TABLE 4. RELATIONSHIP BETWEEN MASS AND TIME OF CAPTURE, CONTROLLING FOR AGE; SALTON SEA FALL, 1999

Species	N	Slope (g/hr)	SE	P	Adjusted R^2	Adjusted r^2
Orange-crowned Warbler	121	0.015	0.0052	0.004	0.080	—
Adults	56	0.021	0.0077	0.008	—	0.110
Young	65	0.0093	0.0070	0.19	—	0.012
Yellow Warbler	120	0.025	0.0062	<0.001	0.130	—
Adults	59	0.026	0.0093	0.007	—	0.100
Young	61	0.024	0.0084	0.005	—	0.110
Audubon's Warbler	105	0.0096	0.0083	0.25	−0.006	—
Adults	30	0.016	0.016	0.32	—	0.001
Young	75	0.0068	0.0097	0.48	—	−0.007
Wilson's Warbler	51	−0.00032	0.0067	0.96	0.250	—
Adults	28	−0.0014	0.0080	0.86	—	−0.037
Young	23	0.0013	0.012	0.92	—	−0.047
Gambel's White-crowned Sparrow	63	0.014	0.026	0.59	−0.024	—
Adults	40	−0.012	0.033	0.72	—	−0.023
Young	23	0.063	0.040	0.13	—	0.061

Notes: Results reported include models that control for age effect, as well as for each age class separately. Adjusted R^2 refers to results from a statistical model that includes age, Adjusted r^2 refers to results of analysis for each age class separately.

toration plans because of their importance to migratory passerines.

ACKNOWLEDGMENTS

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APPENDIX. SPRING (723.5 NET-HRS) AND FALL (1161.0 NET-HRS) CAPTURE RATES (BIRDS/100 NET-HRS) OF BIRDS AT THE SALTON SEA IN 1999

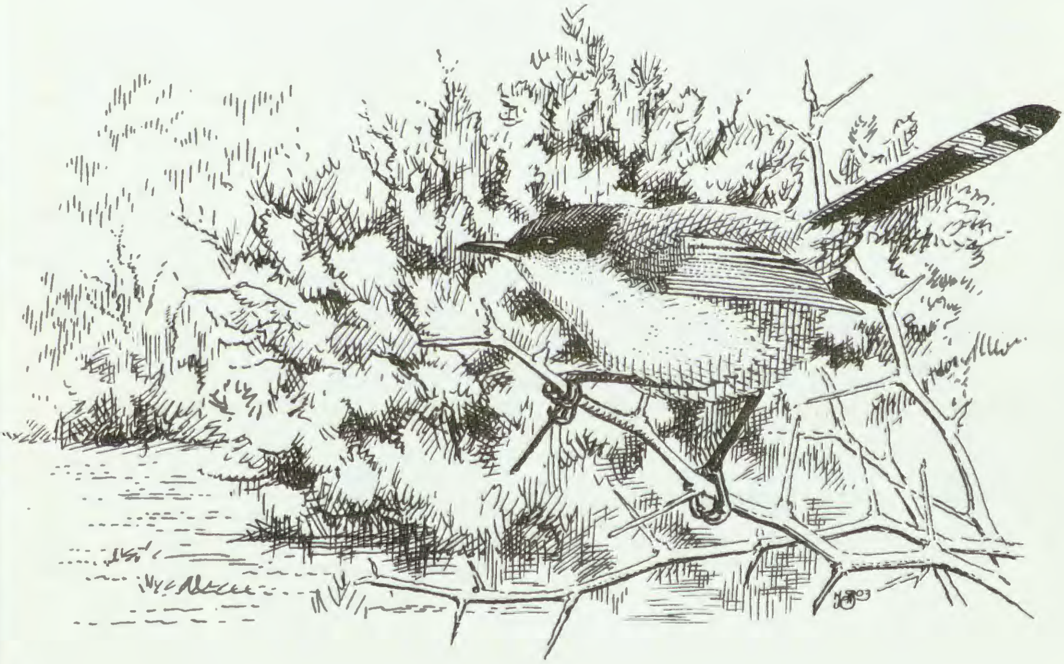
Species	Spring	Fall	Status[a]
Least Bittern (*Ixobrychus exilis*)	0.14	0.00	R
Least Sandpiper (*Calidris minutilla*)	0.14	0.00	M
Sharp-shinned Hawk (*Accipiter striatus*)	0.14	0.00	M
Cooper's Hawk (*A. cooperii*)	0.00	0.09	M
American Kestrel (*Falco sparverius*)	0.00	0.17	R
Common Ground-Dove (*Columbina passerina*)	0.28	0.34	R
Mourning Dove (*Zenaida macroura*)	—[b]	—[b]	R/M
Lesser Nighthawk (*Chordeiles acutipennis*)	0.00	0.09	M
Anna's Hummingbird (*Calypte anna*)	0.00	0.09	R
Rufous Hummingbird (*Selasphorus rufus*)	0.14	0.00	M
Western Wood-Pewee (*Contopus sordidulus*)	0.55	0.00	M
Willow Flycatcher (*Empidonax traillii*)	2.21	3.36	M
Hammond's Flycatcher (*E. hammondii*)	0.97	0.00	M
"Western Flycatcher" (*E. difficilis/occidentalis*)	5.11	0.34	M
Black Phoebe (*Sayornis nigricans*)	0.14	0.95	R
Say's Phoebe (*S. saya*)	0.00	0.17	R
Ash-throated Flycatcher (*Myiarchus cinerascens*)	0.28	0.34	M
Eastern Kingbird (*Tyrannus verticalis*)	0.69	0.00	M
Loggerhead Shrike (*Lanius ludovicianus*)	0.00	0.17	R
Plumbeous Vireo (*Vireo plumbeus*)	0.00	0.09	M
Cassin's Vireo (*V. cassinii*)	0.55	0.00	M
Warbling Vireo (*V. gilvus*)	19.21	0.17	M
Verdin (*Auriparus flaviceps*)	1.52	1.89	R
Cactus Wren (*Campylorhynchus brunneicapillus*)	0.00	0.09	R
Bewick's Wren (*Thryomanes bewickii*)	0.00	0.52	R
House Wren (*Troglodytes aedon*)	0.14	0.17	R
Marsh Wren (*Cistothorus palustris*)	3.32	0.09	R
Ruby-crowned Kinglet (*Regulus calendula*)	2.35	0.86	M
Blue-gray Gnatcatcher (*Polioptila caerulea*)	0.41	0.43	M
Black-tailed Gnatcatcher (*P. melanura*)	0.83	0.09	R
Swainson's Thrush (*Catharus ustulatus*)	3.73	0.00	M
Hermit Thrush (*C. guttatus*)	0.69	0.43	M
Northern Mockingbird (*Mimus polyglottos*)	0.00	0.52	R
Orange-crowned Warbler (*Vermivora celata*)	25.43	12.49	M
Nashville Warbler (*V. ruficapilla*)	4.42	0.43	M
Western Palm Warbler (*Dendroica palmarum palmarum*)	0.14	0.00	M
Yellow Warbler (*D. petechia*)	11.89	10.34	M
Audubon's Warbler (*D. coronata auduboni*)	8.43	14.47	M
Myrtle's Warbler (*D. c. coronata*)	0.00	0.09	M
Unknown Yellow-rumped Warbler (*D. coronata*)	0.00	0.43	M
Black-throated Gray Warbler (*D. nigrescens*)	1.38	0.34	M
Townsend's Warbler (*D. townsendi*)	2.35	0.09	M
Hermit Warbler (*D. occidentalis*)	0.28	0.00	M
American Redstart (*Setophaga ruticilla*)	0.00	0.17	M
MacGillivray's Warbler (*Oporonis tolmiei*)	4.15	2.15	M
Common Yellowthroat (*Geothlypis trichas*)	8.71	5.51	R/M
Wilson's Warbler (*Wilsonia pusilla*)	84.31	3.96	M
Yellow-breasted Chat (*Icteria virens*)	1.11	0.00	M
Western Tanager (*Piranga ludoviciana*)	4.98	0.17	M
Green-tailed Towhee (*Pipilo chlorurus*)	0.00	0.09	M
Abert's Towhee (*P. aberti*)	1.11	2.30	R
Chipping Sparrow (*Spizella passerina*)	0.14	0.17	M
Brewer's Sparrow (*S. breweri*)	0.00	0.26	M
Sage Sparrow (*Amphispiza bellii*)	0.14	0.00	M
Savannah Sparrow (*Passerculus sandwichensii*)	0.00	0.09	R/M
Song Sparrow (*Melospiza melodia*)	6.77	0.09	R
Lincoln's Sparrow (*M. lincolnii*)	1.52	1.38	M

APPENDIX. CONTINUED

Species	Spring	Fall	Status[a]
Swamp Sparrow (*M. georgiana*)	0.14	0.00	M
Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*)	0.69	5.08	M
Mountain White-crowned Sparrow (*Z. l. oriantha*)	0.28	0.43	M
Oregon Junco (*Junco hyemalis oreganos*)	0.00	0.26	M
Black-headed Grosbeak (*Pheucticus melanocephalus*)	0.55	0.00	M
Blue Grosbeak (*Guiraca caerulea*)	0.41	0.34	M
Lazuli Bunting (*Passerina amoena*)	0.97	0.00	M
Red-winged Blackbird (*Agelaius phoeniceus*)	0.00	0.34	R
Brown-headed Cowbird (*Molothrus ater*)	0.83	0.00	R
Hooded Oriole (*Icterus cucullatus*)	0.00	0.09	M
Bullock's Oriole (*I. bullockii*)	0.55	0.00	M
House Finch (*Carpodacus mexicanus*)	0.28	0.26	R
Lesser Goldfinch (*Carduelis psaltria*)	0.14	0.00	R
House Sparrow (*Passer domesticus*)	0.00	0.09	R

[a] R = resident, M = migrant, R/M = resident and migrant.

[b] Unbanded species not distinguishable to individual.



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DENSITY AND ABUNDANCE OF BURROWING OWLS IN THE AGRICULTURAL MATRIX OF THE IMPERIAL VALLEY, CALIFORNIA

DAVID F. DESANTE, ERIC D. RUHLEN, AND DANIEL K. ROSENBERG

Abstract. In concert with conversions of Sonoran desert habitat of the Imperial Valley, California, to intensive agriculture, Burrowing Owl (*Athene cunicularia*) populations dramatically increased in abundance. To quantify the abundance of breeding owls in the agricultural matrix of the Imperial Valley, we conducted surveys in randomly (N = 6) and non-randomly (N = 9) selected 25-km^2 blocks during 1992 and 1993. Based on counts of pairs observed in random blocks, we estimated a density of 2.1 ± 0.6 pairs/km^2 in 1992 and 2.0 ± 0.4 pairs/km^2 in 1993. Total variation (sampling and spatial) was high; estimated densities ranged from 0–7.4 pairs/km^2 among all 15 blocks sampled. Based on the randomly selected blocks, we estimated a total population size of 5600 (95% confidence interval: 3405–7795) owl pairs within the agricultural matrix of the Imperial Valley, indicating one of the largest concentrations of the Burrowing Owl in its entire range. Because the owls nest almost entirely along irrigation drains and canals, this population remains vulnerable to changes in methods of water conveyance.

Key Words: agroecosystems; *Athene cunicularia*; Burrowing Owl; California; Imperial Valley; Sonoran desert.

DENSIDAD Y ABUNDANCIA DEL TECOLOTE LLANERO EN LA MATRIZ AGRÍCOLA DEL VALLE IMPERIAL, CALIFORNIA

Resumen. De acuerdo con los cambios del hábitat de desierto Sonorense del Valle Imperial en California, a agricultura intensiva, la abundancia de las poblaciones del Tecolote Llanero (*Athene cunicularia*) han incrementado dramáticamente. Para cuantificar la abundancia de tecolotes reproductores en la matriz agrícola del Valle Imperial, llevamos a cabo censos en bloques de 25-km^2 seleccionados al azar (N = 6) y sistemáticamente (N = 9) durante 1992 y 1993. Con base en el conteo de parejas observadas en los bloques al azar, estimamos una densidad de 2.1 ± 0.6 parejas/km^2 en 1992 y 2.0 ± 0.4 parejas/km^2 en 1993. La variación total (muestras y espacial) fue alta; la densidad estimada varió de 0–7.4 parejas/km^2 entre los 15 bloques muestreados. Con base en los bloques seleccionados al azar, estimamos un tamaño poblacional total de 5600 (95% de intervalo de confianza: 3405–7795) parejas de tecolotes dentro de la matriz agrícola del Valle Imperial, indicando una de las mayores concentraciones de Tecolotes Llaneros en todo su rango. Debido a que casi todos los tecolotes anidan a lo largo de los drenajes y canales de riego, esta población permanece vulnerable a los cambios en los métodos de conducción del agua.

Palabras clave: Agroecosistemas; *Athene cunicularia*; California; desierto Sonorense; Tecolote Llanero; Valle Imperial.

The Western Burrowing Owl (*Athene cunicularia hypugaea*) was once widespread and fairly common over western North America, but its distribution and abundance has changed markedly during the 20th century. Although many populations have declined in abundance (James and Espie 1997), some to the point of at least temporary local extirpation (e.g., Johnson 1997), others have increased since European occupation. Nowhere is this clearer than in the Imperial Valley of southeastern California.

Historically, Burrowing Owls presumably occurred within the Imperial Valley in low densities, similar to those in the undisturbed portions of the Sonoran Desert in which the Imperial Valley is embedded (Garrett and Dunn 1981). In response to the intensification of agriculture in the early 1900s (Clemings 1996), the Burrowing Owl population within the Imperial Valley became one of the largest and most dense populations of this species in California (e.g., Coulombe 1971, Rosenberg and Haley *this volume*) and probably throughout its range. Understanding this species' ecology in apparently thriving populations may lead to greater insights in managing declining populations. As a first step in addressing this, we conducted a large-scale survey of the agricultural habitats within the Imperial Valley in 1992 and 1993 to quantify density. Here we report the results of that survey, compare densities of Burrowing Owls in the Imperial Valley to those elsewhere in California, and discuss the potential importance of the Valley's population in light of declines elsewhere in California (DeSante et al. 1997, Johnson 1997, Trulio 1998).

METHODS

This survey was conducted as part of a larger survey of Burrowing Owls in all of California west of the Great Basin and desert areas (DeSante et al. 1997; D. DeSante et al., unpubl. data). For this study, we divided the Imperial Valley into 183 5 × 5 km blocks, of which 112 blocks comprised a strata defined as the agricultural matrix of the Imperial Valley. We randomly selected 6% (N = 7) of these 112 blocks and distributed copies of these seven blocks taken from 1: 24,000 USGS topographic maps to colleagues at the Sony Bono Salton Sea National Wildlife refuge and the Imperial Irrigation District for surveying. Because of time and logistic constraints, only six of the seven randomly selected blocks were surveyed in at least one year (Fig. 1). In addition, we surveyed nine other 5 × 5 km blocks in the agricultural matrix strata of the Imperial Valley. These blocks were selected opportunistically. These blocks were distributed over much of the agricultural areas of the Imperial Valley (Fig. 1).

Surveys were carried out by local ornithologists and by agency biologists following training provided to facilitate standardization of survey methods. Observers surveyed each block between dawn and 10:00 and/or between 16:00 and dusk between 15 May and 15 July, during both 1992 and 1993. We computed density as number of pairs counted/km^2 for each year and sampling strategy (random or nonrandom). Observers searched blocks for owls for an average of approximately 10 hrs/block. We estimated the number of breeding pairs of Burrowing Owls (defined as in DeSante et al. 1997) by multiplying the area of the sampled region by the estimated mean density. We assumed that if an owl was present within the block it would be detected. Because this assumption was unlikely met, our estimated numbers are likely negatively biased.

Habitat within the study area was characterized by agricultural fields, framed by a system of concrete irrigation delivery ditches, irrigation canals, and earthen drains managed by the Imperial Irrigation District and landowners. This characterization was made at the scale of the 5 × 5 km sample blocks, as most of the area sampled was comprised of this agricultural matrix. All pairs observed were found along the system of irrigation ditches, canals, and drains immediately bordering the agricultural fields.

RESULTS

We estimated an average density of approximately two owl pairs/km^2 during 1992 and 1993 within the randomly selected blocks (Table 1). Estimated densities were on average >25% higher in the non-randomly selected blocks, although low precision resulted in overlapping 95% confidence intervals (Table 1). Estimated densities in both the random and non-random blocks varied considerably, ranging from 0–7.4 pairs/km^2. The variation between years was small relative to the variation among blocks (Table 1). However, sampling variation that resulted from detection probabilities of <1.0 and which were likely variable among blocks was partially responsible for the observed variation (sensu White 2000). Counts conducted in both years within a block often differed by >80% (Fig. 1). The large variance contributed to imprecise estimates of density, and hence estimated population size. Based on counts within the randomly selected blocks during 1993, the year all six blocks were sampled, we estimated a total population size of 5600 pairs (95% confidence interval: 3405–7795). The high densities in the non-random blocks give further support to such high densities and the large population size as estimated from the small number of random blocks.

DISCUSSION

Based on qualitative assessments, California has one of the largest populations of both resident and wintering Burrowing Owls (James and Ethier 1989, Sheffield 1997). Density estimates from this survey and other surveys conducted in a similar manner elsewhere in California (DeSante et al. 1997; D. DeSante et al., unpubl. data), suggest that a majority (approximately 70%) of the California breeding population of the Burrowing Owl (excluding the Great Basin, Mojave, and Colorado deserts, and Colorado River valley portions of California) nests within the Imperial Valley. Although the small number of randomly selected blocks sampled and the unknown detection probability lessens the strength of these results, particularly for the comparison of relative abundance among regions, it is clear that the density and abundance of Burrowing Owls is exceptionally high within the Imperial Valley.

The densities reported here are likely among the highest throughout the Burrowing Owl's range, especially when considering the large areal extent of the lowland area of the Imperial Valley (approximately 2810 km^2). Similarly high densities (3.3 pairs/km^2) were estimated within the Imperial Valley by Coulombe (1971) within an 8-km^2 area during the breeding seasons of 1965–1967. More recently, Rosenberg and Haley (*this volume*) estimated 8.3 pairs/km^2 within an approximately 12-km^2 study area. These localized results provide additional evidence to support the high densities estimated from this study. The only other estimate of such high densities over a reasonably large area (35.9 km^2) that we are aware of was Millsap and Bear's (2000) estimate of 6.9 pairs/km^2 for the subspecies *A. c. floridana* in southern Florida. What is extraordinary about our findings, however, is the apparently large areal extent of high densities. Given this large area, the estimated densities, and that detection probability was <1.0 (i.e., a higher number existed than was counted), more

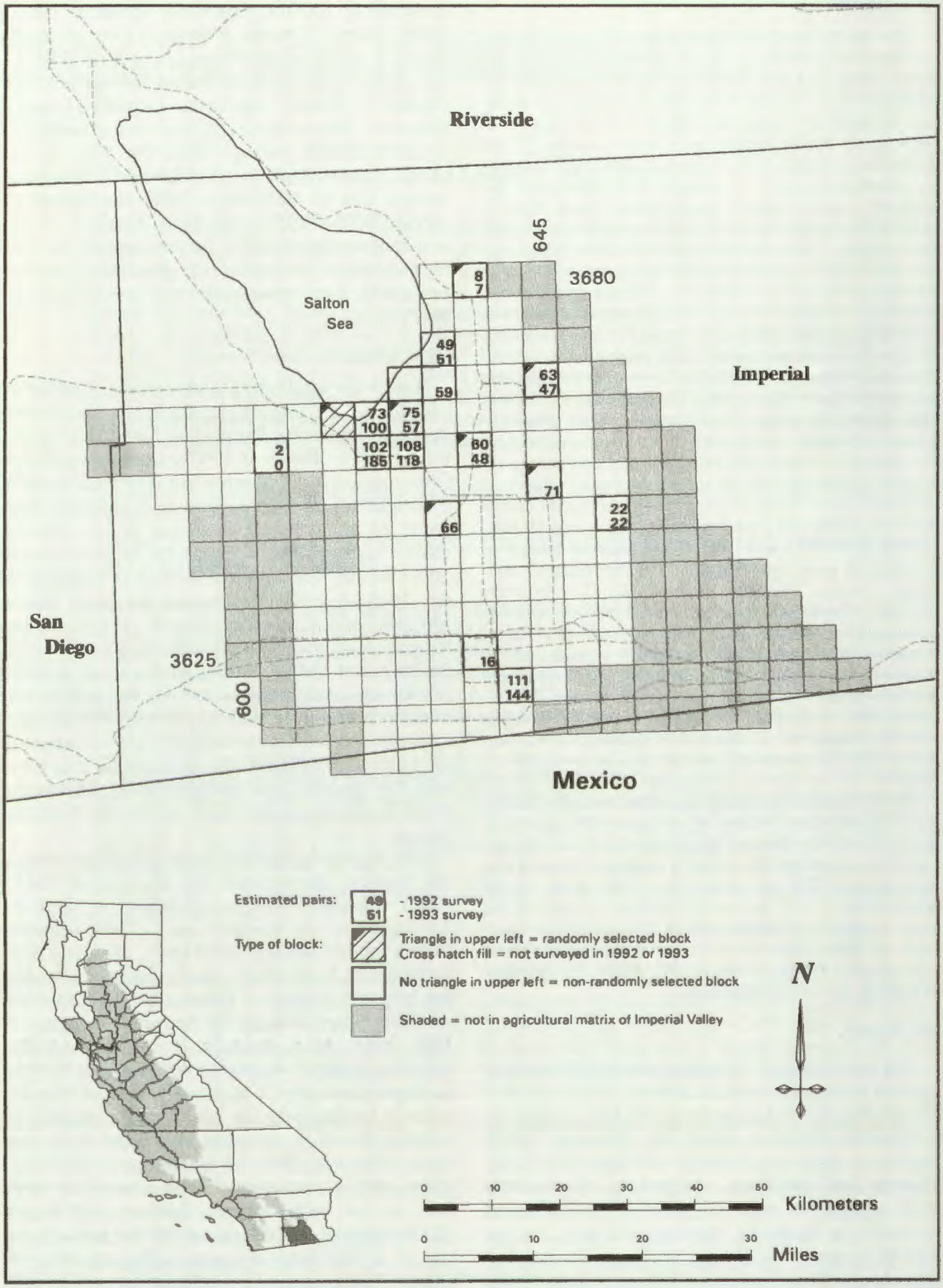
Riverside
645
3680
Salton
Sea
Imperial
San
Diego
3625
600
Mexico
8
7
49
51
59
63
47
73
100
75
57
102
185
108
118
60
48
2
0
71
66
22
22
16
111
144
Estimated pairs:
49
51
- 1992 survey
- 1993 survey
Type of block:
Triangle in upper left = randomly selected block
Cross hatch fill = not surveyed in 1992 or 1993
No triangle in upper left = non-randomly selected block
Shaded = not in agricultural matrix of Imperial Valley
N
0
10
20
30
40
50
Kilometers
0
10
20
30
Miles

TABLE 1. Estimated Burrowing Owl Densities (Owl Pairs/km^2) in 25-km^2 Blocks Sampled within the Agricultural Matrix of the Imperial Valley, California, during May–July 1992 and 1993

	1992					1993				
			Estimated density					Estimated density		
Block type	Number of blocks	Owl pairs	Mean	SE	Range	Number of blocks	Owl pairs	Mean	SE	Range
Random	4	206	2.1	0.6	0.3–3.0	6	296	2.0	0.4	0.3–2.8
Non-random	7	467	2.7	0.7	0.1–4.4	9	695	3.1	0.8	0.0–7.4
All	11	673	2.5	0.5	0.0–4.4	15	991	2.6	0.5	0.0–7.4

than 11,000 (95% confidence interval: 6810–15,590) adult Burrowing Owls inhabited the agricultural ecosystems of the Imperial Valley during the surveys.

Although such a large population of a species considered to be declining in parts of its range (James and Espie 1997) could, at least theoretically, serve as an important source population for future management strategies, its current value for persistence of declining populations elsewhere in California may not be great. Potential dispersal from the Imperial Valley population to declining populations may be limited by unsuitable intervening habitat and by the dispersal characteristics of the resident Imperial Valley population itself, although juvenile dispersal remains unknown (Rosenberg and Haley *this volume*). Given the wide distribution of Burrowing Owls across their range in California, the value of a large but localized potential source population to regional persistence may not be great. However, given the rapid development of much of the grassland and desert regions of California, the apparent extirpation of the species in the Coachella Valley immediately north of the Imperial Valley, the reduction in numbers in other parts of California (DeSante et al. 1997, Johnson 1997, Trulio 1998), and the lack of a statewide conservation strategy, the importance of the Imperial Valley population may increase.

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←

FIGURE 1. Distribution of 5 × 5 km blocks in which Burrowing Owls were counted in 1992 and/or 1993 in the Imperial Valley, CA. Shaded areas represent portions of the Imperial Valley above sea level and without a major agricultural matrix. Non-shaded areas represent agricultural matrix of the Imperial Valley and include the 112 blocks from which a random sample of seven blocks were selected. Numbers embedded in the blocks are the number of Burrowing Owl pairs counted in 1992 (upper right) and 1993 (lower right). The cross-hatched block was randomly selected but was not surveyed. The numbers outside of the blocks refer to the southwest corner of the 5 × 5 km block referenced by the Universal Transverse Mercator system of the block. The UTM values shown are 10^{-3} of the given value.

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THE ECOLOGY OF BURROWING OWLS IN THE AGROECOSYSTEM OF THE IMPERIAL VALLEY, CALIFORNIA

DANIEL K. ROSENBERG AND KATHERIN L. HALEY

Abstract. Burrowing Owls (*Athene cunicularia*) are common in some agroecosystems, yet their ecology in these environments is poorly known. To address this, we collected demographic and space-use data on the Burrowing Owl in the Imperial Valley of southeastern California during the breeding season, 1997–2000. Within our 11.7 km^2 study area, we estimated a very high density of Burrowing Owls (8.3 pairs/km^2) which remained relatively constant during the study. Owls nested predominately on the edges of constructed drains and canals that bordered agricultural fields. Clutch size ranged from 4–8 (mean = 6.7) eggs/clutch and varied little among years. Productivity averaged 2.5 young/nest and varied considerably among individuals and years. Adult annual survival rates for males (0.65) and females (0.62) were similar or higher than reported for other Burrowing Owl populations. We observed high nest-site fidelity for adults, with 85% remaining within 400 m of the previous year's nest. Females moved greater distances than males between breeding seasons; distances were greater for owls whose nests failed. Few juveniles (20 of 124, 16%) were subsequently observed as adults. This, together with a lack of a declining dispersal function, suggested juveniles frequently emigrated from the study area. Based on estimates of nocturnal movements of males, we estimated low selection for the type of crops in which they foraged. They foraged primarily (>80%) within 600 m of their nest, but long-distance movements (2–3 km) often resulted in large estimates (113.7 ± 30.4 ha) of the area traversed (minimum convex polygon method) and the area used (45.3 ± 18.2 ha; fixed kernel method). Because of the high densities of owls, home ranges overlapped considerably. Our estimates of demographic parameters and the space-use properties of Burrowing Owls contrast with those reported from non-agricultural areas. Our results suggest agricultural areas can provide high quality habitat if burrows are available, which in our study area was determined by the farmers tolerance of burrows along the canals and drains bordering their property.

Key Words: agroecosystems; *Athene cunicularia;* Burrowing Owl; California; dispersal; Imperial Valley; reproductive rates; survival rates.

LA ECOLOGÍA DE TECOLOTES LLANEROS EN LOS AGROSISTEMAS DEL VALLE IMPERIAL, CALIFORNIA

Resumen. Los Tecolotes Llaneros (*Athene cunicularia*) son comunes en algunos agroecosistemas, no obstante su ecología en estos ambientes es poco conocida. Con este propósito, durante las temporadas reproductivas de 1997–2000 se colectó información sobre la demografía y el uso espacial del Tecolote Llanero en el Valle Imperial del sureste de California. Dentro del área de estudio (11.7 km^2) se estimó una densidad muy alta de tecolotes (8.3 parejas/km^2) la cual permaneció relativamente constante durante el estudio. Los tecolotes anidaron predominantemente en los bordes de los drenajes y canales que rodean a las parcelas. El tamaño promedio de las nidadas fue de 4–8 huevos por nido (media = 6.7) y varió poco entre años. El promedio en la productividad fue de 2.5 juveniles/nido y varió considerablemente entre individuos y años. Las tasas anuales de supervivencia en machos adultos (0.65) y hembras adultas (0.62) fueron similares o más altas que las reportadas para otras poblaciones de Tecolotes Llaneros. Se observó también que los adultos muestran una alta fidelidad al sitio de anidación, con el 85% permaneciendo dentro de una distancia de 400 m del nido utilizado el año anterior. Las hembras se movieron a mayores distancias que los machos entre temporadas reproductivas, las distancias fueron mayores para aquellos tecolotes cuyos nidos fracasaron. Pocos juveniles (20 de 124, 16%) fueron observados posteriormente como adultos. Esto, junto con la ausencia de una función de dispersión disminuida, sugirió que los juveniles emigraron del área de estudio. Con base en estimaciones de movimientos nocturnos de los tecolotes machos, se estimó que hubo poca selección por el tipo de cosecha en la cual se alimentaron. Ellos forrajearon principalmente (>80%) dentro de un distancia de 600 m de su nido, aunque los movimientos a mayores distancias (2–3 km) a menudo resultaron en estimaciones mayores (113.7 ± 30.4 ha) del área atravesada (método del polígono mínimo convexo) y del área utilizada (45.3 ± 18.2 ha, método fijo kernel). Debido a la alta densidad de tecolotes, las áraes utilizadas se traslaparon considerablemente. Nuestras estimaciones de los parámetros demográficos y de las propiedades del uso del espacio de los Tecolotes Llaneros contrastan con aquellas reportadas para áreas no agrícolas. Nuestros resultados sugieren que las áreas agrícolas pueden proporcionar un hábitat de alta calidad si hay madrigueras disponibles, lo cual en nuestra área de estudio estuvo determinado por la tolerancia de los agricultores a la presencia de las madrigueras a lo largo de los canales y drenajesque rodean a sus propiedades.

Palabras claves: Agroecosistemas; *Athene cunicularia*; California; dispersión; tasa reproductiva; tasa de supervivencia; Tecolote Llanero; Valle Imperial.

The Burrowing Owl (*Athene cunicularia*) is a burrow-nesting owl characteristic of grasslands and deserts throughout western North America, Florida, and Central and South America (Haug et al. 1993). The Western Burrowing Owl (*A. c. hypugaea*) was once widespread and fairly common over western North America. Population declines led to listing of the Burrowing Owl as endangered, threatened, or a species of concern in Canada, Mexico, and in a number of U.S. states (James and Espie 1997). Declines likely reflect eradication or control of fossorial mammals, intensive pesticide use, and conversion of grasslands to agriculture and residential or commercial development (Haug et al. 1993, Trulio 1997, Desmond et al. 2000, Gervais et al. 2000).

California has one of the largest populations of both resident and wintering Burrowing Owls (James and Ethier 1989). Particularly high numbers and densities occur in the Imperial Valley, located in southeastern California (Coulombe 1971; DeSante et al. *this volume*). Historically, Burrowing Owls were present within the Imperial Valley in low densities similar to those in undisturbed habitat of the surrounding Colorado (Sonoran) desert (DeSante et al. *this volume*). Intensification of agriculture in the 1900s (Clemings 1996) enabled Burrowing Owl populations of the Valley to increase greatly. Increasing development and changing patterns of water conveyance in southern California (e.g., Clemings 1996) may have major impacts on the distribution and abundance of Burrowing Owls in the region.

Despite the large population of Burrowing Owls in the Imperial Valley, there have been few investigations of their ecology. Coulombe (1971) and DeSante et al. (*this volume*) documented the concentration of Burrowing Owls along the various watercourses. Although their research provided a framework for understanding these issues, a quantitative approach to the demography and space-use ecology of this species is needed to develop scientifically credible management strategies.

To address this need, we initiated studies of the owl's demography and space-use patterns within the agroecosystem of the Imperial Valley. In this paper, we examine (1) patterns of distribution of Burrowing Owls; (2) rates of and factors affecting survival, reproduction, and between-year movement; and (3) patterns of space-use of individuals. We explore factors that affect individuals and how this may ultimately affect the dynamics of the population.

STUDY AREA

The study area was at the southern rim of the Salton Sea, 40 km north of El Centro, California (Fig. 1). We divided the study area into several subareas. We captured and marked Burrowing Owls only in the Intensive Study Area (ISA), which totaled 1175 ha (Fig. 1). The second subarea (Area B; Fig. 1) extended 0.8 km beyond the ISA. Together, these two areas represented the Demography Study Area (DSA). The third subarea (Area C; Fig. 1) extended 0.8 km (1999) or 1.6 km (2000) beyond the DSA. Most (81%) of the ISA consisted of privately owned agricultural fields. The remainder encompassed a segment of the Sonny Bono Salton Sea National Wildlife Refuge (hereafter, Refuge; Fig. 1). The Refuge maintained a set of 35 nest boxes situated between roads and fields. Design of nest boxes were similar to those described by Trulio (1995).

The study area was characterized by agricultural fields framed by a system of concrete water-delivery ditches and canals, and earthen drains. Drains were deep (up to 8–9 m), dredged waterways maintained by the Imperial Irrigation District. Within this agricultural matrix Burrowing Owls nested almost entirely within or along drains, ditches, and canals. Fields were intensively managed for year-round production of vegetables and cattle feed. Primary crops were Sudan grass (*Sorghum bicolor*), Bermuda grass (*Cynodon dactylon*), alfalfa (*Medicago sativa*), onions (*Allium cepa*), and corn (*Zea mays*).

METHODS

DENSITY ESTIMATION

To estimate the density of Burrowing Owls we first estimated the probability of detecting nesting pairs of Burrowing Owls within the ISA. We divided the study area into approximately 20 800-m blocks, and surveyed each alternating block outside of the Refuge (N = 7) from 14 to 30 April 1998. We surveyed all roads and watercourses that bordered fields three times, two by vehicle and one on foot. We conducted surveys at vehicle speeds ≤10 km/hr with two observers during the morning (30 min before sunrise to 4 hrs after) and evening (3 hrs before sunset until sunset) when wind speeds were <15 km/hr. We used both behavioral and physical evidence of nesting to determine if a pair occupied a given burrow (e.g., Millsap and Bear 1997). To estimate the probability of detecting nesting owls, we applied the removal model of Zippin (1958), which estimates population size as a function of the number of new individuals, or nests as in this study, that are encountered on each survey (Otis et al. 1978:28).

DIET

We estimated the diet composition of Burrowing Owls from regurgitated pellets. We collected pellets from randomly selected nests (2000) and from nest boxes within the Refuge (1998 and 2000). All pellets from a given nest and year were treated as a single sample. We estimated the relative frequency of consumption by recording the occurrence of each taxonomic order. Because earlier observations indicated that the frequency of rodents in the diet may strongly influence productivity (D. Rosenberg et al., unpubl. data), we computed an index of rodent consumption. Skeletal remains were counted to estimate the minimum number of rodents consumed. The index was computed for each sample as the ratio of the minimum number of rodents consumed/number of pellets. We

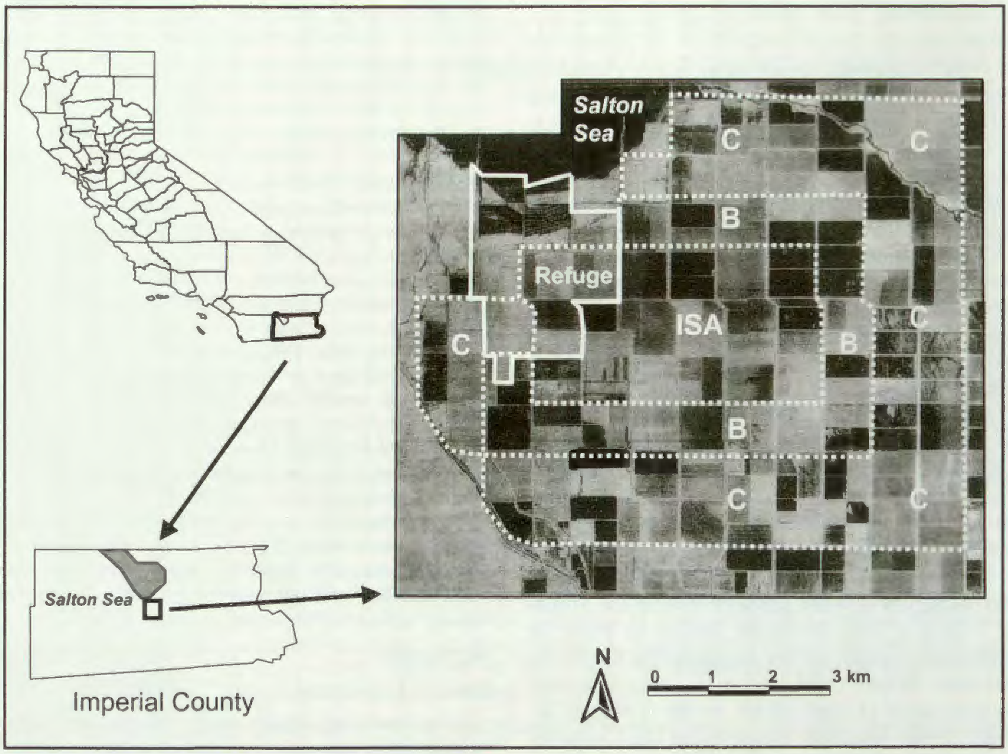

FIGURE 1. Study area in the Imperial Valley of southeastern California. Owls were banded within the Intensive Study Area (ISA) and resighted with equal effort in both the ISA and Subarea B, collectively termed the Demography Study Area. In addition, we attempted to resight owls in Subarea C, but with lower effort. All areas with owl nests within the Refuge were included in the ISA.

estimated the relative degree of variation of the index between years as the coefficient of variation (standard deviation/mean ×100).

Capture and Reobservation

We attempted to capture and mark a large segment of the population within the ISA. We captured Burrowing Owls during May 1997 and April–July 1998–2000. We captured adult owls using spring-net traps baited with a caged mouse, and two-way burrow traps (Bothelo and Arrowwood 1995). We captured young with a one-way trap, modified from that described in Banuelos (1997). We removed young from nest boxes by hand. We marked young and adult Burrowing Owls with an aluminum alpha-numeric color band (Acraft Sign and Nameplate Co., Ltd., Edmonton, Alberta, Canada) and a non-locking No. 4 U.S. Fish and Wildlife Service band. We assigned sex based on presence/absence of brood patch, plumage coloration, and behavioral observations (Haug et al. 1993).

Within the DSA (Fig. 1) we attempted to identify all marked individuals and locate their nests. Resighting efforts involved two vehicular surveys, as described above (see Density Estimation), supplemented by sightings made incidental to the surveys. We conducted a single vehicular survey for marked owls in subarea C (Fig. 1). Because of the lower effort and presumably lower resighting rates, we did not include observations of marked owls from this outer area for survival estimation but included these data for estimation of movement patterns and emigration rates.

Productivity and Breeding Phenology

To estimate productivity, we randomly selected 30 nests from privately-owned agricultural land within the ISA (1999 and 2000) and all occupied nest boxes within the Refuge not subject to experimental feeding from a concurrent study (1998, N = 13; 1999, N = 6; 2000, N = 7; Haley 2002) within the Refuge. We used the same criteria as described above (Density Estimation) to determine if a pair occupied a given burrow; only occupied nests were included for productivity estimation. Nests for which we could not estimate productivity due to limited visibility of nests or an inability to determine whether or not the nest was successful were excluded from analyses, resulting in sample sizes of 23–29 nests outside of the Refuge each year.

We defined productivity as the maximum number of 21–28-d-old young seen simultaneously at a nest during a series of five 30-min watches, each separated by at least 6 hr (Gorman et al. 2003). We aged young via visual techniques described by Haug et al (1993) and Priest (1997). Observations were made from a vehicle at a distance of 80–200 m, using either binoculars or 20–60× spotting scopes during the morning or evening as defined previously. We examined the influence of diet (rodent index), intraspecific competition, and year on productivity from the randomly selected nests in 1999 and 2000. We used the minimum nearest-neighbor distance (log-transformed) and number of nests within 600 m (radius of foraging concentration; see RESULTS) as an index of intraspecific competition. We used a generalized linear model with a negative binomial response probability distribution and a log-link function (SAS Institute 1993). We chose this regression model because count data, such as the number of young, often conforms to a negative binomial distribution, and because this model, when the data are so distributed, provides a more powerful approach with fewer assumptions than other methods (White and Bennetts 1996).

We estimated Burrowing Owl reproductive biology by examining nest boxes within the Refuge and the Refuge headquarters, approximately 10 km east of the ISA. In 1999 and 2000, we evaluated date of first laying, clutch completion, and hatching, and measured clutch size and nest success. We monitored all nest boxes with evidence of owl use weekly until eggs were seen. During each visit, we used an infrared probe (Sandpiper Technologies, Manteca, CA) to observe nest contents. Once eggs were seen, we visited nests at 3 to 4-d intervals to estimate clutch completion dates. A clutch was defined as complete when the number of eggs did not increase by more than one egg/72 hr (Haley 2002). We estimated hatch success as the percent of eggs that hatched/nest.

BETWEEN-YEAR MOVEMENTS

To estimate movement patterns, we used data from owls marked in 1998–1999 and resighted in 1999–2000. We estimated movements of both juveniles and adults. However, we evaluated movement functions and factors associated with movements only for adults because we likely underestimated movement rates for juveniles (see RESULTS).

We did not attempt to differentiate between adults undergoing breeding dispersal (sensu Greenwood 1980) and those moving x distance from their nest the previous year. Rather, we simply modeled distances moved between years under the notion that, based on movement data alone, there is no exact distance that can be considered fundamentally different than any other. We compared two functions, a hazard rate and a negative exponential. The hazard rate model has properties similar to those of the exponential but allows for a "shoulder" (i.e., a distance interval at which the probability to move remains constant) near zero distance. We explored the two functional forms because based on theory, a decreasing probability of movement as distance increases should exist and there were sampling and biological reasons (e.g., Olson and Van Horne 1998) to expect a shoulder near zero distance. In such cases, the hazard-rate function is often useful (e.g., Buckland et al. 1993). The hazard-rate function we used was of the form $\Pr(x) = 1 - \exp(-[x/\sigma]^{-b})$ and the negative exponential function was expressed as $\Pr(x) = \exp(-x/\lambda)$ (Buckland et al. 1993). To describe the probability density function, we rescaled the function by c, where c was the value of the integration of the function evaluated from zero to the furthest distance an owl was observed to move between years. We selected the most appropriate function with Akaike's Information Criterion, adjusted for small-sample size (AICc; Burnham and Anderson 1998) for adults with sexes and years pooled, and then used AICc to compare models fit as sex, year, or sex- and year-specific.

The size and geometry of the area in which movements can be detected may result in the appearance of underlying movement functions that fit models such as the exponential (Porter and Dooley 1993) or hazard-rate. We evaluated this by recreating a set of movements with a uniform probability for which distances from zero to the maximum movement distance we observed (3065 m) all had equal probabilities of occurring. We assigned each owl located in 1998 and relocated in 1999 with a new location for 1999 based on a random direction of movement and a random distance that followed a uniform distribution. Only those individuals that would have been within the DSA (and thus detected) were considered relocated. We fit these data to the same function that was selected for the observed distribution of movements. We graphically approximated the point at which the probability of moving declined from the expected uniform pattern. Similar dispersal patterns between the simulated and the observed distances would suggest that observed movement patterns were affected by the size and geometry of the study area.

We developed ten *a priori* models to explore factors that may affect the distance adults moved between years. We examined each model with multiple regression and used AICc as a basis for model selection. The response variable was the log-transformed distance an adult owl moved between years and explanatory factors included a combination of year, distance to the nearest nest, and whether or not the owl's mate was still present on the study area. The simplest model considered was a no-effects model in which only an intercept term (representing average distance moved) was estimated. For those individuals for which we estimated productivity and movement, we included as a parameter in the model whether or not their nest was successful in the previous year. We compared nine *a priori* models for this smaller data set. In both sets of analyses, we used data only from individuals that were seen in two successive years and for which both members of the pair were initially banded.

SURVIVAL

We used mark-recapture analysis to estimate apparent (i.e., we assumed no emigration from study area occurred) survival rates of Burrowing Owls first captured as adults. We excluded individuals first captured as young because we determined sex of only 17 of 242 marked young, and these were unlikely representative of the population. We fitted modified Jolly-Seber-Cormack models to the mark-recapture data using Program MARK (White and Burnham 1999). We developed ten *a priori* models to estimate survival rates. We used AICc weights (w) to compare the relative likelihood of each model. We used these weights to estimate an average survival rate from all models considered. Model averaging allows inference to be based on all models considered, thus increasing the inferential validity over that of a single model approach (Burnham and Anderson 1998). We assessed goodness-of-fit for the global model using 1000 bootstrap simulations to evaluate the likelihood of the observed deviance (White and Burnham 1999).

Apparent survival rates reflect both mortality and emigration; however, we were interested in estimating "true" (sensu Franklin et al. 1996) survival rates. To allow estimation of survival, we estimated emigration rates of adult Burrowing Owls from observed movements of individuals between 1998–1999. We then estimated survival as

$$\hat{S} = \hat{\phi} + \hat{E}$$

where $\hat{S}$, $\hat{\phi}$, and $\hat{E}$ are the estimated probabilities of annual survival, apparent survival, and emigration of individuals from the DSA, respectively (Burnham et al. 1996). To simplify estimation, we assumed owls emigrated just before nesting and thus experienced no mortality between emigration and the time of resighting. Because the probability of emigration is a function of the location of an individual from the boundary of a study area (e.g., Barrowclough 1978), we randomized observed distances among owls and randomly selected an angle of movement to estimate a new location. We did this separately for males and females because of the differences in observed movement patterns (see RESULTS). We estimated the probability of emigration as:

$$\bar{\hat{E}} = \left(\sum_{i=1}^{R} n^{*}/n\right) \Big/ R,$$

where n^* was the number of adults with estimated locations outside of the study area, n was the number of marked owls in year t that survived and were relocated in year $t + 1$, and R was the number of replications of the random process of recreating movement patterns. We used $R = 1000$ replications and used the mean of $\hat{E}$ as our best estimate of emigration. This method of estimating emigration assumes that the observed distances reflect the true distribution of distances moved, such that individuals that moved outside of the study area and were not detected had movement patterns similar to those owls that were detected. This assumption was supported by the rapidly declining dispersal function (see RESULTS), similar patterns of movement for owls located in the center of the study area as for those located throughout (D. Rosenberg, unpubl. data), and a relatively uniform environment within the study area (homogeneity assumption of Zeng and Brown 1987).

SPACE USE

In May 1998, we radio-tracked six male owls to gain quantitative insight into the owls' space-use patterns. We used necklace-design radio transmitters (4.5 g) with a 20-cm antennae (Holohil Systems, Ltd., Carp, Ontario, Canada). We captured owls that nested within a 0.4 × 0.8 km area along the edge of the road and fields within the Refuge. We attempted to track owls each night from 2000 to 0400 hrs from 5 June–13 July. The receiving antenna assembly consisted of two H-configured antennae (Telonics, Mesa, AZ) separated by a cross boom and connected to a null combiner, mounted to a 2-m rotating tower with a fixed compass. The tower was secured in the bed of a truck, making the antennae height approximately 3 m above ground, following methods described in Gervais et al. (2003).

We established a grid system of stations at approximately 400 m intervals to obtain biangulation data. This allowed a formal search method to negate the potential bias of observers returning to known sites of occurrence, such as nests (Rosenberg and McKelvey 1999). We attempted to obtain locations of a given owl every 15 min. Only locations computed from estimates of the angle of the owl from two stations within 5 min were included in analyses. We omitted all observations that led to locations greater than 1 km from the telemetry stations because of their greater expected error (Gervais et al. 2003).

We estimated home ranges to estimate the area used (kernel methods) and the area traversed (minimum convex polygon, MCP). We used a fixed kernel estimator with least squares cross validation (LSCV) and also an adaptive kernel to estimate area used (Worton 1989). To estimate home range size we used programs KERNELHR (fixed kernel; Seaman et al. 1998), HomeRanger (adaptive kernel; Hovey 1999), and Telem (MCP; K. McKelvey, pers. comm.).

We evaluated factors that potentially affected the owls' likelihood of use. We evaluated distance of owl locations to field edge, distance to nest, and within each field the crop type, dominant crop height, and percent bare ground. The data structure consisted of a sample of cells (30-m² pixels) in which the individual was located by radio telemetry and a sample of randomly selected cells (Design III of Manly et al. 1993). Random cells were sampled from within a circle with a radius equal to the maximum distance an individual was located from its nest (Rosenberg and McKelvey 1999). The binary response variable was coded 1 if an individual was located in a particular cell, 0 if random. We used logistic regression to estimate selection as the odds ratio of use (Hosmer and Lemeshow 1989:40), Proc Logistic (SAS Institute 1994) to obtain parameter estimates, and AICc weights to evaluate the relative likelihood of a given model as being the best among those we considered (Burnham and Anderson 1998).

We developed seven *a priori* models to estimate habitat selection. We evaluated distance to the nest as either a log-function or a 3rd-order polynomial. We categorized crops using two pooling regimes based on density of vegetation: (1) crops with closed canopy structure during the study period (hay, wheat [*Triticum aestivum*], Sudan grass, Bermuda grass, alfalfa, and corn) or an open canopy structure (no crops, onions, and cotton) and (2) simply whether or not standing crops existed. Although cotton becomes dense near maturity, it was relatively open during the study. For each field, we estimated average crop height and percent of bare ground during the mid-point of the space-use study. We subjectively pooled crop types into simple classes that we expected would influence owl foraging behavior to accommodate the small number of observations/owl and the large number of different crop types. We expected a negative relationship of foraging with increasing density of vegetation, and based on central place foraging behavior of the owls, a strong decrease of use with distance from the nest. Although we were interested in investigating the selection for edge habitat, we were unable to do so because of the

TABLE 1. NEAREST NEIGHBOR DISTANCES (M) OF BURROWING OWL NESTS WITHIN THE INTENSIVE STUDY AREA, IMPERIAL VALLEY, CA, 1998–2000

Year	N	Range	Mean	SE	Median
1998	106	13–760	125.4	11.2	98.6
1999	93	8–818	149.1	15.2	101.1
2000	94	7–806	165.9	15.9	121.5

confounding effect of distance from the nest given all nests were located in edge habitat.

RESULTS

NEST DENSITY AND DISTRIBUTION

Based on the number of new nests found in the three surveys (37, 8, 0 nests), we estimated a 0.85/survey detection probability under the Zippin model. This very high detection/survey results in counting most of the Burrowing Owls within the study area from two (98%) or three (99.9%) surveys. Thus, our estimates of density based on counts should have negligible bias.

Density of nesting pairs of Burrowing Owls remained fairly constant during the three years of the survey within the ISA. In each year, we located approximately 100 nesting pairs (1998: 106; 1999: 93; 2000: 94). From these counts, we estimated an average crude (entire area) density of 8.3 pairs/km^2 and an average linear occurrence of 2.9 pairs/km of nest (edge) habitat. Nesting pairs of owls were exceptionally dense along drains and canals, resulting in an average nearest neighbor distance ranging from 125–166 m across years (Table 1). Nests, excluding those in nest boxes, were located primarily along drains (43%), delivery ditches (43%), and canals (11%), with little variation among years.

DIET

Based on frequency of occurrence in pellet samples, the diet was dominated by arthropods, particularly Orthoptera (grasshoppers and crickets), Coleoptera (beetles), and Dermaptera (earwigs; Fig. 2). Small mammals (primarily house mouse [*Mus musculus*], pocket mouse [*Perognathus* spp.], deer mouse [*Peromyscus* spp.], and Botta's pocket gopher [*Thomomys bottae*]) were the dominant vertebrate prey, though birds were frequent in 2000. The average number of rodents/pellet was similar in 1998 (0.10 ± 0.04; CV = 148%) to 2000 (0.13 ± 0.03; CV = 115%).

BREEDING PHENOLOGY AND PRODUCTIVITY

Burrowing Owls in the Refuge generally initiated breeding in April and May and extended into late summer. Egg-laying began as early as 24 April in 1999 and prior to our first observations on 7 April in 2000. Clutches were completed as early as 30 April (1999) and 9 April (2000), but average dates were 14 May (SE = 4.2 d, N = 6 nests) and 29 April (SE = 3.5 d, N = 17 nests), respectively. Pairs with early season nest failures that relaid did so as late as mid-July in 1999 and 2000. Clutch size was similar between years (1999: 6.5 ± 0.2, N = 17; 2000: 6.9 ± 0.3, N = 19), ranging from 4–8 eggs/nest attempt. Young hatched within 1–6 (3.3 ± 1.1, N = 4) days of one another in 1999 and 3–7 (4.3 ± 0.6, N = 9) days in 2000, resulting in large size variation among siblings (Haley 2002). Based on this large variation of hatch date within a clutch, females apparently began incubation prior to clutch completion. Hatching success in 1999 (70.5% ± 14.8, N = 6) was similar to 2000 (84.4% ± 6.9, N = 8) in 2000. Dates of newly hatched young ranged from 13 May–20 June in 1999 (mean 3 June ± 3.6 d, N = 10) and 30 April–June 22 in 2000 (mean 16 May ± 3.4 d, N = 16).

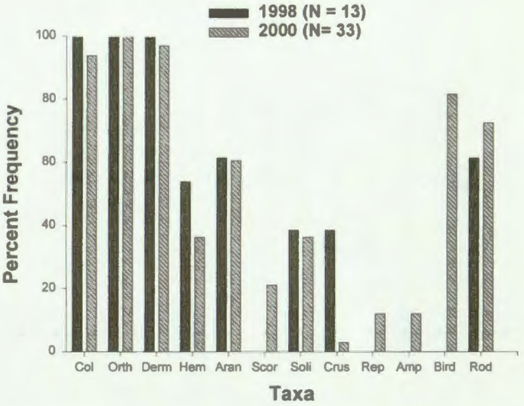

FIGURE 2. Diet of Burrowing Owls based on the % frequency of taxa within pellet samples, Imperial Valley, CA, 1997–2000. Taxa included Coleoptera (Col, beetles), Orthoptera (Orth, grasshoppers and crickets), Dermaptera (Derm, earwigs), Hemiptera (Hem, true bugs), Araneae (Aran, spiders), Scorpionida (Scor, scorpions), Solpugida (Soli, wind scorpions), Crustaceans (Crus), Reptiles (Rep), Amphibians (Amp), Birds (Bird), and Rodents (Rod). The sample size for each year is the number of nests from which pellets were collected.

Productivity varied dramatically among nests and years within the ISA. Nest failure ranged from 0 to 50% among years and location (Table 2). Productivity, as estimated for all nesting attempts and for only those that were successful, was similar between nests on private (natural nests) and Refuge (nest boxes) lands. Productivity averaged 2.5 ± 0.2 young/nest with a maximum of 7 young observed. We failed to find explanatory factors related to productivity other

TABLE 2. COMPARISON OF BURROWING OWL PRODUCTIVITY, IMPERIAL VALLEY, 1998–2000

		No. of young/nest				No. of young/successful nest		
Location[a]	Year	N	$\bar{X} \pm$ SE	Range	% failed	N	$\bar{X} \pm$ SE	Range
Private Lands	1999	23	1.8 ± 0.3	0–4	26.1	17	2.5 ± 0.3	1–4
	2000	29	3.0 ± 0.3	0–5	10.3	26	3.4 ± 0.3	1–5
Refuge Lands	1998	13	2.3 ± 0.6	0–7	30.8	9	3.3 ± 0.6	1–7
	1999	6	1.0 ± 0.5	0–3	50.0	3	2.0 ± 0.6	1–3
	2000	7	3.9 ± 0.6	1–6	0	7	3.6 ± 0.6	1–5

Note: Productivity was defined as the maximum number of young 14–21 d old observed during five 30-min observations (Private) or as the number observed within nest boxes (Refuge).

[a] Nests within private lands were selected randomly from all nests located within the ISA excluding the Refuge. Nests within the Refuge were from all active nest boxes, excluding those randomly selected to receive experimental manipulation.

than year. In 2000, the only year that we had estimates of both productivity and rodent consumption for an adequate sample of nests, productivity was unrelated to the rodent index ($N = 28$ nests, $\beta = -1.3 \pm 1.0$). Although there was high variability in nearest-neighbor distances (7–596 m) and number of neighboring nests (1–19), neither nearest-neighbor distance ($N = 52$, $\beta = -0.04 \pm 0.11$) nor number of nests within 600 m ($N = 52$, $\beta = 0.01 \pm 0.03$) were related to productivity based on the regression model with year and either the nearest-neighbor distance or number of nests as explanatory factors. So although productivity varied by year, we were unable to isolate factors associated with individual variation of productivity.

BETWEEN-YEAR MOVEMENTS

Adult Burrowing Owls exhibited strong fidelity to their nest sites and their mates. Of adult Burrowing Owls of known sex observed in two successive years (N = 91 [1998–1999] and 83 [1999–2000]), over 85% nested within 400 m of their previous year's nest (Fig. 3). Based on data from nest boxes (known nest chamber), 48% (11 of 23) and 65% (11 of 17) of nests had at least one member of the pair nesting in the same box between 1998–1999 and 1999–2000, respectively. The strong nest-site fidelity corresponded well with mate fidelity: >80% of pairs for which both members were banded and found in a successive year remained with the same mate (1998–1999: 19 of 22 pairs, 86.4%; 1999–2000: 16 of 20 pairs, 80%).

The hazard-rate function was clearly a more appropriate model than the exponential ($w = 1.0$) and demonstrated a rapidly declining likelihood to move long-distances (Fig. 4). There was strong evidence that the hazard-rate function was sex and year specific ($w = 1.0$) and fit the data ($P > 0.05$ for each sex and year). Males

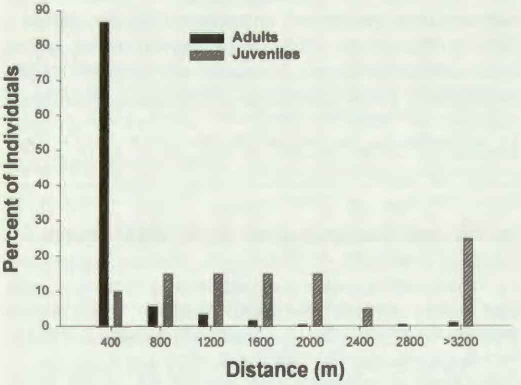

FIGURE 3. Frequency histogram of between-year movement distances of adult (N = 174) and juvenile (N = 20) Burrowing Owls from the Intensive Study Area, Imperial Valley, CA, 1998–2000. The percent of individuals located in two consecutive years is shown within 400-m distance intervals, starting at ≤400 m.

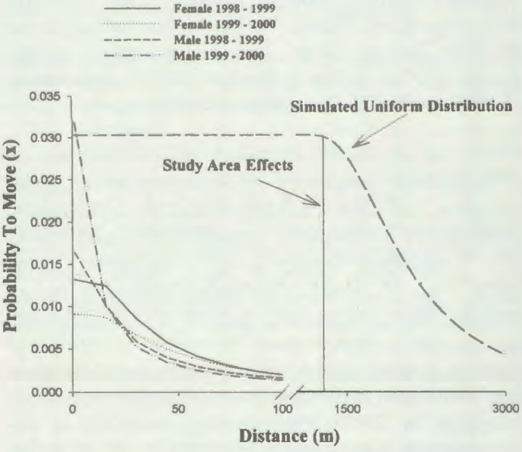

FIGURE 4. We described movement data by the hazard-rate model, $f(x) = 1 - \exp(-[x/\sigma]^{-b})$, fit to distance data of adult female and male Burrowing Owls, 1998–2000. The y-axis is the probability of an individual moving to a nest location *x* distance (m) from their previous year's nest site. "Study Area Effects" shows the estimated dispersal distance at which negative bias occurs given a uniform distribution of movements with a maximum of 3 km.

TABLE 3. Comparison of Models of Factors Affecting Between-year Movement Distances of Adult Burrowing Owls, Imperial Valley, CA, 1998–2000

Models[a]	r^2	ΔAICc[b]	w[c]	r^2	ΔAICc[b]	w[c]
A. 1998–2000, without nest success data	Males (N = 80)			Females (N = 60)		
Year, gone, neighbor, neighbor × year	0.03	6.2	0.02	0.03	11.8	0.01
Year, gone, log(neighbor), log(neighbor) × year	0.03	11.7	0.01	0.02	12.6	0.01
Year, gone, neighbor	0.03	8.0	0.01	0.02	9.3	0.01
Year, gone	0.02	4.4	0.06	0.01	6.1	0.03
Gone, neighbor	0.01	5.7	0.03	0.01	6.1	0.03
Year, neighbor, neighbor × year	0.03	8.0	0.01	0.03	8.5	0.01
Gone	0.01	3.5	0.09	0.01	3.0	0.12
Neighbor	0.01	3.5	0.09	0.01	3.0	0.12
Year	0.02	2.1	0.18	0.01	3.0	0.12
No effects (intercept only)	0.00	0.0	0.52	0.00	0.0	0.56
B. 1999, with nest success data	Males (N = 25)			Females (N = 14)		
Gone, neighbor, success	0.17	6.0	0.02	0.50	6.5	0.01
Gone, log(neighbor), success	0.16	6.6	0.01	0.49	6.9	0.01
Gone, success	0.16	2.4	0.12	0.48	0.7	0.22
Gone, neighbor	0.10	3.9	0.05	0.11	8.2	0.01
Neighbor, success	0.07	4.9	0.03	0.33	4.3	0.04
Gone	0.10	0.0	0.38	0.10	3.3	0.06
Neighbor	0.01	2.6	0.11	0.02	4.4	0.04
Success	0.07	1.1	0.23	0.30	0.0	0.33
No effects (intercept only)	0.0	4.4	0.04	0.0	0.2	0.29

[a] Factors in the models may include whether or not the mate was observed within study area ("gone"), distance to the nearest neighboring nest ("neighbor") or its log-transformed value, the year before the movement event ("year"), and whether or not the nest was successful ("success").
[b] The difference in AICc from the model with the lowest value (Burnham and Anderson 1998).
[c] The relative likelihood of the model, based on AICc (Burnham and Anderson 1998).

had a more rapidly declining function than females (Fig. 4) in both 1998–1999 (males: $\sigma = 14.9 \pm 7.2$, $b = 1.2 \pm 0.1$; females: $\sigma = 30.9 \pm 12.1$, $b = 1.5 \pm 0.2$) and 1999–2000 (males: $\sigma = 6.6 \pm 2.9$, $b = 1.1 \pm 0.2$; females: $\sigma = 36.5 \pm 17.6$, $b = 1.3 \pm 0.2$). We observed long distance movements of >3 km for females (N = 3) and never observed males moving >1.5 km. These results demonstrate the higher likelihood of males to remain near their previous year's nest and the small, but higher likelihood for females to move greater than several hundred m. In contrast, the estimated dispersal functions for the owls with simulated distances followed the expected uniform probability until approximately 1.2 km, at which point the declining slope resembled a negative exponential function (Fig. 4). The very different distance at which the simulated movements showed a declining probability of movement relative to the owl data provided strong evidence that the estimated movement patterns were not negatively biased due to study area constraints (Fig. 4), and thus allowed us to evaluate biological factors responsible for the observed patterns.

Individuals had a unique propensity for movement: distance individuals moved between 1998–1999 was positively correlated ($r = 0.67$, $P < 0.001$, N = 45) with distance moved between 1999–2000. However, we identified few factors associated with how far individuals moved. Based on data for which both members of a pair were banded (N = 66 [1998–1999], N = 68 [1999–2000] pairs), we found little evidence that year, whether or not the mate of the owl was presumed dead (i.e., never seen again), or distance to the nearest nest were associated with distance moved (Table 3a). Based on a subset of the data for which nest success was known, there was some evidence that both nest success and whether or not an owl's mate was presumed dead were associated with distance moved (Table 3b). Distance moved by males and females was associated weakly with nest success and the presence of their mate the following year (Table 3b). For both sexes, distance moved tended to be much greater for individuals whose nests failed, though estimates lacked precision (Table 4).

As expected, dispersal distance of juvenile owls was much greater than between-year movement of adults (Fig. 3). There was no evidence of a decline in the dispersal functions of juvenile owls as distance increased from the natal nest. That finding, in addition to only 20 of 124 (16.1%) juveniles that were banded and reobserved in a following year, suggests that a large proportion of the young emigrated from the study area (sensu Turchin 1998). Some juveniles did remain near their natal nest (Fig. 3). Of five

TABLE 4. COMPARISON OF DISTANCES MOVED (M) BETWEEN SUCCESSIVE YEARS IN RELATION TO AGE, SEX, NEST SUCCESS, AND LOSS OF MATE FOR BURROWING OWLS, IMPERIAL VALLEY, CA, 1998–2000

Summary statistic	Males				Females				Juveniles
	Mate gone	Mate present	Nest successful	Nest failed	Mate gone	Mate present	Nest successful	Nest failed	Pooled
N	38	42	20	5	18	42	10	4	20
Range	0–904	0–1363	0–346	5–643	0–3652	0–3089	0–639	194–3652	0–4300
Mean[a]	27.1	24.5	18.2	66.7	49.4	30.0	36.6	544.6	992.3
95% CI[b]	12.4–59.4	13.6–44.2	6.8–48.4	9.4–473.4	12.6–194.8	13.7–65.6	9.3–144.3	138.4–2143.1	453–2173
Median	25.0	26.0	26.5	194.0	151.0	30.0	46.5	397.0	1462.0

[a] Back-transformed from ln(distance).
[b] Computed from back-transformed SE (ln(distance)).

young banded at nest boxes that were relocated the following year, one nested in its natal nest with a non-parent mate.

SURVIVAL

The large sample of marked owls and their high recapture probabilities resulted in precise estimates of survival. From 1997–1999, a total of 239 adults were marked and released during 1997–1999; only 11 were marked during 1997. During 1998–2000, we identified over 140 marked adults each year, with similar numbers of males (N = 147) and females (N = 148). The global model, Model $\{\phi_{g*t}, P_{g*t}\}$, fit the data (P = 0.08). The models with the highest likelihoods were those that allowed recapture probabilities to vary by sex and constrained survival rates to be equivalent among years (Table 5). High estimated recapture probabilities for males (1.0 ± 0) and females (0.91 ± 0.06) suggested most marked owls were reobserved if present in the study area. There was little evidence that apparent survival rates varied appreciably among years; 95% confidence intervals overlapped for weighted annual estimates for both sexes. There was weak evidence that males had higher apparent survival rates than females. Based on estimates weighted from all models and using the interval from 1998–1999 for comparative purposes, apparent survival rates of males (0.64 ± 0.04) were marginally higher than those of females (0.58 ± 0.05; Table 5), but 95% confidence intervals overlapped.

To allow estimation of actual survival rather than apparent survival, we estimated the likelihood for an adult to disperse from the DSA. We estimated an emigration rate of 0.01 and 0.04 for males and females, respectively. Using these estimates of emigration and the apparent survival rates from the weighted average, we estimated an annual survival probability of 0.65 and 0.62 for males and females, respectively. This suggests that the difference in apparent survival rates between males and females was partially due to differential emigration, consistent with the differences in the movement patterns between sexes.

SPACE USE

Owls used areas nearest their nest most intensively, but included a relatively large area in their home ranges. On average >80% of foraging locations were within 600 m of their nest (Fig. 5). The area traversed averaged 113.7 ± 30.4 ha (Table 6), with high (33.7 ± 3.4%) overlap among owls. Estimates of the mean area used varied from 45.3 ± 18.2 ha (fixed kernel) to 184.5 ± 65.1 (adaptive kernel; Table 6). The difference between estimates from the fixed and

TABLE 5. MODEL DESCRIPTION AND RESULTS OF SURVIVAL ANALYSES OF ADULT BURROWING OWLS, IMPERIAL VALLEY, CA, 1997–2000

Model	Description	k[a]	ΔAICc[b]	AICc weight[c]	$\hat{\phi}$ (SE) females[d]	$\hat{\phi}$ (SE) males[d]
$\phi(s), P(s)$	Survival and recapture probability allowed to vary by sex	4	0.0	0.30	0.55 (0.04)	0.64 (0.04)
$\phi(\cdot), P(s)$	Common survival but recapture probability allowed to vary by sex	3	0.2	0.27	0.61 (0.03)	0.61 (0.03)
$\phi(s + t), P(s)$	Survival allowed to vary among time similarly between sexes; recapture probability allowed to vary by sex	6	0.9	0.20	0.57 (0.05)	0.61 (0.05)
$\phi(s), P(\cdot)$	Survival allowed to vary by sex but common recapture probability	3	1.9	0.12	0.53 (0.04)	0.65 (0.04)
$\phi(t), P(s)$	Survival allowed to vary by time and recapture probability by sex	5	3.5	0.05	0.63 (0.04)	0.63 (0.04)
$\phi(\cdot), P(\cdot)$	Common survival and recapture probability among all individuals	2	4.7	0.03	0.60 (0.03)	0.60 (0.03)
$\phi(s \times t), P(s)$	Survival allowed to vary by sex and time; recapture probability allowed to vary by sex	8	6.5	0.01	0.57 (0.06)	0.66 (0.05)
$\phi(t), P(s \times t)$	Survival allowed to vary by time; recapture probability allowed to vary by sex and time	8	7.3	0.01	0.63 (0.04)	0.63 (0.04)
$\phi(s \times t), P(t)$	Survival allowed to vary by sex and time; recapture probability allowed to vary by time	8	10.1	0.002	0.56 (0.06)	0.67 (0.05)
$\phi(s \times t), P(s \times t)$	Survival and recapture probability allowed to vary by sex and time	10	10.2	0.002	0.58 (0.06)	0.66 (0.05)

[a] Number of parameters in the model.

[b] Difference in small-sample size corrected AIC (AICc) from model with the lowest AICc; smaller values indicate a more desirable model.

[c] Aikaike's weights, an estimate of the likelihood of the model within the set of models considered (Burnham and Anderson 1998).

[d] Estimate for year effect models is based on survival between 1998–1999.

TABLE 6. ESTIMATED HOME RANGE SIZE FOR SIX RADIO-TAGGED MALE BURROWING OWLS NESTING WITHIN THE SONNY BONO SALTON SEA NATIONAL WILDLIFE REFUGE, IMPERIAL VALLEY, CA, MAY–JULY 1998

		Area estimate (ha)		
Owl	No. telemetry locations	100% MCP[a]	95% adaptive kernel	95% fixed kernel
A	71	158	191	13
B	17	68	187	8
C	55	247	491	122
D	77	80	73	65
E	29	63	85	53
F	52	66	80	11
Mean (SE)		113.7 (30.4)	184.5 (65.1)	45.3 (18.2)

[a] Minimum convex polygon.

adaptive kernel were often large because of the different levels of smoothing in areas farthest from the nest, where data were sparse. The fixed-kernel estimates probably underestimated the area used because of the high concentration of locations near the nest, whereas the adaptive kernel probably overestimated area because of the few distant locations.

Habitat selection patterns varied among owls. The strongest single effect was simply distance from the nest (Table 7, Fig. 5). The models with only distance had similar weights to models that also included whether or not cover existed. Although cover may have been a factor in foraging habitat selection for some owls (Table 7), estimates were imprecise (regression coefficient for cover, β, for log(distance) model: −0.31 ± 0.18; for polynomial (distance) model: −0.35 ± 0.58). Although small sample sizes made inferences from finer-scale analyses weak, several crop types were used more than others, relative to availability. Selection, however, varied with distance from the nest (Fig. 6). At locations near the nest, edge and fields without crops ("bare") had the greatest use relative to availability, whereas at distances >600 m selection was greatest for hay fields (Fig. 6). The large variation among owls (Fig. 6) was probably due to distance from the nest, maturity of the crop (i.e., accessibility), and management of a particular field, as well as individual patterns of habitat selection.

DISCUSSION

NEST DENSITY AND DISTRIBUTION

The Burrowing Owl population in the Imperial Valley of California is perhaps the largest continuous population throughout the species' range and surely one of the most dense populations over such a large area (DeSante et al. *this volume*). Coulombe (1971:Table 2) estimated 3.3 pairs/km^2 within an 8-km^2 area of the Imperial Valley during the breeding season of 1966–1967. In southern Florida, Millsap and Bear (2000) reported a density of 6.9 pairs/km^2 for the Florida subspecies (*A. c. floridana*), which they estimated from a relatively large area (35.9 km^2) relative to most other studies. Our estimate of 8.3 pairs/km^2 is one of the highest reported.

Estimates of density are sensitive to the area considered; small areas delineated by the existence of individuals may result in very high densities. For example, Desmond et al. (1995) reported ≥20 pairs/km^2 of owls in black-tailed prairie dog (*Cynomys ludovicianus*) colonies within areas of <35 ha. The spatial variability of owl densities within our study site was due

TABLE 7. COMPARISON OF HABITAT SELECTION MODELS OF MALE BURROWING OWLS (N = 6), IMPERIAL VALLEY, CA, MAY–JULY 1998

	Log (distance)		3rd-order polynomial (distance)	
Model[a]	$\hat{w}$[b]	Range (w)[c]	$\hat{w}$[b]	Range (w)[c]
Distance, crop type	0.06	0–0.20	0.07	0–0.24
Distance, crop cover	0.20	0–0.87	0.26	0–0.77
Distance	0.20	0–0.67	0.20	0–0.54
No effects (intercept only)	0.00	0	0.00	0

[a] Factors in the models may include distance from the nest as either a log effect or as a 3rd-order polynomial, and two different schemes of pooling different habitat types: (1) whether or not the field contained crops with dense cover ("crop type") or (2) whether or not the field had cover by a crop.

[b] The mean of the relative likelihood of the model, based on AICc (Burnham and Anderson 1998).

[c] The range of *w* among owls.

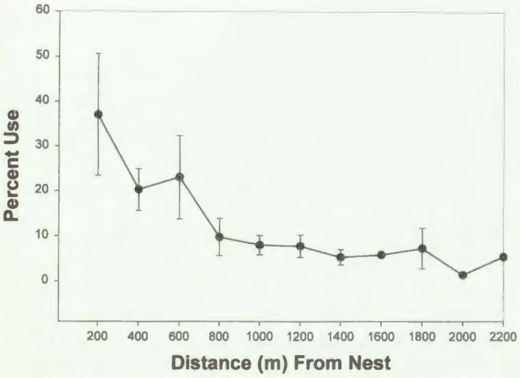

FIGURE 5. Frequency distribution of percent of locations ($\bar{X}$ ± SE) of six male Burrowing Owls radiotracked in the Imperial Valley, CA (June–July 1998).

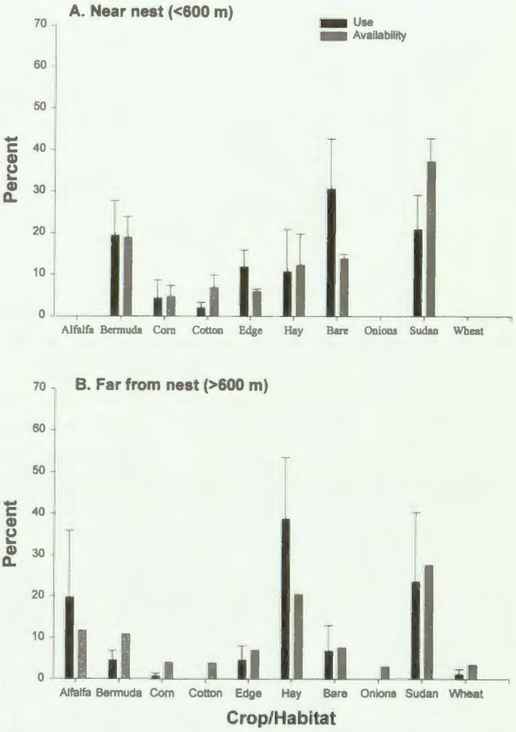

FIGURE 6. Comparison of the percent use among foraging habitats by six male Burrowing Owls, Imperial Valley, CA, June–July 1998. The error bar represents the SE among the owls. The percent use and availability of each type differed based on locations near (A) and far (B) from the nest. Estimates are based on locations gathered from nocturnal telemetry (owl use) or % composition of habitats within a circle with a radius equal to the maximum distance an owl was located from its nest (availability).

in part to the scarcity of burrows in some areas. High spatial variation in nest distribution is characteristic of Burrowing Owl populations (Desmond et al. 1995, Trulio 1997, Millsap and Bear 2000), and results in high variation of nearest-neighbor distances.

Burrowing Owls often live in close proximity to conspecifics, but defend the immediate area near their nest (Coulombe 1971; D. Rosenberg, pers. obs.). We found pairs nesting as close as 7 m to each other, with an average nearest-neighbor distance of 147 m. In a study area about twice the size of ours, Millsap and Bear (2000) reported mean nearest-neighbor distances of 176 m. There have been few studies investigating whether a benefit is gained by their clustered distribution, which often resembles a colonial nesting pattern. Green and Anthony (1989) found nest success was lower for owls that nested within 110 m of another pair, suggesting competition for resources. Although we found high variability in nest densities, we failed to find evidence, based on number of young/female, that competition drives nest distribution. Further investigation into the costs and benefits of the clustered distribution of nests will provide insight into the proximate and ultimate causes of the spatial distribution of Burrowing Owl nests.

DIET

The diet of Burrowing Owls in our study area, dominated numerically by invertebrates, is probably typical of populations within intensive agricultural ecosystems. The very broad diet we observed is characteristic of Burrowing Owls (Haug et al. 1993). During the breeding season, their diet likely represents opportunistic foraging near the nest site, consistent with central place foraging theory (e.g., Orians and Pearson 1979). In many populations, there is a seasonal shift in diet, with an increase in consumption of vertebrates during the non-breeding season (reviewed in Haug et al. 1993; Silva et al. 1995). This may not be the case in the intensive agroecosystems of the Imperial Valley, where York et al. (2002) found dominance by Orthoptera in both the breeding and non-breeding season. Given the estimate of 14 individual Orthoptera/stomach (York et al. 2002) and assuming a pellet egestion rate of 24 hr (Haug et al. 1993), an adult owl consumes about 5000 Orthoptera/yr. Based on an estimate of 13,000 adult owls in the Imperial Valley (DeSante et al. *this volume*), Burrowing Owls consume >65 million Orthoptera/yr. Although the effect of Burrowing Owl predation on crop pests remains unknown, the owls' high density and heavy predation of pest species suggest it may be important.

Analysis of pellet samples in our study area and of stomach contents (York et al. 2002) suggested very low consumption of rodents in the Imperial Valley relative to other populations in California (D. Rosenberg et al., unpubl. data). The rodent index was highly variable among nests and was likely influenced by field-specific crop management. For example, after a field burn we observed greater numbers of rodent remains around owl burrows (K. Haley, pers. obs.). The flood method of irrigation may limit rodent populations. York et al. (2002) hypothesized that Burrowing Owls select small rodents over arthropods and that the low frequency of rodents in their diet in the Imperial Valley was due to low abundance and availability, consistent with findings of strong selection for rodents for a Chilean Burrowing Owl population (Silva et al. 1995).

Birds were another primary vertebrate consumed. They were much more frequent in the diet of owls in the Imperial Valley than in other areas of California (D. Rosenberg et al., unpubl. data). Prey included both small passerines, such as Wilson's Warbler (*Wilsonia pusilla*), as well as larger birds that were apparently scavenged, such as American Avocet (*Recurvirostra americana*). Birds may be an important component of the diet, especially during the breeding season when energetic demands are high.

BREEDING PHENOLOGY AND PRODUCTIVITY

The owls' nesting season is longer than elsewhere in California (D. Rosenberg et al., unpubl. data), with egg-laying extending into July, usually following nest failure. Indeed, a nest with 10–14 d old young was found during December (J. Govan, pers. comm.), giving further support to our hypothesis that year-round food availability may be greater in the Valley than elsewhere in the subspecies' range. The only other record of late-season breeding by Burrowing Owls was in Florida in an area also with high densities of owls (Millsap and Bear 1990). Despite the potential for an extended breeding season and frequent renesting following nest failure (D. Catlin and D. Rosenberg, unpubl. data), we did not observe double-brooding, which has been infrequently observed elsewhere (Millsap and Bear 1990, Gervais and Rosenberg 1999).

Clutch size within a species is believed to be a response to variation in protein and energy availability (Williams 1996, Nager et al. 1997). Burrowing Owls produce large clutches (up to 11 eggs; Haug et al. 1993), usually associated with high rodent abundance (D. Rosenberg, pers. obs.). In the Imperial Valley, we have never observed clutch size >8 during our study period; of these, few individuals typically fledge. Although an average of six eggs were laid per clutch, an average of only 2.5 young survived to 21–28 d old.

We failed to identify factors other than year associated with individual variation in productivity. We explored only two components of those often postulated to be associated with individual variation of productivity in birds: quality of diet and competition for food resources (Newton 1998). We failed to find that our index of rodent consumption or the presence of neighboring owls were related to productivity. Although it is likely that our finding of a year effect on productivity was related to food resources, our index, which estimated the abundance of only one of the many prey resources, was not indicative of individual variability in productivity. How well our estimate provided a reliable index to rodent consumption at the individual nest level is unknown. Unlike other sites in California (D. Rosenberg, unpubl. data), birds were a common component of the diet, and indeed may be more important than rodent consumption for providing sufficient energy and nutrients for a large brood. Other factors affecting individual variation in productivity that may be operative for Burrowing Owls include vulnerability to predation, parental condition, age of adults, and previous reproductive history. These factors remain to be explored with our data and future experimental studies.

That food supply limits clutch size and the number of fledglings of many bird species has been well demonstrated (Newton 1998:145). Indeed, Haley (2002) found an increase in productivity of food-supplemented Burrowing Owls in the Imperial Valley. We hypothesize that clutch size of Burrowing Owls in the Imperial Valley is limited primarily by nutrient and energy availability. We further speculate that the mechanism of reducing brood size occurs through infanticide (Wellicome 2000) and increased predation through exposure of young at the burrow (Botelho 1996), both of which are influenced by food supply. Determining the separate roles of nutrient and energy limitation in clutch size (e.g., Nager et al. 1997) and factors causing mortality of nestlings will require careful observation and experimentation.

BETWEEN-YEAR MOVEMENTS

Burrowing Owls typically remained with their mates in successive breeding seasons. Our finding of greater than 80% mate retention is similar to the high (92%) rate Millsap and Bear (1997) reported in Florida. However, high annual mortality meant that only approximately 40% of the pairs would have both members alive by the following breeding season. Following loss of mates, through divorce, emigration, or death, new pairs were formed; some owls moved considerable distances (e.g., >3 km) before new nest pairs were formed.

Our findings on between-year movements are in general agreement with prior studies throughout the owl's North American range. Our results are similar to the high nest-site fidelity of adults reported for the Florida subspecies by Millsap and Bear (1997) and for a migratory population nesting in Canada (Wellicome et al. 1997). Lutz and Plumpton (1999) reported lower rates for a migratory population in Colorado. Adult between- or within-year movement distances of over 40 km have been detected for both resident (J. Rosier et al., unpubl. data) and migratory (Wellicome et al. 1997) populations. The size of our study area, however, was too small to detect movements >4 km using only mark-recapture methods.

Adult Burrowing Owls, particularly females, will nest in locations distant from their previous year's nest, consistent with avian dispersal patterns (Greenwood 1980). We found such movements often followed nest failure, similar to results from Colorado (Lutz and Plumpton 1997) and grasslands in California (J. Rosier et al., unpubl. data). Millsap and Bear (1997) found that longer-distance movements were associated with loss of a mate. We found evidence for this as well, but our data provided stronger support for nest failure as the predominant factor associated with movements.

Natal dispersal patterns are poorly understood and distance distributions are typically underestimated for most bird species (Barrowclough 1978, Koenig et al. 2000). Natal dispersal patterns in Burrowing Owls are no exception. From the non-declining dispersal function (sensu Turchin 1998), it was clear that our study area was too small to properly estimate this important parameter. Natal dispersal distance of up to 300 km was reported by Wellicome et al. (1997) from a migratory population. Millsap and Bear (1997) reported a median natal dispersal distance of between 0.4–1.1 km; our median distance was similar (1.5 km), and we suspect it was severely underestimated. Careful attention to the problems of estimating dispersal, particularly natal dispersal (e.g., Koenig et al. 2000), will be required to provide a better understanding of the population ecology of this species.

SURVIVAL

It was interesting, but not surprising, that adult survival rates were similar between males and females. We suspect that causes of mortality differ between sexes, though annual mortality is similar. Costs of reproduction are likely higher for females, particularly if nutrients required for reproduction are limiting. Predation within the burrow by fossorial mammals and snakes may be an important mortality factor. If so, this should affect adult females more than males because only females incubate eggs and brood young (Haug et al. 1993). Alternatively, the male's high visibility and the greater amount of time spent foraging during the breeding season may make males more vulnerable to other predators and vehicles. Few accounts of cause-specific mortality exist. Clayton and Schmutz (1997) quantified cause-specific mortality for two Canadian populations; vehicle collisions were the predominate mortality factor for adults in fragmented environments, whereas predation by raptors and mammals predominated in the larger grassland ecosystems. Millsap (2002), in an urban environment in Florida, found vehicle collisions responsible for 70% of banded owls found dead. A deeper understanding of cause-specific mortality is needed to more fully understand factors affecting Burrowing Owl populations.

Our estimate of survival rates of Burrowing Owls is one of the few not based on return rates, which typically underestimate survival. Lutz and Plumpton (1997) reported adult survival rates that varied between 0.17 to 0.71 among years within a migratory population in Colorado. In Canada, Clayton and Schmutz (1997) estimated adult survival rates based on known fate data (radio telemetry) and generally found low rates, although they varied from 0.38–1.0 for a 4-mo period. In a study design similar to ours, Millsap and Bear (1997) found annual survival rates of females generally lower (0.52–0.69) than males (0.62–0.81), and in areas of moderate housing development they tended to be similar to our estimates (Millsap 2002).

Based on the natural history of Burrowing Owls, it is likely that population dynamics are more sensitive to juvenile than adult survival (e.g., Emlen and Pikitch 1989). Indeed, that few adults but many juveniles moved long distances and that mortality rates of adults are high, suggest that *ex-situ* recruitment of young into the breeding population is an essential feature of the dynamics of the relatively stable population we studied. Martin et al. (2000) reported similar findings for White-tailed Ptarmigan (*Lagopus leucurus*) and suggested that recruitment from external populations may be an important and common feature of avian population dynamics. In the Imperial Valley, the Burrowing Owl population is probably structured as a continuous population rather than as a set of distinct "external" populations. Indeed, genetic data suggest high mixing of individuals throughout central and southern California (Korfanta 2001).

Because of the high emigration rate of juveniles from our study area, as evidenced by the non-declining movement function we observed (Fig. 3), estimates of juvenile survivorship would have been severely underestimated from our data. Precise and unbiased estimates of juvenile survivorship will be important in order to model the dynamics of this population, as well as to explore how sensitive the dynamics of the population are to juvenile survivorship.

SPACE USE

Burrowing Owls tend to remain near their nest site during nocturnal foraging. Similar to our results, >80% of the nocturnal telemetry locations were within 600 m of the nest during the breeding season in the agricultural matrix of the Central Valley, California, and Saskatchewan, Canada (Haug and Oliphant 1990, Gervais et al. 2003). Haug and Oliphant (1990) reported male Burrowing Owls selected grass-forb areas and avoided agricultural fields during nocturnal foraging. However, their estimates of selection did not take into account distance from the nest. Because nest sites were all located within grass-forb areas (Haug and Oliphant 1990), distance alone may explain the apparent patterns of habitat selection they reported. Our results and those of Gervais et al. (2003) demonstrate that agricultural fields are often used by Burrowing Owls. Indeed, the high owl densities in the Imperial Valley, predominated by crops, suggest agricultural fields can provide quality foraging habitat. The structure of vegetation within an agricultural field is dynamic and changes throughout the growing season likely affect owl selection. Some crops, such as alfalfa, are grown without cultivation for several years, sometimes as long as six years (A. Kalin, pers. comm.). In such cases, rodent populations may increase with a parallel increase in selection by foraging Burrowing Owls.

Home range size of adult Burrowing Owls is highly variable. Estimates (MCP method) ranged from 14–480 ha ($\bar{X}$ = 240 ha) in a matrix of grazed pastures and cereal crops in Canada (Haug and Oliphant 1990) and averaged 189 ha in the Central Valley of California (Gervais et al. 2003). We found similarly high variation, regardless of the estimator used. Variation in home range size is likely due to availability of prey, reproductive success (i.e., energy demand), and characteristics of the landscape that affect the distribution of resources (Newton 1979, Kenward 1982, Haug and Oliphant 1990, Carey et al. 1992). Management practices that affect prey availability, such as field burning and harvest, were also likely responsible for the individual variation we observed in patterns of space use. Sampling variation may be responsible for much of the observed differences in estimated home range size; this deserves further attention for estimation of home ranges in general (White and Garrot 1990).

MANAGEMENT CONCERNS

In the Imperial Valley, the availability of burrows is largely dependent on the management practices of private landowners and the Imperial Irrigation District. Most of the burrows in our study site likely resulted from water seepage, muskrats (*Ondatra zibethicus*; Coulombe 1971), and gophers. When gophers reach the concrete lining, they often burrow to the surface (A. Kalin, pers. comm.), creating an initial tunnel the owls can enlarge. We also found nests within burrows initially created by the round-tailed ground squirrel (*Citellus tereticaudus*), as did Coulombe (1971). Within the agroecosystems of the Imperial Valley, the abundance of these species and their ability to provide burrows that the owls can modify as nests are determined largely by local farming practices and methods of water conveyance.

The single largest management concern for the Burrowing Owl population in the agroecosystems of the Imperial Valley is how the irrigation system is managed. Dredging of drains and grading of roads has the potential to destroy nests (Coulombe 1971; this study). Indeed, several adults and their nests were buried during road grading operations (D. Catlin and D. Rosenberg, unpubl. data). Flooding from overflow of delivery ditches also cause nest destruction and death of young (K. Haley, pers. obs.). A potential problem is the growth of tall vegetation along drains, which prevents owls from nesting; however, current management practices generally reduce or eliminate vegetation along drains. Collaboration among the Imperial Irrigation District, state and federal agencies, and landowners, such as local farmers, will be instrumental in developing strategies to allow maintenance of the irrigation system while minimizing destruction to nests. Burrowing Owls and their nests are protected under both state and federal laws but such protection in intensively managed ecosystems is difficult. Research on developing feasible methods to reduce the likelihood of destroying nests or entrapping adult owls will be essential in developing conservation strategies.

Another issue that may affect Burrowing Owl populations in the Imperial Valley is the presence of contaminant residues from current and former agricultural practices. Previous findings suggest low levels of contamination by organochlorines; *p,p′*DDE, the only organochlorine detected in eggs, was relatively low in the Imperial Valley (Gervais et al. 2000). Species that consume a large proportion of their diet from aquatic environments have been reported with high levels of *p,p'*DDE and selenium within the Imperial Valley (Setmire et al. 1990, 1993). The predominance of terrestrial-based prey resources in the diet, particularly Orthoptera, may be responsible for the relatively low levels of both *p,p'*DDE and selenium reported by Gervais et al. (2000). The results of Gervais et al. (2000) were based on a small sample from within the Refuge and from only a single year; however, Gervais and Catlin (in press) found similar levels of *p,p'*DDE within and adjacent to the Refuge in 2002. Although we did not evaluate contaminate residues, the relatively high rates of adult survival and the proportion of nesting attempts that produced young do not currently indicate a problem. However, effects could occur if current patterns of pesticide use change or if natural stressors interact with pesticide exposure (Gervais and Anthony 2003).

The large numbers of Burrowing Owls in the agricultural matrix of the Imperial Valley remain vulnerable to changes in land use (e.g., urbanization) and water distribution. Although the concentration of Burrowing Owls within the Imperial Valley is clearly due to farming practices, presumably a large but sparse population existed prior to agricultural development. The few areas of native habitat that remain in the Imperial Valley may be important for the persistence of Burrowing Owls in the Imperial Valley if changes in agricultural practices prevent nesting along the irrigation system. Successful conservation strategies for Burrowing Owls in the Imperial Valley will require both a thoughtful consideration of how future changes in agricultural practices may affect populations and an evaluation of the role of native habitat for population persistence.

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TYPE C BOTULISM IN PELICANS AND OTHER FISH-EATING BIRDS AT THE SALTON SEA

TONIE E. ROCKE, PAULINE NOL, CHARLES PELIZZA, AND KEN K. STURM

Abstract. In 1996, type C avian botulism killed over 10,000 pelicans and nearly 10,000 other fish-eating birds at the Salton Sea in southern California. Although botulism had been previously documented in waterbirds at the Sea, this die-off was unusual in that it involved primarily fish-eating birds. The American White Pelican (*Pelecanus erythrorynchos*) was the species with the greatest mortality in 1996. Since 1996, mortality has recurred every year but losses have declined (<2000 birds/year), with relatively more Brown Pelicans (*P. occidentalis*) than White Pelicans afflicted. In 2000, morbidity and mortality of Brown Pelicans with type C botulism (1311) approached the numbers afflicted in 1996 (2034). In recent years, mortality reached a peak earlier in the summer, July and August, in contrast to 1996 when mortality reached a peak in September. An exotic fish species, tilapia (*Oreochromis mossambicus*), has been implicated as the source of toxin for birds at Salton Sea, but the source of toxin for fish is unknown.

Key Words: avian botulism; *Clostridium botulinum* type C; fish-eating birds; pelicans; Salton Sea; tilapia.

BOTULISMO TIPO C EN PELÍCANOS Y OTRAS AVES PISCÍVORAS EN EL MAR SALTON

Resumen. En 1996, el botulismo aviar tipo C mató a más de 10,000 pelícanos y cerca de 10,000 aves piscívoras en el Mar Salton en el sur de California. Aunque el botulismo se ha documentado previamente en aves acuáticas marinas, esta mortandad fue inusual e involucró principalmente a las aves piscívoras. El Pelícano Blanco (*Pelecanus erythrorynchos*) fue la especie con mayor mortandad en 1996. Desde 1996, la mortandad se ha repetido año con año pero ha disminuido (<2000 aves/año); los Pelícanos Pardos (*P. occidentalis*) fueron relativamente más afectados que los Pelícanos Blancos. En el 2000, la morbidez y mortandad de Pelícanos Pardos con botulismo tipo C (1311) se aproximó al número de los afectados en 1996 (2034). En años recientes, la mortalidad alcanzó el máximo a principios del verano, Julio y Agosto, en contraste a 1996 cuando la mortalidad alcanzó el máximo en Septiembre. Un pez exótico, la Tilapia (*Oreochromis mossambicus*), ha sido implicado como la fuente de toxina para las aves del Mar Salton, sin embargo la fuente de la toxina para los peces se desconoce.

Palabras claves: Aves piscívoras; botulismo aviar; *Clostridium botulinum* tipo C; Mar Salton; pelícanos; Tilapia.

In 1996, nearly 20,000 pelicans and other fish-eating birds at the Salton Sea became sick or died in a large outbreak of type C avian botulism (Friend 2002). The American White Pelican (*Pelecanus erythrorhynchos*) was the species most afflicted, with losses of approximately 9000 birds. Over 2000 endangered California Brown Pelicans (*Pelecanus occidentalis californicus*) were also affected, although many of these (>500) were taken to rehabilitation centers, treated, and ultimately released. Sixty other avian species were found dead during this outbreak, totaling nearly 4500 birds. Among these were Snowy Egrets (*Egretta thula;* N = 779), Ring-Billed Gulls (*Larus delawarensis*; N = 612), Great Egrets (*Ardea alba*; N = 270), Western Sandpipers (*Calidris mauri*; N = 190), Great Blue Herons (*Ardea herodias;* N = 172), Black-Crowned Night-herons (*Nycticorax nycticorax*; N = 169), Eared Grebes (*Podiceps nigricollis*; N = 143), Black-necked Stilts (*Himanoptus mexicanus*; N = 125), and American Avocets (*Recurvirostra americana*; N = 107) (U.S. Fish and Wildlife Service (USFWS), unpubl. data). Over half a million dollars were spent on carcass collection and rehabilitation efforts during this single epizootic (USFWS 1997).

Botulism was first documented at the Salton Sea in 1917, and large-scale outbreaks in waterfowl and shorebirds in the Sea and surrounding wetlands recurred frequently since that time (Friend 2002). However, in the 1990s, botulism outbreaks in waterfowl at the Sea generally declined. The 1996 outbreak was unusual in several respects. Prior to this event, large die-offs of fish-eating birds were not typically associated with type C botulism; most previous reported botulism outbreaks that involved mainly fish-eating birds were caused by type E toxin (Rocke and Friend 1999). Type C botulism mortality in fish-eating birds has generally been documented as an incidental finding related to outbreaks in waterfowl (National Wildlife Health Center (NWHC), unpubl. data). Fish, specifically tilapia (*Oreochromis mossambicus*) were immediately suspected to be the source of toxin for the birds, although perusal of available literature failed to reveal a previously established association between fish and type C botulism in birds. Tilapia are exotic to the U.S. and were introduced in the Salton Sea and its drains in the 1960s, presumably to control vegetation (Costa-Pierce and Doyle 1997). By the 1970s tilapia were the most abundant fish in the Sea in terms of biomass (Dill and Cordone 1997); the population peak of 1996 was estimated to be approximately 20 million (R. Riedel, pers. comm.).

The 1996 botulism outbreak at the Salton Sea resulted in the largest die-off of pelicans ever reported from any cause. Smaller die-offs of pelicans occurred at the Salton Sea in 1994 (N = 108) and 1995 (N = 10), and several were diagnosed with type C botulism, but until the large outbreak in 1996 the risk of type C botulism in pelicans was not recognized. Here we document losses of pelicans and other fish-eating birds from type C botulism at the Salton Sea from 1994 to 2001 and describe the investigation of the larger outbreak in 1996.

MATERIALS AND METHODS

INVESTIGATION OF AVIAN MORTALITY

Sick and dead birds at the Salton Sea were recovered primarily with airboats and other boats, and occasionally affected birds were found by walking shorelines. Severely moribund birds were euthanized by cervical dislocation, although most of the moribund Brown Pelicans were taken to rehabilitation centers (USFWS, unpubl. data). Blood samples were drawn from selected sick birds by jugular venipuncture, allowed to clot, and centrifuged to collect serum. The serum samples were placed at −20°C and shipped frozen to NWHC for testing. Selected carcasses were submitted to NWHC for necropsy; the remainder was incinerated on-site. During necropsy, a gross examination, including mass and other measurements, a description of wounds and abnormalities, and an evaluation of overall body condition with respect to fat reserves and pectoral muscle development, was conducted on each carcass. Samples of organs were tested for a variety of microbes, parasites, and toxins as indicated by gross findings and field information provided by the submitter.

Tissues for histopathology were fixed in 10% buffered formalin, embedded in paraffin, sectioned for light microscopy, and stained with hematoxylin and eosin for routine examination, Ziehl-Neelsen acid-fast for mycobacteria, and/or Grocott silver for fungi. Bacteria were isolated by inoculation of tissues onto 5% sheep red-blood agar and eosin-methylene blue plates (DIFCO laboratories, Detroit, MI), incubated at 37°C for 72 hr, and then characterized with the API-20E system (Analytab Products, Plainview, NY). Tissues for virus isolation attempts were processed according to Docherty and Slota (1988) and Senne (1989). The presence of botulinum toxin in heart blood or serum was evaluated using either the mouse neutralization test (Quortrup and Sudheimer 1943) or the enzyme-linked immunsorbent assay (Rocke et al. 1998). The remains of fish found in the proventriculus of some carcasses or those regurgitated by sick birds were likewise tested for botulinum toxin.

When exposure to organophosphorus or carbamate agricultural pesticides was suspected, brains were screened for cholinesterase activity. Cholinesterase assays were performed according to Ellman et al. (1961) as later modified by Dieter and Ludke (1975) and Hill and Fleming (1982), including incubation (18 hr at 37°C) and retesting of samples with initially low enzyme activities. Cholinesterase inhibition was calculated by comparison with normal published values (Hill 1988) or control values determined by NWHC (Smith et al. 1995). Liver lead residues were determined according to Boyer (1984).

To determine whether any changes had occurred in temporal patterns of sick and dead pelican recovery from 1994–2001, we summarized available data that had been collected each year by staff of the Sonny Bono Salton Sea National Wildlife Refuge (SBSSNWR) during botulism outbreaks.

FISH INVESTIGATIONS

In mid-August and mid-September of 1996, during the peak mortality in birds, we collected 80 dead tilapia, ten from eight different locations in the Sea and along the shoreline. Only fresh carcasses, with pink to bright red gills, were selected. From a few locations in mid-August and mid-September, we also collected 41 moribund tilapia that were sluggish, exhibited poor fright response, and were easily caught with a dip net. In addition, in mid-September we collected 58 apparently healthy tilapia near the deltas of the Alamo, New, and Whitewater rivers using gill nets or minnow traps with assistance of personnel from the California Department of Fish and Game. All fish collected were immediately placed on ice in the field and either necropsied the same day or frozen as soon as possible for later necropsies. Sampled fish averaged 73 g in mass and most ranged from 12 to 15 cm in total body length.

In the laboratory, fish carcasses were rinsed and intestinal tracts were removed from all those collected and ground with a mortar and pestle with minimal amounts of sterile saline added if necessary. The samples were placed at 4°C overnight for toxin extraction, and then centrifuged at 3000 rpm in a Sorvall RI6000 (Global Medical Instrumentation Inc., Clearwater, MN) to separate fluid from the sediment. The fluid was tested for type C botulinum toxin by ELISA and/or by mouse test. We also tested 30 of the healthy fish captured for the presence of *C. botulinum* spores by inoculating intestinal contents into Cooked Meat Medium (Difco) in an anaerobic hood and incubating for five d at 37°C. Culture supernatants were then tested for the presence of type C botulinum toxin by ELISA. Samples from sick fish, including intestinal contents and fluid from the peritoneal cavity, were also cultured for bacteria by inoculating the material into several tubes of brain heart infusion broth (Difco) with 3% added NaCl and incubating at 20°C and 37°C for 24 hr. Broth cultures were streaked onto thiosulfate-citrate-bile sucrose agar (Bekton Dickson, Sparks, MD); colonies were subcultured on blood agar plates (Bek-

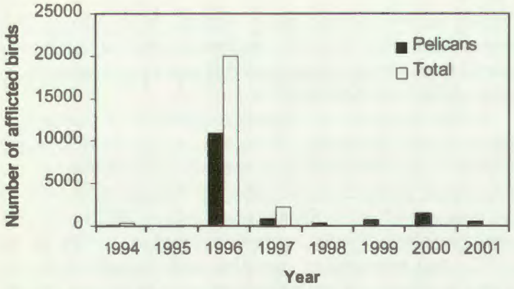

FIGURE 1. Estimated numbers of pelicans and total fish-eating birds (if available) affected by avian botulism at the Salton Sea, 1994–2001.

TABLE 1. PELICANS AFFECTED BY BOTULISM AT THE SALTON SEA, 1994–2001[a]

	White Pelicans		Brown Pelicans		
Year	Sick[b]	Dead	Sick[b]	Dead	Total affected
1994	—[c]	89	—	19	108
1995	—	7	—	3	10
1996	300	8539[d]	905	1129	10,873
1997	181	304	143	234	862
1998	24	94	133	121	372
1999	23	54	444	203	724
2000	103	88	994	317	1502
2001	69	45	342	110	566

[a] USFWS, SSNWR unpubl. data.

[b] When possible, sick birds were sent to rehabilitation centers.

[c] Data unavailable.

[d] Number includes birds that were euthanized.

ton Dickson) for 24 hr incubation and then identified using the API-20E system.

RESULTS

AVIAN DIAGNOSTICS 1994–2001

Every year since 1994, type C botulism has been diagnosed as the cause of death of pelicans submitted to NWHC from the Salton Sea, and numerous pelicans were picked up sick or dead (Fig. 1). During 1996, 22 of 41 carcasses/tissues of fish-eating birds sent from the Salton Sea to the NWHC between 21 August and 18 September tested positive for type C botulinum toxin by mouse test and/or ELISA. Heart blood samples from four of 11 White Pelicans and eight of 13 Brown Pelicans submitted for testing were found to contain type C botulinum toxin. Other species submitted that tested positive for type C botulinum toxin during this time were single individuals of the Great Blue Heron, Black-crowned Night-heron, Snowy Egret, Eared Grebe, Northern Shoveler, and Green-winged Teal, and three individuals of the Great Egret. Fish remains recovered from the Great Blue Heron also tested positive for type C toxin. Thirty-two carcasses tested were negative for type E botulinum toxin. Eight carcasses were tested for the presence of cholinesterase inhibition and were found to have normal levels. Two were tested for lead poisoning and were also negative. None of the birds examined had any significant gross or histologic lesions, and no significant pathogens were found by microbial analyses.

In subsequent years, specimens were sent to the NWHC in late spring and early summer to confirm the onset of outbreaks. Once the diagnosis of type C botulism was confirmed, sick and dead pelicans and other fish-eating birds were documented as having the disease based on observation of clinical signs. These include bilateral paresis or paralysis of leg, neck, and wing muscles, which are manifested in the birds' inability to lift their heads, ambulate, or fly, as well as paralysis of the nictitating membrane (Rocke and Friend 1999). Estimates of botulism mortality by pelican species and year are included in Table 1.

TEMPORAL PATTERNS OF BOTULISM OUTBREAKS, 1996–2001

During 1996, the first disease-stricken pelicans were detected on 15 August. It was estimated the outbreak had begun within the prior two wks. Ninety-five percent of the total affected pelicans that year were detected during the months of August and September, when 4234 and 5897 individuals were collected respectively. Collection rates dropped significantly to 537 total birds in October and 16 in November when the outbreak subsided.

The August/September peak in the number of birds afflicted with botulism continued in 1997, 1998, and 1999, when 75%, 87%, and 88%, respectively, of total affected birds were detected in those months, although mortalities were first detected in May 1998 and in July 1999 and continued through November. In 2000 and 2001, botulism outbreaks at the Sea reached a peak in July and August and subsided in September. During 2000, 72% of affected birds were collected in July and August and only 13% in September. Collections of total affected birds during 2001 reached a peak in August at 45%, whereas collections in June, July, and September totaled 14%, 18%, and 15%, respectively. No data were available in SBSSNWR records to compare temporal patterns of mortality in pelicans for 1994 and 1995.

TILAPIA SAMPLING, 1996

Type C botulinum toxin was detected in the gastrointestinal tracts of both sick and dead tilapia at various sites around the Sea. The highest percent of fish with toxin (50–60%) were found

FIGURE 2. Percentage of dead tilapia collected in 1996 that were positive for type C *botulinum* toxin.

dead in or near the deltas of the New, Alamo, and Whitewater rivers (7–38% at other areas; Fig. 2). In mid-August, only five moribund fish were collected (Salton Sea State Recreation Area (SRA) 2, Wister 1, and Bombay Beach 1), but three (60%) of these were found to contain type C botulinum toxin. Despite attempts to culture other bacteria from their intestinal contents, no significant growth was detected. During a collection in mid-September, 36 moribund fish were caught (Salton Sea SRA 11, Bombay Beach 25), but only three (8%) were found to contain type C botulinum toxin. Most of the fish in the second collection had gross external signs of bacterial septicemia, including hemorrhage of the skin and bases of fins and extensive ascites. *Aeromonas* spp., *Pseudomonas* spp., and *Vibrio* spp. were isolated from most of the moribund fish. Of the 58 apparently healthy tilapia tested in mid-September, none were found to contain type C botulinum toxin in their intestinal contents. Two of ten fish collected at the New River were culture positive for *C. botulinum* type C, although none of the 20 fish collected at the Alamo and Whitewater River deltas were culture positive.

DISCUSSION

Prior to the botulism outbreak at the Salton Sea in 1996, type C botulism in fish-eating birds was considered infrequent (Rocke and Friend 1999). Pelicans were diagnosed with the disease in 1994 and 1995 at Salton Sea and occasionally elsewhere in North America, but rarely in numbers exceeding 100, and often fewer than ten (NWHC, unpubl. data). Botulism was not considered a major threat to pelican populations. However, it has been estimated that White Pelicans lost to botulism in 1996 represented nearly 15% of the western population of that species (USFWS 1997). Additional die-offs of this magnitude could be detrimental to this population. Fortunately, since 1996 the die-offs have been considerably smaller, both in the severity and in the number of species afflicted. However, botulism outbreaks vary from year to year, most likely depending on local environmental conditions (Rocke and Friend 1999).

Interestingly, comparative mortality rates in Brown and White pelicans have changed over the period covered by this review. From 1994 to 1997, losses from type C botulism in White Pelicans were greater than in Brown Pelicans. This trend reversed in the last four years (1998–2001), with losses in Brown Pelicans higher than White Pelicans (Table 1). The reason for this trend is unknown. It might reflect differences in feeding behavior between the two pelican species as fish communities in the Sea change, or it might reflect differences in toxin availability as a result of year-to-year variation in environmental conditions. In 1996 large numbers of tilapia were available and pelicans could readily choose between healthy, sick, and dead fish, both species most likely preferring the easily caught sick, yet still live fish. As tilapia populations declined over the last few years (Riedel et al. 2002), pelicans may have been forced to settle for dead prey with increasing frequency, a behavior perhaps more readily adopted by Brown Pelicans. Alternatively, pelican migration and use patterns may also result in differences in populations at risk for each species from botulism each year. These differences may be reflected in the apparent temporal shift in botulism outbreaks at the Sea. From 1996–1999, the peak in numbers of afflicted birds at the Sea occurred during August and September, regardless of the date of onset. In 2000–2001, outbreaks appear to have begun in May and June and reached a peak in July and August, a month or so earlier than they had in previous years. Brown Pelicans may have been the species at greatest risk for botulism intoxication during these past few years, as most White Pelicans tend to arrive at the Sea later in the season (USFWS, unpubl. data). Unfortunately, there are few data available to calculate populations at risk during botulism outbreaks for either species of pelican, and a number of unknown interacting factors may have been responsible for the trends observed. Currently the California Brown Pelican population remains stable (D. Anderson, pers. comm.), and losses from botulism to date have been insignificant in relation to the total population.

Fish have previously not been documented in the literature as a primary source of type C botulinum toxin for birds. However, the presence of type C toxin in freshly dead and sick tilapia is strong evidence that these fish are the source of toxin for fish-eating birds in the Salton Sea. Unfortunately, it is unknown how tilapia acquire the toxin. One possibility is that fish consume invertebrates or some other food source that contains pre-formed toxin. Laboratory studies have shown that tilapia are sensitive to type C botulinum toxin (Lalitha and Gopakumar 2001; T. Rocke, unpubl. data). Another possible explanation is that tilapia acquire toxin when botulinum spores in their gut germinate and the bacteria proliferate and produce botulinum toxin. Toxic infections such as this occur in animals that are stressed or otherwise compromised from disease or nutritional factors, and as a result, their intestinal environment becomes conducive for spore germination and anaerobic bacterial growth. These types of infections have been documented in human infants (Midura and Arnon 1979), horses (Swerczek 1980), and other animals (Minervin 1967). Bacterial and parasitic infections, high temperatures, and reduced oxygen levels are likely important stressors for tilapia in the Salton Sea (Kuperman and Matey 1999, Riedel et al. 2002; NWHC, unpubl. data). Studies are ongoing to evaluate the role of tilapia in the initiation of outbreaks in fish-eating birds. A greater understanding of the dynamics of this disease may help managers prevent another large outbreak from happening at the Salton Sea and will aid research and management in other parts of the continent where botulism occurs in fish-eating birds.

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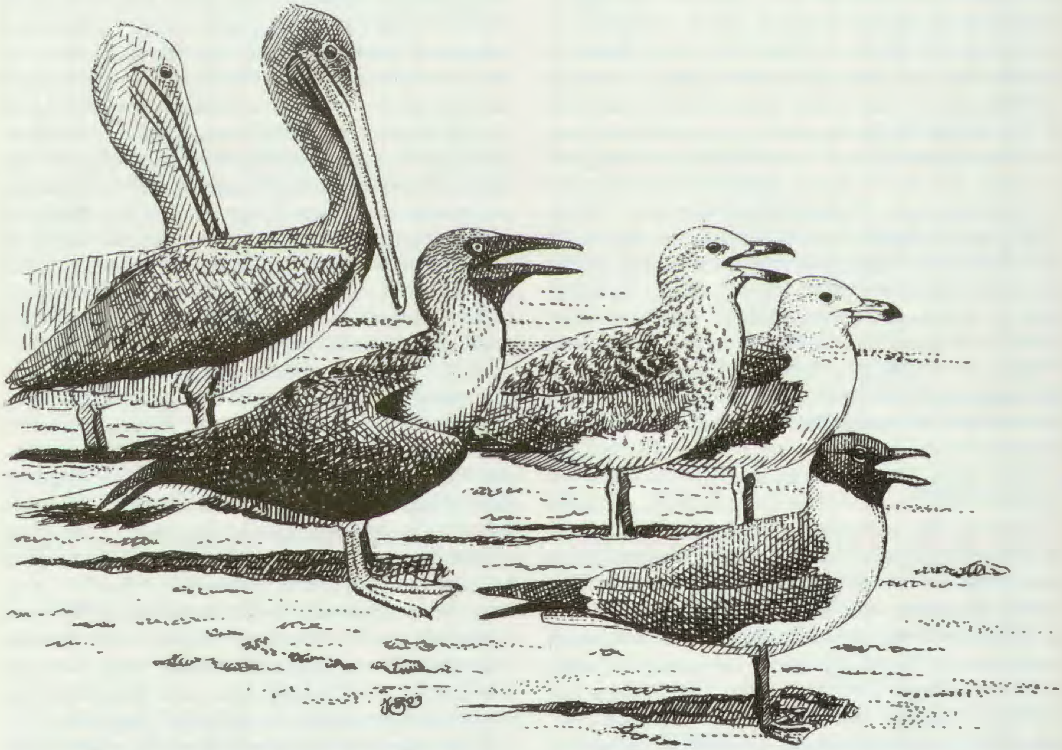

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INVESTIGATION OF A LARGE-SCALE EARED GREBE (*PODICEPS NIGRICOLLIS*) DIE-OFF AT THE SALTON SEA, CALIFORNIA, IN 1992

Carol U. Meteyer, Daniel J. Audet, Tonie E. Rocke, William Radke, Lynn H. Creekmore, and Ruth Duncan

Abstract. An estimated 150,000 Eared Grebes (*Podiceps nigricollis*) died at the Salton Sea between 16 December 1991 and 21 April 1992. This represented the largest documented mortality event of Eared Grebes at the time and approximately 6% of the North American population. During the die-off, grebes exhibited several uncharacteristic behaviors, such as congregating at freshwater tributaries, repeatedly gulping freshwater, preening excessively, moving onto land, and allowing close approach and/or capture. Avian cholera was diagnosed in Eared Grebes collected along the north and west shoreline of the Sea late in the die-off but not from the majority of the Eared Grebes dying along the south shore. Gross and histological examinations and diagnostic testing for viruses, bacteria, and parasites did not identify the cause of mortality in the majority of Eared Grebes examined from the south shore of the Sea. Liver concentrations of arsenic, chromium, DDE, mercury, selenium, and zinc were elevated in some Eared Grebes, but none of these contaminants exceeded known thresholds for independent lethality. Poisoning by heavy metals, organochlorine, organophosphorus, or carbamate pesticides, avian botulism, and salt were ruled out as the cause of mortality. Hypotheses for the die-off are interactive effects of contaminants, immunosuppression, a yet unidentified biotoxin or pathogen present in the Salton Sea, impairment of feather waterproofing leading to hypothermia, or a unique manifestation of avian cholera that evades laboratory detection.

Key Words: avian cholera; biotoxin; contaminant; Eared Grebe; mortality; *Podiceps nigricollis*; Salton Sea.

INVESTIGACIÓN SOBRE UNA MORTANDAD A GRAN ESCALA DEL ZAMBULLIDOR OREJUDO (*PODICEPS NIGRICOLLIS*) EN EL MAR SALTON, CALIFORNIA EN 1992

Resumen. Un estimado de 150,000 Zambullidores Orejudos (*Podiceps nigricollis*) murieron en el Mar Salton entre el 16 de Diciembre de 1991 y el 21 de Abril de 1992. Esto representó el evento de mortandad más grande que se haya documentado para el Zambullidor Orejudo en nuestro tiempo y aproximadamente 6% de la población de Norteamérica. Durante el evento los zambullidores exhibieron un comportamiento fuera de lo común, tal como congregarse en los tributarios de agua dulce, tomar agua dulce repetidamente, limpiarse excesivamente las plumas, moverse hacia tierra y permitir la proximidad e incluso la captura. Se les diagnosticó cólera aviar a los zambullidores colectados a lo largo de la playa norte y oeste del Mar Salton hacia el fin del evento pero no para la mayoría de los zambullidores que murieron a lo largo de la playa sur. Examenes brutos e histológicos y las pruebas para diagnosticar virus, bacterias y parásitos no identificaron la causa de la mortalidad en la mayoría de los zambullidores examinados provenientes de la playa sur del Mar Salton. Las concentraciones de Arsénico, Cromo, DDE, Mercurio, Selenio y Zinc en el hígado de los zambullidores fueron elevadas en algunos individuos, pero ninguno de esos contaminantes excedió los niveles conocidos como letales. El envenenamiento por metales pesados, organoclorados, organofosforados o pesticidas, botulismo aviar y la salinidad fueron descartados como la causa de la mortandad. Las hipótesis para explicar la mortandad fue que hubo una interacción entre el efecto de los contaminantes, inmunosupresión en las aves, una biotóxina o algún agente patógeno aun no identificado presente en el Mar Salton, el deterioro en la impermeabilidad de las plumas lo que llevó a hipotermia, o una manifestación singular de cólera aviar que no fue detectada por las pruebas de laboratorio.

Palabras claves: cólera aviar; biotoxina; contaminante; Mar Salton; mortandad; *Podiceps nigricollis*; Zambullidor Orejudo.

From December 1991 through April 1992, thousands of dead Eared Grebes (*Podiceps nigricollis*) accumulated along the shoreline of the Salton Sea, California. During this die-off, many grebes and fewer Ruddy Ducks (*Oxyura jamaicensis*) exhibited uncharacteristic behaviors, such as congregating in large numbers at fresh water tributaries, repeatedly gulping freshwater, preening excessively, and moving onto land allowing close approach and/or capture. Sick birds became increasingly lethargic and then died without evidence of paralysis or other neurologic impairment. The magnitude of the die-off attracted extensive media and scientific interest and much speculation as to cause.

The majority of North American Eared Grebes migrate through the Salton Sea area, numbering between the hundreds of thousands to over one million in several years (Jehl 1996, Jehl and McKernan 2002). The grebes arrive at Salton Sea after food supplies have become depleted at fall molting/staging areas such as Mono Lake and Great Salt Lake (Storer and Jehl 1985, Jehl 1988). Some overwinter at the Salton Sea (numbers vary greatly annually), whereas others continue south to winter in the Gulf of California, Mexico. The Salton Sea population of grebes normally reaches a peak during February when birds return from Mexico and congregate before departing in March or April for northern breeding grounds. Wintering grebes at Salton Sea consume vast quantities of aquatic invertebrates, primarily pileworms (*Nianthes succinea*), water boatmen (Corixidae), and amphipods (Jehl and McKernan 2002).

Mortality events of Eared Grebes along the Pacific Flyway have been previously documented in Gulf of California, Mexico (Nishikawa et al. 1984, Jehl et al. 2002), Great Salt Lake, Utah (Jensen and Cotter 1976), and Mono Lake and the Salton Sea, California (Jehl 1988, 1996). Although none were of the magnitude that occurred at Salton Sea during the winter of 1991–1992, beached-bird counts for a grebe die-off at Salton Sea from January to March 1989 were extrapolated to 39,600 grebes and may have been much higher (Jehl 1996). Most previous Eared Grebe die-offs involved <10,000 individuals. Jehl (1988) estimates an average mortality of Eared Grebes at Mono Lake at 1370 to 3628 birds/yr. Many die-offs were attributed to severe weather (Jehl and Bond 1983, Ryser 1985, Jehl 1988), avian cholera (National Wildlife Health Center (NWHC), unpubl. data), or food shortages (Jehl 1988, Jehl et al. 2002). Jensen and Cotter (1976) reported 5000 Eared Grebes died of bacterial infection (*Erysipelothrix rhusiopathiae*) in Great Salt Lake, Utah, in 1975. The causes for many mortality events involving grebes remain undiagnosed (Nishikawa et al. 1984, Jehl 1988) or were never investigated (Jehl 1996). This paper reports the size of the grebe die-off in 1991–1992 and the extensive investigation to determine the potential role of various disease agents, contaminants, or biotoxins.

METHODS

ESTIMATION OF NUMBER OF DEAD EARED GREBES

Biologists from the Salton Sea National Wildlife Refuge picked up Eared Grebes along 169 km of Salton Sea shoreline plus 40 km of shoreline associated with freshwater drains and wetlands adjacent to the Sea. Dead birds were collected between 16 December 1991 and 21 April 1992. Biologists felt this encompassed three peaks in mortality: the first began 16 December 1991, the second 19 January 1992, and the more major event that occurred 19 February through April 1992. However, low-level ongoing mortality may have also been occurring without detection during this time. Aerial and shoreline surveys documented that all beaches contained dead birds in approximate proportion to the number of live grebes concentrated offshore. While it was not possible to pick up carcasses from the entire area, carcasses were collected from complete surveys during February and March 1992 that covered 64 km (31%) of the most accessible shoreline (Fig. 1). An estimate of the total Eared Grebe mortality was then calculated by extrapolating the number of carcasses picked up in the area thoroughly surveyed to the total shoreline where the carcasses were documented. Carcasses were either saved for necropsy, frozen for later chemical analysis, or incinerated.

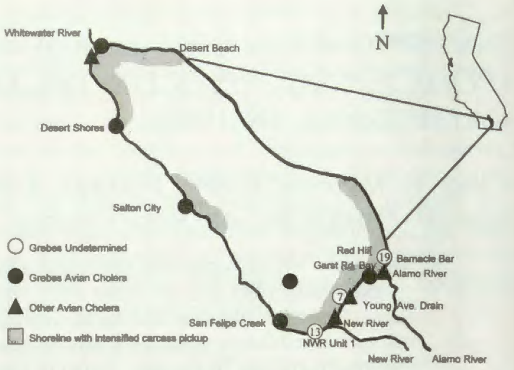

FIGURE 1. Distribution of birds collected and submitted to the National Wildlife Health Center during the 1992 Eared Grebe die-off at the Salton Sea, California. The numbers inside the symbols indicate the number of birds with that diagnosis submitted from that site.

DIAGNOSTIC EVALUATION

Gross examination

Fifty Eared Grebes, six Ruddy Ducks (*Oxyura jamaicensis*), two Herring Gulls (*Larus argentatus*), and single specimens of the American Widgeon (*Anas americana*), Ross's Goose (*Chen rossii*), Ring-billed Gull (*Larus delawarensis*), American Coot (*Fulica americana*), Short-billed Dowitcher (*Limnodromus griseus*), Western Sandpiper (*Calidris mauri*), and American White Pelican (*Pelecanus erythroryhnchos*) were shipped chilled to the NWHC. Within 48 hrs of collection, 23 carcasses were necropsied and 42 carcasses were frozen. Nineteen birds were euthanized; the others were found dead. Collection date and location were recorded as well as sex, age, physical condition, and body mass (four decapitated grebes were not weighed). Birds were categorized as immature if the gonads were undeveloped and thymus or bursa were detectable at necropsy. Birds classified as emaciated had no obvious subcutaneous, pericardial, or intra-abdominal fat; birds in poor to fair condition had trace body fat; birds in good body condition had moderate to abundant fat. Samples were collected for routine bacterial culture, virus isolation, histology, parasitology, and toxicology.

Histopathology

Twenty-four different tissues were sampled from 44 eared grebes (a total of 420 tissues), and fixed in 10% neutral buffered formalin. Tissues were processed as previously described (Meteyer et al. 1997). No histopathology was performed on other species.

Routine bacteriology

Samples of liver (63) and assorted tissues (24) were cultured for aerobic bacteria and salmonella (12) as previously described (Meteyer et al. 1997). Identity of bacterial isolates was determined using the API-20E system (bioMerieux Vitek, Inc, Hazelwood, MO). *Pasteurella multocida* isolates from seven Eared Grebes and five other species were sent to the National Veterinary Services Laboratories (NVSL) in Ames, Iowa, for serotyping (Rhoades et al. 1989) and DNA analysis (Wilson et al. 1992). The same 12 *P. multocida* isolates were sent to the National Animal Disease Center (NADC) to test for presence of dermonecrotizing toxin using a colony-blot assay described by Magyar and Rimler (1991) and Ackerman et al. (1994). The air sac from one American White Pelican was cultured for fungi using Sabauraud's dextrose agar (Remel, Lenexa, KS). Trachea and lungs from seven grebes were cultured for mycoplasma using culture and identification methods described by Goldberg et al. (1995).

Intensive P. multocida *assays*

In addition to routine culture on blood agar, culture attempts using *P. multocida* selective broth (PMSB) and agar (PMSA; Moore et al. 1994) were performed on heart (8), blood (12), intestine (13), brain (2), lung (8), liver (6) and trachea (3) collected from 26 grebes and frozen after necropsy. Extracts from these same frozen tissues were inoculated intraperitoneally into mice. Livers from mice that subsequently died (22) were cultured for aerobic bacteria and for *P. multocida* using PMSA, and isolates were identified as described above.

Tests for Clostridium botulinum *types C and E toxins*

Thirty-four grebes were tested for types C and E avian botulism. Several positive or suspect samples for type C toxin were further tested to determine if type C-1 or C-2 toxin was present. The tests were performed on centrifuged heart blood collected at necropsy or serum from blood collected prior to euthanasia using the mouse protection test (Quortrup and Sudheimer 1943) and antitoxins specific for *botulinum* neurotoxin types C-1, C-1 and C-2 combined, and E. The mice were observed for clinical signs for five to seven consecutive days.

Assay for cyanobacterial toxins

Liver samples from five grebes and the contents of gizzard and intestines from five more grebes were analyzed for cyanobacterial microcystin toxins using enzyme-linked immunosorbent assay (Chu et al. 1989 as modified in An and Charmichael 1994) and a protein phosphatase 2A inhibition assay (Lee 1992).

Virology

Virus isolation was attempted on 91 tissues from 33 grebes, two Ruddy Ducks, and one American Coot. Tissue homogenates were centrifuged and inoculated into duck embryo fibroblast cell culture or the allantoic cavity of 10-day-old chick embryos as previously described by Docherty and Slota (1988) and Senne (1989).

Parasitology

Standard parasitological procedures were used to examine the small intestine from ten grebes and one Short-billed Dowitcher, and the gizzard from two grebes. The mucosa and serosa of intestinal sections were examined grossly; the mucosa was scraped, and the scraped material was sedimented using a standard sedimentation glass. Wet mounts of the sediment were examined under a dissecting microscope. Sections of skin from the back, neck, and wing area of five grebes were also examined for parasites using a dissecting scope. In addition, feathers pulled from these skin sections were dissected, and the feather and feather sheaths were examined directly using a dissecting microscope. The remainder of the parasitological information was obtained from examination of histologic sections of intestinal tract, skin, adrenal glands, liver, and skeletal muscle.

TISSUE AND ENVIRONMENTAL TOXICOLOGY

Tests and methodology are summarized in Table 1. Briefly, liver was analyzed for lead, and brain was measured for cholinesterase (ChE) activity to assess potential exposure to organophosphate or carbamate. Brain was also analyzed for sodium to rule out the possibility of sodium poisoning in the highly saline Sea.

An additional 38 Eared Grebes (five dead, five dying, five healthy; nine recently dead from the north and nine from the south of Salton Sea; six reference Eared Grebes from Camp Pendleton Marine Corps Base, San Diego, CA) were collected by gunshot, euthanized by cervical dislocation, or picked-up within 24 hrs of death to analyze liver for contaminants and heavy metals; further diagnostic information was not collected from these grebes. Ten Ruddy Ducks co-mingling with Eared Grebes at the Salton Sea and showing clinical signs similar to the sick grebes, as described above, were subsequently found dead, and liver from these birds was also collected for analysis. In addition, liver samples from Eared Grebes were collected in 1993 from staging or stopover areas in the Great Basin region (Iron Mountain, Mono Lake, Snow Summit, Great Salt Lake) for similar contaminant analyses (Rattner and Jehl 1997) to provide further comparison to Eared Grebes sampled at the Salton Sea in 1992. After removal from carcasses, all liver samples were immediately frozen in 8-oz chemically clean jars and sent to USFWS's Patuxent Analytical Control Facility (PACF) in Laurel, Maryland, where they were analyzed for heavy metals and organochlorine compounds (Table 1).

Sediment sampling

On 27–28 February 1992, sediment samples were collected in chemically clean jars for organochlorine, heavy metal, and Microtox testing using a petit ponar dredge from areas where grebes were congregating. Surface water samples were also collected for Micro-

TABLE 1. ANALYTICAL TESTS AND METHODS CONDUCTED ON SAMPLES COLLECTED FROM THE SALTON SEA, CALIFORNIA

Test	Analytical technique	Material tested	Reference	Species tested
Sodium	Emission spectrometry	Brain	Windingstad et al. 1987	Grebe (6), Ruddy Duck (2)
Selenium arsenic	Graphite furnace atomic absorption	Sediment, liver, invertebrates	Krynitsky 1987	
Mercury	Cold vapor atomic absorption spectrophotometry	Sediment, liver, invertebrates	Monk 1961	
Lead	Atomic absorption spectrometry	Liver	Locke et al. 1991	Grebe (1), Herring Gull (1), Ruddy Duck (2)
Other metals	Inductively coupled plasma emission spectrometry	Sediment, liver, invertebrates	Haseltine et al. 1981	Grebe (1), Herring Gull (1), Ruddy Duck (2)
Organochlorine pesticides	Gas chromatography/mass spectrophotometry	Sediment, liver, invertebrates	Cromartie et al. 1975	
Organophosphate, carbamate	Gas chromatography	Invertebrates	Belisle and Swineford 1988	
Cholinesterase activity	Visible spectrometry	Brain	Hill and Fleming 1982	Grebe (11), Ruddy Duck (2)
Microbe toxicity (Microtox)	Microbe Model 500 Microtox Unit	Water	Microbics Corporation 1991	

tox testing in 50-ml polypropylene conical centrifuge tubes from three major inflows to the Sea from 27–28 February 1992 and 3–13 March 1992 to evaluate potential effects of local rain events. Water samples were centrifuged for 10 min in preparation for testing. Sediment samples were collected and immediately put on ice. Only sediments not in contact with the dredge surface were analyzed. Thirty samples of pileworms, amphipods, and corixids were collected with light traps or hand-held nets and composited by species into 10-g samples. These invertebrate samples represented food items of the birds and were analyzed for concentrations of metals, 17 organochlorines, 12 organophosphates and carbamates, and 40 additional agricultural pesticides.

A Microtox solid phase test was performed on sediment, and a 100% Microtox test was performed on undiluted water samples using a Microbics Model 500 Microtox (R) unit with procedures and EC50 calculations by Microbic Manual and Software, Microbics, Inc. (1991).

Statistics

Contaminant concentrations in tissues were compared between grebes collected from the north (SSN92) and south ends of the Sea (SSS92). These data sets were initially separated because previous results (Setmire et al. 1993) suggested substantial differences in baseline contaminant levels in sediment and aquatic life between these areas. The SSN92 and SSS92 data sets were also compared to data from Ruddy Ducks collected simultaneously at the Sea (RD92), pre-die-off data collected from Salton Sea grebes in 1989 (SS89; Setmire et al. 1993), and grebes collected from Camp Pendleton in 1992 (CP92). Geometric means were calculated for all data sets with <50% non-detect results; a value of one-half the detection limit was used in the calculation for non-detect values. The data were not normally distributed so non-parametric statistical tests were used. The Mann-Whitney test was used to determine when data sets could be combined for specific contaminants and to test between reference and Salton Sea data sets.

Contaminant concentrations were also compared between Eared Grebes collected at the Salton Sea and Camp Pendleton in 1992, and those collected at other stopover or staging locations in 1993 (Rattner and Jehl 1997). These samples were grouped by locations regardless of date of collection. Salton Sea birds were separated into two groups, those that were dead or clinically ill (symptomatic) and those that were apparently healthy (asymptomatic). The Kruskal-Wallis test was used to look for significant differences between groups. To identify pair-wise significant differences, an ANOVA was conducted followed by a Tukey multiple comparison test. Results were considered only if the results of the ANOVA agreed with the results of the Kruskal-Wallis test. All statistical tests were run on STATGRAPHICS Version 5.0 (Manugistics, Inc. 1994) and the P-value was set at <0.05/number of comparisons.

RESULTS

ESTIMATIONS OF MORTALITY IN EARED GREBES

A total of 46,040 dead birds were picked up over 64 km of shoreline. These represented 47 different species, including 42,587 Eared Grebes. By extrapolation to the 209 km of shoreline on which carcasses were deposited, we estimated that about 150,000 Eared Grebes died at the Salton Sea during the mortality event of 1991–1992.

DIAGNOSTIC EVALUATION

Necropsy findings

Necropsy findings were variable in the 50 Eared Grebes examined (25 female, 24 male, sex undetermined in one; nine immature, 41 adult). Wet and disheveled feathers were a common observation made by field biologists and present in 7/36 Eared Grebes submitted to the NWHC; all those were from the south end of the Sea without a diagnosed cause of death. Grebes varied in body condition: 19 were emaciated (mean 212 g, range 151–290 g); 12 were poor to fair (mean 265 g, range 230–320 g), and 19 were good (mean 321 g, range 230–450 g). The mean mass of Eared Grebes dying from avian cholera was 298 g versus 242 g for those dying from an undetermined cause. Gulls attacked weakened grebes, which appears to explain the bruising over the back of the head, neck, and shoulders seen in 17 Eared Grebes dying from both avian cholera and an undiagnosed cause. No external lesions were seen in 26 grebes. Urate material was seen on the feathers around the vent of 11 grebes but no significant changes were seen in the kidneys microscopically. Livers were swollen and congested in 21 grebes, one grebe had liver fracture with hemorrhage, and two grebes had livers with white spots (one was ultimately diagnosed with avian cholera). Lungs were congested and firm in 31 grebes; 13 of these sank in formalin, suggesting severe edema with possible hemorrhage. Spleens were enlarged and friable in four grebes. Of the ten bone marrows evaluated, three were very pale. The ventriculus of normal grebes contains a large, moist, loose feather pellet; in ten grebes from the Salton Sea, this feather pellet was very dry and compact, suggesting dehydration. Results from microscopic examination of tissues were inconsistent and inconclusive in the grebes that died without a diagnosis. Kupffer cells in the liver and phagocytic cells in the spleen contained structures that resembled red cell fragments in seven grebes and moderate hemosiderin was common in both organs (23 grebes). Small vacuoles were often seen in hepatocytes (32 grebes). All of these are nonspecific changes and their significance remains unknown. Eared Grebes (15) and other species (14) with *P. multocida* isolated had both gross and microscopic lesions consistent with avian cholera (Friend 1999), although the lesions were more subtle in the grebes.

Pulmonary edema was present in 18 grebes. Bacteria were seen in sections of lung in ten of these grebes and *P. multocida* was isolated from nine of them. Microscopic inflammation was seen in the skin of seven grebes, four of which had trauma (gull predation) noted at necropsy. Inflammation was not associated with mites seen in the keratin layer of five grebes. The four grebes with bacteria in the subcutaneous tissue died of avian cholera. Schistosomes were seen in the venous channels of adrenal glands from 15 of 28 grebes, often associated with amyloid. Although mild lymphocytic inflammation was seen along the adrenal periphery of four grebes, this inflammation did not seem directly associated with schistosomes or amyloid and the significance of the adrenal changes is unknown.

The American White Pelican was emaciated, had tan nodules in the lung and severe airsacculitis with sheets of fruiting fungal organisms consistent with aspergillosis.

Bacteriology

No bacteria were isolated from the liver of 27 of 48 Eared Grebes. *P. multocida* serotype 1, the causative agent of avian cholera, was isolated from 15 Eared Grebes, 14 grebes using standard culturing procedures. Of the 15 grebes with isolation of *P. multocida,* 13 were collected dead and nine were from the west or north shores of the Sea. Avian cholera usually kills quickly without chronic loss of mass, which is consistent with our findings. The mean mass of the grebes dying of avian cholera was 298 g whereas the mean mass of grebes without *P. multocida* isolated was 242 g. Analyses of 12 *P. multocida* isolates for unique DNA or potential dermonecrotizing toxin production was negative. The following additional bacteria were isolated from only 1–3 grebes and were not considered significant to the mortality: *Staphylococcus* spp., *Vibrio parahemolyticus, Vibrio alginolyticus, Aeromonas hydrophila, Escherichia coli, Pseudomonas putrifaciens, Pseudomonas* sp., *Enterococcus feacalis, Serratia marcescens, Proteus* sp., and *Hafnia alveii.*

Pasteurella multocida was isolated from liver by routine culture in 14 of 15 non-grebe species submitted. Of these, the only one without *P. multocida* was the American White Pelican, which had gross and microscopic lesions of severe aspergillosis in the lungs and air sacs from which *Aspergillus fumigatus* was isolated.

Intensive P. multocida *assays*

Culture attempts using selective media (PMSB and PMSA) did not yield additional iso-

TABLE 2. Preliminary Screen of Liver Concentrations (µg/g, Geometric Mean) from Composited Dead, Dying and Healthy Eared Grebes Collected from the Salton Sea, California, in 1992

	Arsenic	Cadmium	Chromium	Mercury	Nickel	Lead	Selenium	Zinc	p,p'-DDE
Dead (N = 5)	1.4	2.3	6.7	16	1.8	1.6	47	140	5.7
Dying (N = 5)	2.1	2.1	1.9	7.7	<0.64	<0.64	34	160	1.5
Healthy (N = 5)	0.26	1.9	1.7	14	0.8	<0.77	44	97	<0.019

Note: Concentrations are in dry mass for trace elements and wet mass for DDE.

lations of *P. multocida* from Eared Grebes. Of 49 tissues cultured from 26 grebes, *P. multocida* was only isolated from tissues of three grebes (lung, blood, and intestine), all of which had been previously confirmed by routine culture. Inoculation of mice was slightly more successful. One mouse inoculated with blood from a grebe without isolation of *P. multocida* died one day after inoculation, and *P. multocida* was isolated from the liver of this mouse.

Tests for Clostridium botulinum *type C and E toxin*

The test results from only 24 of 34 grebes blood samples tested for avian botulinum toxins could be interpreted. Of these, two samples were positive for botulism C-1 toxin but these were from grebes that were moderately autolyzed, and the presence of C-1 toxin likely represents postmortem toxin formation. The other ten samples were from grebes that died from avian cholera, and it was determined that the inoculated mice died from *P. multocida* infection that was subsequently isolated from their livers. No *Clostridium* toxin type C-2 or E was detected.

Virology

An enveloped RNA virus was isolated from the lung of one Eared Grebe and from the trachea of another using Muscovy duck embryo fibroblast cell culture. These viruses were not embryo-lethal and were not further characterized.

Mycoplasma *cultures*

A *Mycoplasma* sp. was isolated from the lung of one of seven grebes, but was untypable using conventional methods and was considered an incidental finding.

Parasitology

Cestodes were identified in the intestine of nine of ten grebes. *Acuaria* sp. was identified in both of the gizzards submitted for parasitologic examination. Demoglyphic quill mites (*Paralges* sp.) were found within the sheaths of new emerging contour feathers of the neck and/or wing of four of six grebes and in histologic sections of skin from four others. Mites were not associated with inflammation microscopically and they were not considered to be the cause of the excessive preening in the grebes. Lice (*Pseudomenopon insolens*) were seen in four grebes. The intestine of the Short-billed Dowitcher contained flukes (*Galactosomum* sp.), and nematodes (*Contracaecum* sp. and *Capillaria* sp.).

TISSUE AND ENVIRONMENTAL TOXICOLOGY

Tissue analysis

Lead was not detected in livers of birds tested. No inhibition of brain cholinesterase activity was detected in the 11 Eared Grebes and two Ruddy Ducks tested (median 17.4 ± 0.6 micromoles/min/g and 13.7 ± 0.2 micromoles/min/g respectively). Brain sodium levels in six Eared Grebes and two Ruddy Ducks were within the normal range with respective means of 1675 and 1295 ppm wet mass.

Concentrations of selected contaminants in livers from dead, dying, and apparently healthy grebes collected late February 2002 are presented in Table 2. These data were collected as a preliminary screen to determine if contaminants were potentially implicated in the cause of the die-off. Based on elevated levels of arsenic, chromium, mercury, selenium, and zinc (Ohlendorf et al. 1988; Eisler 2000a–e) in tissue samples, further sampling was justified. Although zinc levels in dead and dying birds were about two-fold higher than in healthy birds and the p,p'-DDE concentrations in liver suggested a trend of increase in DDE from healthy to sick to dead grebes, the concentrations were below lethal thresholds known for birds (Stickel et al. 1970, Blus 1996, Eisler 2000c).

The results of further analysis of Eared Grebes and Ruddy Ducks were not in the lethal range for any metal or contaminant (Table 3). There were no significant differences between results for the north and south 1992 Salton Sea Eared Grebes for arsenic, cadmium, chromium, mercury, selenium or zinc. There were no significant differences between the Salton Sea 1989 and Camp Pendelton 1992 reference sets for cadmium, mercury, or selenium, and there were no significant differences between these reference data and the results for cadmium, chromium, or mercury in birds dying at Salton Sea in

TABLE 3. Comparison of Geometric Mean (Range) of Liver Contaminant Concentrations (μg/g[a]) in Liver from Eared Grebes, Ruddy Ducks, and Food Items of Eared Grebes from the Salton Sea and Liver from Reference Eared Grebes Collected from Staging or Stopover Locations

Location	Species	Collection year	N	Arsenic	Cadmium	Chromium	Mercury	Selenium	Zinc	p,p'-DDE
North Salton Sea	Eared Grebe[b]	1992	9	1.0 (<0.29–37)	2.2 (1.3–12)	1.6 (<1.1–11)	6.1 (0.9–17)	27 (21–46)	150 (110–170)	
South Salton Sea	Eared Grebe[b]	1992	8	0.98 (<0.29–2.6)	2.5 (0.89–11)	1.3 (<0.59–6.1)	8.9 (4.2–15)	30 (17–53)	140 (74–170)	
Salton Sea	Eared Grebe[c,f]	1989	5	nd[d] (<0.1–0.1)	2.5 (1.4–6.7)	nd (<1–1)	5.1 (1.0–13)	13 (2.7–35)	97 (75.6–116)	
Camp Pendleton	Eared Grebe[c]	1992	4	nd (<0.295)	nd (<0.221–1.44)	nd (2.64–5.41)	3.15 (0.933–5.48)	7.01 (3.65–12.1)	64.3 (49.9–72.2)	0.0814 (0.0157–382)
Great Salt Lake	Eared Grebe[c,e]	1988	15	nd (<0.230–2.22)	1.20 (<0.327–3.20)	10.4 (3.08–48.6)	4.47 (0.757–9.34)	6.42 (2.61–11.0)	77.9 (53.8–124)	0.0192 (<0.01–0.100)
Iron Mountain	Eared Grebe[c,e]	1988	5	nd (<0.305)	1.31 (<0.783–3.81)	3.48 (1.30–7.29)	8.57 (5.80–11.3)	17.2 (12.3–21.3)	96.4 (61.6–140)	0.0460 (<0.01–0.296)
Mono Lake	Eared Grebe[c,e]	1988	18	0.376 (<0.187–958)	1.59 (0.778–4.36)	6.35 (2.14–18.7)	6.21 (1.50–17.5)	12.8 (6.42–35.7)	85.7 (53.0–198)	0.0211 (<0.01–0.263)
Snow Summit	Eared Grebe[c,e]	1988	3	nd (<0.302)	3.33 (2.53–4.09)	7.64 (6.33–9.15)	14.3 (11.8–17.2)	27.7 (20.5–35.7)	138 (111–190)	
Salton Sea	Eared Grebe[b]	1992	29	1.04 (<0.297–10.4)	1.63 (0.831–4.23)	10.7 (1.90–39.0)	7.27 (0.184–19.8)	29.0 (17.1–56.2)	133 (86.5–210)	0.0761 (<0.01–2.31)
Salton Sea	Eared Grebe[c]	1992	26	1.56 (<0.297–6.41)	1.44 (0.819–11.3)	7.77 (1.27–23.5)	7.57 (1.26–17.4)	22.9 (12.0–38.1)	137 (80.9–204)	0.0870 (<0.01–1.93)
Salton Sea	Ruddy Duck	1992	10	nd (<0.31–0.48)	0.91 (<0.36–2.0)	2.8 (<0.70–10)	0.22 (<0.08–1.0)	12 (9.2–24)	150 (100–230)	
Salton Sea	Water boatmen[f]	1988–1989	4	0.80 (0.30–2.0)		1.0 (<0.40–2.47)	nd (<0.10–0.12)	2.2 (1.4–3.3)	105 (90.4–121)	
Salton Sea	Water boatmen	1991–1992	14	0.49 (0.16–3.3)		nd (<2.5–7.5)	nd (<0.72)	2.9 (1.2–11)	127 (61–253)	0.028 (0.01–0.09)
Salton Sea	Pile-worms[f]	1988–1989	6	5.1 (2.9–22)		7.5 (1.7–27)	nd (<0.38)	3.1 (0.82–12.1)	58 (32–164)	
Salton Sea	Pile-worms	1991–1992	6	3.9 (1.9–5.1)		3.2 (2.6–5.9)	nd (<0.46)	6.6 (4.7–12)	85 (47–122)	0.13 (0.05–0.31)

[a] Concentrations are in dry mass for trace elements and wet mass for DDE.

[b] Symptomatic (sick/dead birds).

[c] Asymptomatic (healthy birds).

[d] nd = ≥50% of samples had non-detectable concentration.

[e] Data from Rattner and Jehl (1997).

[f] Data from Setmire et al. (1993).

1992. Selenium concentrations were significantly higher (Z = 1.9842, N = 27, P = 0.047) in grebe liver tissues collected during the die-off versus the reference data set, but were lower than selenium values in Ruddy Ducks collected earlier from the Salton Sea (Koranda et al. 1979, Setmire et al. 1990).

Zinc concentrations in the Eared Grebe liver tissues were significantly higher in Eared Grebes collected during the die-off in 1992 versus either reference or pre die-off results but were comparable to levels of selenium in normal Eared Grebes at various stages of their migration/staging (6.42–35.65 ug/g; Rattner and Jehl 1997). These levels are not in a range that would be considered toxic (Eisler 2000c).

Contaminant concentrations in grebes varied among additional samples from asymptomatic grebes in 1992 and from birds at staging (Mono Lake and Salton Sea, California) and stopover points (Iron Mountain and Snow Summit, California) in 1993 (Table 3). No significant differences were found among the various groups in cadmium and p,p′-DDE concentrations. Arsenic values were significantly different among groups in both the Kruskal-Wallis test ($H = 25.9$, $P < 0.001$) and ANOVA ($F = 3.88$, $P = 0.012$). In the pairwise comparison, the Mono Lake group had significantly lower arsenic concentrations than each of the Salton Sea groups. The other groups lacked adequate data for comparison.

Selenium concentrations also were significantly different among sample groups (Kruskal-Wallis test $H = 70$, $P < 0.001$; ANOVA $F = 27$, $P < 0.001$). Selenium values of the Camp Pendleton, Great Salt Lake, and Mono Lake samples were all significantly lower than those of the Snow Summit, Salton Sea symptomatic, and Salton Sea asymptomatic groups. Samples for Iron Mountain and the Salton Sea asymptomatic group were each significantly lower in selenium than that of the Salton Sea symptomatic group; however, there was no significant difference in selenium concentration between Salton Sea symptomatic group and Snow Summit samples.

Zinc concentrations also were significantly different among sample groups for both the Kruskal-Wallis test ($H = 53$, $P < 0.001$) and ANOVA ($F = 14$, $P < 0.001$). The Camp Pendleton, Great Salt Lake, and Mono Lake samples were significantly lower in zinc than those of the Salton Sea symptomatic and Salton Sea asymptomatic groups. However, there was no significant difference in zinc concentration between the Salton Sea and Snow Summit samples.

Microtox assays

Multiple repetitions of the 100% Microtox test for water were inconclusive with an indication of high nutrient input or low level toxicity (B. Walburn and M. Henry, pers. comm.) based on an increase in light output (enhancement) of the test bacteria for all locations. No EC50 could be determined with increased light output.

Sediment chemical analysis

The only organochlorine found above detection limits was p,p′-DDE with all values below 0.1 ug/g (dry mass). The highest concentration (0.098 ug/g), from the Alamo River outlet, was higher than that previously reported (0.064 ug/g) from the same location (Setmire et al. 1990). The median p,p′-DDE concentration (0.04 ug/g) was also higher than a previous calculated median (0.014 ug/g) for the Salton Sea reported in (Setmire et al. 1990).

Cadmium, molybdenum, tin, and beryllium were below detection limits for all locations. Concentrations of arsenic, barium, boron, chromium, copper, manganese, nickel, lead, vanadium, and zinc were all well within the baseline range for soils in the western United States (Shacklette and Boerngen 1984, Severson et al. 1987). Concentrations of arsenic, barium, chromium, copper, nickel, lead, selenium, vanadium, and zinc were lower than previously reported values for the Salton Sea (Setmire et al. 1990). Selenium concentrations from the Whitewater and Alamo river outlets were very similar to previous levels, whereas the New River outlet sample was well below previous levels (Setmire et al. 1990).

Aquatic invertebrate analysis

There were no differences in arsenic ($Z = 0.7882$, $P = 0.431$), selenium ($Z = -0.1214$, $P = 0.903$), or zinc ($Z = -1.173$, $P = 0.203$) between corixid samples collected in 1988–1989 and those in 1991–1992 collected during the Eared Grebe die-off. Similarly, there were no significant differences in the pileworm data sets for chromium ($Z = 1.1726$, $P = 0.241$), selenium ($Z = -1.8412$, $P = 0.066$), or zinc ($Z = 0.0001$, $P = 0.999$). However, sample sizes were small and somewhat variable in both cases, and mean values for pileworms and corixids collected during the 1992 die-off were higher than ones collected in 1989 (Table 3).

Organochlorine, p,p′-DDE, was found in trace amounts in all invertebrate samples ($N = 7$), and trace amounts of all parent and metabolite compounds of DDT were found in one pileworm sample collected at the Alamo River delta. No other organochlorine, organophosphate, or carbamate pesticide compounds were detected.

DISCUSSION

The estimated 150,000 Eared Grebes that died at the Salton Sea in 1992 represented about 6% of the North American population of approximately 2.5 million birds (Jehl 1996). We speculate that this mortality estimate is conservative. Low-level aerial surveys of the Salton Sea throughout the die-off documented many dead grebes floating at sea. Some of these carcasses would likely have become waterlogged and sunk before reaching the shoreline. Some carcasses that reached the shore were destroyed by wave action along the rocky shore and others were likely buried by sand or crushed barnacles. Predation and scavenging of sick and dead grebes was also widespread, with coyotes and gulls observed feeding on carcasses.

Gaps in the data make it difficult to estimate the percent of Eared Grebes that were killed by avian cholera or died from an undetermined cause. Biologists did not collect Eared Grebes from the north end of the Sea during the smaller die-offs in December 1991 and January 1992. When grebes were collected from the north and west shores of the Sea in March 1992 toward the end of the die-off, they were diagnosed with avian cholera. Although biologists felt that symptoms in grebes from the north were similar to those from the south and that the same undiagnosed syndrome was occurring throughout the Sea from December through April, data were unavailable to confirm this hypothesis. From the last week in February through April 1992 the cause of mortality in the majority of grebes (26/32) from the southern end of the Salton Sea continued to be undetermined even though other species picked up from similar southern and northern locations were positive for avian cholera (Fig. 1).

Large epornitics in waterbirds caused by *P. multocida* have been summarized by Friend (1999). For example, during an avian cholera die-off in Chesapeake Bay 31,295 carcasses were picked up. The carcasses were estimated to represent 10–80% of actual mortality and consisted primarily of Long-tailed Ducks (*Clangula hyemalis*), but also included Horned Grebes (*Podiceps auritus*; Montgomery et al. 1979). An estimated 32,000 from a population of 150,000 Eared Grebes died from avian cholera at the Great Salt Lake in 1998 (NWHC, unpubl. data). Most avian cholera mortality events, including the grebe die-offs at both the Salton Sea in 1992 and Great Salt Lake in 1998, are due to *Pasteurella multocida* serotype 1 (Wilson et al. 1995). A notable difference in the Chesapeake Bay event was the isolation of *P. multocida* serotype 3 as the cause of mortality, which is unusual in waterfowl.

Avian cholera was not the cause of all Eared Grebe mortality at the Salton Sea in 1992, and, despite the use of selective and enrichment media and mouse bioassays, *P. multocida* was not isolated from 35 grebes collected at the south end. Furthermore, the isolates of *P. multocida* from this event were not serotypically or genetically unique (all were serotype 1), and assays for dermonecrotoxins, produced by some of the other pathogenic serotypes of *P. multocida,* were not detected, suggesting that the *P. multocida* isolates were not uniquely pathogenic. For 35 birds, no cause of death could be determined.

Salt toxicosis was considered a potential cause of the illness because grebes were congregating and appeared to be drinking at the freshwater inflows. Brain sodium levels, however, did not confirm toxicity. Furthermore, Eared Grebes have been found to tolerate high salinity levels at Mono Lake, California (Mahoney and Jehl 1985), as well as salinity as high as 160,000 mg/L at Great Salt Lake, Utah (Jehl 1988), which is four times greater than the salinity of the Salton Sea during the 1992 mortality.

Concentrations of selenium and zinc were significantly higher in livers of dead grebes from 1992 than in healthy grebes collected along the California coast, but water, sediment, and invertebrate samples from the Salton Sea did not have significant concentrations of either of these inorganic constituents, suggesting no biological pathway for exposure at the Sea. Ohlendorf et al. (1988) and Ohlendorf and Marois (1990) found Eared Grebes had the greatest level of selenium bioaccumulation compared to many other waterbirds. Rattner and Jehl (1997) found higher selenium concentrations in livers from normal Eared Grebes collected at Mono Lake compared to Salton Sea, and selenium levels from grebes at Snow Summit were nearly as high as those of grebes that died at the Salton Sea.

Even though the liver concentrations of zinc in dead grebes from the Salton Sea were among the highest reported for grebes (J. Skorupa, pers. comm.), zinc dietary concentrations were within acceptable ranges and below any known mortality threshold (>2000 mg/kg) for birds (Gasaway and Buss 1972, Eisler 2000c), and liver levels were elevated but below the toxic range for domestic poultry (200–700 ppm; Puls 1988). Eisler (2000c) suggested that zinc concentrations in field-collected samples are highly variable and difficult to interpret as interactions of zinc with many chemicals (including cadmium, chromium, mercury, and selenium) may alter patterns of accumulation, metabolism, and toxicity. Rattner and Jehl (1997) showed that the body condition of Eared Grebes can greatly influence the size of the liver; birds in poor body condition have higher concentrations of some elements due to liver atrophy. Body condition can fluctuate dramatically in Eared Grebes as part of their normal annual cycle (Jehl 1997). More severe reduction in body condition can occur as a result of decreased food supply (Jehl et al. 2002) or illness. Many of the grebes that were necropsied were emaciated with associated liver atrophy, which might have increased the concentrations of zinc and other elements in this study. Even so, levels of these elements were not in the range known to be toxic. Interestingly, Morris et al. (1986) and Hudson et al. (1984) reported excessive drinking in birds as a sign of zinc toxicosis, and some of the pathology in the Eared Grebes, such as red cell fragments and hemosiderin in the spleen and liver have also been reported in zinc toxicosis (Droual et al. 1991).

The liver p,p′-DDE levels found in the initial screen of grebe tissue had an ascending trend from healthy to sick to dead birds. However, levels found in dead grebes were well below any toxic thresholds for DDE (Stickel et al. 1970, Ohlendorf and Miller 1984, Blus 1996). Median concentrations of arsenic, chromium, and mercury in grebe livers were not at levels known to cause independent lethality (Eisler 2000a,b,d).

The Salton Sea is a nutrient-rich body of water receiving extensive agricultural fertilizers from the Imperial and Coachella valleys and waste inflows from Mexico entering through the New River. These high nutrient loads in association with warm temperatures promote algal blooms with the potential to produce associated biotoxins. Analysis for cyanobacterial toxins in livers and upper gastrointestinal contents of grebes were difficult to interpret because of a lack of clinical and lethal threshold concentrations for microcystins in wild birds. Biotoxins associated with algal blooms in a saline sink such as the Salton Sea are not well documented. Prior to and in the early stages of the mortality event, the Salton Sea area received an abnormally high amount of rain. However, without proper water sampling prior to, during, and following major rain events, pulses of nutrients or other contaminants that might be associated with heavy rains cannot be estimated.

It is interesting to note that the outflow of the New River, which flows north from Mexico, is at the south end of the Salton Sea where the undiagnosed grebe mortality occurred. During a 1963 die-off at a sewage lagoon in Canada (Nero 1968), four species of grebes became wet shortly after landing, presumably from contact with waste detergents, and spent almost all of their time on shore preening. This description of loss of water-proofing and obsessive preening is very similar to the activity seen in grebes at the Salton Sea. Loss of water-proofing can compromise buoyancy and lead to hypothermia (Nero 1968). Obsessive preening and loss of buoyancy might interfere with the grebes' ability to acquire adequate food. Water intake for Eared Grebes is usually via water content in prey (J. Jehl, pers. comm.), and inadequate food consumption could lead to dehydration as well as poor body condition. Unfortunately, deaths associated with hypothermia, poor nutrition, and dehydration are difficult to definitively diagnose, although Eared Grebes that were killed by avian cholera during this die-off (usually a very short clinical course before death) had an average mass of 298 g while the average mass Eared Grebes that died from an undetermined cause was only 242 g.

In summary, avian cholera killed numerous grebes and other waterbirds at Salton Sea in 1992, particularly at the northern end of the Sea, but did not appear to be involved in the death of the majority of the Eared Grebes from the southern end of the Sea. Contaminant concentrations in the livers of Eared Grebes (Tables 2, 3) were below acute mortality (Ohlendorf and Miller 1984; Eisler 2000a–e). Selenium levels measured in Salton Sea grebes were in the range reported to potentially cause reproductive problems (Heinz et al. 1988, 1989; Ohlendorf et al. 1988, 1989; Ohlendorf and Marois 1990) but not mortality (Eisler 2000e). Tests for avian botulism, salmonella, viral infections, and salt toxicosis were also negative. Potential causes of the undiagnosed mortality may have been related to interactive effects of an as yet unidentified biotoxin, contaminants, or contaminant-related immunosuppression (Fairbrother and Fowles 1990, Whiteley and Yuill 1991) that might make the grebes vulnerable to a pathogen at concentrations below detection, a difficult to isolate manifestation of avian cholera, or hypothermia and poor nutrition as a consequence of loss of feather waterproofing. Studies at the Salton Sea continue and have expanded to include investigations of the role of microbial toxins and factors that could lead to hypothermia as potential causes for the die-offs. Until one or more specific etiologies are identified, it is difficult to devise methods to reduce losses in grebes. Although smaller die-offs of Eared Grebes are not unusual in winter, a die-off of the magnitude seen in 1992 has not recurred.

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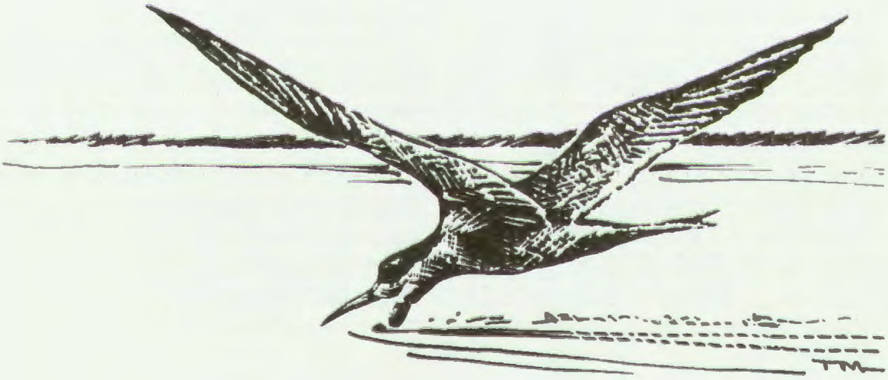

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THE SALTON SEA: A CONSERVATION CONUNDRUM OR PARADIGM FOR SUCCESS?

W. DAVID SHUFORD AND KATHY C. MOLINA

Abstract. Despite current broad support for improving the ecological health of the Salton Sea, the outcome of proposed plans, if adopted, is uncertain. History tells us that the depth of scientific knowledge of an area is not necessarily an accurate predictor of the success of conservation efforts. While the opportunity is ripe for adaptive management to ensure healthy bird and fish populations at the Salton Sea, many challenges must be met to accommodate various, perhaps mutually exclusive, restoration objectives, including providing water of sufficient quality in an arid state with a large and rapidly expanding human population, maintaining the Sea as a repository for agricultural and urban wastewater, controlling salinity, reducing eutrophication, and enhancing recreation and economic opportunities. It will be particularly difficult to return the ecosystem to a self-maintaining state, as intensive long-term management appears to be necessary. Salton Sea restoration should be part of a binational effort to restore lost and degraded wetland, riparian, and terrestrial habitats throughout the entire Colorado River Delta region. For effective management, scientific advancement at the Salton Sea must be coupled with bridging the social and natural sciences via scientific engagement in the political and regulatory processes. Long-term and broadscale conservation of waterbird populations in western North America must involve training of scientists in landscape-level thinking and the ability to apply political solutions and management knowledge to real world problems. Such efforts will be enhanced by addressing the root problems of our environmental crisis—overpopulation and overconsumption. Major paradigm shifts are needed in the scientific community's willingness to directly engage in societal problem solving and in the public's appreciation for intact natural ecosystems as well as highly managed ones that provide alternative habitat for wildlife.

Key Words: adaptive management; connectivity; conservation training; paradigm shift; self-maintaining processes; societal engagement.

EL MAR SALTON: ¿ENIGMA DE CONSERVACIÓN O PARADIGMA DEL ÉXITO?

Resumen. A pesar del amplio apoyo actual en favor de mejorar la salud ecológica del Mar Salton, es incierto el resultado que tendrán los planes propuestos si éstos se adoptan. La historia nos dice que la profundidad del conocimiento científico de un área no permite necesariamente predecir acertadamente el éxito de los esfuerzos de conservación. A pesar de que existe una buena oportunidad para un manejo adaptativo que asegure la presencia de poblaciones saludables de aves y peces en el Mar Salton, deben superarse muchos desafíos que implican consensuar múltiples objetivos de restauración, tal vez mutuamente excluyentes. Éstos incluyen la provisión de agua de buena calidad en un estado árido con una gran y creciente población humana, el mantenimiento del mar como un sumidero de agua de desecho de las actividades urbanas y de la agricultura, el control de la salinidad, la reducción de la eutrofización y la mejora de las oportunidades económicas y de recreación. Será particularmente difícil retornar el ecosistema a un estado de auto-mantenimiento, dado que parece necesario desarrollar un intenso plan de manejo a largo plazo. La restauración del Mar Salton debería ser parte de un esfuerzo binacional para restaurar los humedales, las áreas riparias y los ambientes terrestres perdidos y degradados en toda la región del delta del Río Colorado. Para un manejo eficiente, el progreso científico en el Mar Salton debe combinarse con la interacción de las ciencias sociales y naturales a través de la participación científica en los procesos políticos y regulatorios. La conservación a largo plazo y en gran escala de las poblaciones de aves acuáticas en el oeste de América del Norte debe involucrar el entrenamiento de los científicos en pensar a nivel de paisaje y en la habilidad de aplicar soluciones políticas y conocimientos de manejo a los problemas del mundo real. Estos esfuerzos se verán beneficiados si se refieren a los problemas de raíz de nuestra crisis ambiental: sobrepoblación y consumo desmedido. Se necesitan cambios importantes de paradigma en la predisposición de la comunidad científica a involucrarse directamente en resolver problemas sociales y en el aprecio público por ecosistemas naturales intactos y sistemas manejados que provean ambientes alternativos para la vida silvestre.

Palabras clave: cambio de paradigma; compromiso social; conectividad; entrenamiento en conservación; manejo adaptativo; procesos de auto-mantenimiento.

Within the Colorado River Delta region (Figure 1 in Patten and McCaskie *this volume*) there has been extensive loss and degradation of wetland, riparian, and terrestrial habitat on both sides of the U.S.-Mexico border, particularly in the Salton Sink (Patten et al. 2003) and the Delta itself (Anderson et al. 2003, Cohen et al. 2003). This diminishment of wetland and riparian habitat stems mainly from water diversions and development to meet the agricultural and urban needs of ongoing human population expansion in the southwestern United States, northwestern Mexico, and the coastal plain of southern California (Cohen et al. 2003). Overallocation of water has left remaining wetland and riparian habitats in the lower Colorado River region dependent on wastewater returns or irregular releases of floodwaters that exceed upstream diversion capacities. Beyond inadequate water supplies and direct habitat destruction, known and potential threats to the region's birds and habitats include salinization, eutrophication, contamination, introductions of exotic plants and animals, elevated occurrence of diseases, and human disturbance (Anderson et al. 2003, Cohen et al. 2003, Mora et al. 2003, Rocke and Friend 2003). Because the water supply and threats to wildlife transcend international borders, there is a recognized need for binational management and conservation planning to restore wildlife habitat in the Colorado River Delta region (Anderson et al. 2003, Cohen et al. 2003). Although to date such binational cooperation has been limited, the opportunities for it are great, and some progress is being made at the local and regional level on both sides of the border.

A series of events in the 1990s, including large-scale bird die-offs that aroused extensive media attention coupled with the death of a congressman championing environmental cleanup and economic development, catalyzed renewed interest in restoration of the Salton Sea (Garrett et al. *this volume,* Molina and Shuford *this volume*). Regardless of whether people considered the Salton Sea a natural ecosystem or an artificial one maintained by agricultural wastewater (Patten and Smith-Patten *this volume*) but serving as *de facto* mitigation for extensive wetland loss and degradation in the region, there soon developed widespread support for managing this ecosystem to counteract increasing salinity, eutrophication, large-scale bird die-offs from diseases and unknown causes, and potential risks from contaminants of agricultural and urban runoff (Tetra Tech 2000). The blueprint for successful management, however, is still being developed. Because of the massive scale of proposed projects and competing restoration goals, it remains unclear if efforts at the Salton Sea will serve as a model for successful restoration throughout the Colorado River Delta region or whether because of the ecological and political complexities it will remain an unsolvable conservation conundrum.

HISTORICAL PERSPECTIVE

Historically, there was limited knowledge of the status of birds at the Salton Sea (Patten et al. 2003, Garrett et al. *this volume*). Jehl (1994) concluded from a review of avifaunal changes at eight saline or alkaline lakes in western North America, including the Salton Sea, that scanty historical records precluded detailed analyses of faunal changes, and even if data existed they would be poor indices of changes at the population or species level. In California, it is clear that historical efforts to document the status of the state's avifauna by Grinnell and others did not focus on large inland lakes. Of the various avifaunal monographs produced in the first half of the 20th century (e.g., Tyler 1913, Grinnell 1923) none dealt specifically with the waterbird fauna of any of the state's large inland lakes, such as Lower Klamath Lake, Tule Lake, Goose Lake, Honey Lake, Eagle Lake, Lake Tahoe, Mono Lake, Owens Lake, Tulare Lake, or the Salton Sea. For the sites most severely degraded—Tulare Lake and Owens Lake—we do not even really know what was lost. Of those that remain, the avifauna of many is still either poorly known or poorly documented in the literature. Given the wide variation in the extent of degradation of California's large lakes, history suggests that prior scientific knowledge alone is not a good measure of the likelihood of conservation success, as societal or political realities may trump faunal or ecological understanding.

OPPORTUNITIES AND CHALLENGES AT THE SALTON SEA

Unlike many contentious environmental issues, there currently is a broad consensus for the need to improve the health and sustainability of the Salton Sea ecosystem on behalf of its bird populations while enhancing opportunities for human recreation and economic development. The challenge, given the great loss of historic wetlands in California and adjacent Mexico, is to manage habitats such as the Salton Sea that rely on wastewater so in the long term they can sustain avian populations and diversity. Although many important ecological questions will remain unanswerable in the short term, particularly the ecosystem-level remedies for disease events and transmission, the quest for sustainability must rely on action rather than waiting for research to solve problems (Cairns 1999). Key problems at the Salton Sea are caused by increasing salinity—from upstream diversions of the Colorado River, agricultural use in the Imperial Valley, and, particularly, by evaporation in the Sea itself—and by eutrophication from inflows of nutrients from agricultural and urban sources (Tetra Tech 2000, Holdren and Montaño 2002, Schroeder et al. 2002). Although the role of increasing salinity and eutrophication in large-scale bird die-offs at the Salton Sea are unknown, the recent drastic increase in bird mortality there appears to reflect an ecosystem in severe stress (Rocke and Friend 2003). Current initiatives to transfer water from the Imperial Valley to meet increasing demands in urban centers throughout southern California, if realized, will lessen the inflow of fresh water to the Sea, thereby exacerbating the difficulties of reducing its salinity (CH2M HILL 2002). Reduction of salinity will likely require innovative technological and engineering solutions at the Sea and the continued importation of fresh water. Providing additional water of sufficient quality to the Salton Sea will be especially challenging in a state with a large and rapidly expanding human population and a federal mandate to reduce its reliance on Colorado River water. Severe impacts on bird reproduction from concentrations of selenium and heavy metals from agricultural drain waters at Kesterson National Wildlife Refuge and agricultural evaporation ponds in the San Joaquin Valley (Skorupa and Ohlendorf 1991) provide cautionary tales of the difficulties of dealing with imported and degraded water in enclosed water systems in arid regions with high evaporation rates. Although contaminants are not known to have caused large-scale reproductive harm to birds nesting at the Salton Sea, potential impacts should be monitored periodically, given that DDE, selenium, and boron occur in levels of concern in birds foraging in the Salton Sea and the Imperial Valley (Setmire et al. 1993). Such monitoring should be conducted on a regional scale encompassing the entire Colorado River Delta ecosystem (Mora et al. 2003).

The Salton Sea's setting—alternately stark, seasonally very harsh, at times odiferous, and far from a large conservation constituency—is an additional impediment to be overcome to increase public support for restoration. Although efforts to increase recreation at the Salton Sea should provide economic benefits and broaden support for restoration, advanced planning is needed to avoid increased human disturbance at isolated river mouths and other sites where large numbers of birds or sensitive species concentrate (Shuford et al. 2000, 2002b).

One of the desirable attributes of an ecosystem is the ability to maintain natural processes, such as succession, energy flow, and nutrient cycling, without constant management intervention (Cairns 1999). Proposed alternatives to maintain or reduce the salinity of the Salton Sea currently all call for large engineering projects and intensive long-term management (Tetra Tech 2000). It is likely that a self-maintaining system at the Salton Sea will not be possible unless salinities are allowed to increase to the point where the food chain will be devoid of fish and dominated by brine shrimp (*Artemia* spp.) and brine flies (*Ephydra* spp.). Although such a system might not serve the highest biological diversity, it might in the long term be the only viable alternative given ecological, financial, and political constraints.

CONSERVATION SUCCESS STORIES

Mono Lake serves as a conservation success story (Hart 1996), yet knowledge of its avifauna was poor when activists began to raise consciousness about its plight. Expansion of scientific knowledge closely paralleled increasing activism, contention, and education about the lake's important wildlife and aesthetic values; the latter proved crucial in building broad public support. From a scientific standpoint, the recipe for success at a single site involves a combination of ongoing data collection, analysis, and publication, a willingness to work with conservation groups, and the dedication to engage in political, judicial, and regulatory processes.

At the Salton Sea, science has begun to make great strides via funding of reconnaissance studies and research and monitoring of disease events, and by providing a strong voice in the Salton Sea Restoration Project via the Salton Sea Science Office. It remains to be seen, though, whether scientists will engage extensively over the long haul in all crucial steps in the process.

CONNECTIVITY AND LONG-TERM SUCCESS

There is an increasing understanding of the need to conserve the extensive and often disjunct wetland systems upon which waterbirds depend, wetlands that may span extensive areas of one or more continents (Haig et al. 1998). Protection of Eared Grebes (*Podiceps nigricollis*) at one site, such as Mono Lake, will not suffice if tens of thousands die at the Salton Sea or elsewhere. Consequently, we need to understand the suite of sites needed, linkages among sites, and the ecology of individual sites. This is particularly so in the arid West where fluctuating climate conditions can shrink or expand wetlands in short time frames. Survey efforts will have to encompass the entire range of key sites, as declines or increases at particular sites may just reflect geographic shifts of relatively stable populations (e.g., interior Snowy Plovers, *Charadrius alexandrinus*; Page et al. 1991). Similarly, ecological processes that sustain populations may vary greatly among sites.

In the long run, landscape-level thinking will have to be supported by both landscape-level training and active engagement in conservation issues. Noss (1996, 1997) bemoaned both the loss of naturalists and the failure of universities to produce conservation biologists. These problems stem from increasing scientific reliance on computers and statistics, at the expense of extensive field knowledge, and on insistence in training in academic paradigms when what may be needed is the ability to apply political solutions and management knowledge to real world problems. Our point is that even if we are willing to get into the trenches in conservation battles we may be ill-equipped for success. Cairns (1999) discussed the importance of the coming together of the social and natural sciences despite the often bitter fragmentations of human society and isolation of disciplines in educational institutions. While this may sound utopian, he emphasized that visions of a better future can be very powerful and produce major paradigm shifts. Likewise, further education is needed to increase the public's appreciation both for intact natural ecosystems and highly managed ones that provide alternative habitat for wildlife.

Another key avenue for scientists to enhance chances for long-term conservation success is to speak out on the root problems of our environmental crisis—overpopulation and overconsumption. Some leading scientists are outspoken in this arena (e.g., Ehrlich and Ehrlich 1990), whereas many others, surely very aware of the problems, are silent. To speak out one must be willing to take the heat. For example, the lead author of a poster on the relation of population growth to the possibility of Salton Sea restoration, presented at another recent symposium, was quickly labeled a racist for bringing up the issue of immigration. Scientists need to define the biological basis for solutions even if at first these prove unpopular.

CONCLUSIONS

Whether the Salton Sea proves to be an intractable environmental issue because of greater value placed on other human needs or desires, or a model for conservation success will depend in part upon whether scientists continue to add needed knowledge via research and, just as importantly, engage environmentalists, bureaucrats, managers, politicians, and the public in devising creative solutions to improving the ecosystem's health. A failure to do so will not bode well for the long-term conservation of waterbird communities in western North America. Decades ago, Linsdale (1930) noted the passive approach of ornithologists to bird conservation in California. Will we scientists sit by and chronicle the demise of the bird life of the vast and highly-productive ecosystems of the Salton Sea region without actively promoting conservation efforts? We hope not.

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