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WITHIN- AND BETWEEN-YEAR DISPERSAL OF AMERICAN AVOCETS AMONG MULTIPLE WESTERN GREAT BASIN WETLANDS

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ABSTRACT.—Connectivity of discrete habitat patches may be described in terms of the movements of individual organisms among such patches. To examine connectivity of widely dispersed alkali lake systems, we recorded post-breeding and subsequent breeding locations of color-banded American Avocets (*Recurvirostra americana*) in the western U.S. Great Basin, from 1995–1997. Among individuals observed during the post-breeding/premigratory season, over half of the 188 breeding adults were observed at lakes other than their breeding locations, whereas 70% of 125 post-fledged young were observed only at their natal lake systems. Of 46 breeding adults observed in consecutive years, only eight (17%) dispersed between different lake systems. Only 8% of chicks were observed after their first year, and only 1.3% returned to the natal area in subsequent breeding seasons. Adult and recently fledged birds from the southernmost breeding site were regularly observed in post-breeding aggregations at lakes several hundred kilometers to the north, suggesting seasonal differences in habitat quality at the lake systems studied. These results indicate the importance of maintaining habitat for post-breeding movements. *Received 10 Dec. 1998, accepted 3 April 1999.*

Concurrent with the recognition that habitat fragmentation is a key threat to regional biodiversity, the role of dispersal in maintaining connectivity between populations and subpopulations has become a major focus in assessing extinction risks and other dynamics of populations and communities (Saunders et al. 1991, McPeek and Holt 1992, Taylor et al. 1993, Dunning et al. 1995, With et al. 1997, Haig et al. 1998). For vertebrate populations, dispersal studies generally have focused upon movements within contiguous habitats or among adjacent patches. Although appropriate for some species, this approach fails to account for a significant proportion of dispersal events among more mobile species, especially those that inhabit discrete, widely-dispersed patches of habitat. In addition, connectivity measures require monitoring of multiple sites as both potential sources and recipients of dispersers. Such interchange among patches has been incorporated to varying degrees into numerous spatial models of populations (see Doebeli and Ruxton 1997, Ims and Yoccoz 1997, Wiens 1997), but empirical measures of such rates of exchange are often difficult to determine for vertebrate metapopulations.

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Specifically, studies of avian dispersal are largely limited by the spatial scale that researchers are able to effectively monitor dispersing individuals and by a traditional focus on return rates rather than on broader dispersal patterns. Typically, such studies focus on a population inhabiting a single site or a few neighboring areas, with the probabilities of detection for dispersers decreasing geometrically with distance from the point of origin (Barrowclough 1978, Cunningham 1986).

To determine large-scale connectivity patterns among discrete wetlands of the western Great Basin, we examined movements of banded American Avocets (*Recurvirostra americana*) among major lake systems of an otherwise arid region. In addition to monitoring dispersal in relation to breeding sites, we also examined premigratory movements of individuals, an often neglected aspect of individual life histories that may be a critical connective element of patchy landscapes (Haig et al. 1998).

METHODS

From 1995 to 1997, we color-banded and observed American Avocets at four major alkali lake systems in high desert regions of the western Great Basin: Summer Lake and Lake Abert in Lake County, Oregon; Goose Lake in Lake County, Oregon and Modoc County, California; and Honey Lake in Lassen County, California (Fig. 1). Interlake distances range from 45–315 km. Avocet breeding locations in the region, other than our study areas, were scarce during the years of the study; although additional local breeding popula-

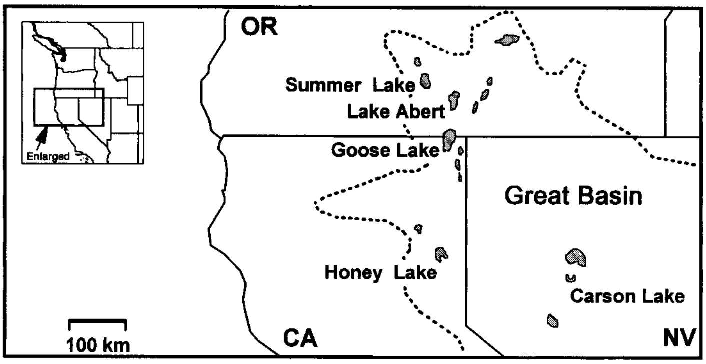

FIG. 1. Avocet study areas of the western Great Basin.

tions occur sporadically in response to suitable water conditions (Neel and Henry 1996; Oring and Reed 1996; L. W. O., pers. observ.). During breeding periods, our efforts at Summer Lake and Honey Lake were focused on managed wetlands adjacent to the main lake bodies: the Summer Lake Wildlife Area (SLWA) and Jay Dow, Sr. Wetlands (JDW), respectively, although we also conducted regular surveys along the entire lake shorelines.

During the three breeding seasons, 339 incubating adults were captured at nests and given unique combinations of color bands. Recently hatched chicks ($n = 457$) and flightless fledglings ($n = 19$) were captured and individually marked opportunistically near nesting areas. In 1995, an additional 61 individuals in post-breeding flocks were captured and banded at Summer Lake. All birds were given U.S.D.I. numbered aluminum and celluloid or Darvic™ plastic leg bands. In 1996 and 1997, radio transmitters were attached to aluminum leg bands and placed on 185 adult avocets, distributed among the four lake systems (Plissner et al. in press). Hatch-year birds were given brood-specific band combinations, with individuals identified by colored plastic tape wrapped around the numbered aluminum band. Sexes of adults were distinguished by relative bill curvature (Hamilton 1975) whenever possible but were deferred to judgments during banding in cases of conflict with observations of resighted individuals.

Banded avocets were resighted during the breeding and post-breeding periods at each lake, from April through September of each year. The Summer Lake WA and Jay Dow, Sr. Wetlands were surveyed weekly throughout the field season. Because of difficulties in accessing most of the lakeshores, the four main lakes were surveyed less frequently by foot and from vehicles and hovercraft. In 1996 and 1997, complete surveys of the three Oregon lakes were conducted weekly during the breeding and post-breeding periods. Aerial surveys and previous monitoring efforts at Honey Lake indicated relatively little use of the main lake body by avocets throughout the breeding and post-breeding periods (L.W.O., unpubl. data). Nevertheless, focal lake sites in proximity to Jay Dow, Sr. Wetlands were regularly surveyed. Observers recorded band combinations observed with 20–60× telescopes. Breeding status was assigned to birds observed at nests or in the presence of young chicks. As a conservative measure, only birds observed after 1 August were assumed to be post-breeding. We use the term "dispersal" to refer to movements between different lake systems; whereas we refer to birds returning to the same lake system as "philopatric". We also report anecdotal observations of banded avocets from wintering areas in California.

Resightings were subsequently screened against lists of known band combinations. Because of occasional band loss and the fact that some pairs of band colors became difficult to distinguish as they faded over time (Robinson and Oring 1997a), alternatives were considered for those observations that did not correspond to known combinations. If only a single alternative combination existed, the sighting was retained in the dataset. Other observations were discarded. Observations of individuals breeding in different years (bird-years) were considered independent for all summaries and analyses. Frequency data were analyzed using G-tests with Williams correction (Excel macro based on Sokal and Rohlf 1981).

RESULTS

Within year movements.—During the study period, we monitored postfledging/postbreeding movements for 476 hatch-year and 339 breeding adult American Avocets (151 females, 170 males, 18 unknown gender) banded in the western Great Basin. One bird, originally banded as a chick, was subsequently recaptured and rebanded as a nesting adult. Eight individuals were observed at nests during two breeding seasons. Of the total monitored, 125 chicks (26%) and 188 adults (55%) observed during nesting periods were resighted during the subsequent post-fledging/post-breeding periods (i.e., after 1 August). Among

TABLE 1. Post-breeding locations of adult American Avocets in the western Great Basin, 1995–1997.

		Post-breeding location[b]			
Breeding location	Adults monitored[a]	Honey Lake	Goose Lake	Lake Abert	Summer Lake
Honey Lake	105	12	2	10	9
Goose Lake	57	0	17	11	12
Lake Abert	50	0	5	16	12
Summer Lake	133	0	4	42	62

[a] Includes seven individuals observed at nests during two breeding seasons.
[b] Multiple post-breeding locations included for 30 individuals.

adults resighted during the post-breeding period, 53% were observed at lakes other than where they had bred (Table 1). There was no significant difference in proportions of males (53.5%, $n = 99$) and females (52.6%, $n = 76$) that dispersed from breeding locations to other lake systems ($G_w = 0.014$, $P > 0.05$). Furthermore, of observed post-fledged young, 30% (38 of 125) were resighted away from their natal lake systems (Table 2), a significant difference from the adult rates of post-breeding dispersal ($G_w = 15.59$, $P < 0.05$). Five chicks and 16 adult breeders dispersed following fledging or breeding from Honey Lake to post-breeding locations among the northern three lakes, while no birds from the northern three lakes were observed postbreeding/post-fledging at Honey Lake. Four chicks and three adults were reported from wintering areas along the northern California coast (Humboldt Bay and San Francisco Bay) after leaving Goose Lake and Honey Lake natal/breeding areas. Prior to being reported on the wintering grounds, all seven birds were observed on at least one of the three Oregon lakes during the post-breeding period.

Between-year movements.—We monitored between-year dispersal locations for 454 chicks and 259 adult American Avocets (137 females, 122 males). Altogether, 197 birds were observed in the region in multiple years, including 51% of all banded adults and 8% of chicks. Of 46 adults that were observed in the region in consecutive breeding seasons, 38 (83%) returned to the same lake. Eight additional adults that bred at Honey Lake in 1995 were not observed the following year but returned to breed in 1997. Overall, return rates for chicks were 0.4% for birds observed in their first post-natal breeding period (i.e., at age 1) and 1.3% for birds observed during their first two post-natal breeding seasons (i.e., ages 1 or 2). Of eleven banded chicks resighted during subsequent breeding seasons, seven (64%) returned to the natal lake system. The other four chicks, all banded at Honey Lake, dispersed to Oregon lakes in subsequent breeding seasons. No adults dispersed from Honey Lake to the northern lakes between years, and no birds of any age class from Goose, Abert, or Summer Lakes dispersed south to Honey Lake during subsequent breeding periods. Four birds (three males and one female) were observed during the breeding period of all three study years. Three of the four were observed at Honey Lake during all three years. The other individual bred at Summer Lake in 1995 and 1996 and was observed at Lake Abert during the breeding period in 1997. Only four individuals that bred in 1996 and 1997 were observed during the post-breeding period of the previous year. One of the four nested in 1997 at Summer Lake after nesting and spending the post-breeding

TABLE 2. Post-fledging locations of American Avocets in the western Great Basin, 1995–1997.

		Post-fledging location			
Natal location	Chicks monitored	Honey Lake	Goose Lake	Lake Abert	Summer Lake
Honey Lake	201	21	0	6	2
Goose Lake	169	0	45	12	14
Lake Abert	10	0	0	5	1
Summer Lake	97	0	1	2	16

period at Lake Abert in 1996. The other three bred and spent the post-breeding period at the same lake in both years.

DISCUSSION

Our results demonstrate within and between year patterns of dispersal at a regional scale. Earlier studies of movement patterns of avocets and other recurvirostrids focused on rates of philopatry and dispersal of individuals within a single wetland (Cadbury and Olney 1978, Watier and Fournier 1980, Sordahl 1984, Cadbury et al. 1989, James 1995, Robinson and Oring 1997b) or relied upon occasional surveys and anecdotal reports of marked individuals from areas away from the study area (Robinson and Oring 1996). By regularly monitoring birds at multiple, distant lake systems, we were better able to define the movement patterns and extent of movements at a scale more appropriate to the life history of the species. Still, we recognize the fact that, in order to gain an objective measure of dispersal, monitoring of more distant sites in multiple directions from breeding areas would be required.

Return rates of individuals we observed differed somewhat from those described for avocets in an earlier Great Basin study at Honey Lake, California. Robinson and Oring (1997b) estimated that 21–25% of avocets chicks that were known to have survived to breeding age returned to the natal site to breed, whereas we observed 64% of known survivors (i.e., individuals observed after their hatch-year) returning to the natal lake system. In relation to the total number of chicks banded, however, our return rates were lower (4.2%, Robinson and Oring 1997b; 1.3%, this study), suggesting that survivorship of chicks was likely the distinguishing variable. Return rates of breeding adults were significantly different in the two studies (24%, Robinson and Oring 1997b; 18%, this study; $G_w = 4.24$, $P < 0.05$). Relative to other species of Charadriiformes (Oring and Lank 1984), natal and breeding philopatry rates of avocets in the western Great Basin were low, perhaps resulting from the extensive annual variability in breeding habitat suitability.

The small number of interlake breeding and natal dispersal events during the three years of the study suggests limited, but adequate (Wright 1951), gene flow among Great Basin breeding populations. Furthermore, the pattern of both post-breeding and between year dispersal suggests an unbalanced pattern of connectivity, perhaps indicative of source-sink metapopulation dynamics (Pulliam 1988), with Honey Lake/Jay Dow, Sr. Wetlands serving as a source population in relation to the three Oregon lakes. This hypothesis is further supported by observations that productivity at Jay Dow, Sr. Wetlands has generally been higher than at the other study areas (S.M.H. and L.W.O., unpubl. data). Historically, in a system with high interannual variability in habitat patch quality resulting from fluctuations in precipitation (Engilis and Reid 1997, Robinson and Warnock 1997), sources and sinks may have shifted periodically. Such shifts would characterize a rescue effect metapopulation (Brown and Kodric-Brown 1977), in which local populations, in danger of extinction if isolated, nevertheless persist as their numbers are buffered by immigration from populations with more favorable breeding conditions (Stacey et al. 1997). As a recently developed, managed wetland, the Jay Dow, Sr. Wetlands may in fact now be a stable source for avocet populations at other wetland systems throughout the western Great Basin.

Post-breeding movements also suggested seasonal differences in the use of various wetlands within the region. Primary breeding areas such as the managed wetlands (Jay Dow, Sr. Wetlands and Summer Lake WA) were relatively less important as post-breeding habitats, whereas the major lake bodies, particularly the three northern waterbodies in our study (Goose Lake, Lake Abert, and Summer Lake), supported much higher densities of birds in late summer and early fall than during the breeding season (Warnock et al. 1998). Our observations of post-breeding dispersal from Honey Lake to northern lakes may reflect differential habitat suitability of the lake systems during this time period. Avocets from Honey Lake also have been reported in post-breeding flocks at water bodies east and south of the breeding/natal lake system (Robinson and Oring 1996, 1997b; Plissner et al. in press); indicating a multidirectional exodus from this particular breeding area in late summer and early fall. As an alternative to hypotheses of seasonal resource tracking, other studies have suggested that premigratory movements of birds are exploratory or otherwise associated with identification of future breeding areas (Morton et al. 1991, Reed and Oring 1992, Reed et al. in press). Our results, however, do not provide evidence for associations between post-breeding locations and subsequent nest sites, as would be expected for support of this hypothesis.

The observed patterns of dispersal movements were confirmed by radio telemetry data (Plissner et al. in press), which also demonstrated a northerly trend in post-breeding movements of avocets between Carson Lake, Churchill County, Nevada (Fig. 1) and the three Oregon lakes of this study, without evidence of southward post-breeding movements by Oregon breeders. Telemetry data further indicated that a very high proportion of post-breeding adults (71%) frequented wetlands other than their breeding locations. In addition, radio-tagged individuals frequently were not detected at any of the primary lakes during some telemetry surveys, suggesting even greater rates of movements away from breeding locations during the time period. Therefore it is likely that visual resightings of individuals represent a conservative estimate of the extent of post-breeding movements in the region. Nevertheless, these data provided information on movements across multiple years and for first-year birds, which can not be obtained effectively using current telemetry methodologies.

Post-breeding locations may also be associated with specific migration routes and/or wintering areas for these populations. All birds reported during the fall/winter along the northern California coast, including those originating from Honey Lake, were last observed at one of the three northern lakes. Previous reports suggest that birds originating from Honey Lake primarily migrate to wintering areas in California's Central Valley and coastal areas from San Francisco Bay south to the central coast of Sinaloa, Mexico (Robinson and Oring 1996, Robinson et al. 1997). Numbers of avocets at the northern extreme of the species' winter range (Humboldt Bay, California), however, have been increasing since 1960 (Evans and Harris 1994), and it is clear that many of these birds originated from breeding areas throughout the western Great Basin. Although further data are needed from other wintering areas, it appears possible that birds that aggregate at post-breeding areas in the northwestern Great Basin may overwinter along the northern California coast, whereas others, even from the same breeding area, may migrate directly south and west to more southerly post-breeding and wintering sites.

Our studies of American Avocet movements in the western Great Basin indicate that a dispersal-based evaluation of habitat connectivity requires an understanding of movements at multiple temporal and spatial scales. Based solely upon movements of individuals between breeding sites, connectivity among the different wetlands of the region would appear to be weak. Rates of post-breeding movements among different lake systems, however, was substantially higher, providing evidence of a strong link between the different systems. An apparent northward trend in long-distance post-breeding dispersal suggests that the northern lake systems may provide better resources for avocets during this time period, while the same trend in between-year movements may be simply a geographic artifact of the location of a source population relative to other study populations with lower productivity. This hypothesis also is supported by observations of avocets from Jay Dow, Sr. Wetland at stopover areas farther south (Robinson and Oring 1996), suggesting a multi-directional exodus of post-breeding birds from Honey Lake breeding sites. Thus, avocets use a large array of Great Basin wetlands within and among years, suggesting that conservation efforts should consider this complexity in defining appropriate habitat conservation strategies.

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