

POSTBREEDING MOVEMENTS OF AMERICAN AVOCETS AND IMPLICATIONS FOR WETLAND CONNECTIVITY IN THE WESTERN GREAT BASIN

JONATHAN H. PLISSNER,¹ SUSAN M. HAIG,^{1,3} AND LEWIS W. ORING²

¹USGS Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, Oregon 97331, USA; and ²Department of Environmental and Resource Sciences, University of Nevada, 1000 Valley Road, Reno, Nevada 89512, USA

ABSTRACT.—Wetlands in the western Great Basin of the United States are patchily distributed and undergo extensive seasonal and annual variation in water levels. The American Avocet (*Recurvirostra americana*) is one of many shorebird species that use these wetlands as breeding and migratory stopover sites and must adjust to variable conditions. We used radio telemetry to determine postbreeding, premigratory movement patterns of avocets throughout the region. In 1996 and 1997, 185 breeding adults were captured and fitted with radio transmitters at five breeding areas in Oregon, California, and Nevada. Regular aerial and ground surveys were conducted at the five main study areas from June through September, or until all avocets had left a site. Other wetlands in the western Great Basin also were surveyed by aircraft for the presence of radio-marked birds. Fifty-six percent of radio-marked avocets were still detected in the region at least eight weeks after capture. Each of these individuals was detected at an average of 2.1 lakes (range 0 to 6), with 74% found at more than one lake system. Forty radio-marked individuals moved at least 200 km between wetlands prior to migration, most of which dispersed northward. Male and female patterns did not differ significantly. Overall, movements may be associated with a prebasic molt, exploitation of a superabundant food source in northern lakes, and reconnaissance for future breeding efforts or staging sites. These results also demonstrate wide-ranging patterns of dispersal in this species and suggest a need for the consideration of large-scale habitat connectivity issues in establishing conservation strategies for shorebirds in the western Great Basin. Received 21 October 1998, accepted 8 July 1999.

THE MOVEMENT of individuals among habitat patches has long been a focal topic in various subdisciplines of theoretical and applied ecology. Recently, the relevance of such movement patterns to conservation biology also has been noted, e.g. in defining metapopulation structure, explaining the dynamics of metapopulations, and as a key element in maintaining habitat and landscape connectivity (Haig et al. 1998). Patterns of individual movements, however, typically have been described only at relatively local levels, largely because detectability of marked individuals decreases with distance from the source (Barrowclough 1978). Landscapes with discrete habitat patches (i.e. wetlands) offer opportunities to more readily monitor movements of species whose distributions are restricted to such habitats (Skagen and Knopf 1993, Farmer and Parent 1997, Warnock and Bishop 1998).

The Great Basin of the western United States is characterized by a mosaic of wetlands within a xeric landscape. To varying degrees, most of these wetlands are ephemeral, and all are subject to high annual and seasonal variability in water levels and salinity. Anthropogenic and climatic effects on the region have resulted in large-scale alteration and loss of wetland habitats (Grayson 1993, Engilis and Reid 1997), but relatively little is known about the ecology of these systems.

These wetlands are important breeding and migratory stopover sites for many North American waterbirds, including more than 30 species of shorebirds, 9 of which regularly breed in the region (Oring and Reed 1997, Warnock et al. 1998). The region is critically important for populations of American Avocets (*Recurvirostra americana*) during most stages of their life history (Nehls 1994, Neel and Henry 1997, Warnock et al. 1998). To better determine the interrelationships of wetlands as they pertain to avian populations, we investigated the extent and

³ Address correspondence to this author. E-mail: haigs@fsl.orst.edu

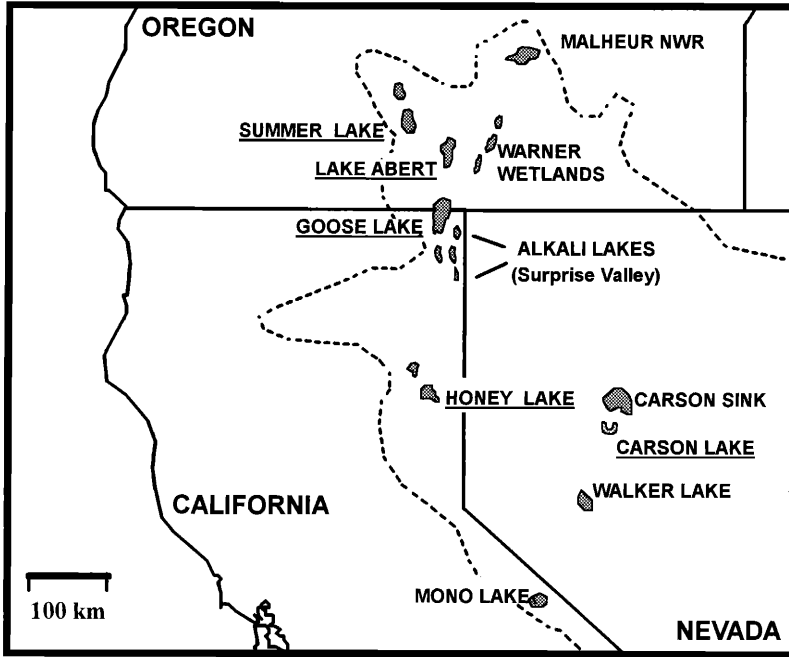


FIG. 1. Major wetland systems of the western Great Basin. The main study areas (banding locations) are underlined. Dashed line indicates approximate boundary of the Great Basin.

variability of postbreeding movements of American Avocets in the western half of the Great Basin.

STUDY AREA AND METHODS

Our study areas (see Fig. 1) included most of the major alkali lake systems in the western Great Basin, from Malheur Lake, Oregon (43°20'N, 118°45'W) and Carson Lake, Nevada (39°19'N, 118°42'W), west to Summer Lake, Oregon (42°50'N, 120°45'W) and Honey Lake, California (40°09'N, 120°15'W). The region is characterized by high desert habitats with dispersed alkaline wetlands. Annual precipitation is low but variable (\bar{x} = 10 to 30 cm per year; Engilis and Reid 1997), which contributes to extensive annual fluctuations in water levels (Keister 1992). Two of the principal lakes of the study, Abert and Goose, have dried completely less than 10 times in the past century, but other lake basins in the region are nearly desiccated in many years, although not during the current study period (Johnson et al. 1985, Keister 1992, L. Oring unpubl. data). High rates of evapotranspiration and agricultural demands for water from lakes and inflow streams result in large within-year fluctuations in water levels as well (Neel and Henry 1997).

American Avocets are long-legged shorebirds that forage for aquatic invertebrates in the water column

and sediments of shallow water (Boettcher et al. 1995). They breed primarily in interior wetlands of western North America and migrate to coastal wintering areas from northern California and eastern Texas to Honduras and in South Carolina and Florida (Robinson et al. 1997). Avocets return to the western Great Basin beginning in late February, with the primary nesting period extending from early May through June (Gibson 1971, Robinson et al. 1997). Monogamous pairs jointly tend semicolonial nests in sparsely vegetated habitats, typically within 50 m of water (Robinson et al. 1997). Both parents remain with broods for several weeks following hatching of the precocial young. Males and females can be distinguished by differences in bill curvature.

In 1996 and 1997, we color-banded and radio-marked 185 breeding adult avocets at five wetlands. At Summer Lake (Oregon) and Honey Lake (California), 20 adults were captured and tagged in each of the two years. At Lake Abert (Oregon), Goose Lake (Oregon/California), and Carson Lake (Nevada), 15 birds were captured in 1996 and 20 in 1997. Incubating adults tending clutches 10 or more days old were captured with traditional walk-in nest traps in 1996 and with custom-designed, spring-loaded nest traps in 1997. All trapped birds were given a unique combination of colored plastic leg bands that identified the year, site, and individual bird. Radio transmitters (2.5 g; Holohil Systems Ltd. model PD-2sp)

were attached with epoxy to aluminum bands, coated in plastic, and placed on the bird's leg. The placement of radios on the tibiotarsus was tested on captive avocets to assess the potential for injury or effects on behavior. We also conducted field tests of unattached transmitters to determine how antenna position and submersion in water and mud affected radio detectability and signal strength. The expected life of the radios was four months.

Beginning on approximately 1 June of each year, we conducted ground surveys at the five wetlands using hand-held Yagi antennas and a radio-tracking truck (at Honey Lake). Multiple vantage points were chosen to maximize coverage at each wetland. Coverage was not intended to be complete but rather to reduce the number of individuals to be sought during subsequent aerial surveys. Air and ground surveys were conducted on a weekly basis (except Carson Lake in 1996) until the final week of September, or until birds were known to have left the lake basin.

From mid-June through the final week of September, weekly surveys of the three Oregon lakes were conducted from a Piper Super Cub with hand-held or wing-mounted Yagi antennas. Flight paths included the entire perimeter of each lake. The estimated range of radio detection at the flight altitude of 18 m above ground level was approximately 2 km. In 1996, three aerial surveys also were conducted in Surprise Valley, southeast of Goose Lake. Two surveys were conducted at Honey Lake, and single flights were made at Malheur National Wildlife Refuge, the Warner Wetlands (east of Lake Abert), and the Carson Lake region (Carson Lake, Stillwater National Wildlife Refuge, and Carson Sink). These surveys were conducted using a Cessna 206 aircraft with mounted Yagi antennas. In 1997, Honey Lake, the Carson Lake region, and the Surprise Valley lakes were surveyed biweekly throughout the time period. The Malheur wetlands were surveyed on two occasions, and three flights included coverage of the southern Warner Valley, Oregon, and the Long Valley Basin, California.

Marked birds also were recorded during visual surveys conducted throughout the study period at areas with large concentrations of avocets. These surveys were carried out on foot and from vehicles and hovercraft, approximately on a weekly basis, at all focal lakes except Carson Lake.

RESULTS

Radio detection rates and avocet persistence in region.—Avocets were relocated an average of $5.1 \pm \text{SE of } 0.28$ times ($n = 185$) after their initial capture and tagging, with mean numbers of detections varying significantly among sites ($F = 5.25$, $df = 4$ and 180 , $P < 0.001$) but not be-

tween years ($F = 1.83$, $df = 1$ and 183 , $P = 0.18$). At Summer, Abert, and Goose lakes, where resighting and telemetry efforts were comparable, radios were detected 2.66 times more often than individuals were observed directly, with little variance among the three sites.

Of the 185 radio-marked avocets, 125 (67.6%) were detected within the region at least one month after capture. Fifty-eight percent of radio-marked individuals ($n = 107$) were accounted for after 1 August; however, only 28.1% remained into September. Combining both years of the study, 25 radio-marked individuals (13.5%) were detected during the final week of September, when surveys were terminated. Persistence rates were somewhat higher in 1997 than in 1996, and comparisons of visual and radio detections suggested that early radio failures (primarily resulting from antenna loss) were more common in 1996 (10%) than in 1997 (2%). Persistence also varied among breeding locations ($F = 4.67$, $df = 4$ and 180 , $P < 0.01$). On average, birds that bred at the three northern lakes remained in the region approximately two weeks longer than birds that nested at Honey and Carson lakes (Fig. 2). No radio-marked avocets were found at Honey Lake after 8 August in 1996 or after 21 July in 1997.

Despite a high probability of detection, individuals were not detected during a substantial proportion ($\bar{x} = 34.6 \pm 3.5\%$) of the survey weeks between the date they were banded and their ultimate disappearance from the study area (or termination of surveys). Incomplete survey coverage during some weeks likely contributed to some of the weeks that birds were missed. Nevertheless, during weeks with complete coverage of the major lake systems, an average of $19.2 \pm 3.4\%$ of the birds subsequently detected in the region were not located during the surveys. These frequent gaps in detection during one or more survey weeks between relocations suggest that birds often moved to areas within the region that were not included in the surveys, or that they left the region and then returned. Therefore, the extent of movements that we recorded is very conservative.

Movements among wetlands.—Following capture, avocets remained for varying periods of time at the lake system where they bred before moving to other systems within the region or disappearing from the study area (Fig. 3). Altogether, 47% of the radio-marked birds were

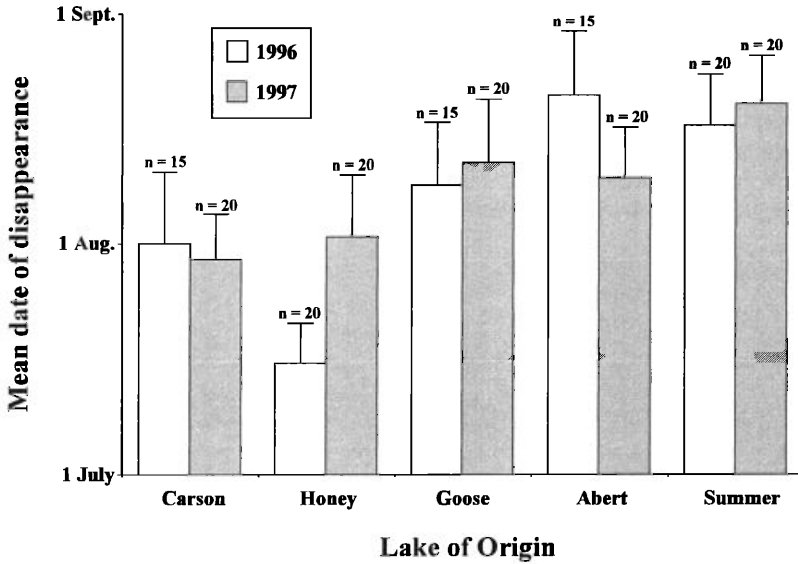


FIG. 2. Persistence of radio-marked American Avocets in the western Great Basin. Values are $\bar{x} \pm SE$.

observed only at their lake of origin. Even among birds that were detected until the end of the annual study period, a large proportion (32%) remained sedentary.

Nevertheless, most of the breeding avocets in the western Great Basin used multiple wetlands during the postbreeding/premigratory

period, regardless of their point of origin (Table 1). On average, individuals were detected at 0.82 ± 0.09 (range 0 to 4) lake systems in addition to the breeding locality. Birds that moved among different wetlands also returned to previously visited lakes, resulting in a higher number of documented movements ($\bar{x} = 1.03$

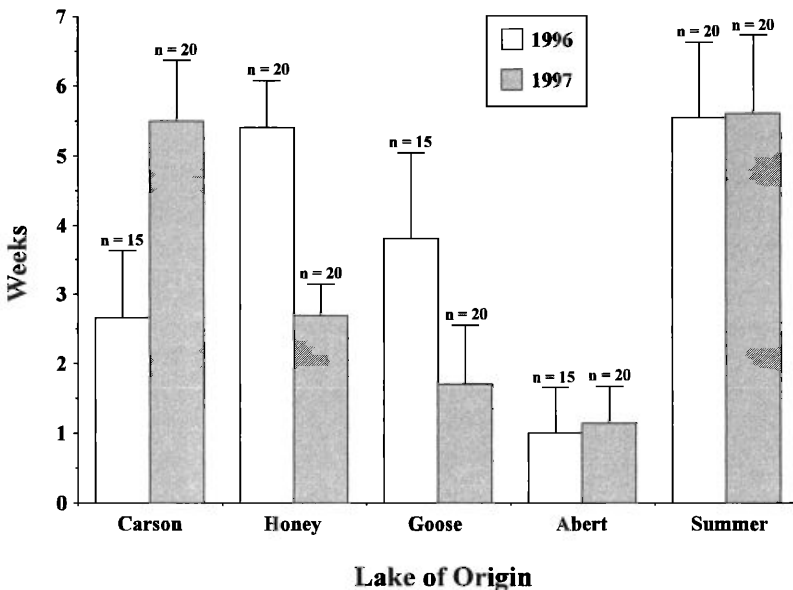


FIG. 3. Persistence of American Avocets at their breeding location prior to departure or disappearance. Values are $\bar{x} \pm SE$.

TABLE 1. Summary of postbreeding movements of radio-marked American Avocets detected during ground and aerial surveys in the western Great Basin, 1996 and 1997. Sample sizes are numbers of birds marked at each banding location.

Encounter location	Banding location				
	Summer Lake (<i>n</i> = 40)	Lake Abert (<i>n</i> = 35)	Goose Lake (<i>n</i> = 35)	Honey Lake (<i>n</i> = 40)	Carson Lake (<i>n</i> = 35)
Summer Lake, OR	36	18	12	6	3
Lake Abert, OR	18	21	12	9	5
Goose Lake, OR/CA	2	3	22	8	2
Honey Lake, CA	0	0	0	40	0
Carson Lake, NV	1	0	0	2	28
Malheur NWR, OR	3	0	0	0	0
Warner Wetlands, OR	0	0	1	1	0
Surprise Valley, CA	1	5	6	5	1
Alkali Lake, NV	0	0	1	0	0
Carson Sink, NV	0	3	4	5	11

± 0.13 , $n = 185$). Seventeen percent of radio-marked individuals were detected at more than two lakes, and 26% made at least two interlake movements during the postbreeding period. For birds that were detected after banding ($n = 161$), the mean minimum distance traveled among the lake systems within the region was 145.0 km. For avocets known to have remained in the western Great Basin through the last week of September, the mean number of lakes used was 2.12. We found no differences between the sexes in the number of movements, number of lake systems visited, or persistence in the region (t -tests, all $P > 0.1$, $n = 87$ females and 79 males). In addition, we detected no consistent patterns of movement among lakes by individuals that were observed at multiple locations.

During eight survey weeks when all lake systems were surveyed thoroughly, only 8 of 110 birds (7%) that bred at the northern three lakes (and none originating at Summer Lake) were detected at either of the California or Nevada sites. However, 23% of the adult avocets that nested at Carson Lake and 28% of those that nested at Honey Lake were located at Summer, Abert, or Goose lakes, resulting in a significant northerly directional bias in movements between these two subregions (G -test with Williams' correction, $G = 11.32$, $P < 0.001$).

Throughout the postbreeding period, the relative use of individual lakes varied dramatically, both within and between years (Fig. 4). Honey, Summer, and Goose lakes had consistent patterns of use by radio-marked individuals. The proportion of birds using Lake Abert,

however, differed between the two years, with lake usage substantially lower in 1996 than in 1997.

DISCUSSION

Avocet movements.—Postbreeding movements have been described for other species of waterbirds (Haig et al. 1998). However, by monitoring regional movements of individuals from multiple local breeding populations, our study provided some of the most extensive data on premigratory movements of a shorebird species (see Reed and Oring 1992, Warnock et al. 1998, Reed et al. 2000). Dietrich and Hötter (1991) also described patterns of extensive postbreeding movements by color-banded Pied Avocets (*Recurvirostra avosetta*) in the North Frisian region of Germany. During the molt period, 30% of the observed individuals moved among different postbreeding locations, up to 200 km apart, along the coast of the Waddensee. Similarly, Robinson and Oring (1996, 1997) observed postbreeding movements of American Avocets in the Great Basin. These studies, however, relied largely on opportunistic resightings, did not include broad-scale survey efforts, and therefore were insufficient for determining the extent of movements and the patterns of use of wetlands throughout the region.

As is true for most migratory birds, postbreeding movements of avocets have not been well studied. Our results point to three overlapping factors that likely contribute to the large-scale movements we observed in the western Great Basin: (1) the potential benefit of

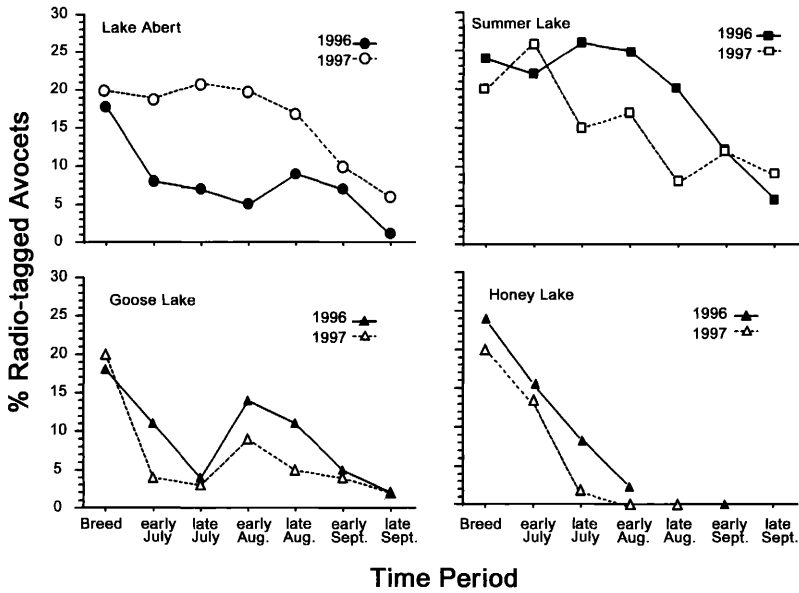


FIG. 4. Seasonal use of western Great Basin lakes by radio-marked American Avocets. Percentages refer to the total number of birds radio-marked for the study each year (85 in 1996 and 100 in 1997).

flocking during molt, (2) use of a superabundant food source in northern lakes, and (3) assessment of potential breeding or staging sites. First, movements during this period may be associated with molt (Dietrich and Hötter 1991, Hohman et al. 1992, Yarris et al. 1994). Adult avocets undergo a complete prebasic molt during the postbreeding period (Robinson et al. 1997), but the extensive movements throughout the period suggest that flight is not limited for any considerable time during the molting period. Thus, moving to areas such as Summer and Abert lakes during this potentially energetically stressful time may provide benefits such as easy foraging (not available at Honey Lake in 1996 and 1997) and increased awareness of predators by birds that join flocks.

Avocets may move north because of abundant invertebrate resources, potentially critical for premigratory fattening. The disappearance of birds from Honey Lake by early August and the late summer influx of tens of thousands of avocets to Summer Lake, Carson Sink, and Lake Abert attest to abundant food resources at these water bodies during the postbreeding period (Neel and Henry 1997, Warnock et al. 1998). These numbers far outweigh local breeding estimates, hence they suggest that specific factors attract avocets to these areas. An enig-

matic result of these movements is that some Carson Lake birds move north despite the fact that postbreeding numbers of avocets in the Carson area generally are comparable to those at Abert and Summer lakes (Neel and Henry 1997, Warnock et al. 1998). This suggests that competition for food does not drive Carson Lake breeding birds to undertake northward flights of 300 km or more.

The northerly bias in the direction of postbreeding movements is counter to the principal migratory vector of avocets during this time period. Avocets banded at Honey Lake in summer were recovered in autumn 250 and 480 km south of the banding site (Robinson and Oring 1996). Thus, postbreeding avocets can and do move in the typical migratory direction to specific foraging areas, although many move north prior to fall migration.

Finally, although overall numbers remain high at many lakes throughout the postbreeding period, our results demonstrate that some individuals move more extensively than would be expected if they were simply moving from breeding areas to join flocks at postbreeding staging or molting areas. Thus, they may be carrying out reconnaissance of areas for future breeding or staging sites (Morton et al. 1991, Reed and Oring, 1992, Reed et al. 2000). At

Great Basin wetlands, avocets nest in close proximity to water (Robinson et al. 1997) and therefore are more likely to be sensitive to fluctuations in lake levels than are other shorebirds that breed in adjacent upland habitats. Thus, assessment of alternative nest sites should be more important for avocets than for species that nest farther from shorelines. However, prospecting for future breeding areas during the postbreeding period would be most advantageous if conditions at that time accurately reflected nest-site quality during the following breeding season, an assumption that is unlikely given that lake levels vary widely from year to year and are largely determined by weather conditions during the winter. Robinson and Oring (1997) found relatively low breeding-site fidelity (24.3%) among avocets at Honey Lake, which suggests that prospecting takes place at some point in the annual cycle. Also, it should be noted that few avocets breed at Summer Lake or Abert Lake (Warnock et al. 1998); thus, only forays to other sites should be considered prospecting. Hence, the role of reconnaissance remains unclear.

Methodological considerations.—Methods for tracking movements of birds include visual identification of uniquely marked individuals and remote detection of birds using radio telemetry, satellite, or transponder technologies. Each method has advantages and limitations depending upon the system under study and the specific questions being addressed. Many of the lake systems of the western Great Basin are vast (10,100 to 60,700 ha; Neel and Henry 1997, Oring and Reed 1997), and large portions of each basin are inaccessible by surface transportation. Further, the semicolonial nature of avocet breeding facilitates a focused search effort for breeding individuals, but postbreeding birds are more widely dispersed across wetlands. Thus, consistent and thorough coverage of these areas for visual surveys of marked individuals is impossible.

Our data indicate that detectability of individuals was significantly greater using radios than from visual resighting efforts (Plissner et al. 1999). Consequently, reliance upon visual resightings alone led to a different interpretation of otherwise similar results. For example, visual observations of color-banded avocets strongly suggest that prior to migration, postbreeding individuals move to areas with abun-

dant food resources, and these observations provide little evidence for exploratory movements. This interpretation results from fewer observations of individuals at multiple sites, suggesting little movement of individuals among postbreeding sites.

Although radio telemetry reduces biases associated with low detectability of individuals, such concerns are not eliminated (White and Garrott 1990). Individuals may move beyond the boundaries of the study area, or radio signals may not be detected even when an animal is present in the search area. Therefore, we present comparative results that are descriptive of general patterns of regional movements by avocets rather than quantitative analyses of numbers, survivorship, phenology, and home-range areas. Nevertheless, the number of weeks in which individuals were not detected, despite complete coverage of the study areas, indicates that our estimates of movement frequency and extent are conservative.

The probability of detecting an individual within each study area was high for nearly all weeks of our study. By using a combination of ground and aerial methods, a missing individual would have to be absent for at least two search attempts to be considered absent for a given week. Prohibitive access to large lakes, however, did not allow direct comparisons of ground-based and aerial telemetry methods. In general, the greater range of detection and accessibility of remote locations were advantages of aerial methods, but with large numbers of transmitters, scanning rates may limit effective coverage of areas from aircraft alone. Our transmitters varied in signal strength in response to position of antenna and submersion in water and mud; however, preliminary field tests indicated that these effects were minimal for aerial monitoring. It is therefore likely that undetected individuals were not present in the sites covered by our surveys.

Importance of large-scale studies.—Connectivity of habitat patches is a crucial element in defining the structure of landscapes (Taylor et al. 1993, With et al. 1997). Haig et al. (1998) suggested that the development of conservation strategies for wetlands requires a broader perspective of the connectedness of individual patches across the landscape and that bird movements may be a key element in defining this connectivity. Numerous studies have doc-

umented that seasonal migration and between-year dispersal, especially by individuals of younger age classes, may link habitats across a large geographic scale. Our study demonstrates that within-year movements of individuals also may determine the extent to which populations use habitats on a regional basis.

Our results demonstrate the need for multi-year studies to elucidate patterns of habitat use, particularly in systems that fluctuate drastically in habitat quality (Robinson and Warnock 1997). The different patterns of use of Summer and Abert lakes between the two years of our study are particularly instructive. Our results, as well as those of Warnock et al. (1998), demonstrate high interannual variation in the use of these two systems by shorebird populations. These differences likely are attributable to changes in factors such as salinity, which in turn affect the availability of invertebrate prey for the birds (Rubega and Robinson 1997). The diversity of lake systems in the region, however, provides multiple options for birds to locate suitable foraging sites.

Most efforts to develop conservation strategies for shorebirds have focused on protection of major migratory staging and stopover areas along coastlines (Myers 1983, Harrington and Perry 1995, but see Skagen and Knopf 1993). It is apparent, however, that current strategies (such as the nascent National Shorebird Conservation Plan) must recognize the need for multifaceted approaches to protecting these species. For populations inhabiting highly dynamic systems such as the Great Basin, attempts to identify individual sites for special conservation status likely will not result in effective conservation for waterbirds (Haig and Oring 1998). As we have demonstrated, individual birds, even during relatively short periods of their lifetimes, are likely to use multiple wetland systems within a region and may vary their use of these systems annually.

In summary, our investigation of individually marked American Avocets during the post-breeding period provided insight into the appropriate scale for landscape studies of waterbirds, documented the importance of determining connectivity of habitat patches through individual movements, and identified unexpected behavioral patterns that would not have been detected in population-level studies. Our results suggest a need for additional studies to

improve our understanding of life-history strategies that will enable the development of effective conservation strategies for other shorebird species.

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