birds were present on the breeding grounds. The information gained from this work provides details on overall patterns of space use by individuals in the population and allows for assessment of appropriate management strategies that will insure their viability throughout a substantial portion of the annual cycle.

STUDY AREA AND METHODS

From 1995 to 1997, adult killdeer were color-banded and observed in the vicinity of the Jay Dow, Sr. Wetlands, a 540-ha area containing 16 managed water bodies in Lassen County, northeastern California. The study area is located adjacent to the southern shore of Honey Lake, a 23,000-ha alkaline lake basin of the western Great Basin. Lake levels fluctuate extensively both seasonally and between years, and occasionally the lake is dry. The region is characterized by desert scrub habitat interspersed with a variety of wetland systems (Reed et al. 1997).

Adults were trapped and banded at nests during incubation periods. All birds were given U.S. Department of Interior numbered aluminum bands and 3–5 celluloid or Darvic™ plastic-colored leg bands. The use of space by banded killdeer was studied February through September 1995–97 (1995: 61 females, 61 males; 1996: 65 females, 63 males; 1997: 82 females, 96 males). Sixteen individuals (2 females, 14 males) were observed during all 3 years of the study, and 29 birds (13 females, 16 males) were

observed in 2 separate years. For our analyses, we considered observations on birds returning in multiple years to be independent.

The study area was surveyed for marked birds daily from April through July and at least weekly during the remaining months. Observations were conducted throughout the day, although a majority (64%) of sightings were made before 1200 hr. All areas around the Honey Lake basin (up to 20 km from Jay Dow, Sr. Wetlands) where substantial numbers of killdeer occurred were also surveyed periodically. Observers identified individuals using binoculars and spotting scopes, and indicated locations of killdeer on field maps derived from aerial photographs of the study area and point coordinates from a Trimble Pathfinder Basic Plus global positioning system (Trimble Navigation, Sunnyvale, California, USA). Locations were subsequently plotted on a geographic information system coverage of the area (MapInfo, Version 3, Troy, New York, USA) from which coordinates of each position could be derived and distances from reference points could be calculated. In 1995, a subset of the observed birds (45 of 122) was outfitted with radiotransmitters (Powers 1998). Locations of radioed individuals were entered into the same MapInfo data set as were visual resightings, and all locations were combined for analysis.

Observations were divided into time periods in relation to breeding stage. The prenesting time period included observations of birds prior to the laying of a pair's first egg of the year. The nesting period commenced with egg laying and lasted until hatching (approximately 3.5 weeks) or nest failure. All observations following termination of a bird's final nest of the year were designated as postnesting, regardless of the fate of eggs and chicks. Multiple nesting attempts by individuals within a year and time periods between nest attempts were analyzed separately. If marked young were observed after 25 days posthatching, we considered the brood to have successfully fledged (L. W. Oring, University of Nevada, unpublished data). In such cases, we designated the first 25 days posthatching as a chick-rearing period, when dependent young (fledglings) were present. We designated subsequent observations as postfledging.

We used 2 approaches to analyze space use of killdeer. First, we determined distances of individuals from reference points (nest locations). We determined mean and maximum dis-

tances for all individuals with at least 10 recorded positions for each time period of interest. A paired comparisons analysis of individuals observed during both morning and afternoon indicated that individuals were located farther from nests early in the day (Wilcoxon paired-sample test, $P \leq 0.001$, $n = 702$), when movements were more frequent (L. W. Oring, University of Nevada, unpublished data). Because relative numbers of morning and afternoon observations were consistent across time periods and between sexes, we combined observations from all times of day for subsequent analyses. In order to reduce effects of serial autocorrelation, we limited analyses to observations of individuals that were separated by at least 2 hr (Powers 1998). To do so, observations recorded <2 hr apart were randomly selected for inclusion or omission in the analysis. Multiple sightings of individuals within the same day accounted for 14% of all observations. We did not analyze distance measures for time periods between successive nesting attempts within a year because the appropriate nest to use as a reference point could not be objectively determined. For prenesting periods, distances were computed to the first nest site attended for the year. Postnesting distances were computed relative to the final nest location for the individual. For distance-from-nest analyses, we did not exclude any observations that may have represented occasional excursions beyond designated home range boundaries (Burt 1943, Jewell 1966). However, we considered temporal patterns of longer distance movements separately by examining the frequency of such distant observations relative to nesting activity.

The second approach estimated home range sizes for individuals using the fixed-kernel method of the program KERNELHR (Seaman et al. 1998). Recent comparisons of methodologies have indicated that kernel density estimates are among the most accurate measures of space use, particularly for distributions of data points that are not bivariate normal (Worton 1995, Seaman and Powell 1996) and for moderately autocorrelated data (Swihart and Slade 1997). Estimated ranges incorporated 95% of the utilization distribution for each individual. Bandwidth (the smoothing parameter) was selected automatically for each area estimate, using the least squares cross validation (LSCV) method. This method does not provide a reliable estimator of bandwidth when several

data points are very close together (e.g., individuals frequently observed at the nest site; Seaman and Powell 1996). We therefore omitted 12% of the initial home range estimates from further analysis when this method resulted in choice of a very small bandwidth for the data. Because sample size has a significant effect on estimated home range size (Bekoff and Mech 1984, Harris et al. 1990, Hansteen et al. 1997), particularly with <50 data points (Seaman et al. 1999), we corrected our area estimates by fitting data to the results of a simulation model in which locations were randomly sampled from a home range composed of 16 bivariate normal distributions (Seaman et al. 1999). The regression equation for the curve generated by the simulation model was

percent relative bias (PCB) = $1.076977 + 988.1066(1/n) - 3.929.401(1/n^2)$,

where n is the number of sample points. The corrected home range was then calculated from the equation $A = 100\breve{A}/(PCB + 100)$, where A is the corrected estimate and $\breve{A}$ is the LSCV-based estimate generated by KERNELHR (Seaman et al. 1999). This method validated comparisons of home range sizes based on different sample sizes, without losing data from subsampling methods that would be necessary to equalize sample sizes.

Because both distance measures and home range estimates deviated significantly from normal distributions and did not normalize following standard transformation procedures, we used nonparametric procedures to analyze differences between groups. Wilcoxon 2-sample tests were used for analyses of differences in distances and home range size associated with sex, reproductive success, and proximity to nearest water body. We used Wilcoxon paired-sample tests to examine sex differences among mated individuals. Kruskal-Wallis tests were used to determine overall effects of year and breeding stage on distances from nest and home range size. Where effects were significant, we subsequently conducted multiple comparisons using a Tukey-Kramer test for differences among ranked distance and area data. Differences between means are reported for $q > q_{0.05,277,3}$. In addition, we computed the power of pairwise comparisons of means yielding nonsignificant differences. To do so, we determined power for corresponding parametric analyses and used 95% of the value as an ad-
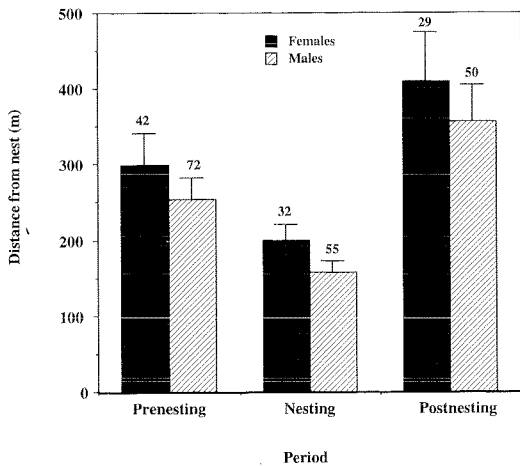
Fig. 1.   Mean (± SE) distances of killdeer from nest locations at Jay Dow, Sr. Wetlands, Lassen County, California, USA, 1995–97. Numbers on each column indicate numbers of individuals. Males and females did not differ for any period ($P >$ 0.10, power < 0.34).
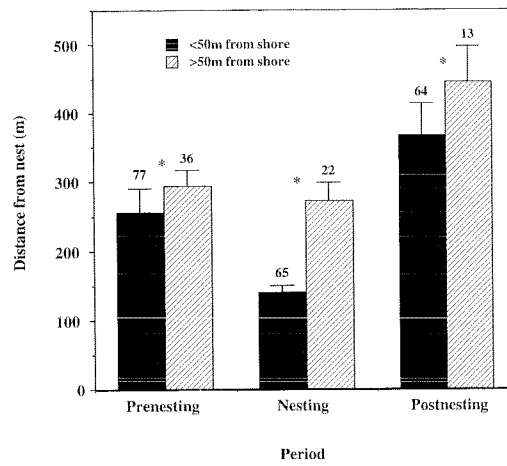

Fig. 2.   Mean (± SE) distances of killdeer from nest locations at Jay Dow, Sr. Wetlands, Lassen County, California, USA, in relation to proximity of nest to pond shoreline, 1995–97. Numbers on each column indicate numbers of individuals. Significant differences ($P <$ 0.05) indicated by *.

justment for the nonparametric test (Siegel and Castellan 1988). We assigned effect sizes equal to the square root of SSH/N, where SSH is the sum of squares of the hypothesis and N is the total sample size (SAS Institute 1994). We analyzed frequency data on long distance movements using G-tests, with Williams correction (Sokal and Rohlf 1981).

RESULTS

Distances from Nests

Killdeer remained closer to nest sites during nesting periods than either prenesting ($P \le$ 0.001) or postnesting ($P \le$ 0.001; $mean_{prenest} =$ 270 m, $mean_{nest} =$ 173 m, $mean_{postnest} =$ 375 m). The maximum distances that birds were observed from nest sites were greater postnesting than either before ($P <$ 0.05) or during ($P \le$ 0.001) nesting periods ($mean_{prenest} =$ 723 m, $mean_{nest} =$ 639 m, $mean_{postnest} =$ 1,107 m). Overall, females tended to be observed farther from nest sites than did males ($P =$ 0.057, pow-

er = 0.06). Although this tendency held for all time periods (prenesting, nesting, and postnesting), there were no differences between sexes during any specific period (Fig. 1). Furthermore, there was no difference between the sexes in the maximum distance that individuals were observed away from nests during the prenesting ($P =$ 0.312) and postnesting ($P =$ 0.522) periods. While tending nests, however, females were observed at greater distances from nests than were males ($P =$ 0.018). Among mated pairs, females were observed at greater distances than males from nest locations (Table 1). The distance of nests from the nearest water body also influenced movements relative to nest sites (Fig. 2), as individuals with nests >50 m from the nearest water body ranged farther from nests during prenesting ($P \le$ 0.001), nesting ($P \le$ 0.001), and postnesting periods ($P =$ 0.048).

Hatching success did not influence postnesting distances from final nests of the year ($mean_{successful} =$ 314 ± 34 m, $n =$ 46; $mean_{unsuccessful}$

Table 1.   Home range size (ha) and distances from nest sites (m) of paired killdeer at Jay Dow, Sr. Wetlands, Lassen County, California, USA, 1995–97.

	Home range size						Distance from nest					
		Females		Males				Females		Males		
Period	n	Mean	SE	Mean	SE	P	n	Mean	SE	Mean	SE	P
Prenesting	35	3.88	0.66	4.56	0.92	0.724	59	292	32	262	33	0.049
Nesting	27	5.28	1.12	5.50	1.25	0.674	25	189	23	147	17	0.009
Postnesting	6	1.70	0.36	4.37	1.29	0.131	22	374	60	358	91	0.579

Table 2. Distances from nest and home range sizes of nesting male and female killdeer within and between years, 1995–97, at Jay Dow, Sr. Wetlands, Lassen County, California, USA.

| | Home range size (ha) | | | | | | Distance from nest (m) | | | | | |
| | Females | | | Males | | | Females | | | Males | | |
	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE
Nest attempt												
First	22	6.15	1.23	51	5.43	1.09	19	193	26	35	162	17
Second or third	17	3.52	1.00	29	3.26	0.65	13	207	40	20	149	26
Year												
1995	20	6.32	1.41	36	3.30	0.66	26	193	24	34	125	15
1996	9	3.58	1.34	24	4.41	0.93	2	220	154	10	200	42
1997	11	3.95	0.92	20	7.34	2.42	4	228	72	11	219	34

= 458 ± 75 m, n = 34; P = 0.288, power = 0.47). For adults that successfully fledged young, maximum distances away from the nest increased following brood independence (mean$_{prefledge}$ = 575 m, n = 20; mean$_{postfledge}$ = 1,582 m, n = 8; P = 0.016).

Within years, movements during nesting were similar for initial and subsequent nest attempts (Table 2) among females (P = 0.683, power = 0.16) and males (P = 0.322, power = 0.09). Among years, however, the mean distances of males from active nests did vary (Table 2, P = 0.011); however, there was no yearly variation among females (P = 0.836).

In general, the variance in distances that individuals were seen from nest sites tended to be high. Observations of 60% of all individuals included locations >2 standard deviations farther than the mean distance from the nest. The frequencies of these long distance movements, however, did not differ for prenesting, nesting, and postnesting time (P > 0.05). However, 27% of all individuals were observed at distances >1 km from nest sites, with more postnesting individuals (44%) observed away from the nest than individuals during either the prenesting (22%; P = 0.048) or nesting (18%; P ≤ 0.001) periods. Within sexes, there was a difference between time periods for males (P ≤ 0.001) but not for females (P > 0.10). Only 11% of males moved greater than 1 km during the nesting period, whereas 29% of females were observed at least once at such distances from active nests (P < 0.05).

Home Ranges

For birds observed on at least 10 occasions during each of the periods (prenesting, nesting, and postnesting), the mean yearly home range size was 6.0 ha (range = 1.0–25.9 ha, median = 3.10 ha, n = 10). Prenesting females and males had home range sizes of 4.24 ± 0.61 ha ($\bar{x}$ ± SE, n = 44) and 6.73 ± 1.02 ha (n = 78). Nesting home ranges of females were 5.05 ± 0.82 ha (n = 40), while males inhabited areas of 4.64 ± 0.74 ha (n = 80). Between nest attempts, females and males used areas of 6.52 ± 1.74 ha (n = 12) and 4.80 ± 0.83 ha (n = 19). Following nesting, areas used were 6.35 ± 2.15 ha (n = 24) for females and 7.13 ± 1.56 ha (n = 45) for males.

We found no differences in the size of areas used by male or female killdeer across all stages of the breeding season (Fig. 3). Furthermore, there were no differences in size of areas used by individual members of pairs (Table 1; P = 0.529, n = 79). Nesting home ranges of killdeer
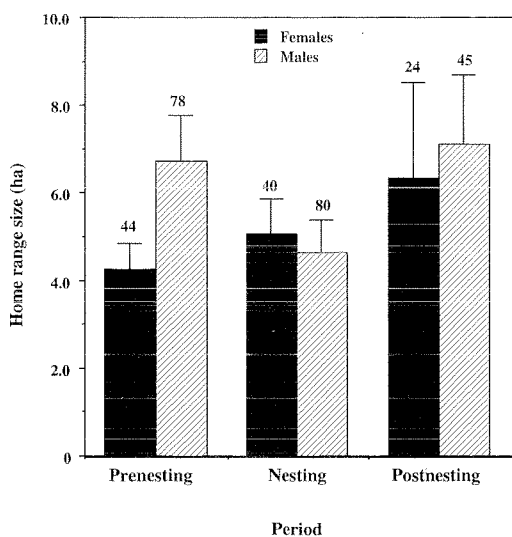

Fig. 3. Killdeer home range size in relation to nest stage for individuals nesting at Jay Dow, Sr. Wetlands, Lassen County, California, USA, 1995–97. Numbers on each column indicate numbers of individuals. There were no differences between sexes or across nest stages (P > 0.05).

also did not vary in relation to the brood attempt within a season ($P = 0.146$) or between years ($P = 0.607$; Table 2), or in relation to the distance of the nest from water bodies ($P = 0.902$, power $= 0.22$).

DISCUSSION

In studies of avian space use, habitats used prior to and after breeding often are ignored, even though these areas may be critical for survivorship. Studies that have considered habitat use during these time periods have focused upon areas disjunct from breeding grounds, such as staging and molting areas (Hohman et al. 1992; Skagen and Knopf 1993; Yarris et al. 1994; Warnock et al. 1998; Plissner et al. 1999, 2000). For many species, however, seasonal shifts in space use also occur at smaller spatial scales (Stenger and Falls 1959, Stefanski 1967, Burger 1984). Among many populations, such as killdeer in the Great Basin, individuals remain on or near the breeding area during much of the nonbreeding portion of the annual cycle. In such cases, it is important to recognize the link between various stages of the annual cycle (Myers 1981).

The killdeer population at Jay Dow, Sr. Wetlands is not resident throughout the year, but individuals are known to be present in the breeding area in some years from February through mid-November. Pairing occurs primarily in March and April, with most egglaying occurring from April through June (L. W. Oring, University of Nevada, unpublished data). During the period when killdeer are present, Great Basin habitats undergo extensive seasonal changes, particularly in water availability and quality, which would likely be reflected in shifts in killdeer home ranges. To this end, our home range results suggest that the area used during nesting only represents a fraction of the total area used by individuals during the entire portion of the year that they are present locally. Our estimates of overall home range sizes for this population are 65% larger than those reported by Powers (1998) using an adaptive-kernel estimator. These differences may have resulted in part from the different methods used in the analyses (Seaman and Powell 1996). Additionally, her study was based solely on radio-telemetry data and did not include prenesting locations of individuals, which likely significantly increase the overall area utilized by individuals during the season.

Even within stages of the annual cycle, home ranges and distances from nests can vary considerably among individuals at the same site. At Jay Dow, Sr. Wetlands, killdeer nests were located adjacent to ponds as well as up to several hundred meters from water in desert sagebrush habitat. One third of all nests were located in sagebrush habitat >50 m from shorelines (L. W. Oring, University of Nevada, unpublished data). Birds nesting in desert areas were more often observed far from nests, as they used distant ponds for foraging, belly-soaking, and brood-rearing (Bent 1929; Bunni 1959; Schardien and Jackson 1979; Mundahl 1982; L. W. Oring, University of Nevada, unpublished data).

Sex-specific patterns of space use may be associated with mating systems (Emlen and Oring 1977). Male killdeer may have greater investment in resource (nest-site) defense than do females (Brunton 1988*a,b*). Killdeer also exhibit biparental care and share in territorial defense of nests and chicks, although there are sex differences in both efforts (Bunni 1959; Brunton 1988*a,b*). Therefore, prenesting differences in distances that pair members were found away from nest sites may reflect different roles in territory establishment and defense. Males, which were found in greater proximity to future nest sites, are more active in territorial defense (Mundahl 1982; Brunton 1988*a,b,c*, 1990). Males also show greater site tenacity than do females both within and between breeding seasons (Lenington and Mace 1975, Powers 1998). In addition, males remained closer to the nest site during the period when nests were being tended. In addition to exhibiting greater effort in nest defense, male killdeer also spend more time incubating eggs than females (Brunton 1988*b*). Sightings of males at nests, therefore, were likely to skew the mean distances of the sexes toward greater proximity by males. Nevertheless, we also found that males were less likely than females to make longer distance movements away from the nest site during this time period.

While linear distance measured from nests differed by sex, corresponding home range sizes of males and females did not differ. These contrasting results suggest that home range size alone may be insufficient for describing killdeer space use. In the study population, home range sizes were highly variable, and the shape of home ranges may be more closely associated

with environmental factors, sex, and nest period.

Largely because of territory structure within the study area, kernel methods provided the best estimators of home range size (Worton 1995). However, corrections to kernel-based home range estimators, as reported here have not been applied previously. The correction factor we applied was based on simulation of a complex home range distribution (a mixture of 16 bivariate distributions). It is possible that, although substantially more realistic than distributions created from fewer bivariate normal distributions, the simulated home range is not representative of actual individual utilization distributions, and the regression curve does not provide an accurate correction factor. In addition, the regression equation generated does not provide an exact correction for small sample sizes, and our analyses may have been subject to error based on the variance about the curve. Nevertheless, results of subsampling indicated that our adjustments reduced the error in the area estimates.

Despite some problems, home range studies provide crucial information on patterns of area used by individuals and populations. The results of our approach, analyzing multiple temporal scales of movements and area used, indicate the importance of considering different life history stages in determining both the appropriate scales for questions of habitat use and the proper analyses of results. In general, home range studies have been applied more toward mammalian than avian species, largely because mobility of the latter generally hampers efforts to thoroughly monitor movements of individuals throughout their range. It is therefore difficult to assess whether movements are part of normal activity within a home range or excursionary movements. Our results indicate that a large percentage of individuals engage in relatively long distance movements before, during, and after the breeding periods. The nature of these movements (reconnaissance, dispersal, etc.) requires more extensive monitoring relative to their correlation with migratory behavior and past and future breeding. Further work also is needed to assess finer scale issues, particularly in relation to specific habitat types and quality.

MANAGEMENT IMPLICATIONS

Spatial issues are particularly critical considerations in regions such as the western United States Great Basin, where breeding habitat for shorebirds is highly variable, patchily distributed, and often isolated geographically from other suitable breeding and foraging areas (Reed et al. 1997). To persist in the region, individuals must be able to respond to unfavorable conditions by utilizing alternative habitats for nesting, acquiring prey, and–or avoiding predators. Using our results in conjunction with other recent studies of waterbirds in the Great Basin (Haig and Oring 1998), it is apparent that an understanding of how different species use these areas and respond to natural climatic changes is critical to planning strategies for preserving alternative habitats at both local and regional scales.

In the Great Basin, movements of killdeer are restricted largely to the local breeding area, but individuals use diverse habitats surrounding a wetland. When shoreline conditions are unfavorable for nesting or predation rates are high, individuals respond by moving to more vegetated, upland habitats in the local area (L. W. Oring, University of Nevada, unpublished data). Management options for killdeer and species that respond similarly (e.g., willets, *Catoptrophus semipalmatus*; S. M. Haig, U.S. Geological Survey, unpublished data), therefore, require a focus on multiple habitats surrounding individual wetlands. Although we did not address specific habitat associations, we demonstrated that, within local populations, space use varies in relation to nest location. Killdeer will nest in upland habitats at some distance from water sources, and our results indicate that these individuals will travel greater distances from the nest than individuals nesting nearer to water. Therefore, the distribution of nests in relation to water bodies will affect the area requirements for the population, at least in terms of the spatial geometry of utilized area, if not the total acreage. Management of populations relies upon determining the distribution of nesting individuals and adjusting estimates of space requirements accordingly, rather than assigning a fixed mean utilization area surrounding each nest. Furthermore, our data also indicate that management needs for such species must not focus solely on territories and home ranges occupied around active nests, but must also consider space use both prior to and following nesting, when individuals often travel farther throughout the local area.

Unlike killdeer, species such as American av-

ocets (*Recurvirostra americana*) locally restrict their activities to aquatic habitats, yet move hundreds of kilometers among wetlands during the breeding and postbreeding periods (Plissner et al. 1999, 2000). Conservation strategies for such a mobile species require focus on preserving multiple wetlands as alternative nesting, molting, and staging locations. Such differences in space use among a single taxonomic group (e.g., shorebirds) suggest the importance of understanding habitat utilization by a diversity of species in order to develop effective local or regional wetland conservation plans.

ACKNOWLEDGMENTS

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