

DISTRIBUTION AND ABUNDANCE OF COLONIAL HERONS AND EGRETS IN CALIFORNIA, 2009–2012^a

W. DAVID SHUFORD, Point Blue Conservation Science, 3820 Cypress Dr., #11, Petaluma, California 94954; dshuford-RA@pointblue.org (current address: 1040 Helen Ct., Petaluma, California 94954)

JOHN P. KELLY (current address: 1424 Santa Fe Drive, Encinitas, California 92024) and T. EMIKO CONDESO, Audubon Canyon Ranch, Cypress Grove Research Center, P. O. Box 808, Marshall, California 94940

DANIEL S. COOPER, Cooper Ecological Monitoring, Inc., 255 Satinwood Ave., Oak Park, California 91377

KATHY C. MOLINA, Section of Ornithology, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007

DENNIS JONGSOMJIT, Point Blue Conservation Science, 3820 Cypress Dr., #11, Petaluma, California 94954

ABSTRACT: As part of an 11-state inventory in the western United States organized by the U.S. Fish and Wildlife Service, we coordinated censuses of 15 species of breeding colonial waterbirds throughout California from 2009 to 2012. Here we describe the status of the five widespread species of colonial ardeids in California during that period, combining the results of surveys from the air, boats, and ground. Statewide, we estimate 5517 pairs of the Great Blue Heron (*Ardea herodias*) nesting at 399 sites, 7973 pairs of the Great Egret (*Ardea alba*) at 182 sites, 1888 pairs of the Snowy Egret (*Egretta thula*) at 79 sites, 2678 pairs of the Cattle Egret (*Bubulcus ibis*) at 20 sites, and 2443 pairs of the Black-crowned Night-Heron (*Nycticorax nycticorax*) at 104 sites. For four of these species, the numbers of colonies and breeding pairs were highest near the coast and in the Central Valley, much lower in the Great Basin, Cascade Ranges, Sierra Nevada, and southern deserts. By contrast, about two-thirds of the statewide total of nesting pairs of the Cattle Egret was in the Imperial Valley. The Central Valley was particularly important to the two most numerous species, holding about three-quarters and one half of the state's nesting pairs of the Great Egret and Great Blue Heron, respectively. The survey period coincided with drought, which greatly reduced potential foraging habitat in many regions and may have restricted herons' distribution and depressed their abundance. In the lack of broad-scale surveys during a wet climatic period, no quantification of the effect of drought on herons is possible, though such data are available for other colonial waterbird species. Although the populations of the five herons appear to be stable or increasing, considerable uncertainty in the magnitude and direction of trends remains because of substantial year-to-year variation in numbers of nests and a lack of a robust broad-scale monitoring program suited to these species. Plans for long-term monitoring of ardeids and other colonial waterbirds must account for the large fluctuations in their distribution and abundance over short-term cycles of drought and flood, and factor in the expectation of greater environmental fluctuations with continuing climate change.

Initiatives to promote the conservation of waterbirds throughout North America recognize the importance of inventorying and monitoring. Such work is crucial for determining conservation status, detecting population

^aAppendices 1 and 2 and Tables S1–S5 are available at archive.westernfieldornithologists.org/archive/V51/Shuford-et-al-herons.

trends, assessing habitat health, and evaluating whether management and environmental change are affecting waterbirds (Kushlan et al. 2002). To help fulfill this need, from 2009 to 2012 the U.S. Fish and Wildlife Service coordinated the Western Colonial Waterbird Survey, a broad-scale inventory of 19 species of colonial waterbirds in 11 western states (www.fws.gov/mountain-prairie/migbirds/species/birds/western_colonial/index.html). Goals were to document the species composition, size, and location of colonies; estimate minimum regional population sizes for each breeding species; produce an atlas of colonies; and establish a baseline for development of a long-term monitoring program for colonial waterbirds in the West. To date, a lack of adequate data on population sizes and trends of waterbirds has hampered efforts to set population and habitat goals for conservation of these birds in California (Shuford 2014b, Shuford and Dybala 2017).

To ensure adequate coverage of the vast expanse of the West, regional experts organized and implemented the surveys at the state level. In California, Point Blue Conservation Science coordinated surveys of 15 primary species of colonial waterbirds with the extensive aid of many collaborating organizations and individuals (Shuford 2014a). Results of those surveys, with comparisons to prior surveys in the late 1990s, have been published for three tern species and two gull species (Shuford et al. 2016, Doster and Shuford 2018). Here we report on the distribution, number of colonies, and estimated number of pairs nesting in California from 2009 to 2012 for five species of colonial ardeids: the Great Blue Heron (*Ardea herodias*), Great Egret (*Ardea alba*), Snowy Egret (*Egretta thula*), Cattle Egret (*Bubulcus ibis*), and Black-crowned Night-Heron (*Nycticorax nycticorax*). Early assessments of herons' status in California were based on anecdotal information, and more recent efforts to quantify the abundance of the state's nesting ardeids have substantial limitations (Belluomini 1978, Schlorff 1982). Nevertheless, we compare the 2009–2012 results to these prior assessments and other broad-scale and regional surveys or monitoring programs extending over multiple years and interpret results on the basis of environmental conditions during the 2009–2012 survey period. We discuss current and future threats to colonial waterbirds in California, and outline how the recent surveys can aid in development of a strategy for monitoring colonial waterbirds throughout the western United States.

STUDY AREA AND METHODS

Background and Overall Approach

In organizing statewide surveys, we based the timing and extent of field work on a combination of extensive information gathered on the locations of historical and recent colonies, broad-scale knowledge of wetlands and other potential foraging and nesting habitats from extensive surveys of migrant and breeding shorebirds and waterbirds across much of California since the 1980s (e.g., Shuford et al. 1998, 2006, 2007, Molina and Sturm 2004, Kelly et al. 2006, Shuford 2010), discussions with a broad network of collaborators developed over the years, and, of course, available funding.

Shuford supplemented searches for information on colonies from published and unpublished literature and databases (e.g., California Natural

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Diversity Database), by communicating with various field biologists prior to field work, and by pursuing additional leads when out in the field. These efforts were greatly enhanced by biologists who shared survey data from continuing local or regional monitoring projects or who, under subcontract to our project, conducted or coordinated surveys of one or more species in regions where they had extensive knowledge (and contacts) and/or had conducted surveys in the past.

Because it was not feasible to survey all 15 target species statewide in the same year under the same environmental conditions, we took a regional approach by year. Thus the five species of ardeids discussed here were surveyed by region along with other species of colonial waterbirds. Field work in 2009 focused on selected species that breed mainly in northeastern California; in 2010 on remaining species in northeastern California plus the Black Tern (*Chlidonias niger*) in the Central Valley; in 2011 on additional species in the Sacramento Valley, Sacramento–San Joaquin River delta, and the northern and central coastal slope (especially the San Francisco Bay area); and in 2012 on the San Joaquin Valley, the coastal slope of southern California, the Salton Sea and Imperial Valley, and the Owens, Mojave, and lower Colorado River valleys. Observers surveyed from the ground, boats, and aircraft. Methods varied by species, colony site, and region depending on the species' nesting habits and local conditions, such as variation in nest substrates, proximity of other nesting species, and accessibility of colony sites. Aerial surveys were particularly valuable for photographing some remote colonies and for visually covering large areas, such as the Central Valley, that would have been impossible to survey adequately by other methods alone.

At each colony, observers tried to count or estimate the number of active nests or nesting pairs for each species. Active nests were defined as those that, at the time of the survey, were attended by an adult(s), held eggs or young, or showed signs of occupancy (e.g., extensive guano) earlier in the current breeding season. Guano-stained nests were counted only during late-season surveys because of the likelihood of pairs from early-season nests later re-nesting. It was possible in some cases, but not in others, to identify the species responsible for guano-stained nests that were not occupied by adults or young. At four colonies in coastal southwestern California, we apportioned 156 nests of either the Black-crowned Night-Heron or Snowy Egret to species according to the ratio of the identified nests for each species (when the total of identified nests for the two species combined was at least one third the number of unidentified). At seven colonies that did not meet this criterion we were unable to apportion to species the 169 nests of this species pair, leading to an undercount of nests for the two species. At the few sites where it was not possible to estimate the number of nesting pairs by counting nests, we relied on counts of adults and converted these to an estimate of active nests or nesting pairs (see Appendix 2 and Tables S1–S5; see Appendix 1 for glossary of abbreviations used in this supplemental material available at archive.westernfieldornithologists.org/archive/V51/Shuford-et-al-herons).

As much as possible, we timed surveys around peak nesting according to published accounts (e.g., Pratt and Winkler 1985, Kelly et al. 2006, 2007) or the personal knowledge of local experts. To do so, we needed to account for phenology varying by species in multi-species colonies. Individuals within

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a colony may breed asynchronously, or the time of breeding may vary from year to year or from site to site in the same year (e.g., Kelly et al. 2006, 2007). Because logistical constraints usually allowed for only one count per site, we tried to time visits to a colony to optimize counts for all species, given these complications of phenology. Phenological variation was less of an issue where multiple counts were possible. For example, some collaborators identified “peak nesting” for each species as the highest of multiple counts across the season (e.g., Kelly et al. 2007). Others, such as those covering the Sacramento and San Luis National Wildlife Refuge (NWR) complexes and the Sacramento Regional County Sanitation District Bufferlands, provided the raw data from multiple counts from which we identified the time of peak nesting.

Estimating Regional and Statewide Populations

Although surveys for many of the species addressed by the Western Colonial Waterbird Survey included only the interior of California (see Shuford 2014a for definition), those for herons covered the entire state, including the coast, and hence provide minimum statewide population estimates. To obtain a statewide estimate for each species, we summed the regional estimates, which, with a few exceptions, included the single best (peak) count for each colony during the specific year of the regional survey. The totals approximate the number of nests, which we used as a proxy for the number of nesting *pairs* (i.e., one nest equals one pair).

Survey Protocols

In California, observers generally followed the protocols of the Western Colonial Waterbird Survey (Jones 2008). Still, it was necessary to refine these or adopt other methods for situations not covered by that document. Here we summarize the methods by survey region and year; further details of methods are in Appendix 2. We selected census methods and protocols that we judged that would provide the most accurate estimates depending on the species involved, logistical constraints around the colony, the need to minimize disturbance, and the difficulty of covering such a large state.

Northeastern California: 2009

This study area included all or portions of Siskiyou, Modoc, Shasta, Lassen, Plumas, Sierra, Nevada, Placer, El Dorado, Alpine, and Mono counties. Although much of this sparsely populated region is relatively arid, marshes, lakes, and reservoirs offer extensive potential nesting habitat for waterbirds. These habitats are scattered widely, primarily at elevations from 1220 to 1830 m (4000 to 6000 ft) on plateaus, in large valleys, or in basins receiving drainage from nearby mountains. The breeding season of 2009 followed 3 years of drought, as documented by data for the two geographic climate divisions that together compose most of our northeastern California study area (Figure 1A). Consequently, several terminal lakes, reservoirs, or wetlands in this region were nearly or completely dry.

Although field work in this region in 2009 focused on other species of colonial waterbirds that in California breed entirely or mainly in the interior on islands in lakes, reservoirs, or wetlands, we also censused any herons nesting on these islands, those nesting (mainly in marshes) at Clear Lake, Lower

Klamath, and Tule Lake national wildlife refuges, and colonies of Great Blue Herons at other known or potential colony sites in the region (Appendix 2).

Northeastern California: 2010

Although the main target species in 2010 were three other widespread or locally numerous breeders not surveyed in this region in 2009, the Eared Grebe (*Podiceps nigricollis*), Black Tern, and Forster's Tern (*Sterna forsteri*), we also surveyed for local colonies of herons and ibis. Our efforts focused on valleys of the Cascade Range, Klamath Mountains, and Sierra Nevada, the Modoc Plateau, and the Great Basin desert of all or portions of Siskiyou, Shasta, Modoc, Lassen, Plumas, Sierra, Nevada, Placer, and El Dorado counties. Although precipitation in northeastern California in the winter of 2009–10 was close to the long-term mean (Figure 1A), the previous three years of drought still left many shallow marshes or lakes in the region as small remnants if not dry.

At the two sites in northeastern California where we found egrets and night-herons nesting in 2010, we estimated the number of nesting pairs from a count of adults because our visits were late in the season and/or nests were tucked in dense patches of trees (Appendix 2)

Central Valley: 2011 and 2012

The Central Valley, surrounded by mountains except at its western outlet into the San Francisco Bay estuary, is about 645 km long and 65 km wide. It is divided into the Sacramento Valley, draining southward, the San Joaquin Valley, draining northward, and the Sacramento–San Joaquin River delta, where these rivers converge. The San Joaquin Valley is further divided into the San Joaquin Basin and the usually closed Tulare Basin. Over 90% of the Central Valley's historic wetlands have been lost (Frayer et al. 1989, Fleskes 2012), and, overall, habitat for breeding waterbirds typically is scarce. The dominant land use in the Central Valley is agriculture, and certain irrigated crops can provide habitats in which breeding ardeids forage. These include the extensive areas of cultivated rice (*Oryza sativa*) in the Sacramento Valley and smaller areas in the delta and San Joaquin Basin, and flood-irrigated alfalfa (*Medicago sativa*) throughout the Central Valley. Other potential habitats for foraging herons in the Central Valley include managed wetlands on refuges and duck clubs (limited summer water), basins for storage of flood water or recharge of groundwater (e.g., South Wilbur Flood), reservoirs, stream and river edges, agricultural lands flooded by spring runoff after winters of exceptionally high precipitation, and grasslands and other uplands that provide suitable prey such as small rodents. In the Central Valley most herons nest in riparian woodland, various exotic trees in suburban parks and residential areas, and large stands of eucalyptus in rural areas.

Our censuses of ardeids in the Central Valley spanned two breeding seasons. We surveyed the Sacramento Valley and the delta in 2011. Precipitation in this region in the winter of 2010–11, preceding the 2011 breeding season, was well above average, but was preceded by a winter of average precipitation following three very dry winters (Figure 1A). In 2011, we searched ardeid colonies in the Sacramento Valley and delta by a combination of (extensive)

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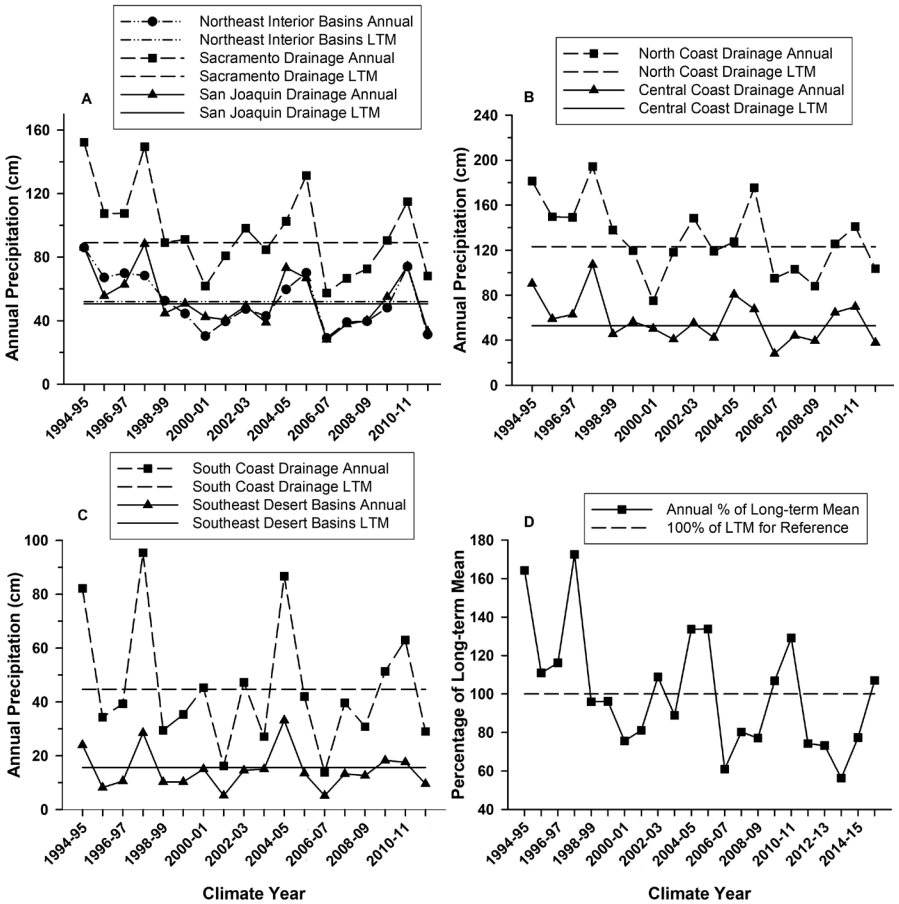


FIGURE 1. Annual precipitation for the climate years (1 July–30 June) 1994–95 to 2011–12, compared to the respective long-term means (LTM, $n = 117$ yrs), for the following climate divisions of California: (A) the Northeast Interior Basins, Sacramento Drainage, and San Joaquin Drainage; (B) the North Coast Drainage and the Central Coast Drainage; (C) the South Coast Drainage and the Southeast Desert Basins; and (D) annual precipitation for all of California, as a percentage of the long-term mean (LTM, $n = 119$ yrs), for the climate years 1994–95 to 2015–16. Data from the Western Regional Climate Center (www.wrcc.dri.edu/divisional.html).

aerial, ground, and (limited) boat surveys (Appendix 2). Although most potential habitat was on the floor of the Central Valley, we also looked for colonies along rivers, creeks, wetlands, ponds, and reservoirs in the Sierra Nevada foothills on the east and along east-flowing drainages of the Coast Ranges to the west.

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We surveyed the San Joaquin Valley for ardeids in 2012, locating and counting colonies by the same methods described for the Sacramento Valley and delta in 2011. Although drier than the Sacramento Valley and delta, the San Joaquin Valley is also dominated by agriculture. Habitat for nesting and foraging waterbirds persists mainly at managed wetlands, along rivers and streams, and at water-recharge basins, reservoirs, and other water bodies. The breeding season of 2012 was preceded by a very dry winter; the drought prevailing since 2006–07 had been broken only in 2010–11 (Figure 1A).

Northern and Central Coast: 2011

This region, from the Oregon border on the north to San Luis Obispo County on the south, includes the intensively developed counties around San Francisco Bay, with its extensive (primarily estuarine) wetlands. In the more sparsely populated counties to the north and south, the land generally rises steeply from the sea and the coast is punctuated with only occasional estuaries and river mouths. In these regions, precipitation in the winter preceding the 2011 breeding season was well above average, in contrast to the prior winter of slightly above average precipitation following three very dry winters (Figure 1B). Surveys in this region were largely ground-based nest counts; aerial and boat surveys were limited (Appendix 2).

Southern Coast: 2012

The area surveyed for ardeid colonies on the coastal slope of southern California included the coastal plain, interior valleys, and some montane valleys or depressions, all draining west to the Pacific Ocean. This region, much of which is highly developed, encompasses southern Santa Barbara, southern Ventura, southern Los Angeles, Orange, western Riverside, southwestern San Bernardino, and western San Diego counties. The pattern of rainfall in the years preceding the survey of this region paralleled that over most of the rest of California: three very dry winters from 2006–07 to 2008–09, above-average precipitation in 2009–10 and 2010–11, and a very dry winter in 2011–12 (Figure 1C).

Colonies were largely in plantings of non-native trees near estuaries, wetlands, and reservoirs or other water bodies. Surveys in this region were almost exclusively of nests counted from the ground (Appendix 2).

Salton Sea and Imperial Valley: 2012

The Salton Sea, in Imperial and Riverside counties, is a large saline lake formed in the early 1900s when floodwaters of the Colorado River overwhelmed water-diversion structures and flowed unconstrained into the Salton Sink for over a year. Its current input consists mainly of tailwater from irrigation of the adjacent Imperial Valley to the south by water imported from the Colorado River. The sea's level is currently on a trajectory of steady decline. Around the south end of the Salton Sea, wetlands of the Sonny Bono Salton Sea NWR and the Wister and Finney–Ramer units of Imperial Wildlife Area (WA) offer additional waterbird habitat. Ardeids also sometimes nest in stands of eucalyptus or other large trees in the Imperial Valley and, more recently, the Coachella Valley. The 2012 breeding season in this region was preceded by a very dry winter in 2011–12, preceded by two winters of above

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average precipitation after three very dry ones starting in 2006–07 (Figure 1C). Precipitation's effect on waterbirds in this desert region appears minimal, however, as inflows to the sea are primarily from agricultural tailwater.

Along with the goals of the broader 11-state project, surveys of colonial waterbirds at the Salton Sea and Imperial Valley in 2012 aimed to provide a basis for comparison with the results of comprehensive surveys in this region in 1999 (Shuford et al. 2000, Molina and Sturm 2004, Molina and Shuford 2013). In this area, observers used a combination of aerial, airboat, and ground surveys (Appendix 2).

Lower Colorado River, Mojave River, and Owens River Valleys: 2012

Elsewhere in the deserts of southern California, there is limited habitat for nesting ardeids along the lower Colorado River, Mojave River, and Owens River where flood-irrigated crops and pastures, and some adjacent wetlands, allow foraging. Precipitation patterns for these areas were like those for the Salton Sea (Figure 1C). Searches for colonies in this region were largely aerial, supplemented by ground-based counts at newly discovered or previously known colonies (Appendix 2).

Klamath River Country: 2012

Using prior data on colony locations (from Bob Claypole, California Natural Diversity Database, and John Hunter) and knowledge of potential nesting habitats, from 27 May to 2 June Shuford searched from the ground for active heron colonies in Shasta, (mainly) western Siskiyou, and northern Humboldt counties as detailed in Appendix 2.

DATA SUMMARY AND PRESENTATION

Ecoregions

We summarize the distributions of colonies of the five species of ardeids by “ecoregions” as defined in the Jepson Manual (Hickman 1993). The Jepson system is hierarchical, apportioning California among three floristic provinces divided into 10 regions and 23 subregions. The California Floristic Province, the largest, encompasses six regions: Northwestern California, Cascade Ranges, Sierra Nevada, Great Central Valley, Central Western California, and Southwestern California. The Great Basin Province includes the Modoc Plateau and East of Sierra Nevada regions; the Desert Province the Mojave Desert and Sonoran Desert regions. In our results we also distinguish the Sacramento Valley and San Joaquin Valley subregions of the Great Central Valley (Figure 2). In the Jepson system, the Sacramento–San Joaquin River delta is not a distinct subregion but parts of it are included in both the Sacramento Valley and San Joaquin Valley subregions.

Mapping

The maps showing the distribution and relative size of colonies of each species were created in ArcMap version 10.5.1 (ESRI, Inc.); values for categories of relative abundance were based on natural breaks in the data.

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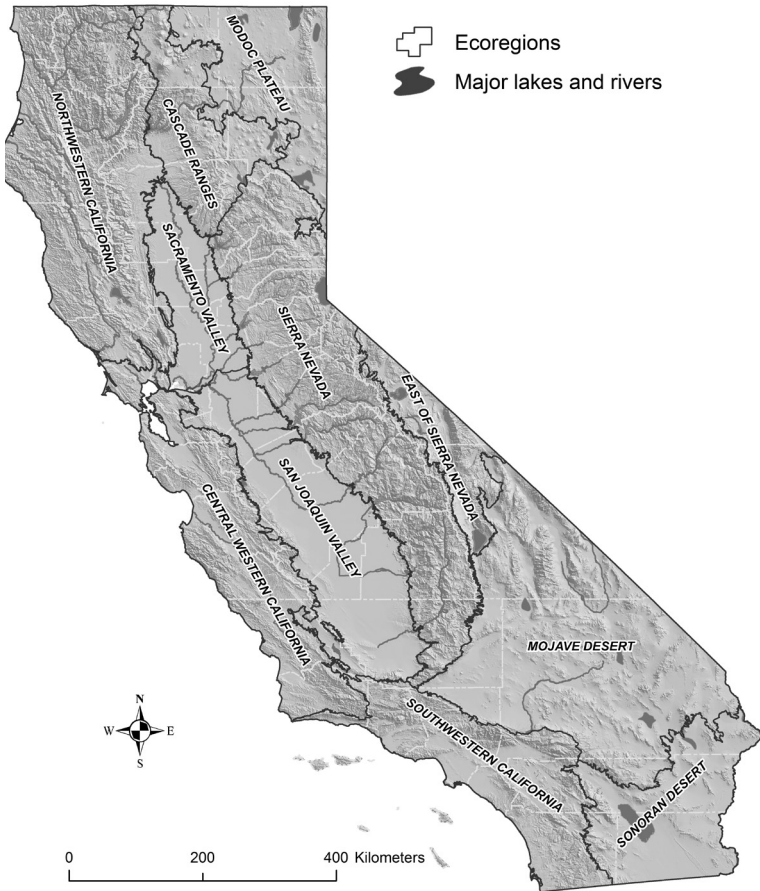


FIGURE 2. Ecoregions—based on the Jepson Manual’s geographic subdivisions of California (Hickman 1993)—used for mapping and summarizing data from statewide surveys of waterbird colonies, 2009–2012.

RESULTS

Here we describe the patterns of distribution and abundance of the five species from 2009 to 2012 by region. Details on the location and size of individual colonies are in Tables S1–S5 (archive.westernfieldornithologists.org/archive/V51/Shuford-et-al-herons).

Great Blue Heron

During our study, an estimated 5517 pairs of Great Blue Herons were breeding at 399 sites in California (Table 1). Colony sites ranged in elevation from about -71 m (-233 ft) below sea level at the Salton Sea, Imperial County, to 2163 m (7095 ft) along the upper Owens River, Mono County

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TABLE 1 Estimated Minimum Numbers of Pairs (and Colonies) of Five Species of Ardeids from Broad-scale Surveys throughout California^a

Years	Great Blue Heron	Great Egret	Snowy Egret	Cattle Egret	Black-crowned Night-Heron
1969	1737 (56)	401 (11)	227 (4)	0 (0)	822 (10)
1970	2298 (76)	594 (20)	303 (5)	0 (0)	1205 (11)
1971	2004 (104)	432 (13)	525 (6)	50 (1)	1225 (10)
1972	2553 (112)	725 (21)	985 (8)	100 (1)	1035 (11)
1978	3065 (133)	853 (30)	3704 (12)	7612 (7)	939 (16)
1982	2859 (111)	1245 (34)	851 (15)	3400 (5)	1192 (17)
2009–2012	5517 (399)	7973 (182)	1888 (79)	2678 (20)	2443 (104)

^aData for 1969–1982 from Schlorff (1982), for 2009–2012 from this study. See text for cautions warranted in interpreting differences, given the limited information on the thoroughness of the surveys 1969–1982.

(Table S1). Although not the most numerous, the Great Blue Heron was the most widespread species of ardeid in the state, occurring in all 11 ecoregions. The number of colonies was greater than that of any other species (Tables 1 and S1, Figure 3). Over half (54%) of the Great Blue Heron colonies observed during our survey were small (<10 active nests each; Table S1). Smaller colonies tended to occur in areas far from extensive wetlands or flood-irrigated agriculture, including suburban neighborhoods with fairly limited foraging habitat nearby. Colonies were particularly concentrated in the Sacramento and San Joaquin valleys, which each accounted for about 27% of all breeding pairs (Table 2). These herons were also numerous in the three coastal ecoregions and at the Salton Sea. Colonies were located mainly in stands of tall trees around coastal estuaries, large inland water bodies, and along major rivers and creeks adjacent to rice fields, other flooded-irrigated forage crops, or wetlands. Less frequently nest sites were on rocky or tule-mat islands, and on artificial structures. Colonies around the periphery of the Central

TABLE 2 Percentage of Nesting Pairs by Ecoregion for Five Species of Ardeids from Statewide Surveys in California, 2009–2012

Ecoregion ^a	Great Blue Heron	Great Egret	Snowy Egret	Cattle Egret	Black-crowned Night-Heron
Northwestern California	7	3	7	1	13
Central Western California	8	8	32	0	14
Southwestern California	9	2	20	5	18
Sacramento Valley	27	56	29	14	36
San Joaquin Valley	27	19	6	17	9
Cascade Ranges	1	1	0	0	0
Sierra Nevada	5	3	<1	0	0
Modoc Plateau	1	6	2	0	7
East of Sierra Nevada	1	0	0	0	3
Mojave Desert	<1	0	0	0	<1
Sonoran Desert	13	2	4	64	<1

^aAs defined in the Jepson Manual: Higher Plants of California (Hickman 1993; Figure 2).

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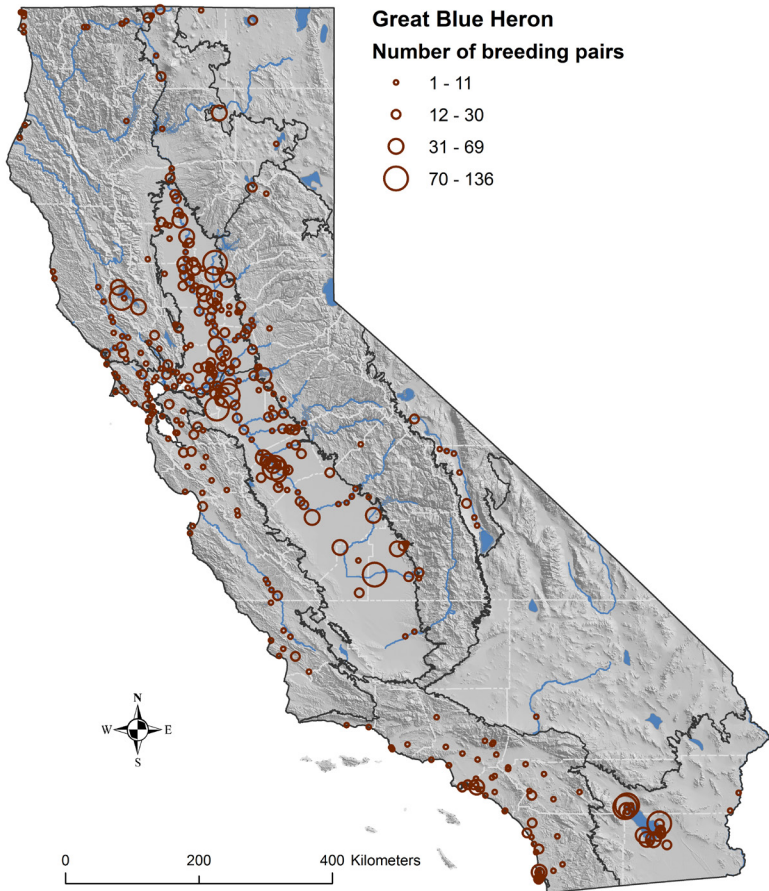


FIGURE 3. Distribution and relative size of Great Blue Heron colonies in California from statewide surveys, 2009–2012 (colony details in Table S1, archive. westernfieldornithologists.org/archive/V51/Shuford-et-al-herons).

Valley and in the adjacent foothills tended to be smaller. Most colonies in the Sacramento Valley and northern San Joaquin Valley were along the main rivers (Figure 4). Most of the largest colonies in southern California were at the Salton Sea (Table S1, Figure 3).

Great Egret

We estimate a total of 7973 pairs of Great Egrets distributed among 182 colonies (Table 1). These ranged in elevation from about -68 m (-224 ft) at the Salton Sea, Imperial County, to 1367 m (4484 ft) at Clear Lake NWR, Modoc County (Table S2). Great Egret colonies occurred in 9 of 11 ecoregions, being

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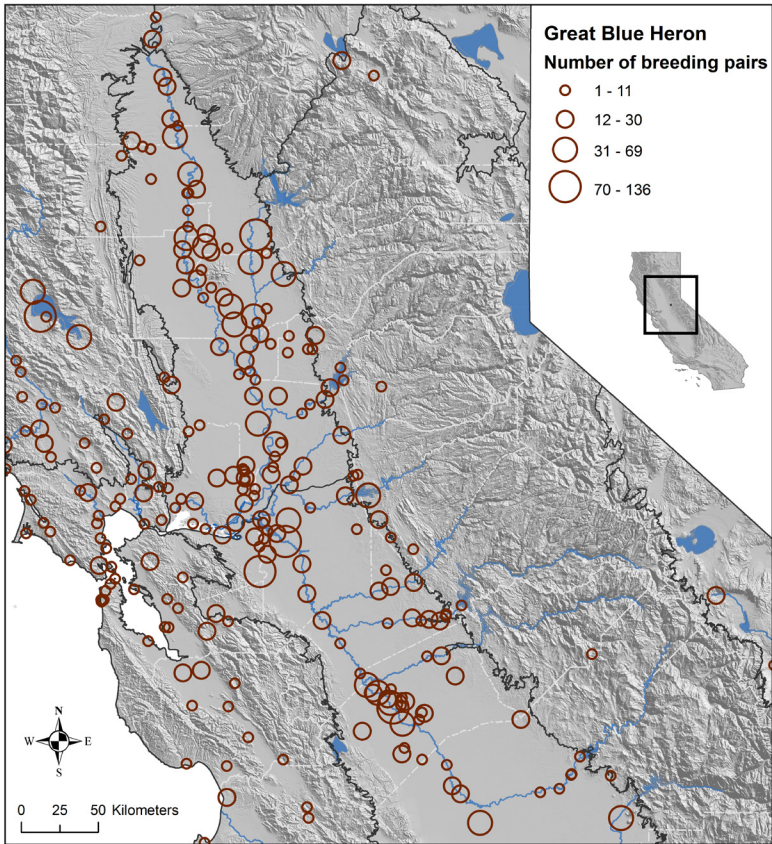


FIGURE 4. Distribution and relative size of Great Blue Heron colonies in areas of concentration in the Sacramento Valley, Delta, northern San Joaquin Valley, and central coast of California from statewide surveys, 2009–2012 (colony details in Table S1, archive.westernfieldornithologists.org/archive/V51/Shuford-et-al-herons).

absent only in the East of the Sierra and Mojave Desert ecoregions (Table S2, Figure 5). Otherwise the overall distribution of the Great Egret was fairly similar to that of the Great Blue Heron. The Great Egret, however, nested in fewer and generally larger colonies (only 31% with <10 nests each) than the Great Blue Heron. Also, in comparison to the Great Blue, it was more concentrated in some ecoregions and sparser in others (cf. Figures 3–4 with 5–6). Great Egrets were particularly concentrated in the Sacramento and San Joaquin valleys, home to 56% and 19%, respectively, of the statewide total of estimated breeding pairs (Tables 2 and S2). Like those of the Great Blue Heron, colonies of the Great Egret tended to be smaller toward the periphery of the Central Valley and in the adjacent foothills. Colonies were closely associated with the major rivers

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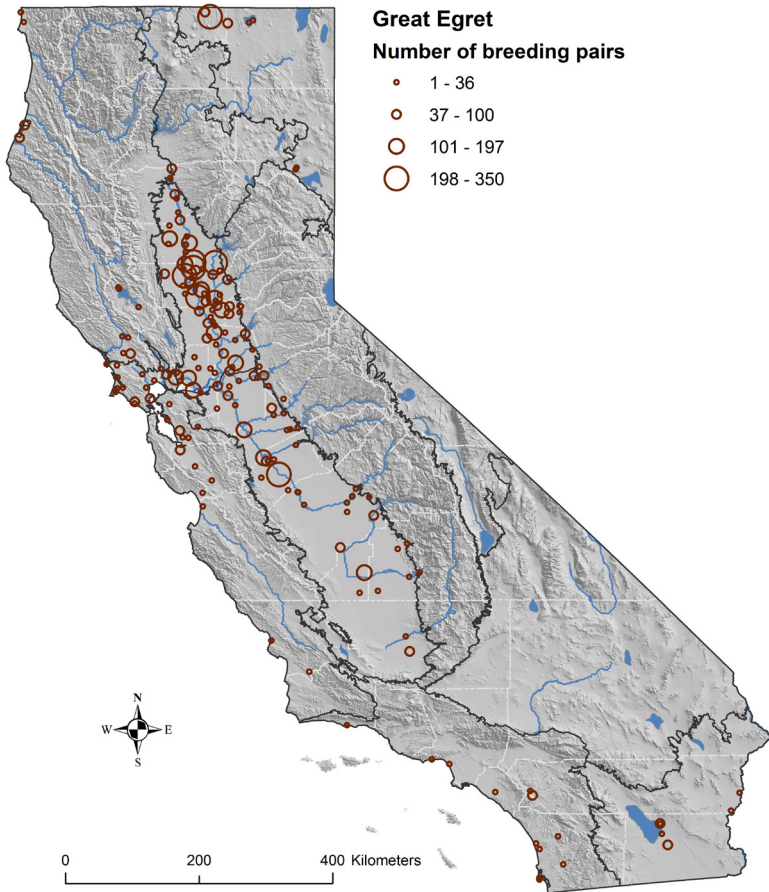


FIGURE 5. Distribution and relative size of Great Egret colonies in California from statewide surveys, 2009–2012 (colony details in Table S2, archive. westernfieldornithologists.org/archive/V51/Shuford-et-al-herons).

(Figure 6). Great Egrets and Great Blue Herons frequently nested in mixed colonies; the two species' nesting and foraging habitats overlap substantially. The Great Egret's particularly high concentration in the Sacramento Valley may reflect its heavy use for foraging of that region's extensive rice fields. Roadside surveys across the Sacramento Valley in the late May and early June 2012 found densities of the Great Egret greater than those of the Great Blue Heron in flooded wetlands, alfalfa, rice, and irrigated pastures (Point Blue unpubl. data).

Snowy Egret

We estimate that 1888 pairs of the Snowy Egret, distributed among 79 sites, nested in California between 2009 and 2012 (Table 1). This estimate is

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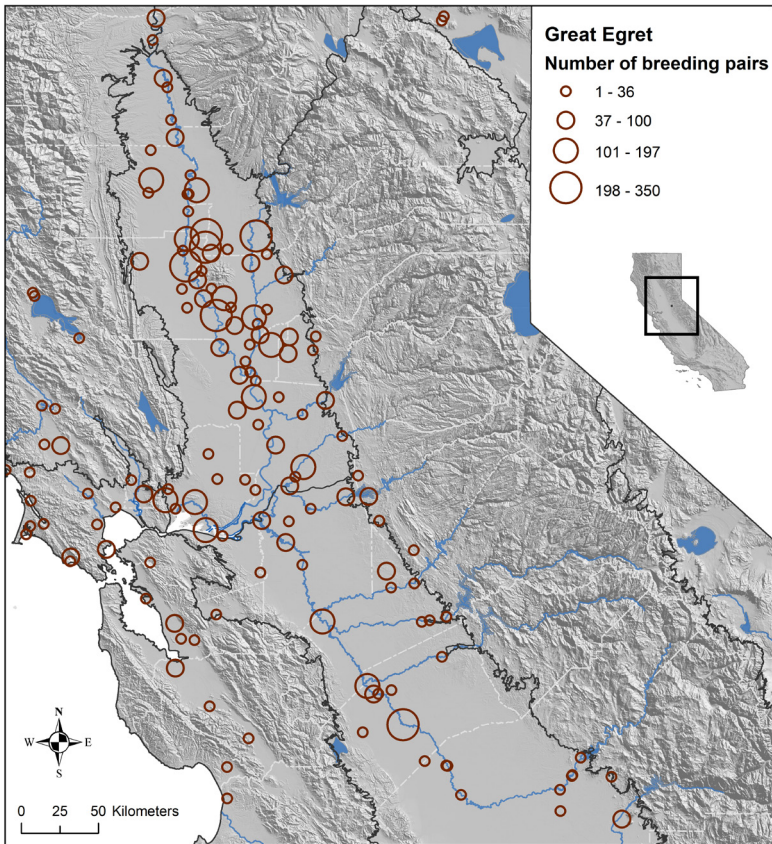


FIGURE 6. Distribution and relative size of Great Egret colonies in areas of concentration in the Sacramento Valley, Delta, northern San Joaquin Valley, and central coast of California from statewide surveys, 2009–2012 (colony details in Table S2, archive. westernfieldornithologists.org/archive/V51/Shuford-et-al-herons).

probably low, as it was not possible to distinguish used nests of the Snowy Egret from those of the Black-crowned Night-Heron or Cattle Egret at several sites surveyed late in the season. Similarly, at the East Hacienda Flood Basin in the southern San Joaquin Valley, large numbers of small white egrets on nests within dense tamarisk or willows could not be distinguished to species during an aerial survey. In addition, because nesting of these species is less synchronized than that of the larger herons (Kelly et al. 2007), peak colony sizes and the number of breeding pairs may have been substantially greater than reflected in our observations. Still, we confirmed Snowy Egret colonies in 8 of the 11 ecoregions. Only in the Cascade Ranges, East of the Sierra, and Mojave Desert ecoregions were they lacking (Tables 2 and S3, Figure 7). Colonies ranged in elevation from about -68 m (-224 ft) at the Salton Sea,

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Imperial County, to 1250 m (4100 ft) at Leavitt Lake, Lassen County (Table S3). The numbers of pairs and colonies of the Snowy Egret were greatest in the San Francisco Bay area, the Sacramento Valley, and southwestern California (Tables 2 and S3, Figure 7). The smaller species—Snowy Egret, Cattle Egret, and Black-crowned Night-Heron—frequently established mixed colonies in trees in residential neighborhoods, parks, or other human-dominated environments, as well as in some more remote locations in the lower strata of trees in which Great Blue Herons and Great Egrets were also nesting.

Cattle Egret

During our study, an estimated 2678 pairs of Cattle Egrets nested at 20 sites in California (Table 1). Colonies ranged in elevation from about -68 m (-224 ft) at the Salton Sea, Imperial County, to 456 m (1495 ft) at the San Jacinto wastewater-treatment plant, Riverside County (Table S4). Cattle Egret colonies occurred in only 5 of the 11 ecoregions, and the vast majority of egrets were in just 3 (Tables 2 and S4, Figure 8). The Imperial, San Joaquin, and Sacramento valleys held 64%, 17%, and 14% of the statewide total, respectively (Table 2). In the Imperial Valley, most of the egrets were at a single colony at Ramer Lake in the Finney-Ramer Unit of the Imperial WA; the remainder were at two sites at the Salton Sea. Away from the Imperial Valley, most Cattle Egrets nested in mixed-species colonies (mainly with Snowy Egrets and night-herons) in ornamental trees close to human habitation.

Black-crowned Night-Heron

Our estimate for the Black-crowned Night-Heron is 2443 pairs nesting at 104 sites (Table 1), ranging in elevation from about -68 m (-224 ft) at the Salton Sea, Imperial County, to 2173 m (7128 ft) at Laurel Pond, Mono County (Table S5). These night-herons occupied 9 of the 11 ecoregions, but three coastal ecoregions and the two in the Central Valley accounted for 90% (Tables 2 and S5, Figure 9). Of these, the Sacramento Valley held the greatest proportion at 36% of the statewide total. Although many night-herons were nesting in mixed-species colonies with small egrets in ornamental trees close to human habitation, many others were nesting in native trees in more isolated settings in mixed-species colonies that also included Great Blue Herons and Great Egrets.

Other Species

Surveys on the coastal slope and deserts of southern California in 2012 documented breeding of two other species of herons that have spread north into California in recent decades. In 2012, three pairs of the Little Blue Heron (*Egretta caerulea*) were nesting with Snowy Egrets on the grounds of Sea World, Mission Bay, San Diego County (F. Zern and J. Pea pers. comm.), where it has nested at least intermittently since 1992. Likewise, Yellow-crowned Night-Herons (*Nyctanassa violacea*) nested in 2012 at Sea World (1 nest) and at the Imperial Beach Sports Park adjacent to the Tijuana River estuary, San Diego County (2 nests; F. Zern, J. Pea, and J. Szabo pers. comm.). At least one pair of the Yellow-crowned Night-Heron has nested at the latter site annually since California's first confirmation of the species' successful nesting there in 2006.

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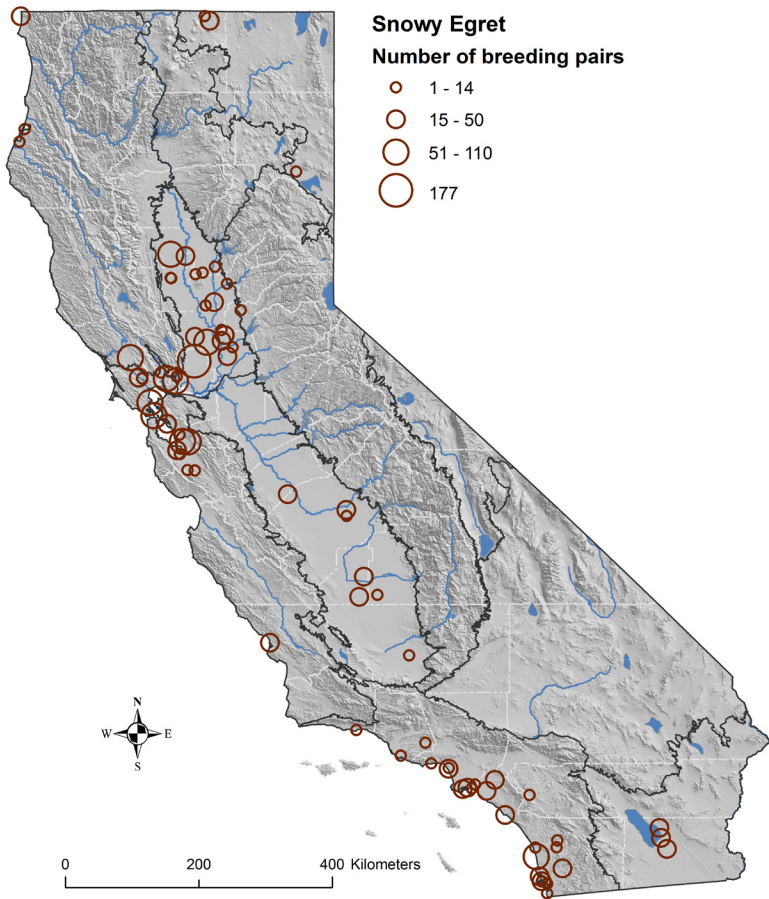


FIGURE 7. Distribution and relative size of Snowy Egret colonies in California from statewide surveys, 2009–2012 (colony details in Table S3, archive. westernfieldornithologists.org/archive/V51/Shuford-et-al-herons).

DISCUSSION

Population Trends

Most colonial ardeids in California experienced historical declines and have since recovered to an unknown degree. The Great and Snowy egrets were decimated by the ravages of plume hunters at the end of the 19th century but began to rebound by about 1910 (Grinnell and Miller 1944). By 1943, the Great Egret was “considered common on the remaining suitable portions of its former range” (p. 58), and the latter was then “fairly common in favored places” (p. 59). These authors also reported numbers of the Great Blue Heron as reduced in “recent years” (p. 56), especially in southern California, and the

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Black-crowned Night-Heron as “formerly abundant, now greatly depleted locally” (p. 60). By contrast, the Cattle Egret was first recorded in California in 1962 and first documented breeding in the state at the Salton Sea in 1970 (120 nests). Its numbers increased rapidly at least until the 1990s (Schlorff 1982, Patten et al. 2003, Molina and Sturm 2004).

Statewide, regional, and local inventorying and monitoring of California’s heron colonies did not commence in earnest until the late 1960s (e.g., Schlorff 1982, Pratt 1983). The California Department of Fish and Game conducted statewide inventories of colonial ardeids in six years from 1969 to 1982 (Schlorff 1982; Table 1). The results are hard to interpret because the limited information on those surveys’ methods (Schlorff 1982) suggests they were far less complete than those from 2009 to 2012 (see Methods). Belluomini (1978), however, judged that the steady increase in numbers of nests over the span of at least the first four inventories, 1969–1972, was “as much an increase in the knowledge of heronry locations as an increase in breeding activity.” Still, from 1969 to 1982, the various species’ patterns of change in the number of breeding pairs (nests) and colony sites differed (Table 1). The numbers of pairs and colonies of the Great Blue Heron and Great Egret increased overall, but for the Great Blue both metrics dipped in 1982. Overall the number of pairs and colonies of the Snowy Egret increased, with a large spike in pairs in 1978. For the Cattle Egret, one small colony in 1971 and 1972 grew to a peak of 7612 pairs at 7 colonies in 1978 then declined to 3400 pairs at 5 colonies in 1982. Numbers of pairs of the Black-crowned Night-Heron were relatively stable over time while the number of colonies increased modestly. The number of colonies of each species detected from 2009 to 2012 was much greater than in any year from 1969 to 1982 (Table 1), likely reflecting increased survey effort. With respect to the number breeding pairs, however, those for 2009–2012 were much greater than those for 1969–1982 for the Great Blue Heron, Great Egret, and Black-crowned Night-Heron but not for the Snowy and Cattle egrets, whose numbers were more variable (Schlorff 1982).

Regional studies clarify trends in portions of California. Kelly et al. (2006) reported stability or increases in the number of nests of the four main species nesting in the San Francisco Bay region from 1994 to 2005. The Great Blue Heron and Black-crowned Night-Heron showed no significant linear trend, the Snowy Egret showed a marginally significant linear increase, and the Great Egret showed a significant increase, reflecting primarily a sharp increase in 2004 and 2005. From 2001 to at least 2016, the number of Black-crowned Night-Herons nesting in the central and northern San Francisco Bay region declined steeply, at an average rate of -4.9% per year ($b = -0.049$, $P < 0.0001$). Apparently the decrease is related to increases in the frequency of potential nest predators disturbing the colonies (Kelly and Robinson-Nilsen 2011; Audubon Canyon Ranch unpubl. data).

In coastal southern California, the numbers of breeding herons have increased in recent decades, particularly since the 1990s. The increases have been driven largely by the establishment of new colonies in urban settings, though patterns vary by species and subregion. The Great Egret, however, is the one species that has shown a pattern of consistent increase across the region (Unitt 2004, Lehman 2019, Cooper and R. A. Hamilton unpubl. data). In 2012 the total population in southwestern California was about 150 pairs

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or <2% of the statewide total (Tables 2 and S2). Although in the last 20 years the number of Snowy Egret colonies in Los Angeles, Santa Barbara, and San Diego counties has increased, in the latter county the increase in colonies has not been accompanied by a clear increase in the species' numbers (Unitt 2004:133, San Diego CBC data *vide* P. Unitt). Likewise, there is evidence of increases in nesting Black-crowned Night-Herons in Los Angeles County (Cooper and R. A. Hamilton unpubl. data) and at one site in Santa Barbara County (Lehman 2019), but little evidence for changes in the species' abundance in San Diego County (Unitt 2004:144, P. Unitt pers. comm.).

Molina and Sturm (2004) described annual variation in the number of breeding pairs and colonies of five species of ardeids at the Salton Sea from 1986 to 1999. That variation was greatest in the Snowy Egret, Cattle Egret, and Black-crowned Night-Heron, which all reached peaks in 1992 or 1993 when numbers dwarfed those in most other years. By contrast, the number of nesting pairs of the Great Blue Heron was lowest in the early 1990s, and annual variation in the Great Egret was the lowest of the five species. The overall patterns are uncertain, however, as survey effort varied annually, especially prior to 1991 (Hurlbert et al. 2007). Our surveys at the Salton Sea in 2012 found numbers of all five ardeid species lower than in 1999, the year of the last comparable survey (Molina and Shuford 2013).

The applicability of sources of data on ardeid numbers away from colonies is limited. Although all of the five species we address occur in California year round, it is not clear whether numbers in winter are augmented substantially by seasonal influxes of birds from outside of California or how well-suited Christmas Bird Counts (CBC) are to tracking trends in these waterbirds. The Breeding Bird Survey (BBS) gathers data on many species of birds, including ardeids, but its methods are not adapted to surveying colonial waterbirds and undersample marshes (Bystrak 1981, Robbins et al. 1986).

For the periods 1968–2012 and 2002–2012 (i.e., through the last year of our surveys), the BBS showed no significant trends for California for four of the five species we considered (Sauer et al. 2014). The exception was the Great Egret, which showed a significant positive trend in both periods. Although the Cattle Egret showed no significant trends, the BBS data for it were particularly inadequate.

Hurlbert et al. (2007) also assessed variation in the numbers of waterbirds at the Salton Sea, using data from local colony surveys (1987–1999), the two local CBCs (mainly 1968–2004), and the BBS for the western United States (1968–2002). Fluctuations in fish-eating waterbirds, including ardeids, tracked fish populations closely over their two cycles of boom and bust from the 1970s to the early 2000s. Molina and Sturm (2004) concluded that because potentially suitable habitat for colonial waterbirds had remained constant from the mid-1980s to late 1990s, rapid increases in the numbers of nests of some waterbirds, including the Great Blue Heron but no other ardeid, in the mid- to late 1990s were best explained by changes in the availability of food rather than of nest sites (but see under Threats below).

For the period 1978–2014, Pandolfino and Handel (2018) compared trends of various species, including ardeids, on CBCs in the Central Valley with those from the BBS for all of California and the West. The Great and Snowy egrets both showed significant increases on both the Central Valley

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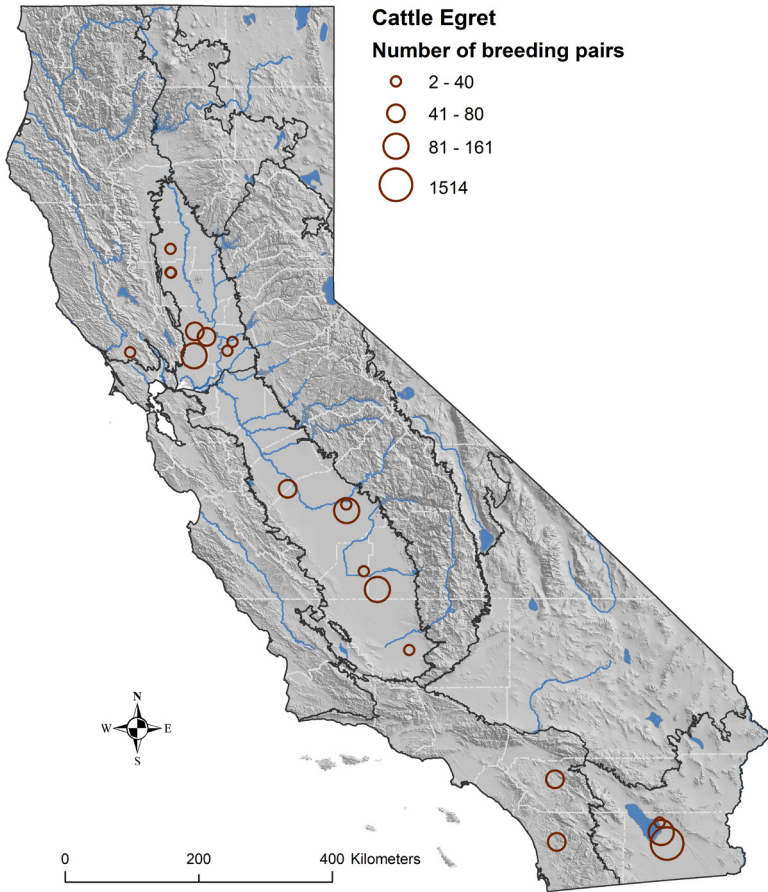


FIGURE 8. Distribution and relative size of Cattle Egret colonies in California from statewide surveys, 2009–2012 (colony details in Table S4, archive. westernfieldornithologists.org/archive/V51/Shuford-et-al-herons).

CBCs and California BBS routes. By contrast, the Great Blue Heron showed a small but significant decrease on CBCs and no significant trend on the BBS. For the Black-crowned Night-Heron there was no significant trend in either set, and for the Cattle Egret the lack of a significant trend on CBCs was paired with an increasing but weakly supported significant trend on the BBS.

It is possible that some of the patterns Pandolfino and Handel (2018) described from Central Valley CBCs may in part reflect changes in distribution rather than in abundance. Fleskes et al. (2018) analyzed trends in the abundance and distribution of waterfowl and their habitats in the Central Valley from 1973 through 2000. During this period, wetlands increased throughout the Central Valley. By contrast, the extent of rice fields flooded after harvest

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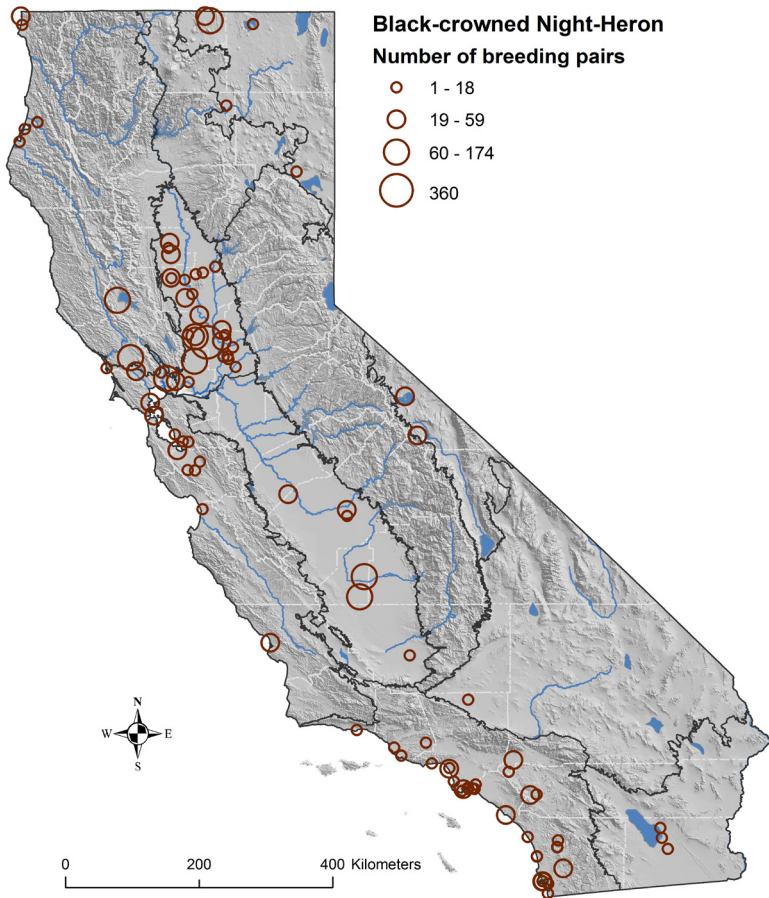


FIGURE 9. Distribution and relative size of Black-crowned Night-Heron colonies in California from statewide surveys, 2009–2012 (colony details in Table S5, archive. westernfieldornithologists.org/archive/V51/Shuford-et-al-herons).

increased greatly to the north in the Sacramento Valley but decreased to the south in the San Joaquin Valley. The result was a pronounced shift in the availability of winter waterfowl habitat, and of the waterfowl themselves, to the north. Some heron species might have shifted north as well. Although numbers of Great Blue Herons on CBCs in the Central Valley did not increase, this species' apparent stability might in part reflect the Great Blue's relying less on rice fields than does the Great Egret; in 2012 we found the egret's density in rice fields to be greater than that of the heron (Point Blue unpubl. data). The sample of CBC circles Pandolfino and Handel (2018) analyzed was more heavily weighted to the Sacramento Valley, where most of the Central Valley's rice is grown, than to other subregions, so the Great Egret might be

overrepresented because of disproportionate coverage of areas where rice cultivation was expanding.

Given the limitations of all these studies, there is still considerable uncertainty in the direction and magnitude of changes in populations of California's breeding herons over the last 40 to 50 years. The clearest case is that of the Cattle Egret, which increased rapidly soon after the initial discovery of a colony of about 120 pairs at the Salton Sea in 1970 (Patten et al. 2003). By 1978 the Imperial Valley hosted over 7000 breeding pairs (Belluomini 1978), and in 1992 it reached a peak of about 30,000 pairs (Molina and Sturm 2004). From 1986 to 1999, however, numbers (of uncertain accuracy) varied greatly from one year to the next, often by many thousands (Molina and Sturm 2004). Thus annual variation rather than a downward trend could account for the 2012 estimate for the Imperial Valley/Salton Sea being only 25% of the total in 1999, when last surveyed (Molina and Sturm 2004, Molina and Shuford 2013). Water conservation mandated by recent transfers of water from the Imperial Valley to San Diego and other coastal cities may also have reduced the suitability of this valley to the Cattle Egret, given its dependence there on irrigated agriculture for foraging. Notably, from 2003 to 2011, an average of 85,869 acre-feet of water was saved annually by fallowing of fields and increased efficiency of irrigation (Velasco 2013). Alternatively, it may simply be that after peaking the number of Cattle Egrets nesting in that region has dropped to a lower level around which it is currently fluctuating.

Data for the other four species suggest their numbers have been stable or increasing in recent decades (Schlorff 1982, Molina and Sturm 2004, Kelly et al. 2007, Sauer et al. 2014, Pandolfino and Handel 2018). Among these, however, the Great Egret is the only species that shows strong evidence of an increasing population in California. Annual variation for the Snowy Egret and Black-crowned Night-Heron may be so great that it masks any underlying long-term trends, as it does for the Cattle Egret in recent years.

Elevational and Latitudinal Ranges

The upper elevational limits of breeding of each of the five species in California was closely associated with the northern latitudinal limit of its breeding in western North America. The Great Blue Heron and Black-crowned Night-Heron, which each bred up to about 2160 m (7100 ft) in California, breed the farthest north (Dunn and Alderfer 2017). By contrast, the Cattle Egret bred up to just 456 m (1495 ft) in California, and it does not breed as far north as the other four species. The Great and Snowy egrets are intermediate in these limits with respect to the other species.

Climatic Variation

Over the last 20 years California's climate has varied widely, from very wet to extremely dry. Surveys of the state's interior from 1997 to 1999, a period with precipitation well above average (Figure 1D), addressed some colonial waterbirds but not herons (Shuford 2010). Conversely, the 2009–2012 surveys, which did include them, overlapped with the extended drought that began in 2006–07. Despite being interrupted by one year of heightened precipitation (129% of long-term mean), this dry period persisted four years beyond the completion of our surveys in 2012 (Figure 1D). The dry period

from 2011–12 to 2015–16, alone, is considered the most severe statewide drought in the historical record (Swain 2015, Wang et al. 2017). Furthermore, the 2000–2018 drought in southwestern North America, including California—driven by natural variability superimposed on drying from anthropogenic warming—was the second driest 19-year period since 800 CE (Williams et al. 2020).

The lack of long-term monitoring of the populations of colonial waterbirds in most of the interior of California limits the conclusions we can draw on the drought's effects. But data for this region for a set of species inventoried both 1997–1999 and 2009–2012 provides some potentially valuable insights (Shuford 2014a, Shuford et al. 2016, Doster and Shuford 2018). In the latter period, breeding populations of the Ring-billed Gull (*Larus delawarensis*), California Gull (*L. californicus*), Caspian Tern (*Hydroprogne caspia*), Black Tern, and Forster's Tern were greatly reduced in northeastern California. Those of the latter three species were also much reduced in the Central Valley and so throughout the inland portion of their California breeding ranges. Drought likely affected herons and other waterbirds unsurveyed in one or both periods. Effects on most species, whether monitored or not, undoubtedly intensified after 2012, as the drought continued four more years. Kelly and Condeso (2014) investigated the effects of the amounts and volatility (storminess) of seasonal rainfall on changes in the numbers of heron nests in the San Francisco Bay area, 1991–2010. They found that the number of nests of the Great Blue Heron and Great Egret in this region declined or grew more slowly after winters of both wetter- or drier-than-average rainfall. Those of the Snowy Egret and Black-crowned Night-Heron declined or grew more slowly immediately after spring (nesting) seasons when the volatility of rainfall was greater than usual and two years after winters when this measure was greater than usual. From this they predicted regional declines in the growth or resilience of heron population should the amount and volatility of rain in northwestern California increase. Furthermore, future effects may be even greater, given projections of 21st-century increases in the frequency of wet extremes and smaller increases in dry extremes (Swain et al. 2018).

Accuracy and Challenges of Nest Counts

It is often difficult to determine how close counts or estimates of the numbers of nests or breeding pairs of ardeids are to the actual number present. Many factors can influence the counts' accuracy, such as the size of the area to be searched and availability of resources. Cycles of wet and dry affect habitat availability in different regions from year to year, complicating comparisons when colonies in different regions are surveyed in only one year during a multi-year survey period. The number of nests or adults present (or visible) varies through a breeding season, hindering comparisons when counts of different colonies span an extended period within that season. The detectability of nests and adults varies with the surrounding landscape, nest substrate or vegetation type, the species' behavior and color, observers' experience, etc. We were not able to quantify how such factors might have influenced the accuracy of counts from 2009 to 2012.

Ideally, all surveys should be conducted in a single year, as colonies' locations and size can change as water levels and the availability of nest sites

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or foraging areas fluctuates annually. Our regional approach of spreading surveys over several years encompasses potentially substantial unknown annual variation in colonies' size and distribution. However, annual variation in colony-site selection and use largely reflects the adaptive responses of herons and egrets to the local landscape within their foraging range. Local annual responses are substantially masked (or averaged out) at larger scales of measurement (Kelly et al. 2018). Thus our analysis of regional or multiregional differences in the numbers of nesting herons is unlikely to be affected strongly by smaller-scale processes and colony-site differences between years. Nonetheless, unknown interregional shifts of the population could confound interpretation of the results of a four-year survey partitioned among regions.

Regardless, summing counts taken over more than one year, as we have done, is often the only feasible way to estimate a total population size when the goal is a census of multiple species distributed among large numbers of colonies spread over a broad area (e.g., see Carter et al. 1992 for California seabirds). In just one of four years from 2009 to 2012 was precipitation above average, which likely reduced the year-to-year variation in numbers of nests within that interval. Still, it seems likely that summing the regional estimates yielded a minimum value for the statewide populations of the five species, as very dry conditions in two years may be expected to have depressed the numbers. Furthermore, given the huge area we surveyed, we undoubtedly missed some colonies.

Timing the counts to the peak of nesting is always desirable. This is not always easy to do, however, particularly for species such as the Black-crowned Night-Heron and Snowy Egret for which the timing of peak nesting may vary considerably, annually or by site in the same year (Kelly et al. 2006). For such species, it is preferable, if feasible, to take multiple counts across the season. Late-season counts may include so many used nests that it may not be possible to assign them to species by the ratio of nests of these species still active in the colony. For some seabirds, however, peak nest counts can substantially underestimate the number of breeding pairs (Seavy and Reynolds 2009). It is unclear to what degree this potential bias affected our estimates of the numbers of nesting herons. Nevertheless, our counts are indices of the population so should be comparable to future estimates if surveys follow the same methods, are done at the same time in the nesting cycle, and are done under reasonably similar environmental conditions.

Species that nest on varied substrates may be relatively easy to count on one substrate but not on another. For example, nests of the Great Blue Heron on open islands are straightforward to count from aerial photos, but this technique works poorly when the birds are nesting in trees with leafy canopies. In such cases visual counts of nests from the air or ground are preferable.

When nests are partially screened by vegetation the accuracy of nest counts may vary with the vegetation type. At the extreme end, species like egrets and night-herons may nest in tall marsh vegetation where few if any nests are visible from the periphery of the marsh. In such cases, numbers of nests can be estimated from counts of the number of adults flying out of the colony. Converting numbers of adults to an estimate of pairs, however, introduces uncertainty, as the proportion of adults remaining at the nest site may vary over the course of the breeding season. Using a conversion factor

implies the assumption that all adults present are breeding and their nests are at the same stage of the breeding cycle. The latter in particular is a risky assumption because the timing of nesting in a colony may vary considerably by species, by individual within a species, and from year to year (Kelly et al. 2006, 2007, Hothem et al. 2010).

A more typical challenge is obtaining good counts of nests in leafed-out trees. The foliage may obscure a nest, or an entire tree may block the view of more distant trees in which herons are nesting. Observers may compensate by surveying from multiple vantage points, but such options may be limited by impenetrable vegetation or restricted access to private property. For early-nesting species like the Great Blue Heron it may be possible to count nests before the trees are well leafed out. But this often is just a partial solution. In multi-species colonies other species may start nesting later when trees are fully leafed out. Such seasonal variation in foliage is not an issue for colonies in evergreen trees.

Aerial surveys can provide a good overview of a colony, particular those of the Great Egret and Great Blue Heron, which tend to nest at or near the top of the canopy. From a fast-moving plane, however, the time available for counting nests is short. This problem can be alleviated somewhat if the colony can be circled several times. Also, the ease of locating a colony on an aerial survey depends on the colony's size and species composition. Large colonies, particularly those dominated by white-plumaged egrets, are much easier to detect than are smaller colonies, particularly those with just a few pairs of drab-plumaged herons. Censusing arboreal colonies by means of photographs is challenging because nests may be within multiple layers of the canopy, making it hard to piece together photos of a three-dimensional object taken from various angles. During aerial surveys, it is usually not feasible to photograph large numbers of colonies because of the costs of additional flight time and photo counting. Our study entailed many days of aerial surveys, particularly for colonies along the rivers of the Central Valley. We initially contemplated making rough counts of the nests from the plane and then going back on the ground to make a more leisurely and accurate count. It was often not possible, however, to get close to colonies on the ground because of private property, impenetrable vegetation, or sloughs to cross. Or, just a portion of the colony might be visible from the only access point. In such cases, mapping the locations of nests is helpful, as is watching the colony long enough that young may stand up in nests that were not initially visible, or adults returning to the colony may reveal nests when they land.

To facilitate comparisons of the results of future statewide inventories with ours, we recommend the use of the most accurate method of counting for each species, nest substrate, and time of the season and, insofar as possible, replication of our protocols and methods. Modifications may, of course, be needed or desirable depending on conditions at the time of a future inventory or advances in knowledge or technology that may improve surveys' accuracy over what is currently possible.

Future Monitoring

One of the primary goals of the Western Colonial Waterbird Survey was to establish a baseline for long-term monitoring of these species throughout

the western United States (Seto 2008). Such an inventory is a prerequisite for a long-term monitoring program, as are standardized protocols and methods for surveying colonial waterbirds (e.g., Steinkamp et al. 2003, Jones 2008). Steinkamp et al. (2003) emphasized thinking beyond measuring change in numbers over time so that the information collected can be used effectively to improve management. They noted that the geographic scale and objectives will greatly influence the design of the program. For example, is the main objective to detect population declines that may require action to remediate, or is the main interest in documenting colony locations? Another key element is deciding the scale on which the program will focus for evaluating the status and trends of waterbird populations. Any monitoring at the scales of the state or the West as a whole will require collaboration with groups that focus their current monitoring at smaller scales. Ideally, protocols and methods can be standardized, modified, or adapted so that trends can be accurately assessed, and compared geographically, for the range of scales important to collaborators.

Other key decisions are whether particular species or populations deserve priority for monitoring, whether to monitor all populations or just sample or select populations, the frequency of surveys within and in successive years, and the magnitude of change targeted for detection with reasonable precision over a specified period (Steinkamp et al. 2003). The Pacific Flyway Council (2013, 2018) considered these factors when prioritizing the monitoring of western populations of the Double-crested Cormorant (*Phalacrocorax auritus*) and American White Pelican (*Pelecanus erythrorhynchos*) in response to predation of these species on fish of conservation concern or economic or social value.

In California, decisions on a frequency for monitoring of ardeid colonies should take into account the state's great annual variation in precipitation, the substantial annual variation in the breeding numbers of some species, and the rates of abandonment of old and establishment of new colonies. We recommend surveys at short intervals, ideally annually, as the extent of wetlands or other water bodies may vary markedly over short periods, the extent of flood-irrigated crops in which herons forage may decrease substantially during severe droughts, and the variability of precipitation may increase with climate change (Swain et al. 2018). While the desired levels of precision and ability to detect trends should inform sampling effort, resource limitations may dictate survey frequency.

Given that attempts to inventory all heron colonies in California on a regular basis are not feasible, any statewide monitoring program will need to adopt a statistically robust sampling framework. This should reduce sampling error resulting from spatial and temporal variation in densities of waterbirds influenced by habitat or other factors, variability in colony attendance by the stage of the nesting cycle, and differences in the probability of detecting birds by species and habitats and over time (Steinkamp et al. 2003).

Any monitoring program for ardeids in California can draw lessons from efforts at the local and regional level (e.g., Molina and Sturm 2004, Kelly et al. 2006), from the California-wide surveys 1997–1999 (Shuford 2010) and 2009–2012 (Shuford 2014a), and from the recent multi-state surveys (Cavitt et al. 2014). The results of experiments with unmanned aerial drones for

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wildlife surveys (e.g., Ogden 2013) suggest that the way biologists monitor waterbirds may change rapidly in coming years.

Even a well-designed and -executed monitoring program may falter without institutional support to maintain training of biologists and volunteers to survey in a standardized manner. The program's administration must coordinate the collection and analysis of the data, disseminate the results, and instigate research and management when action is warranted.

Threats to Waterbirds

Colonial waterbirds face a host of threats, which have changed over time. But the greatest threat to these birds in California currently is the combination of habitat loss, degradation, and fragmentation, driven by an expanding human population. Other threats to waterbirds in California include increasing competition for water from municipal and agricultural interests; changing or detrimental agricultural, municipal, or industrial practices in altered habitats; poor or toxic water quality and oil spills; diseases; subsidized and introduced predators; invasive species; human disturbance; conflicts with human interests; interspecific conflicts; and the long-term effects of climate change (Shuford 2010, 2014b).

California's drought from 2006 to 2016 emphasizes the importance of reliable water supplies for wetlands and irrigated crops that are prime foraging habitats for waterbirds. Although waterbirds are adapted to periodic droughts, there are, of course, limits to their adaptability. The effect of precipitation may cut both ways, however, as Kelly and Condeso (2014) reported that on the central California coast both too much or too little rainfall, or increases in the volatility of that rainfall, are likely to depress the growth rates of heron populations. It remains to be seen if these patterns are similar in the interior, where foraging habitats tend to be more ephemeral, than on the coast, where herons forage predominantly in tidal wetlands.

Furthermore, water diversions for human uses may increase the frequency of predators' access to heron nests if water levels drop or sites dry up until islands, marshes, or emergent trees and snags are no longer surrounded by water. Unless conservation of water improves greatly, competition for water will only increase as the human population expands. In agriculture, ironically, water-conservation measures may decrease the value of some crops to foraging waterbirds if there is a move to drip or sprinkler irrigation of crops that are currently flood irrigated.

Areas of California where overallocation of water supplies has been a particular problem in recent years include the Klamath Basin, Central Valley, and Salton Sea (summaries in Shuford 2010). Some of the potential threats previously identified in these regions have been realized. By 2014, the steady decline in the levels of the Salton Sea had forced the abandonment of the huge colony of Double-crested Cormorants and smaller colony of Great Blue Herons on Mullet Island; the cormorant colony had been by far the largest in the interior of California (Shuford 2014a) and the second largest in the Pacific states (Adkins et al. 2014). Similarly, some nearshore snags herons and egrets formerly used were out of the water in 2012 and no longer suitable for nesting; as of 2020, many snags have fallen and remaining ones are subject to disturbance as water levels have receded further (T. Anderson and S. Przeklasa née

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Haynes in litt.). Also, the Salton Sea's increasing salinity as its water levels drop will ultimately decimate the fish prey crucial to nesting waterbirds. Since our surveys in 2012 the decline in the sea's level has accelerated (waterdata.usgs.gov/ca/nwis/dv?referred_module=sw&site_no=10254005) and is projected to continue. Although the California populations of five species of ardeids appear to be stable or increasing, vigilance is essential as threats like these may increase with an expanding human population and changing climate.

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LITERATURE CITED

- Adkins, J. Y., Roby, D. D., Lyons, D. E., Courtot, K. N., Collis, K., Carter, H. R., Shuford, W. D., and Capitolo, P. J. 2014. Recent population size, trends, and limiting factors for the Double-crested Cormorant in western North America. *J. Wildl. Mgmt.* 78:1131–1142; doi.org/10.1002/jwmg.737.
- Belluomini, L. A. 1978. Statewide heron rookery inventory. Nongame Wildl. Investigations Rep., Proj. W-54-R-10, Job IV-1, Calif. Dept. Fish Game, Sacramento (available from Calif. Dept. Fish Wildl., P.O. Box 944209, Sacramento, CA 94244-2090).
- Bystrak, D. 1981. The North American Breeding Bird Survey. *Studies Avian Biol.* 6:34–41.
- Carter, H. R., McChesney, G. J., Jaques, D. L., Strong, C. S., Parker, M. W., Takekawa, J. E., Jory, D. L., and Whitworth, D. L. 1992. Breeding populations of seabirds in California, 1989–1991, vols. 1 and 2. Report to U.S. Fish Wildl. Serv., Dixon, CA; <https://farallones.noaa.gov/eco/seabird/pdf/news/journal/monitoringand-status.pdf>.
- Cavitt, J. F., Jones, S. L., Wilson, N. M., Dieni, J. S., Zimmerman, T. S., Doster, R. H., and Howe, W. H. 2014. Atlas of breeding colonial waterbirds in the interior western United States. Res. Rep., U.S. Fish Wildl. Serv., Denver; www.fws.gov/mountain-prairie/migbirds/species/birds/western_colonial/.
- Doster, R. H., and Shuford, W. D. 2018. Recent trends in population size and distribution of Ring-billed and California gulls in the western United States, *in* Trends and traditions: Avifaunal change in western North America (W. D. Shuford, R. E. Gill Jr., and C. M. Handel, eds.), pp. 161–179. *Studies of Western Birds* 3. W. Field Ornithol., Camarillo, CA; doi.org/10.21199/SWB3.8.
- Dunn, J. L., and Alderfer, J. 2017. Field Guide to the Birds of North America, 7th ed. Natl. Geogr., Washington, DC.
- Fleskes, J. P. 2012. Wetlands of the Central Valley of California and Klamath Basin, *in* Wetland Habitats of North America: Ecology and Conservation Concerns (D. Batzer and A. Baldwin, eds.), pp. 357–370. Univ. of Calif. Press, Berkeley.
- Fleskes, J. P., Casazza, M. L., Overton, C. T., Matchett, E. L., and Yee, J. L. 2018. Changes in the abundance and distribution of waterfowl wintering in the Central Valley of California, 1973–2000, *in* Trends and traditions: Avifaunal change in western North America (W. D. Shuford, R. E. Gill Jr., and C. M. Handel, eds.), pp. 50–74. *Studies of Western Birds* 3. W. Field Ornithol., Camarillo, CA; doi.org/10.21199/SWB3.2.

DISTRIBUTION OF CALIFORNIA HERON AND EGRET COLONIES

- Framer, W. E., Peters, D. D., and Pywell, H. R. 1989. Wetlands of the California Central Valley: Status and trends. Report of U.S. Fish Wildl. Serv., Portland, OR; catalog.hathitrust.org/Record/102513976.
- Grinnell, J., and Miller, A. H. 1944. The distribution of the birds of California. Pac. Coast Avifauna 27.
- Hickman, J. C. (ed.). 1993. The Jepson Manual: Higher Plants of California. Univ. of Calif. Press, Berkeley.
- Hothem, R. L., Brussee, B. E., and Davis, W. E., Jr. 2010. Black-crowned Night-Heron (*Nycticorax nycticorax*), in The Birds of North America Online (A. F. Poole, ed.), no. 74. Cornell Lab Ornithol., Ithaca, NY; doi.org/10.2173/bna.74.
- Hurlbert, A. H., Anderson, T. W., Sturm, K. K., and Hurlbert, S. H. 2007. Fish and fish-eating birds at the Salton Sea: A century of boom and bust. Lake Reservoir Mgmt. 23:469–499; doi.org/10.1080/07438140709354033.
- Jones, S. L. 2008. Western Colonial Waterbird Survey protocols. Report of U.S. Fish and Wild. Serv., Nongame Migratory Birds Coordinator's Office, Denver; www.fws.gov/mountain-prairie/migbirds/species/birds/western_colonial/.
- Kelly, J. P., and Condeso, T. E. 2014. Rainfall effects on heron and egret nest abundance in the San Francisco Bay area. Wetlands 34:893–903; doi.org/10.1007/s13157-014-0551-0.
- Kelly, J. P., and Robinson-Nilsen, C. 2011. Tidal marsh herons and egrets, in The State of the Birds, San Francisco Bay (M. Pitkin and J. Wood, eds.), pp. 14–15. PRBO Conservation Science and the San Francisco Bay Joint Venture; www.egret.org/sites/default/files/kelly_robinson-nilsen_2011_stateofthebirds_0.pdf.
- Kelly, J. P., Etienne, K., Strong, C., McCaustland, M., and Parkes, M. 2006. Annotated atlas and implications for the conservation of heron and egret nesting colonies in the San Francisco Bay area. ACR Tech. Rep. 90-3-17; www.egret.org/atlas.
- Kelly, J. P., Etienne, K., Strong, C., McCaustland, M., and Parkes, M. L. 2007. Status, trends, and implications for the conservation of heron and egret nesting colonies in the San Francisco Bay area. Waterbirds 30:455–478.
- Kelly, J. P., Millus, S. A., and Condeso, T. E. 2018. Nesting dynamics of four ardeid species at subregional scales: Recovery rates after sudden major declines in nest abundance. Waterbirds 41:223–237; doi.org/10.1675/063.041.0302.
- Kushlan, J. A., Steinkamp, M. J., Parsons, K. C., et al. 2002. Waterbird conservation for the Americas: The North American Waterbird Conservation Plan, version 1. Waterbird Conservation for the Americas, Washington, DC; www.fws.gov/migratorybirds/pdf/management/northamericawaterbirdconservationplan.pdf.
- Lehman, P. E. 2019. The Birds of Santa Barbara County, California, rev. ed.; www.sbcobirding.com/lehmanbosbc.html.
- Molina, K. C., and Shuford, W. D. 2013. Surveys of colonial nesting waterbirds at the Salton Sea in 2012. Report to the Imperial Irrigation District, P.O. Box 937, Imperial, CA 92251.
- Molina, K. C., and Sturm, K. K. 2004. Annual colony site occupation and patterns of abundance of breeding cormorant, herons, and ibis at the Salton Sea. Studies Avian Biol. 27:42–51.
- Ogden, L. E. 2013. Drone ecology. BioScience 63:776–776.
- Pacific Flyway Council. 2013. A monitoring strategy for the western population of Double-crested Cormorants within the Pacific Flyway. Pacific Flyway Council, U.S. Fish Wildl. Serv., Portland, OR; pacificflyway.gov/Documents/Dcc_monitoring.pdf.
- Pacific Flyway Council. 2018. A monitoring strategy for the western population of American White Pelicans: 2018 revision. Pacific Flyway Council, U.S. Fish Wildl. Serv., Portland, OR; pacificflyway.gov/Documents/Awp_monitoring.pdf.
- Pandolfino, E. R., and Handel, C. M. 2018. Population trends of birds wintering in the Central Valley of California, in Trends and traditions: Avifaunal change in

DISTRIBUTION OF CALIFORNIA HERON AND EGRET COLONIES

- western North America (W. D. Shuford, R. E. Gill Jr., and C. M. Handel, eds.), pp. 215–235. *Studies of Western Birds* 3. W. Field Ornithol., Camarillo, CA; doi.org/10.21199/SWB3.12.
- Patten, M. A., McCaskie, G., and Unitt, P. 2003. *Birds of the Salton Sea: Status, Biogeography, and Ecology*. Univ. of Calif. Press, Berkeley.
- Pratt, H. M. 1983. Marin County California heron colonies: 1967–1981. *W. Birds* 14:169–184.
- Pratt, H. M., and Winkler, D. W. 1985. Clutch size, timing of laying, and reproductive success in a colony of Great Blue Herons and Great Egrets. *Auk* 102:49–63.
- Robbins, C. S., Bystrak, D., and Geissler, P. H. 1986. *The Breeding Bird Survey: Its first fifteen years, 1965–1979*. Resource Publ. 157, U.S. Fish Wildl. Serv., Washington, DC.
- Sauer, J. R., Hines, J. E., Fallon, J. E., Pardieck, K. L., Ziolkowski, D. J., Jr., and Link, W. A. 2014. *The North American Breeding Bird Survey, results and analysis 1966–2012, version 02.19.2014*. U.S. Geol. Surv. Patuxent Wildl. Res. Center, Laurel, MD; www.mbr-pwrc.usgs.gov/bbs/bbs2012.shtml.
- Schlorff, R. W. 1982. Heronry inventory. Nongame Wildl. Investigations Rep., Proj. W-54-R-14, Job III-8, Calif. Dept. Fish Game, Sacramento; nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=40685.
- Seavy, N. E., and Reynolds, M. H. 2009. Seabird nest counts: A test of monitoring metrics using Red-tailed Tropicbirds. *J. Field Ornithol.* 80:297–302.
- Seto, N. W. H. 2008. Coordinated colonial waterbird inventory and monitoring in the western United States: Comprehensive breeding season surveys. U.S. Fish Wildl. Serv., Migratory Birds and Habitat Programs, Portland, OR; www.fws.gov/mountain-prairie/migbirds/species/birds/western_colonial/.
- Shuford, W. D. 2010. Inland-breeding pelicans, cormorants, gulls, and terns in California: A catalogue, digital atlas, and conservation tool. Wildl. Branch, Nongame Wildl. Program Rep. 2010-01. Calif. Dept. Fish Game, Sacramento; nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=24095 [minus digital atlas].
- Shuford, W. D. 2014a. Patterns of distribution and abundance of breeding colonial waterbirds in the interior of California, 2009–2012. Report to Calif. Dept. Fish Wildl. and U.S. Fish Wildl. Serv. (Region 8); www.fws.gov/mountain-prairie/migbirds/species/birds/western_colonial/.
- Shuford, W. D. 2014b. Coastal California (BCR 32) Waterbird Conservation Plan: Encompassing the coastal slope and Coast Ranges of central and southern California and the Central Valley. A plan associated with the Waterbird Conservation for the Americas initiative; www.centralvalleyjointventure.org/assets/pdf/BCR32_WaterbirdCon_interactive_10FEB14.pdf.
- Shuford, W. D., and Dybala, K. E. 2017. Conservation objectives for wintering and breeding waterbirds in California's Central Valley. *San Francisco Estuary Watershed Sci.* 15(1): article 4; doi.org/10.15447/sfews.2017v15iss1art4.
- Shuford, W. D., Page, G. W., and Kjelson, J. E. 1998. Patterns and dynamics of shore-bird use of California's Central Valley. *Condor* 100:227–244; doi.org/10.2307/1370264.
- Shuford, W. D., Warnock, N., Molina, K. C., and Black, A. E. 2000. Avifauna of the Salton Sea: Abundance, distribution, and annual phenology. Final report for EPA contract R826552-01-0 to the Salton Sea Authority, 78401 Highway 111, La Quinta, CA 92253.
- Shuford, W. D., Thompson, D. L., Mauser, D. M., and Beckstrand, J. 2006. Abundance and distribution of nongame waterbirds in the Klamath Basin of Oregon and California from comprehensive surveys in 2003 to 2004. Final report to U.S. Fish Wildl. Serv., Klamath Basin Natl. Wildl. Refuge Complex, 4009 Hill Rd., Tulelake, CA 96134.
- Shuford, W. D., Humphrey, J. M., Hansen, R. B., Page, G. W., Stenzel, L. E., and

DISTRIBUTION OF CALIFORNIA HERON AND EGRET COLONIES

- Hickey, C. M. 2007. Summer distribution, abundance, and habitat use of Black-necked Stilts and American Avocets in California's Central Valley. *W. Birds* 38:11–28.
- Shuford, W. D., Sesser, K. A., Strum, K. M., Haines, D. B., and Skalos, D. A. 2016. Numbers of terns breeding inland in California: Trends or tribulations? *W. Birds* 47:182–213; doi.org/10.21199/WB47.3.1.
- Steinkamp, M., Peterjohn, B., Byrd, V., Carter, H., and Lowe, R. 2003. Breeding season survey techniques for seabirds and colonial waterbirds throughout North America. Draft 13 February 2003; www.bu.edu/scscb/working_groups/resources/steinkamp-survey-techniques.pdf.
- Swain, D. L. 2015. A tale of two California droughts: Lessons amidst record warmth and dryness in a region of complex physical and human geography. *Geophys. Res. Lett.* 42:9999–10,003; doi.org/10.1002/2015GL066628.
- Swain, D. L., Langenbrunner, B., Neelin, J. D., and Hall, A. 2018. Increasing precipitation volatility in twenty-first century California. *Nat. Clim. Change* 8:427–433; doi.org/10.1038/s41558-018-0140-y.
- Unitt, P. 2004. San Diego County bird atlas. *Proc. San Diego Soc. Nat. Hist.* 39.
- Velasco, C. A. 2013. From rural to urban: The creation of water markets, agriculture and farmworkers in California's Imperial Valley. M. S. thesis, Columbia Univ., New York; doi.org/10.7916/D88K7H7C.
- Wang, S.-Y. S., Yoon, J.-H., Becker, E., and Gillies, R. 2017. California from drought to deluge. *Nat. Clim. Change* 7:465–468; doi.org/10.1038/nclimate3330.
- Williams A. P., Cook, E. R., Smerdon, J. E., Cook, B. I., Abatzoglou, J. T., Bolles, K., Baek, S. H., Badger, A. M., and Livneh, B. 2020. Large contribution from anthropogenic warming to an emerging North American megadrought. *Science* 368:314–318; doi.org/10.1126/science.aaz9600.

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