

## NATAL AND BREEDING DISPERSAL IN AMERICAN AVOCETS

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**ABSTRACT.**—We banded 811 nestling and 478 adult American Avocets (*Recurvirostra americana*) at a breeding site in northeastern California and observed their occupancy of space over the next one to two breeding seasons. Of the fledged young, 12% were seen after their hatching year, and 4.6% bred within one to two years after hatching. Twelve birds returned and bred at age two, and one individual bred at age one. Only 21 to 25% of avocets estimated to have survived to age two returned and bred; the rest presumably dispersed elsewhere. Females dispersed farther from their hatching site than did males. Overall, 53.6% of banded adults were seen one or two years following banding, but only 24.3% were known to have bred within 20 km of the banding site. There was a significant tendency for adults to avoid returning or to disperse greater distances in the year after they were banded. Approximately 72 to 78% of the adults estimated to have survived for two years after they were banded were seen subsequently; 56% of these birds returned and bred. There were no significant differences between males and females in dispersal distances or breeding return rates. Males responded to nesting failure by dispersing farther the next year, but females did not. There were no relationships between mate retention, dispersal distance, or subsequent success. Avocets were paired upon arrival at their breeding sites, which led to mate changes between years. We suggest that avocet dispersal patterns are life-history adaptations to unpredictable breeding habitats that yield few benefits from site familiarity. Received 26 April 1996, accepted 30 January 1997.

DISPERSAL PATTERNS are thought to be a consequence of mating system (Greenwood 1980, Greenwood and Harvey 1982). In birds, social monogamy with resource defense by males is the norm. Females generally disperse farther than males both for their first nesting attempt (natal dispersal) and for subsequent attempts (breeding dispersal). This pattern is thought to result from an increased ability of males to acquire and defend territories at sites with which they are familiar. For birds that are not socially monogamous, other patterns of sex bias in dispersal distance are explained in terms of resource needs and mate acquisition and are exceptions that prove the rule (e.g. Dunn and Braun 1985, Pruett-Jones and Lewis 1990, Reed and Oring 1993).

Because of the wide variety of mating systems exhibited by shorebirds (Pitelka et al. 1974, Oring 1982), studies of dispersal in this group form important tests of Greenwood's (1980) framework (e.g. Oring and Lank 1982,

Colwell et al. 1988, Oring 1988, Reed and Oring 1993, Jackson 1994). It was originally believed that natal and breeding dispersal were not sex biased in monogamous shorebirds (Oring and Lank 1984). However, the issue proved to be more complex. For example, some studies found no sex bias in dispersal distance in Dunlins (*Calidris alpina*; Soikkeli 1970) and Common Redshanks (*Tringa totanus*; Thompson and Hale 1989), whereas others identified sex-biased dispersal in these species (Jackson 1994). Some monogamous species have sex-biased natal philopatry (Long-billed Curlew [*Numenius americanus*], Redmond and Jenni 1982; Common Ringed Plover [*Charadrius hiaticula*], Jackson 1994), whereas others do not (Semipalmated Sandpiper [*Calidris pusilla*], Gratto 1988; Piping Plover [*Charadrius melodus*], Haig and Oring 1988a). Similarly, some species have sex-biased breeding-site fidelity (Common Redshank; Thompson and Hale 1989, Jackson 1994), whereas others do not (Long-billed Curlew, Redmond and Jenni 1982; Piping Plover, Haig and Oring 1988b).

In order to understand why some monogamous shorebirds might have male-biased phil-

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opatry and fidelity while others do not, Greenwood's logic must be applied carefully. Differences in dispersal tendency among monogamous species might be explained in terms of variations in habitat and social behavior (Thompson et al. 1988). When habitat availability is unpredictable, the benefits of breeding-site fidelity are reduced because a familiar habitat may not be available the next year. Similarly, the importance of mate acquisition increases because both sexes may be forced to breed at a new site many times during their lives. Thus, we predict that monogamous shorebirds in ephemeral habitats would benefit from forming pair bonds early in the season, even prior to arrival at the breeding site, whereas monogamous shorebirds in stable habitats could rely on mutual return to the previous breeding site as a means of acquiring a mate. As a corollary of reduced mate and site tenacity, we predict that monogamous shorebirds in stable habitats should show a sex bias in breeding dispersal (because of benefits of territory familiarity), whereas those in ephemeral habitats should not.

Because American Avocets (*Recurvirostra americana*) use extremely unpredictable habitats, they form an ideal test of the above hypotheses. Avocets are considered specialists in using semipermanent or ephemeral wetlands. They commonly breed inland near shallow saline and alkaline wetlands (Bent 1927, Palmer 1967, Johnsgard 1981, Alcorn 1988) that exhibit extreme annual variation in availability and quality (Castro et al. 1990, Skagen and Knopf 1993, Robinson and Warnock 1997). Prior to this study, information on dispersal and philopatry in avocets was based on only 21 individuals banded at a single site (i.e. Sordahl 1984).

We report results from four years of study of color-banded American Avocets breeding in the western Great Basin (northern California and northwestern Nevada). Our objectives were to: (1) identify the patterns and scale of return to natal and breeding sites; (2) compare these patterns for males and females; (3) document social and temporal aspects of reproduction including age at first breeding, timing of pair formation, and patterns of mate retention; and (4) evaluate potential relationships between dispersal, mate retention, and reproductive success. We also used resightings of

marked adults within a season to compare patterns of within-season breeding dispersal after nesting failure with patterns of between-season breeding dispersal. We allowed the movements of avocets to determine the scale of study by documenting dispersal at multiple distances from the core study site (cf. Jackson 1994) in order to avoid underestimating the importance of long-distance dispersal.

#### STUDY AREAS AND METHODS

*Study areas.*—Avocets were marked from 1992 to 1994 at the Jay Dow, Sr. Wetlands (Dow; 40°10'N, 120°13'W), a research facility of the University of Nevada, Reno located in the Honey Lake Valley (HLV) in northeastern California. The wetlands at Dow were constructed in 1990 and 1991, so few (if any) avocets had previous breeding histories there. Limited banding also was conducted at other sites in HLV including the Dakin and Fleming units of the Honey Lake State Wildlife Area, the Wild Goose Hunting Club, Amedee Hot Springs, and along the shore of Honey Lake itself (hereafter each of these sites is referred to as a wetland complex; Fig. 1).

In Nevada, banding was conducted in 1991 in the Lahontan Valley at two sites (Alberico 1993): Mahala Slough (39°30'N, 119°00'W) and S-Line Reservoir (39°30'N, 118°40'W). Mahala Slough is an ephemeral wetland that was most likely maintained by canal seepage (Lico 1992) and was nearly dry from mid-summer 1991 through the 1995 breeding season (Alberico 1993). S-Line Reservoir is a storage reservoir for the Newlands Irrigation project. Seepage from the reservoir maintains a flooded pasture where a few recurvirostrids breed.

Study areas were subdivided at several spatial scales. Analyses of movements from one year to the next were conducted using: (1) the shortest linear distance between two points, and whether or not movements were among (2) ponds, (3) pond complexes, or (4) wetland complexes (Fig. 1). A pond was defined as an area of wetland surrounded by shoreline and/or dikes. A pond complex was identified by grouping ponds that were separated only by narrow stretches of land (2 to 10 m), and a wetland complex was identified by grouping pond complexes that were more than 2 km from the next nearest wetland.

*Trapping and banding.*—Our final trapping protocol was adopted in 1993 to minimize disturbance of breeding birds (see Robinson et al. 1997: 22). Adults were trapped on the nest after 14 days of incubation. Birds were trapped during the heat of the day when they were highly motivated to incubate and were not kept off the nest for more than 20 min. Eggs were replaced with painted wooden replicas (cf. Reed et al. 1993) and were placed back in the nest immediately after trapping. Members of a breeding pair were not

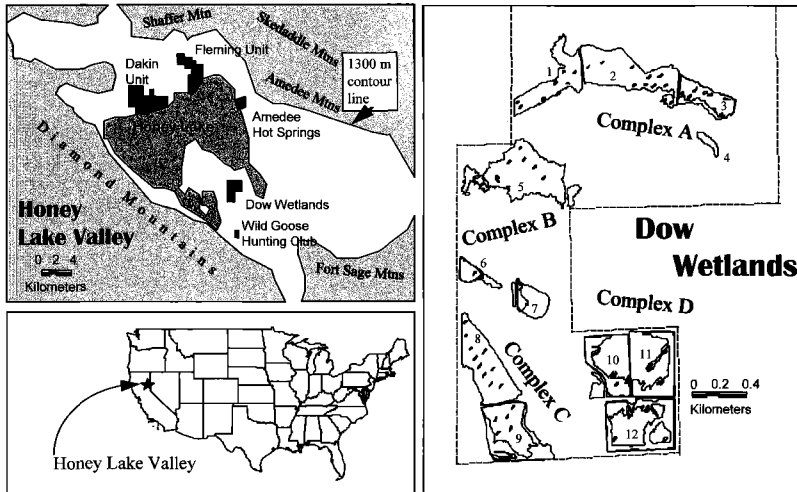


FIG. 1. Wetland complexes in the Honey Lake Valley, California, 1992 to 1994. Detail map illustrates ponds (designated by numerals) and pond complexes within the Jay Dow, Sr. wetland complex.

trapped on consecutive days, and the second bird usually was trapped only when the eggs were hatching. Chicks were banded at the nest within 6 h of hatching or occasionally were caught by hand after leaving the nest.

We banded 591 adults and 1,371 juveniles at HLV from 1992 to 1994 (Robinson and Oring 1996); 32 adults also were banded in the Lahontan Valley in 1991. Adults were banded with unique combinations of three to five UV-resistant colored plastic bands plus a numbered metal federal band. Adults were sexed by bill curvature (Hamilton 1975), and similar numbers of females and males were banded (313:310). Chicks were banded with brood-specific combinations of one to two colored plastic bands plus a numbered federal band. Colored plastic tape placed over the band distinguished individuals within broods.

Resightings at Dow were accumulated at two temporal scales: daily and weekly. Daily resightings were made by field crews of one to two individuals responsible for groups of three to four ponds (0.6 to 1.1 km<sup>2</sup>; Fig. 1). Vehicles and portable blinds were used for concealment to observe birds with 15–60 × spotting scopes. Each crew spent approximately 8 h per day, 6 days per week, in their assigned area. We also systematically surveyed all sites in the HLV every seven days and recorded the identity and location of each marked bird sighted. Whenever we resighted an individual, we attempted to record whether it was in a group (>2 birds), with a single member of the opposite sex, with a single individual of unknown sex, or alone.

*Population measures.*—To estimate numbers of nesting birds, we used weekly counts of avocets present at each wetland complex and estimated clutch initi-

ation dates from all known nests (see Alberico 1995). Median clutch initiation dates were 12 May 1992 ( $\pm$  SD of 13 days), 9 May 1993 ( $\pm$  10 days), and 15 May 1994 ( $\pm$  12 days). However, median dates by wetland complex differed by 5 to 16 days ( $\pm$  7 to 14 days). Because the SD ranged from one to two weeks, we estimated number of nesting birds by counting the numbers of birds present two weeks prior to the median clutch initiation date for the site, on the median initiation date, and two weeks after the median initiation date. At most wetland complexes in most years, these counts closely reflected the numbers of breeding birds (as indicated by numbers of nests), and variability between weeks can be attributed to movements of breeders that failed and initiated a second nest at a new site (Robinson et al. unpubl. data).

At Dow, approximately 54, 61, and 47% of the breeding adults were marked from 1992 to 1994, respectively (including birds banded that year and birds previously banded, but excluding individuals marked as chicks). At Goose, 85% were banded in 1993 and 23.8% in 1994 (Fig. 2). Other wetland complexes in HLV also supported large numbers of breeding avocets. In 1993, approximately 600 avocets bred at Dakin, 150 at Fleming, and 200 at Amedee. In 1994, 330 avocets bred at Dakin, 110 at Fleming, and none at Amedee (these sites were not monitored in 1992). In 1994, 13.3% of adults at Dakin were banded, and 2.4% of adults at Fleming were banded.

For sites under close observation (Dow from 1992 to 1994, Goose in 1993 and 1994, and Dakin and Fleming in 1994), we have accurate estimates of the proportion of chicks banded. These data (including estimates for other locations and years) are shown in Figure 3. At Dow, the proportion of chicks banded

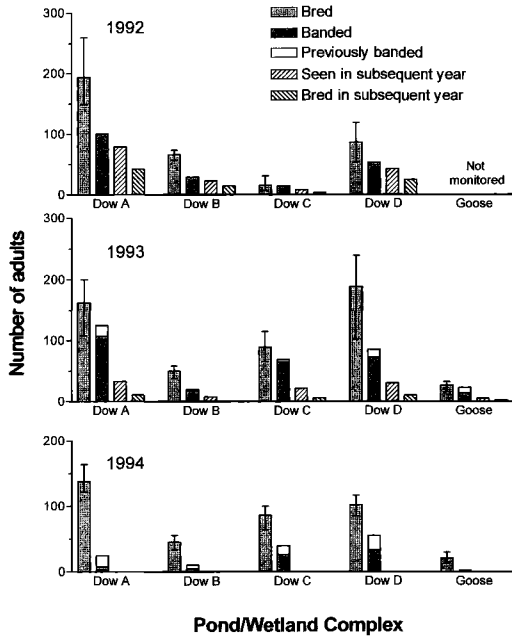


FIG. 2. Banding effort and population estimates for adult American Avocets breeding in the Honey Lake Valley, California, 1992 to 1994.

each year was 91.2, 86.3, and 71.0 from 1992 to 1994, respectively.

By comparing resightings of fledged chicks with resightings during winter or migration (Robinson and Oring 1996) and in subsequent breeding seasons, we estimated the probability of detecting fledged young. Young birds that were resighted after fledging were seen a mean of 1.97 times ( $\pm 1.42$ , range 1 to 11,  $n = 670$ ). Of these individuals, many were resighted only once, and some were not identifiable as individuals due to band or tape loss. Thirty-nine individuals banded as chicks and seen as adults had retained their complete band and tape combinations. These individuals were seen as fledged young-of-the-year a mean of 1.39 times ( $\pm 1.57$ , range 0 to 6); 16 of 39 (41%) that were not resighted as fledglings were later seen alive.

*Dispersal and survivorship measures.*—In addition to our observations of marked birds on the breeding grounds, we obtained sightings of marked birds observed at migration and wintering sites (Robinson and Oring 1996). This secondary migration/winter data set was used to make an approximate separation of mortality and long-distance dispersal probabilities for birds that were never seen at HLV after the year they were banded. The proportion of banded individuals that returned ( $P_{ret}$ ) can be described in terms of the probability of surviving ( $1 - P_{die}$ ) and the probability of dispersing ( $P_{disp}$ ) using the relationship:

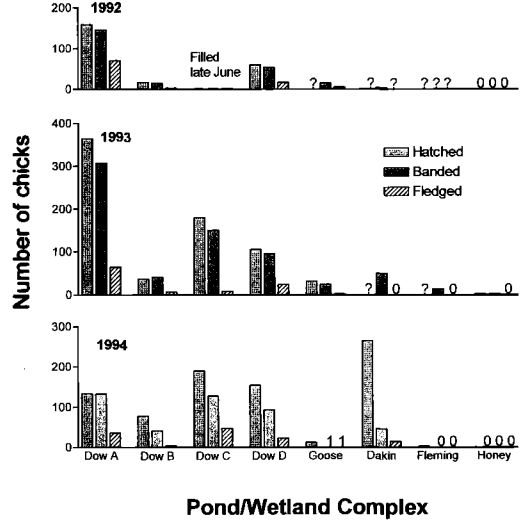


FIG. 3. Banding effort and survivorship for hatching-year American Avocets in the Honey Lake Valley, California, 1992 to 1994.

$$P_{ret} = (1 - P_{die})(1 - P_{disp}). \quad (1)$$

$P_{ret}$  was estimated from all the data on return to HLV. We estimated  $P_{disp}$  using only the HLV return rates for individuals known to be alive based on resightings at migration and/or wintering sites. Equation 1 was then solved for  $1 - P_{die}$  to estimate survivorship.

These calculations rest on the assumption that all individuals survived from the time they were seen during migration or winter until the following breeding season. Thus,  $P_{disp}$  is equivalent to the proportion of marked individuals seen during migration or winter that did not return to HLV divided by the total number of marked individuals seen during migration or winter. When this assumption is not met, it leads to an overestimate of  $P_{disp}$  and a corresponding underestimate of  $P_{die}$ . However,  $P_{die}$  still can be considered a minimum estimate of the proportion of birds that died. As an additional evaluation of this assumption, we calculated two values of  $P_{die}$ . The first assumed that an individual seen during winter or in migration in 1992 or 1993 survived until 1994; the second assumed only that it survived to the next breeding season.

*Statistical analyses.*—We defined an individual as a successful breeder if it hatched chicks during the year it was banded. Because data reported are for only three years, sufficient data for breeding birds in multiple years after they were banded were not available. For all contingency analyses, we excluded resightings of breeding birds outside of HLV where systematic surveys were not conducted. Sample sizes differed for each test due to occasional missing values for mate retention (i.e. if the first mate was un-

TABLE 1. Return to the natal site (or to other sites in the Honey Lake Valley) by American Avocets banded at Jay Dow, Sr. Wetlands, California, 1992 and 1993.

	Year Banded at Dow		
	1992	1993	Combined
No. banded	218	593	811
No. observed fledged	93 (42.7%)	106 (17.9%)	199 (24.5%)
Corrected no. fledged <sup>a</sup>	131 (60.1%)	150 (25.3%)	281 (34.6%)
No. seen in HLV			
One year old	6 <sup>b</sup>	13 <sup>c</sup>	19
Two years old	18 <sup>d</sup>	—	—
One and / or two years old <sup>e</sup> (% of fledged)	21 <sup>f</sup> (16.0%)	13 (8.67%)	34 (12.1%)

<sup>a</sup> Based on 41% of birds later known to be alive but not seen fledged during hatching year.

<sup>b</sup> Three females, three unknown sex.

<sup>c</sup> Seven females, five males, one unknown sex.

<sup>d</sup> Six females, five males, seven unknown sex.

<sup>e</sup> Minimum number of individuals seen whether in one or both years.

<sup>f</sup> Seven females, five males, nine unknown sex.

banded) or breeding success (i.e. if fate of the nest was unknown).

Contingency tables ( $2 \times 2$ ) were analyzed using the conditional binomial exact test (CBET; Rice 1988). These analyses assumed that each observation was independent. For analysis of natal philopatry this was not a problem because no known siblings returned (see Alberico et al. 1992), and no philopatric birds bred together. For analysis of breeding dispersal we avoided including joint nesting attempts twice and maintained independence by conducting separate tests for males and females. Contingency tables larger than  $2 \times 2$  were analyzed using the  $G$ -statistic (Sokal and Rohlf 1981) with Emigh's (1980) correction for continuity ( $G_{adj}$ ).

When probabilities for tests were greater than  $\alpha = 0.05$ , we examined power of the contingency tests. For the CBET and  $G$ -tests, we estimated minimum power using tables for the  $\chi^2$  test in Cohen (1988; see Alberico 1995). This is a minimum estimate because power for the CBET test and  $G$ -test is greater than for the  $\chi^2$  test (Sokal and Rohlf 1981, Rice 1989). To aid in evaluating biological significance of negative results, we also examined  $\beta_{30\%}$  the probability of detecting a 30% difference at the observed sample size. The effect size of 30% was chosen following qualitative suggestions of Cohen (1988). When this power  $> 0.75$ , we concluded that no biologically significant effect was observed.

In cases where percentages for a small subgroup were compared with the rest of the larger statistical population, we calculated 95% confidence intervals (CI) around the subgroup percentages and examined whether the percentage for the larger group fell within the confidence interval. If the larger group percentage fell within the subgroup confidence interval, then we computed  $n_{crit}$  which is the number of observations necessary to narrow the confidence interval around the subgroup percentage and ex-

clude the larger group percentage (at  $\alpha = 0.05$  and  $1 - \beta = 0.80$ ; Sokal and Rohlf 1981).

To maintain experimentwise error rate, significant  $P$ -values were adjusted for multiple tests for the same individuals using the sequential Bonferroni method (Rice 1989). Adjusted  $P$ -values are given after unadjusted values and noted as  $P_{adj}[x]$ , where  $x$  denotes groups of significant  $P$ -values to which the sequential Bonferroni adjustment was applied.

## RESULTS

### NATAL PHILOPATRY AND AGE OF FIRST BREEDING

*Return to the natal site.*—At least 34 individuals were seen in HLV after their hatching year (Table 1). This equals 4.2% of the chicks hatched in 1992 and 1993, or 12.1% of the corrected total number of fledglings ( $P_{ret} = 12.1\%$ ). Some one-year-olds returned to HLV even though they did not breed (Table 1).

Of 19 young avocets banded in 1992 and 1993 and seen during migration or winter (Robinson and Oring 1996), two were seen as nonbreeders in the summer at HLV, two returned and bred at HLV, and 15 were not seen again. Assuming that all birds seen during migration/winter in 1992 and 1993 survived until 1994, then  $1 - P_{disp} = 21.05\%$  (4/19), and the estimated probability that a fledgling survived to breed at age two (i.e.  $1 - P_{die}$ ) was 57.5%.

Of 19 avocets banded as chicks and later seen during migration/winter, 10 had been banded in 1992 and 9 in 1993. Of the 10 banded in 1992, four were seen during migration/winter 1992

and then as breeders in 1994, three were seen during migration/winter 1992 only, two were seen during migration/winter 1993 only, and one was seen during migration/winter 1994 only. Thus, up to three individuals could have died between 1992 and 1993. If these individuals actually died, then  $1 - P_{disp}$  would be 25.0% (4/16) and the survivorship estimate ( $1 - P_{die}$ ) would be 48.4%.

We documented one case of long-distance dispersal from the natal site. A male banded as a chick by R. Gerstenberg at Tulare Basin, California (35°47'N, 119°38'W) in 1985 was captured on a nest at HLV in 1993, 480 km from its natal site.

*Age at first breeding.*—At least 13 avocets that were banded as chicks returned to breed at HLV (1.6% of all nestlings banded, or 4.6% of the corrected total number of fledglings). The sex ratio of these birds (eight females and five males) was not statistically different from 1:1 (binomial  $P = 0.60$ ,  $n_{crit} = 307$ ). Each of these philopatric birds first bred in 1994. Seven females bred at age two, one female bred at age one, and all five of the males bred at age two. Three of the birds that first bred at age two (two females and one male) had been seen as non-breeders at HLV in the previous year.

*Differences between males and females.*—Because of uncertainties associated with band loss, natal dispersal distances could be determined for only five females ( $\bar{x} = 7.3 \pm SD$  of 7.1 km, median = 6.3 km, range 2.0 to 19.4 km) and three males ( $\bar{x} = 1.1 \pm 0.87$  km, median = 0.62 km, range 0.59 to 2.1 km). Compared with males, females had a greater variance in dispersal distance ( $F = 66.9$ ,  $df = 2$  and 4,  $P = 0.030$ ,  $P_{adj}[1] = 0.048$ ) and tended to have greater mean dispersal distance ( $t = 1.93$ ,  $df = 4$ ,  $P = 0.13$ ). These results must be interpreted with caution because dispersal distances for females were not normally distributed (see Fig. 4), and our sample sizes were quite small. Using a non-parametric Kolmogorov-Smirnov test (Sokal and Rohlf 1981, Siegel and Castellan 1988), overall natal dispersal distances for males and females were not statistically different ( $D = 0.4$ ,  $n = 3$  and 5,  $P = 0.92$ ), but the power of this test was low.

All seven females but only two of the five males bred at a pond complex other than their natal one. The status of one additional female was undetermined because her band combi-



FIG. 4. Dispersal distances for American Avocets that returned and bred one and/or two years after banding. Shaded areas show ranges of possible dispersal distances between suitable habitats.

nation was not unique. This fits the pattern of females dispersing farther from their hatching site (CBET,  $P = 0.024$ ,  $P_{adj}[1] = 0.048$ ). Males bred at locations where they had been seen as chicks or fledglings ( $n = 4$ ), whereas females did not ( $n = 5$ ; one male and three females were not seen as juveniles; CBET,  $P = 0.012$ ,  $P_{adj}[1] = 0.035$ ). This result must be interpreted carefully because males were more likely than females to be seen as juveniles ( $G_{adj} = 10.79$ ,  $df = 2$ ,  $P = 0.005$ ,  $P_{adj}[1] = 0.020$ ).

*Hatching success of first-time breeders.*—Hatching success (proportion of breeders that hatched at least one egg) for known first-time breeders (69.2%,  $n = 13$ , 95% CI = 43.2 to 90.6%), did not differ from the that of other breeders (53.5%,  $n = 432$ ; CBET,  $P = 0.28$ ). Hatchability (proportion of eggs hatched) was the same for known first-time breeders ( $\bar{x} = 59.1\%$ , median = 100%) and other breeders ( $\bar{x} = 51.9\%$ , median = 75%; Mann-Whitney  $z = 0.54$ ,  $P = 0.59$ ). All three females that dispersed >2.5 km failed to hatch chicks, whereas the five females that stayed within Dow successfully hatched chicks. The nest of the female that bred at age one was depredated.

BREEDING DISPERSAL BETWEEN YEARS

*Return to HLV.*—Of 199 adults banded in 1992 and 279 adults banded in 1993, 116 (24.3%) returned and bred one to two years after banding, 227 (46.4%) were never seen again, and 140 (29.3%) were seen in subsequent years as non-breeders or migrants at HLV;  $P_{ret} = 53.56\%$  (256

TABLE 2. Long-distance movements (&gt;50 km) within and between breeding seasons by American Avocets that bred in the Honey Lake Valley, California.

Individual	Banding location and year <sup>a</sup>	Nest fate <sup>b</sup>	Resighting data	Distance (km)
<b>Females</b>				
GO:YA	HLV, 1992	S	Reno, bred 1993	60
GOG:YAY	HLV, 1993	S	Summer Lake, bred 1994	325
WK:AY	HLV, 1992	S	Reno, seen 5 May 1993; HLV, bred 1993 and 1994	61
<b>Males</b>				
<i>z</i>				
AR:RK	HLV, 1992	?	Reno, bred 1993	59
KA:RO	HLV, 1994	U	Lake Abert, seen 1994 <sup>c</sup>	261
KY:GA	LV, 1991	U	HLV, seen 1993 and 1994	150
OB:KA	LV, 1991	U	HLV, bred 1993	150
WAW:YGY	HLV, 1993	?	Reno, seen 19 April 1994; HLV, bred 1994	60

<sup>a</sup> HLV, Honey Lake Valley; LV, Lahontan Valley.

<sup>b</sup> S, successful (eggs hatched); U, unsuccessful (eggs did not hatch); ?, unknown.

<sup>c</sup> Last seen at banding location on 12 June 1994 and seen in migratory flock at Lake Abert (north of banding location) on 12 July 1994.

of 478). Of those birds that were seen in HLV, only 56% bred there within two years of being banded (85 of 152, birds banded in 1992 only).

Eighteen of 25 individuals banded as adults and seen during migration or winter (Robinson and Oring 1996: table 2) returned to HLV. Assuming that all birds seen during migration/winter in 1992 and 1993 survived until 1994, then  $1 - P_{\text{disp}}$  was 72.0%, and the minimum probability that an adult bird died within two years after being banded ( $P_{\text{die}}$ ) was 25.6%, which is equivalent to an annual survivorship of 86.2%.

Of 25 individuals seen during migration/winter, 15 were banded in 1992 and 10 were banded in 1993. Of the 15 banded in 1992, two could have died in 1993 but have been assumed to be alive in 1994 (Robinson and Oring 1996: table 2). If these two individuals actually died, then the estimate for  $1 - P_{\text{disp}}$  would be changed to 78.3% (18 of 23), and the probability that an adult bird died within two years after being banded would become 31.6%, which is equivalent to an annual survivorship of 82.7%.

Although many birds did not return to HLV in the year after they were banded, observations in later years and resightings during winter/migration indicated that return rates reflected years spent away from HLV and not mortality. For example, only 35% (93 of 263) of the avocets banded in 1993 were seen at HLV in 1994, whereas 77% (152 of 198) of the birds banded in 1992 were seen in 1993 and/or 1994. Dispersal distances from previous nests were significantly greater for birds that returned in the year after banding ( $x + 1$ ) than for birds

that first returned to breed two years after banding ( $x + 2$ ;  $D = 0.37$ ,  $n = 52$  and  $33$ ,  $P = 0.008$ ). Although these distance data were not normally distributed, birds in year  $x + 1$  probably had greater variance in dispersal distance as well ( $F = 2.37$ ,  $df = 33$  and  $52$ ,  $P = 0.011$ ). The tendency to delay one year before returning to breed did not differ between males and females (23 of 40 females vs. 29 of 47 males that eventually bred returned in year  $x + 1$ ; CBET,  $P = 0.35$ ,  $\beta_{30} = 0.20$ ).

We documented seven long-distance breeding movements between seasons by individuals banded at HLV (Table 2). Prior to their first breeding attempt for the season, five individuals were seen near Reno. Three of these birds eventually settled at HLV for the season, and two bred in the Reno area 60 km from their previous breeding sites. Four of 32 avocets banded in the Lahontan Valley in 1991 also were seen subsequently. All avocet breeding attempts failed in the Lahontan Valley in 1991 due to drought (Alberico 1993), and Mahala Slough did not contain water from 1992 to 1994 (Robinson pers. obs.). Two banded birds were seen later at a borrow pit with a small amount of water near Mahala Slough, one in 1992 and one in 1993. Although it is impossible for these birds to have bred at Mahala Slough in those years, they may have bred elsewhere in the Lahontan Valley. Two other avocets from the Lahontan Valley have been seen at HLV, with one confirmed breeding (Table 2). These constitute probable drought-induced breeding dispersals of 150 km.

*Differences between males and females.*—A

TABLE 3. Arrival dates, departure dates, and residence times (SD in days) of adult American Avocets in the year after they were banded, Honey Lake Valley, California, 1993 and 1994.

	Females			Males			<i>t</i>	<i>P</i>
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>		
Date first seen <sup>a</sup>	21 April	18	79	20 April	17	93	-0.33	0.74
Date last seen <sup>b</sup>	25 June	18	67	2 July	18	74	-0.33	>0.80
Residence time, days <sup>b</sup>	66	24	67	76	23	74	0.75	>0.50

<sup>a</sup> Includes all banded birds whether or not they bred.

<sup>b</sup> Includes only birds seen  $\geq 25$  days after first resighting (the approximate incubation period).

slightly higher proportion of males than females returned and bred (64 males vs. 52 females), but the difference was not statistically significant (one-tailed binomial test,  $P = 0.18$ , 95% CI = 35.8 to 54.4%,  $n_{crit} = 1,501$ ). Sex ratios of avocets that were seen one or two years after banding (whether or not they bred) did not differ from 1:1 (1 year: 110 males, 99 females,  $P = 0.24$ , 95% CI = 40.1 to 53.9%,  $n_{crit} = 5,739$ ; 2 years: 60 males, 58 females,  $P = 0.46$ , 95% CI = 39.8 to 58.3%,  $n_{crit} = 54,890$ ). Taken as a whole, there was no evidence for a sex bias in return rates of adults.

Dispersal distances of males ( $x = 2.67 \pm 4.60$  km,  $n = 45$ ) and females ( $y = 2.50 \pm 3.99$  km,  $n = 36$ ) did not differ ( $D = 0.27$ ,  $P = 0.12$ ; Fig. 4), and males and females showed no difference in tendency to nest on a different pond (20 of 35 females vs. 27 of 43 males moved; CBET,  $P = 0.62$ ). They also showed no difference in tendency to disperse to a different pond complex (17 of 35 females vs. 26 of 43 males moved; CBET,  $P = 0.296$ ). Both of these tests had sufficient power ( $\beta_{30} = 0.24$ ) to detect a 30% difference between males and females.

*Pair formation and mate retention.*—At Dow, most avocets were paired when first observed each year (regardless of whether they stayed and bred). Of 357 individuals seen in at least one year after banding, 162 (45.4%) were first seen in close proximity to a single individual of the opposite sex (35.2% not with a mate, 30% undetermined). Based on the incidence of behaviors such as copulation, nest building, and territoriality (see Hamilton 1975, Alberico 1993), 263 (73.7%) appeared to be paired pre-breeders or breeders when first observed (11.5% alone, 9.2% in a flock, 5.6% unknown). In the year after banding, the sexes did not differ in arrival or departure dates (Table 3). Twelve of 25 females and 21 of 35 males changed mates in the year after they were

banded (CBET,  $P = 0.37$ ; Table 4). The previous mates of seven females (58.3%) and nine males (42.8%) were resighted at least once at HLV in year  $x + 1$ , so mortality or dispersal by a former mate did not explain these mate changes.

*Dispersal, mate retention, and reproductive success.*—Males that had unsuccessful nests had greater variance in linear dispersal distance than did successful males ( $F = 3.9$ ,  $df = 12$  and  $29$ ,  $P < 0.01$ ), leading to a difference between groups that approached significance ( $D = 0.35$ ,  $n = 13$  and  $30$ ,  $P = 0.076$ ). This trend was confirmed at other scales (Table 4): pond (CBET,  $P = 0.044$ ), pond complex (CBET,  $P = 0.028$ ), and wetland complex (CBET,  $P = 0.059$ ). For females, only variance in linear dispersal distance differed between successful versus unsuccessful birds ( $F = 4.49$ ,  $df = 10$  and  $23$ ,  $P < 0.025$ ;  $D = 0.28$ ,  $n = 11$  and  $23$ ,  $P = 0.31$ ); there were no differences in dispersal distance between successful and unsuccessful females at other scales (Table 5).

There was no difference in dispersal distance for avocets that changed or retained mates, whether measured as linear distance (females:  $D = 0.099$ ,  $n = 12$  and  $12$ ,  $P = 1.00$ ; males:  $D = 0.22$ ,  $n = 21$  and  $14$ ,  $P = 0.62$ ) or at other scales (Table 4). In addition, dispersal distance did not differ between birds that were successful versus unsuccessful at their next nesting attempt, whether measured as linear distance (females:  $D = 0.47$ ,  $n = 5$  and  $3$ ,  $P = 0.81$ ; males:  $D = 0.89$ ,  $n = 9$  and  $2$ ,  $P = 0.15$ ) or at other scales (Table 4).

The success of a breeding attempt did not influence return rates, mate retention, or future reproductive success (Table 5). Two of the comparisons had sufficient power to conclude that there was no difference between successful and unsuccessful birds ( $\beta_{30} < 0.20$ ). Success at the previous nest did not influence: (1) whether avocets returned in year  $x + 1$  or  $x + 2$  versus



TABLE 4. Proportion of American Avocets that changed breeding locations at the pond, pond complex, and wetland complex scales relative to nesting success and mate identity ( $P$ -values from conditional binomial exact tests). Column A shows the proportion of birds that changed breeding location and met the first indicated condition, and column B shows the proportion of birds that changed breeding locations and met the other indicated condition.

Scale	Females			Males		
	A	B	$P$	A	B	$P$
<b>Successful (A) vs. unsuccessful (B) in previous breeding attempt<sup>a</sup></b>						
Pond	12/23	8/12	0.215	15/28	12/15	0.044
Pond complex	10/23	7/12	0.210	14/28	12/15	0.028
Wetland complex	1/23	0/12	0.801	1/28	3/15	0.059
<b>Changed (A) vs. did not change (B) mates<sup>b</sup></b>						
Pond	7/12	8/13	0.585	13/21	9/14	0.583
Pond complex	6/12	7/13	0.594	14/21	7/14	0.178
Wetland complex	1/12	1/13	0.501	3/21	1/14	0.296
<b>Successful (A) vs. unsuccessful (B) at their next breeding attempt<sup>c</sup></b>						
Pond	3/5	1/3	0.876	4/9	2/2	0.107
Pond complex	2/5	1/3	0.628	4/9	2/2	0.107
Wetland complex	0/5	0/2	n/a	0/9	0/2	n/a

<sup>a</sup> Power to detect a 30% difference is 0.43 for females and 0.50 for males.

<sup>b</sup> Power to detect a 30% difference is 0.32 for females and 0.43 for males.

<sup>c</sup> Power to detect a 30% difference <0.10 for females and <0.15 for males.

never (females: CBET,  $P = 0.06$ ,  $\beta_{30} = 0.17$ ; males: CBET,  $P = 0.43$ ,  $\beta_{30} = 0.18$ ), or (2) whether avocets returned in year  $x + 1$  versus later or never (females: CBET,  $P = 0.36$ ,  $\beta_{30} = 0.00$ ; males: CBET,  $P = 0.40$ ,  $\beta_{30} = 0.00$ ; Table 5).

#### BREEDING DISPERSAL WITHIN SEASONS

We observed 31 banded adults (12 females and 19 males) that renested after their first breeding attempt failed. Compared with breeding dispersal between years, these birds renested at sites that were farther from their first nests (females:  $\bar{x} = 2.97 \pm 5.53$  km,  $D = 0.69$ ,  $n = 36$  and 12,  $P = 0.0003$ ; males:  $\bar{x} = 2.99 \pm 4.88$  km,  $D = 0.67$ ,  $n = 45$  and 19,  $P < 0.0001$ ). This difference in linear distance was due to an increased tendency to move between ponds (compared with data in Table 4; 16 of 18 males changed ponds, CBET,  $P = 0.045$ ; 10 of 12 females changed ponds, CBET,  $P = 0.051$ ), and not to increased dispersal between pond complexes (males: CBET,  $P = 0.43$ ; females: CBET,  $P = 0.29$ ) or wetland complexes (males: CBET,  $P = 0.21$ ; females: CBET,  $P = 0.46$ ). In 1993 only, 120 avocets (60 pairs) nested along the shore of Honey Lake, but nearly all failed within one week. Marked individuals in this group later renested at Dow.

In sharp contrast to mate switching between years (Table 4), once a pair bond was estab-

lished for the season it was maintained for multiple nesting attempts. Of the birds that renested and whose mates were banded, only one of seven females and none of six males changed mates within a season (vs. between-season mate switching; females: CBET,  $P = 0.054$ ; males: CBET,  $P = 0.0024$ ). Not surprisingly, males and females did not differ in distance dispersed within seasons at any scale (linear distance,  $D = 0.42$ ,  $n = 19$  and 12,  $P = 0.15$ ; pond, CBET,  $P = 0.51$ ; pond complex, CBET,  $P = 0.33$ ; wetland complex, CBET,  $P = 0.77$ ).

#### DISCUSSION

*Natal philopatry.*—Most avocets did not breed until they were at least two years old, although one female bred at age one. A few birds that eventually returned and bred spent a non-breeding summer at their natal site, but most did not (cf. Reed and Oring 1992, Reed and Dobson 1993). Before their first breeding attempt, avocets might visit potential breeding sites at distances of 600 km or more from their natal site (Robinson and Oring 1996).

Fledglings had a relatively high probability of surviving to age two (48 to 57%), and about 21 to 25% of surviving young returned to the HLV. It is important to separate these components, because survivorship is extremely site- and year-specific (see Fig. 3). Females dis-

TABLE 5. Proportion of American Avocets that nested successfully relative to between-season dispersal, mate retention and future success. Column A shows the proportion of birds that were successful and subsequently met the first indicated condition, and column B shows the proportion of birds that were successful and subsequently met the other indicated condition.

	Females			Males		
	A	B	$1 - \beta_{30}^b$	A	B	$1 - \beta_{30}^b$
Returned and bred at Dow (A) vs. elsewhere (B)	19/28	4/7	0.309	25/35	4/5	0.073
Returned and bred at one (A) vs. two years later (B)	13/23	9/17	0.421	16/29	10/18	0.519
Returned one or two years (A) vs. not in three years (B)	22/40	21/54	0.061	26/47	24/45	0.429
Returned next year (A) vs. later or never (B)	24/36	117/185	0.355	31/46	113/173	0.402
Bred successfully the next year (A) vs. failed (B)	14/22	7/9	0.789	19/26	10/16	0.243
Bred successfully the next time (A) vs. failed (B)	21/33	8/14	0.344	27/38	11/20	0.115
Bred with same mate next year (A) vs. new mate (B)	9/14	7/11	0.504	10/15	13/31	0.398
Bred with previous mate (A) vs. new mate (B) <sup>c</sup>	8/12	7/9	0.734	8/13	11/20	0.369

<sup>a</sup> Conditional binomial exact test (CBET).

<sup>b</sup> Power of the test to detect a 30% difference between columns A and B at that sample size.

<sup>c</sup> Column A shows the proportion of individuals that was successful after breeding with a previous mate, and column B shows the proportion of individuals that was successful after changing mates.

persed farther from their hatching site than did males. When measured as linear distances, the difference was significant only for variance in dispersal distance, but when measured at the pond complex scale, the difference clearly was significant. Female-biased dispersal distance was reflected even in the postfledging movements of young. Males usually were seen as fledglings at the pond complex where they eventually returned to breed, whereas females were not. In addition, females tended not to be seen after fledging until they returned to breed.

First-time breeders were just as successful as older birds, implying that site familiarity provides little advantage in breeding success. However, our anecdotal data suggested that nesting success decreased the farther a female dispersed from her natal site. For young birds, then, our results do not clearly indicate whether there is an advantage to breeding at a familiar site.

*Breeding-site fidelity.*—Our data on breeding dispersal were limited by the lack of birds returning in the year after they were banded. Birds that returned the next year nested farther from their previous site than did birds that returned two years later. We believe that this result was a response to banding and/or our presence on the study site. Jackson (1994) also reported dispersal in response to capture of adults at the nest for three shorebird species. More data are needed to evaluate whether this phenomenon results from researcher disturbance or is a response to changes in wetland availability.

Individuals moved up to 325 km between breeding seasons. Sometimes long-distance breeding dispersal was a response to habitat loss and sometimes a response to unknown factors (Table 2). We know that avocets can respond to changes in wetland availability by moving long distances. For example, avocets from HLIV bred in previously dry wetlands in the Reno area in 1993, and avocets banded in the Lahontan Valley dispersed to HLIV after Mahala Slough became dry.

Males and females had an equal tendency to return and breed at HLIV. In addition, for those birds that returned and bred there were no differences in dispersal distance for males and females, whether measured on a linear, pond, or pond complex basis. Thus, females had a greater tendency to disperse at large spatial scales

because they were more likely to go hundreds of km, but at smaller spatial scales dispersal did not differ between the sexes.

Dispersal distance did not differ between birds that changed mates and birds that retained mates. We detected no relationship between successful nesting and return rates, future success, or mate retention. Moreover, dispersing longer distances did not affect subsequent nesting success. Taken as a whole, these results indicate that at the scales we observed, familiarity with the site chosen for nesting played little role in site selection, breeding-site fidelity, or subsequent breeding success. Furthermore, because at least 50% of the avocets arriving at Dow already were paired, mate acquisition probably played only a small role (if any) in determining nesting location for many individuals. We propose that a pair's choice of nesting site is determined by social factors involved in formation of loosely structured breeding colonies and the individual experience of males (e.g. having had a previous nest depredated or observing large numbers of hatched chicks; see Oring et al. 1994).

Perhaps the best insight into the scale at which previous nesting success influences site selection comes from comparisons of dispersal within a season versus between years. The mean dispersal distance for pairs that renested within a season was determined by their tendency to change ponds but not pond complexes or wetland complexes. In contrast, even though their mean dispersal distances were shorter than within-season reneesters, unsuccessful males returning the next year were more likely than successful males to change ponds, pond complexes, and wetland complexes. Apparently, changing ponds can be considered a response to nesting failure, but changing pond complexes or wetland complexes might be related to additional factors. Both males and females seemed to disperse in response to human disturbance in the breeding area (e.g. when they were banded), but only males responded to nesting failures by increasing their tendency to disperse or by increasing dispersal distances. This suggests that site selection was influenced by male experience.

Avocets maintained pair bonds within a season, but only 57% of females and 56% of males paired with a previous mate the next year (Table 5). Because only 53.6% of banded avocets

were seen again at HLV, one might conclude that this is a high degree of mate fidelity. However, for 43 to 58% of the birds that changed mates, the former mate was alive and present at HLV. Avocets that form pair bonds in winter or during migration (Sordahl 1984, this study) may not encounter a previous mate at the breeding site until after they have formed a pair bond (similar to the "accidental loss hypothesis" of Choudhury 1995).

*Comparisons with other recurvirostrids.*—The variable age at first breeding for American Avocets appears to be similar to reports for Pied Avocets (*Recurvirostra avoetia*). Cadbury and Olney (1978) reported that Pied Avocets did not breed until age two or three in the United Kingdom. The majority of birds (65%) that returned within four years of hatching bred at age two. In contrast, Pied Avocets regularly bred at age one in France (Watier and Fournier 1980, Girard and Yésou 1989). James (1995) documented breeding at age one for Black-necked Stilts (*Himantopus mexicanus*).

The tendency for one-year-old American Avocets to return to their natal site as nonbreeders also has been described for Pied Avocets. In Britain, one-year-olds were seen as nomadic nonbreeders but sometimes formed temporary pair bonds and attempted to copulate (Cadbury and Olney 1978). Like American Avocets, Pied Avocets have weak attachment to natal sites (Cadbury and Olney 1978, Watier and Fournier 1980). Cadbury and Olney (1978) calculated that 75% of surviving two-year-olds bred outside of Britain. Of those that returned to the banding site, 12 to 20% returned to their natal colony at age two to four. This natal return rate (25%) compares closely with our calculation of 21 to 25% natal philopatry at HLV.

Unlike the above similarities in natal dispersal, Cadbury et al. (1989) observed much stronger breeding-site fidelity than we observed for American Avocets. This difference in adult movements probably was due to the paucity of breeding sites available in Britain and the tendency for some birds to remain as winter residents (Cadbury et al. 1989). Our annual survivorship estimate of 83 to 86% is similar to Cadbury et al.'s (1989) estimate of 90% for Pied Avocets.

Sordahl (1984) reported 29% breeding site fidelity of 21 adult American Avocets banded at a relatively small site in Utah (after one year).

Not surprisingly, his value is smaller than our observation of 54% returning within a search area of up to 20 km around the banding site.

*Dispersal in monogamous shorebirds.*—Because they nest semicolonially and do not maintain exclusive multi-purpose territories, we predicted that there would be little benefit to breeding-site fidelity in American Avocets. Data from Thompson et al. (1988) support the pattern of decreased site fidelity in semicolonial species. They compared breeding-site fidelity of Common Redshanks and Common Greenshanks (*Tringa nebularia*). Greenshanks, which had dispersed to breeding territories in upland habitats, had greater site faithfulness and mate fidelity than did redshanks, which nested semicolonially in a seasonally variable salt marsh. For greenshanks, return rates for both sexes were high, and there was a clear bias toward male returns. As for avocets in our study, male and female redshanks returned in roughly equal proportions, albeit with a slightly greater tendency for males to return.

Benefits for birds that return to previous breeding sites generally are envisioned at the territory scale. The flexibility in spatial scale for our study allowed us to detect movements at larger spatial scales than are normally studied. In this context, both breeding-site fidelity and the benefits of that fidelity are scale-dependent processes (see Robinson and Warnock 1997). Benefits to site familiarity at spatial scales larger than the territory could favor a tendency for birds to return at a pond complex, wetland complex, or a larger scale. For example, birds with experience at HLV, where coyotes (*Canis latrans*) are the major mammalian nest predator, might be at a disadvantage in breeding areas where red foxes (*Vulpes vulpes*) predominate.

We predicted that there would be no difference in breeding dispersal by male or female avocets. Our results partially support this prediction. We did not observe differences between male and female dispersal distance within the 1,254-km<sup>2</sup> area of HLV, but at larger spatial scales, we detected a slight tendency for females to disperse (as noted for Piping Plovers; Haig and Oring 1988b). Female avocets also dispersed farther from their natal site than did males. If our interpretation of male and female breeding-site fidelity is correct, and there is no sex difference for adults within HLV, then

the sex bias in natal dispersal might provide a necessary mechanism of inbreeding avoidance (Greenwood 1983, 1987).

The effect of unpredictable or changing habitats is an important consideration for predicting sex biases in dispersal. For example, Jackson (1994) compared dispersal of three monogamous shorebirds along the Western Isles of Scotland. Common Ringed Plovers, which bred in fields at different stages of agricultural rotation, had a greater tendency to disperse and dispersed farther than Common Redshanks or Dunlins. Female Common Ringed Plovers were less likely than males to return to within 100 m of their previous year's nest, but there was no difference in the proportion of males and females that returned to within 500 m (i.e. a distance that reflected dispersal away from habitats that became unsuitable for breeding; Jackson 1994).

We predicted that monogamous birds in ephemeral habitats would form pair bonds early in the season and that the pairs would select breeding sites from available habitat. Our observations of natal philopatry and breeding-site fidelity in American Avocets match these predictions. The tendency of avocets to pair during winter or migration (Sordahl 1984, this study) and to select nesting sites together (Hamilton 1975, Robinson et al. unpubl. data) is evidence of a mechanism of mate acquisition that is independent of the availability of a previous breeding site.

*Conservation issues.*—Wetland losses and conversions in North America have led to population declines of American Avocets (e.g. Bent 1927, Page and Gill 1994). The ability of avocets to colonize newly available habitats provides protection from the effects of locally changing patterns of habitat availability, but it will not help them avoid the effects of permanent habitat loss. Simply viewing avocets as highly mobile birds is extremely misleading. Avocets have high fidelity to breeding areas, even if this is at a larger scale than the territory. Furthermore, they show little tendency to disperse in response to nesting failure. Wetlands that are constructed to mitigate loss or contamination of habitat (e.g. California State Water Resources Control Board 1995) would attract breeding avocets if they provided an appropriate ecological equivalent. However, avocets that currently breed in contaminated habitats such as ponds

for disposal of irrigation drainwater (e.g. Skorupa and Ohlendorf 1991) might not disperse, even when the contaminants cause reproductive failure (e.g. Ohlendorf et al. 1989). Use of human disturbance to encourage breeding dispersal the next year could provide a valuable tool for encouraging breeding avocets to relocate.

There is a measurable degree of population connectedness between birds breeding in the Great Basin and central California (as exemplified by the avocet that dispersed from the Tulare Basin to HLV). This connectedness means that reproductive effects on birds breeding in the Tulare Basin might influence avocet population sizes throughout the western United States. The extent of this connectedness is a critical issue for understanding the influence of declining wetland availability and quality on these populations.

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