

LONG-TERM VARIATION IN BREEDING POPULATIONS OF COLONIALY NESTING CORMORANTS AND HERONS IN A SEVERELY IMPAIRED ECOSYSTEM AT CLEAR LAKE, CALIFORNIA

FLOYD E. HAYES^{1,5}, BRYAN J. MCINTOSH², DOUGLAS E. WEIDEMANN¹, BRAD J. BARNWELL³,
AND DONNA MACKIEWICZ⁴

¹Department of Biology, Pacific Union College, 1 Angwin Avenue, Angwin, California 94508

²3736 Gard Street, Kelseyville, California 95451

³Post Office Box 554, Lakeport, California 95453

⁴Post Office Box 1612, Clearlake Oaks, California 95423

⁵Corresponding author; e-mail: floyd_hayes@yahoo.com

Abstract.—Clear Lake, a large and shallow lake in Lake County, northern California, USA, is highly eutrophic and severely impaired by human activities. We studied populations of colonialy breeding Double-crested Cormorants (*Nannopterum auritum*), Great Blue Herons (*Ardea herodias*), Great Egrets (*Ardea alba*), and Black-crowned Night-Herons (*Nycticorax nycticorax*) by counting nests at Clear Lake and associated wetlands during 2006–2024 and compiled historical data (1993–2000). We found 10 colony sites, some subsequently abandoned and others recently colonized. Breeding populations of Double-crested Cormorant and Great Blue Heron declined during 1993–2024, but populations of the former increased and the latter were stable during 2011–2024. Populations of Great Egret and Black-crowned Night-Heron were stable during 2009–2024. The number of nests for all species was unaffected by water level. The causes of long-term population declines are unknown. Future monitoring is needed to better understand long-term trends and the environmental drivers of change.

Key Words.—Ardeidae; *Ardea alba*; *Ardea herodias*; coloniality; nesting; *Nannopterum auritum*; *Nycticorax nycticorax*; Phalacrocoracidae

INTRODUCTION

Located in the coastal ranges of northern California, USA, at an elevation of 402 m above sea level, Clear Lake (38°56'46" to 39°07'23"N, 122°38'04" to 122°54'46"W), in Lake County, is considered the oldest natural freshwater lake in North America (Sims 1988). Although relatively large with a surface area of 176.7 km² and 114 km of shoreline, it is relatively shallow, averaging 8.1 m deep with a maximum depth of 18.4 m (Horne and Goldman 1972). Because of its shallow depth, Clear Lake represents a polymictic and highly eutrophic lacustrine ecosystem with an abundance of nutrients that nourish cyanobacterial and algal blooms, especially during the warm summer months (Goldman and Wetzel 1963; Richerson et al. 1994; Winder et al. 2010), and an abundance of zooplankton and higher trophic level organisms, including many species of fish (Thompson et al. 2014) and waterbirds (Cooper 2004).

Clear Lake and its adjacent wetlands are severely impaired by a long history of human activities, including contamination of mercury (Hg) from a nearby mine, invasive species of aquatic plants and fishes, applications of herbicides and pesticides to control plant and animal pests, loss of wetlands due to modification and reclamation for agriculture and urban development, and cultural eutrophication from excessive nutrient loading (see reviews by Richerson et al. 2000, 2008; Suchanek et al. 2003; Thomson et al. 2013; Smith et al. 2023). In 1949, 1954, and 1957, massive amounts of the organochlorine

pesticide dichlorodiphenyldichloroethane (DDD) were dumped in the lake in an attempt to control aquatic larvae of the Clear Lake Gnat (*Chaoborus astictopus*; Hunt and Bischoff 1960). Shortly after the second and third applications, large numbers of dead Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*) were found along the shoreline. Subsequent studies revealed elevated concentrations of DDD in the tissues of several fishes, frogs, and the piscivorous grebes, providing the first documented instance of biomagnification in which toxic chemicals accumulated in increasingly higher concentrations from lower to higher trophic level organisms (Hunt and Bischoff 1960; Carson 1962; Rudd 1964).

Although the devastating effects of DDD on the grebes of Clear Lake are well documented, resulting in mass mortality of adults and cessation of breeding followed by a gradual multidecadal recovery of their breeding populations (Hayes et al. 2022), the impact of DDD on other piscivorous birds, including cormorants and herons, has not been determined. In March 1895, Chamberlin (1895) described a breeding colony of about 100 Double-crested Cormorant (*Nannopterum auritum*) nests in the vicinity of Reeves Point and a second immense colony stretching across what he estimated as half a mile of shoreline south of The Narrows, providing the only data on its breeding population prior to the application of DDD. No information is available on pre-DDD populations of colonialy breeding herons. After describing the demise of the grebes of Clear

Lake following the application of DDD, Rudd (1964) thought that populations of egrets and herons also were lower than in former years but did not provide any data. The first post-DDD surveys of breeding populations of cormorants and herons at Clear Lake occurred during 1993–1994 as part of a study of biomagnification of DDD and Hg in birds and mammals (Wolfe and Norman 1998). Additional surveys were conducted during 1995–1996, 1998–2000 (for Double-crested Cormorant only during 1995–1996 and 1998–2000), and 2009–2012 (the latter surveys with data we supplied; Shuford 2010, 2014; Shuford et al. 2020a,b), and the nesting of Great Blue Heron in different colonies was briefly summarized by Lyons (2023). These surveys revealed large numbers of breeding Double-crested Cormorants, Great Blue Herons (*Ardea herodias*), and Black-crowned Night-Herons (*Nycticorax nycticorax*), and smaller numbers of Great Egrets (*Ardea alba*).

Given the potential threats of habitat loss, water diversions, introduced species, bioaccumulation and biomagnification of toxic chemicals, climate change, and other threats to waterbirds, monitoring their populations and habitats is crucial for evaluating their conservation status, detecting long-term population trends, assessing habitat quality, and documenting the effects of environmental changes and management practices on waterbirds (Kushlan et al. 2002). We summarize long-term variation in breeding populations of cormorants and herons at Clear Lake based on data from previously published surveys during 1993–2000 and new surveys during 2006–2024. We discuss the potential causes of variation and provide suggestions for future monitoring.

METHODS

Study area.—Clear Lake has three major arms (Fig. 1). Major wetlands occur along large tributaries at the northwest end of the lake (Middle Creek and Rodman Slough), at its outlet at the southeast end of the lake (Anderson Marsh and Cache Creek), and in many shallow areas along the margins of the lake, especially at the mouths of small tributaries (Fig. 1). Riparian forests dominated by willows (*Salix* spp.), Valley Oak (*Quercus lobata*), Fremont Cottonwood (*Populus fremontii*), and California Sycamore (*Platanus racemosa*) occur along the shores of tributaries and portions of the lake, providing nesting habitat for cormorants and herons. Urban development occurs along the shore in several areas of the lake, but not at Rodman Slough, Anderson Marsh, and most of Cache Creek. Recreational boating and fishing are extremely popular, with dozens or hundreds of watercraft on the lake daily during fair weather.

Precipitation occurs mostly during October to May and rarely during June to September (Suchanek et al. 2008), with the water level typically highest during February to April, declining during summer, and lowest October to December (De Leon and Deligiannis 2022).

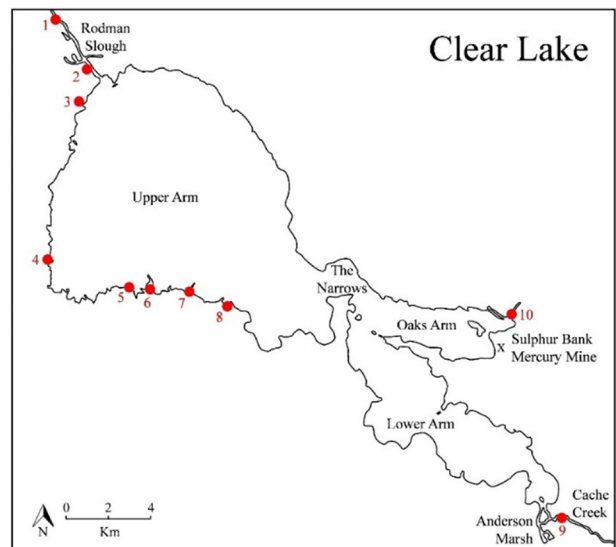


FIGURE 1. Map of Clear Lake, California, and associated wetlands with locations of 10 colony sites of breeding cormorants and herons indicated by red circles. See Table 1 for the number, name, and characteristics of each colony site.

The level of Clear Lake is measured in reference to the Rumsey gauge, which was established by Captain Rumsey at Lakeport in 1873. Zero Rumsey is considered the natural low water level of Clear Lake. Zero Rumsey is equal to 401.805 m (1,318.257 ft) above mean sea level. A full lake, by definition, is reached when the lake measures 2.30 m (7.56 ft) on the Rumsey gauge (<https://www.lakecountyca.gov/DocumentCenter/View/4336/Historical-High-and-Low-Water-Levels-of-Clear-Lake-PDF>). Water level at Lakeport (west shore of Upper Arm) varied dramatically since monitoring of breeding cormorants and herons began in 1993, ranging from 3.22 m (10.58 ft) Rumsey in 2017 to -0.835 m (-2.74 ft) Rumsey in 2022 (Fig. 2), but well within the historical extremes of -1.07 m (-3.50 ft) Rumsey in 1920 and 4.16 m (13.66 ft) Rumsey in 1890 (Suchanek et al. 2003; De Leon and Deligiannis 2022).

Breeding surveys.—During 2006 to 2024, we intermittently searched for breeding colonies of cormorants and herons along the shores of Clear Lake, adjacent tributaries, and the outlet. We did not search any of the colony sites annually, with some searched during more years than others, and some searched up to 10 times within a breeding season. We made visual surveys from a canoe, motorboat, or from land during the breeding season, from 1 January to 14 June, but mostly in late March and throughout April. During each survey we counted or estimated the number of active nests as a measure of reproductive effort (no data were obtained on reproductive success, such as the number of nestlings), and we identified the species that constructed and attended each nest, usually with the aid of binoculars or a telescope. Obtaining an exact count was often difficult due to nests hidden in the foliage and branches of trees,

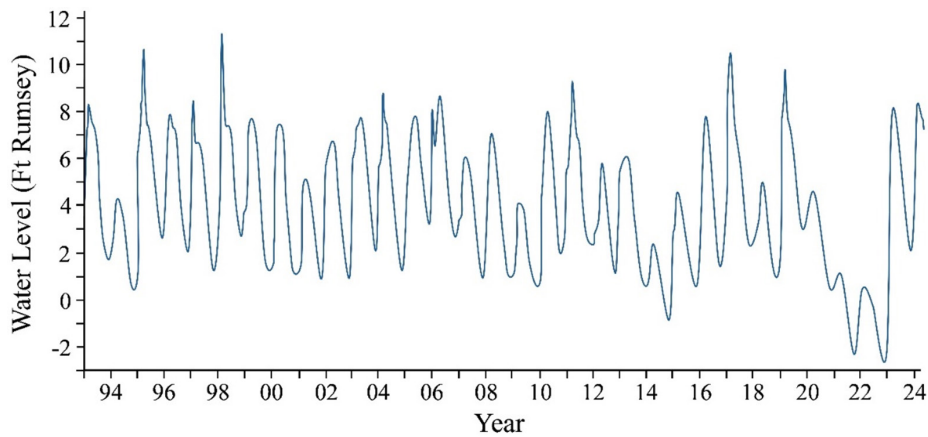


FIGURE 2. Water level at Lakeport, Clear Lake, California, from January 1993 through May 2024. Water level at Clear Lake has historically been measured as number of feet Rumsey (see Methods for definition of this measurement).

especially during April to June. For sites surveyed multiple times, we used the count with the highest number of nests as our measure of reproductive effort. We considered clusters of nests with gaps of less than 1 km from the nearest cluster of nests sub colonies of a single colony. Priority in naming colony sites was given to established names for prominent topographic features rather than urban developments (the latter are more likely to change over time). We obtained coordinates of the approximate center of each colony site from Google Earth (<http://www.google.com/earth>).

Statistical analyses.—We obtained water level data during the study period from the U.S. Geological Survey (http://waterdata.usgs.gov/ca/nwis/uv?site_no=11450000). To examine the relationship between water level and reproductive effort, we used the water level (ft Rumsey) on 15 March (early in the breeding season, when many birds were still deciding when and where to nest) for each year and the total number of nests in all colonies combined during years in which the major colonies of each species were all monitored in Rodman Slough, the Upper Arm, and Cache Creek, including previously published data from 1993–2000. We used Linear Regression (Zar 2010) to regress the number of nests against the independent variables year and water level, separately, for each species (sample sizes were too small to use multiple regression). We used Statistix 10 software (Analytical Software, Tallahassee, Florida) for all descriptive statistics and inferential statistical tests with an $\alpha = 0.05$.

RESULTS

Colony site dynamics.—Colonially breeding cormorants and herons nested in 10 distinct colony sites: two exclusively in the largest tributary of the lake (Upper Rodman Slough and Lower Rodman Slough), seven along the shores of the lake or nearby in small tributaries, and one in the outlet of the lake, Cache Creek (Fig. 1,

Table 1). Four colony sites (Reeves Point, Quercus Point, Cache Creek, and Clearlake Oaks Wetlands) hosted all four study species; the other six sites hosted one to three species (Fig. 3, Tables 1–2). Several colony sites had distinct sub colonies separated by gaps of several hundred meters, including Willow Point (Library Park and Willow Point), Reeves Point (Reeves Point and mouth of Adobe Creek), Long Tule Point (McGaugh Slough and Shirley Slough), and Cache Creek (west and east sections).

Excluding the years 1995–2000, when Shuford (2010, 2014) surveyed some colony sites for cormorants but not herons, two colony sites, Long Tule Point and Cache Creek, were active each year surveyed for 14 y and one site, Quercus Point, was active each year surveyed for 10 y. Two colony sites, Upper Rodman Slough and Lower Rodman Slough, were abandoned without being reused during the study period. Upper Rodman Slough was active each year (although one year was not monitored) from 2011–2019, but no nests were found in 2024, and Lower Rodman Slough was active each year during 2011–2014 but not during 2016–2019 or 2024. Two colony sites, Willow Point and Reeves Point, were intermittently active and inactive. Three recently discovered colony sites were either previously overlooked or represented new colonizations. We detected the Lyons Creek colony site in 2024; if not previously overlooked, it may have been established by Great Blue Herons previously nesting 3.4 km away at Upper Rodman Slough. The Kelsey Creek colony site was first colonized by a single pair of Great Blue Herons in 2021 in an area frequented by birders (including ourselves) who had not seen it during the previous 15 y. We first detected nests at Clearlake Oaks Wetlands in 2020, but we may have previously overlooked these nests. The latter two colony sites remained active annually with an increasing number of nests through 2024.

Species accounts.—The Double-crested Cormorant nested at six colony sites (Table 2) with a maximum

TABLE 1. Colony sites for breeding cormorants and herons at Clear Lake and associated wetlands, including site number corresponding with Figure 1, coordinates (decimal degrees north, west), years surveyed, years active, and species nesting (BCNH = Black-crowned Night-Heron, *Nycticorax nycticorax*; DCCO = Double-crested Cormorant, *Nannopterum auritum*; GBHE = Great Blue Heron, *Ardea herodias*; GREG = Great Egret, *Ardea alba*). Notes and references are a - surveys reported by Wolfe and Norman (1998), b - referred to as Library Park (Shuford 2014), c - surveys reported by Shuford (2014) and Shuford et al. (2020b), referred to as Mouth of Holiday Cove, d - surveys reported by Shuford (2014), e - referred to as east of Quercus Point for Double-crested Cormorant and west of Clear Lake State Park for Great Blue Heron (Shuford 2014, Shuford et al. 2020b), f - surveys reported by Wolfe and Norman (1998), referred to as Slater Island, and g - surveys reported by Shuford (2014) and Shuford et al. (2020b), referred to as Slater Island, Anderson Marsh.

Colony	Coordinates	Years surveyed	Years active	Species
1. Upper Rodman Slough	39.1372, -122.9025	1993–1994a, 2011–2014, 2016–2019, 2024	1993–1994, 2011–2014, 2016–2019	DCCO, GBHE, GREG
2. Lower Rodman Slough	39.1214, -122.8914	2011–2014, 2016–2019, 2024	2011–2014	GREG
3. Lyons Creek	39.1058, -122.8974	2024	2024	GBHE
4. Willow Point	39.0425, -122.9136	2009–2019b, 2024	2009–2016, 2024	BCNH
5. Reeves Point	39.0275, -122.8794	1998–2000c, 2006, 2008–2012, 2014, 2018–2019, 2024	1999–2000, 2006, 2008–2009, 2018–2019, 2024	BCNH, DCCO, GBHE, GREG
6. Long Tule Point	39.0258, -122.8577	1999d, 2006, 2008–2019, 2024	2006, 2008–2019, 2024	DCCO, GBHE
7. Quercus Point	39.0275, -122.8378	1993–1996e, 1998–2000e, 2006, 2008–2011e, 2024	1993–1998, 2000, 2008–2011	BCNH, DCCO, GBHE, GREG
8. Kelsey Creek	39.0203, -122.8158	2006–2024	2021–2024	GBHE
9. Cache Creek	38.9325, -122.6342	1993–1994f, 1999g, 2009–2019g, 2024	1993–1994, 1999, 2009–2019, 2024	BCNH, DCCO, GBHE, GREG
10. Clearlake Oaks Wetlands	39.0175, -122.6611	2020–2024	2020–2024	BCNH, DCCO, GBHE, GREG

count at a single site of 210 nests at Quercus Point during 1993 or 1994 (year not specified; Wolfe and Norman 1998), where we never detected nesting during 2006–2024. Our highest count at a single site was 100 nests at Reeves Point in 2006. Nesting activity began as early as 1 January and peaked in April (Appendix). Our maximum annual count for the lake was 101 nests in four sites in 2024, considerably lower than the 375 nests at three colony sites in 2000 (Shuford 2010). There was a significant negative relationship in the annual number of nests at all major colony sites combined from 1994–2024 (slope = -6.6, $F_{1,12} = 10.75$, $P = 0.007$, $r^2 = 0.47$, $n = 14$ y of data). The number of nests at all major colony sites combined for this species increased significantly for our surveys from 2011–2024 (slope = 5.5, $F_{1,7} = 12.48$, $P = 0.010$, $r^2 = 0.64$, $n = 9$ y; Fig. 4).

The Great Blue Heron nested at eight colony sites (Table 2) with a maximum count at a single site of 121 nests at Upper Rodman Slough in 1993 (Wolfe and Norman 1998), surpassing our highest count of 85 nests at Long Tule Point in 2010. Nesting activity began as early as 6 January and peaked in April (Appendix). The maximum annual count for the lake was 286 nests in three colony sites in 1992 (Wolfe and Norman 1998), exceeding our highest count of 191 in three sites in 2012. The annual number of nests at all major colony sites combined decreased significantly from 1993–2024 (slope = -6.3, $F_{1,9} = 15.73$, $P = 0.003$, $r^2 = 0.64$, $n = 11$ y), but there was no significant relationship during our surveys from 2011–2024 ($F_{1,7} = 2.89$, $P = 0.133$; $n = 9$ y; Fig. 4).

The Great Egret nested at six colony sites (Table 2) with a maximum count at a single site of 20 nests at Cache Creek and our maximum annual count for the lake of 27 nests at three colonies in 2018. Nesting activity began as early as 1 March and peaked in May (Appendix). Despite reporting large numbers of Great Blue Heron nests, Wolfe and Norman (1998) did not report this species nesting at Clear Lake, but it is unclear if they were absent or unreported. The annual number of nests at all major colony sites combined from 2011–2024 did not change significantly ($F_{1,7} = 1.88$, $P = 0.213$; $n = 9$ y; Fig. 4).

The Black-crowned Night-Heron nested at five colony sites (Table 2), with a maximum count at a single site of 102 nests at Willow Point in 2016 and a maximum annual count for the lake of 109 nests at two sites in 2024. Nesting occurred during April to June, peaking later than other heron species (Appendix). Wolfe and Norman (1998) reported only three nests at Quercus Point in 1993 or 1994 (year not specified), where we never detected nesting, but they may not have visited Willow Point. This species was the only heron nesting at Willow Point, with annual counts of 32–104 nests during 2009–2016, mostly at Library Park with smaller numbers within three city blocks to the west and at a campground just south of the park. No nests were detected during 2017–2019, however, when the loud cries of a raptor were broadcast from loudspeakers in trees at Library Park to discourage herons from nesting. We did not survey the colony site during 2020–2023, but of 95 nests we counted in 2024, only one was in Library Park, where no raptor calls were broadcast, while all others were about 150 m to the

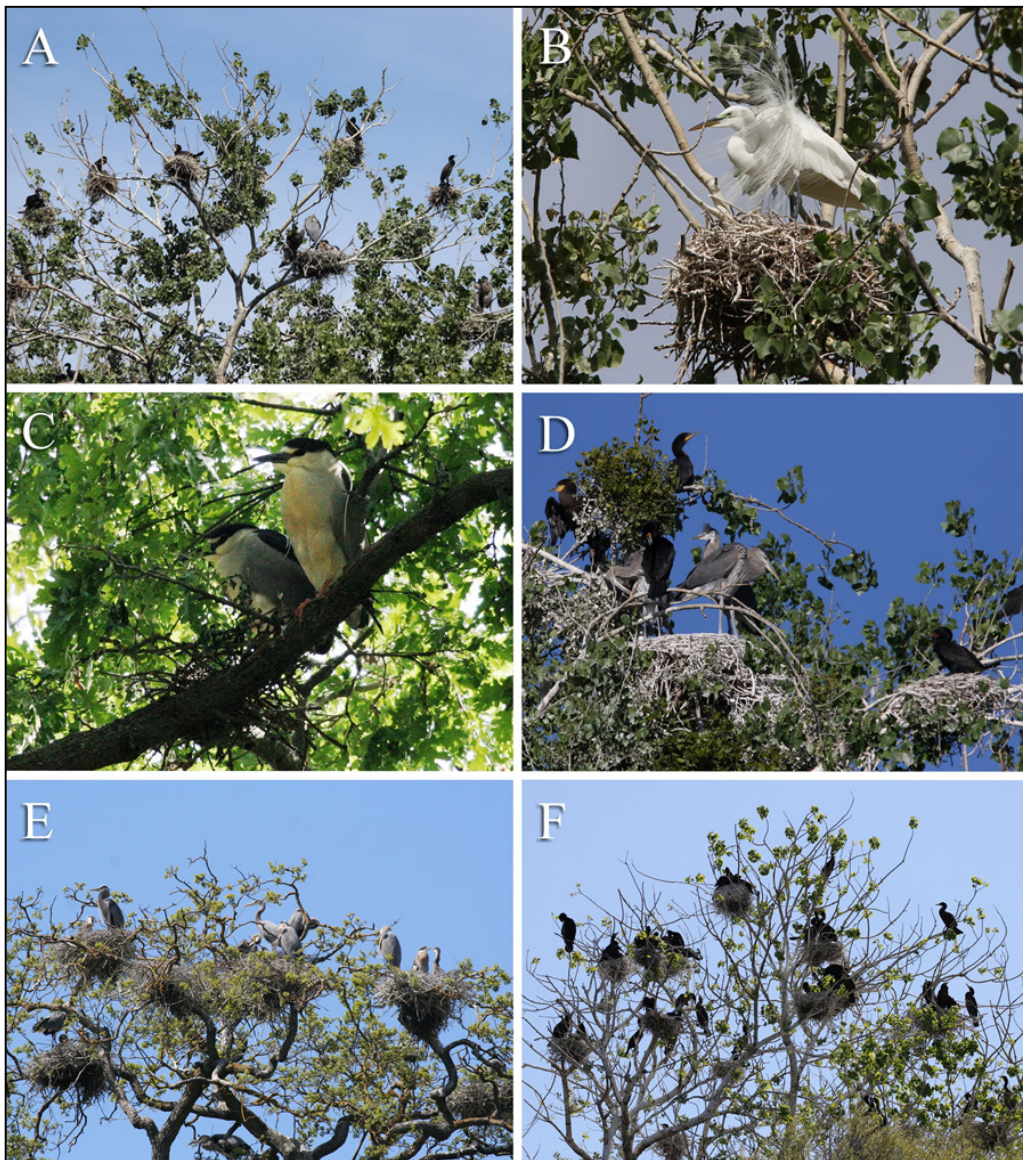


FIGURE 3. Bird species (BCNH = Black-crowned Night-Heron, *Nycticorax nycticorax*; DCCO = Double-crested Cormorant, *Nannopterum auritum*; GBHE = Great Blue Heron, *Ardea herodias*; GREG = Great Egret, *Ardea alba*) nesting at different colony sites at Clear Lake, California, and associated wetlands. **(A)** DCCO and GBHE at Upper Rodman Slough, 24 April 2016. **(B)** GREG at Upper Rodman Slough, 30 May 2017. **(C)** BCNH at Willow Point, 5 May 2012. **(D)** DCCO and GBHE at Reeves Point, 12 May 2017. **(E)** DCCO and GBHE at Long Tule Point, 24 April 2010; **(F)** DCCO at Clearlake Oaks Wetlands, 11 April 2024. (A, C, E, F photographed by Floyd E. Hayes, B and D by Brad J. Barnwell).

south in a campground. The annual number of nests at all major colony sites of Black-crowned Night Herons combined from 2009–2024 did not change significantly ($F_{1,10} = 0.04$, $P = 0.849$, $n = 11$ y; Fig. 4). The annual number of nests at all major colony sites combined and water level were not significantly related for any species ($F_{1,7-12} = 0.02-1.17$, $P = 0.300-0.900$; $n = 9-14$ y).

DISCUSSION

Despite the limitations of our surveys (not all colony sites surveyed annually, surveys occurring at different stages of the breeding season, and more than one survey in

a breeding season for some colony sites), our data reveal considerable fluctuations in the presence and number of nests of each species at each colony site. The higher numbers of Double-crested Cormorant and Great Blue Heron nests in 1993 and 1994 (Wolfe and Norman 1998) compared with our surveys during 2006–2024 revealed a significant decrease in the number of nests for each of these species, in contrast with the dramatic increase in breeding populations of the Western Grebe and Clark’s Grebe during 1992–2019 (Hayes et al. 2022). The large numbers of nesting Double-crested Cormorants in 1895 (Chamberlin 1895) suggest that its breeding population prior to the 20th Century was even higher. These negative

TABLE 2. Number of years surveyed and active, mean (SD) number of nests, and range for breeding cormorants and herons at different colony sites at Clear Lake and associated wetlands during 1993–2024. Notes and references are a - includes 1999 (Shuford 2014, Shuford et al. 2020b), b - includes 1993–1994 (uncertain which year; Wolfe and Norman 1998), 1998, and 1999 (Shuford 2014, Shuford et al. 2020b), c - includes 1993 and 1994 (Wolfe and Norman 1998), d - includes 1993–1994 (uncertain which year; Wolfe and Norman 1998).

Species and colony site	Years surveyed	Years active	Mean (SD)	Range
Double-crested Cormorant				
Upper Rodman Slough	9	7	22.7 (21.6)	0–53
Reeves Point a	13	8	37.6 (59.4)	0–200
Long Tule Point a	17	6	15.4 (27.4)	0–100
Quercus Point b	12	5	67.5 (89.5)	0–210
Cache Creek a	14	4	3.1 (6.8)	0–22
Clearlake Oaks Wetlands	5	5	26.4 (7.8)	21–40
Great Blue Heron				
Upper Rodman Slough c	11	10	39.0 (37.8)	0–121
Lyons Creek	1	1	15	—
Reeves Point	10	5	6.0 (9.0)	0–27
Long Tule Point	14	14	34.6 (32.4)	1–85
Quercus Point c	8	6	19.9 (36.6)	0–100
Kelsey Creek	18	4	0.6 (1.9)	0–8
Cache Creek c	14	14	36.0 (17.7)	8–65
Clearlake Oaks Wetlands	5	5	9.4 (3.4)	6–14
Great Egret				
Upper Rodman Slough	9	5	3.8 (5.5)	0–15
Lower Rodman Slough	9	4	3.0 (5.2)	0–16
Reeves Point	10	2	1.3 (2.8)	0–7
Quercus Point	6	1	0.2 (0.4)	0–1
Cache Creek	12	11	7.1 (5.8)	0–20
Clearlake Oaks Wetlands	5	1	1.0 (2.2)	0–5
Black-crowned Night-Heron				
Willow Point	12	9	47.4 (37.5)	0–102
Reeves Point	11	1	0.5 (1.5)	0–5
Quercus Point d	7	1	0.4 (1.1)	0–3
Cache Creek	12	2	0.8 (1.8)	0–5
Clearlake Oaks Wetlands	5	1	2.2 (4.9)	0–11

trends contrast with the relatively stable or increasing populations of breeding Double-crested Cormorants and Great Blue Herons in the San Francisco Bay region and elsewhere in California (Kelly et al. 2007; Capitolo et al. 2019; Rauzon et al. 2019; Shuford et al. 2020a,b). If the two long-term trends are genuine rather than artifacts of a small sample size from a population that varies stochastically over time, we do not understand the environmental drivers of these trends.

Because breeding population surveys of cormorants and herons did not begin until more than four decades after the last application of DDD on Clear Lake, the immediate and short-term effects of DDD are unknown. Although DDD concentrations in feathers, tissues, and

eggs of grebes at Clear Lake steadily declined in the 1960s and early 1970s (Craig and Rudd 1974), no such studies were conducted on cormorants and herons at the lake until 1993–1994, when much lower and sublethal concentrations of DDD and dichlorodiphenyldichloroethylene (DDE, resulting from the breakdown of the related pesticide dichlorodiphenyltrichloroethane or DDT) were found in the tissues of the Double-crested Cormorant and Great Blue Heron (Wolfe and Norman 1998). These studies revealed a gradual multidecadal decline in the organochlorine pesticides in the lake, which clearly did not contribute to the recent declines of Double-crested Cormorants and Great Blue Herons since 1993.

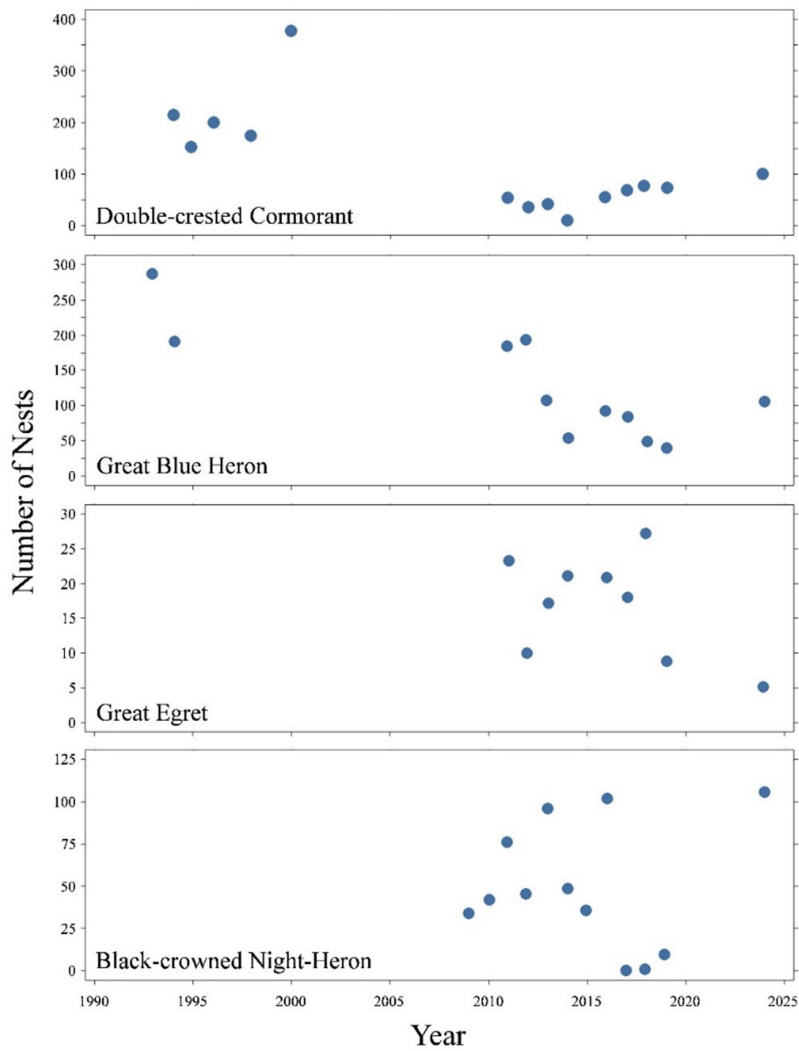


FIGURE 4. Total number of nests per breeding season for Double-crested Cormorant (*Nannopterum auritum*), Great Blue Heron (*Ardea herodias*), Great Egret (*Ardea alba*), and Black-crowned Night-Heron (*Nycticorax nycticorax*), during years when all major colonies in Rodman Slough, Upper Arm, and Cache Creek, Clear Lake, California, were surveyed during 1993–2024.

Mercury (Hg) contamination may also have adversely impacted breeding cormorants and herons. Hg was mined intermittently from the nearby Sulphur Bank Mercury Mine (Fig. 1) during 1872–1957, with increased seepage into the lake after large-scale open pit mining began in 1927 (Suchanek et al. 2000, 2008). Elevated but sublethal Hg concentrations were found in the tissues and feathers of Double-crested Cormorants and Great Blue Herons at Clear Lake in 1993 (Cahill et al. 1997, 1998; Wolfe and Norman 1998), but the growth rates of Great Blue Heron nestlings did not differ from nestlings at other locations uncontaminated with Hg (Wolfe and Norman 1998), suggesting that reproductive effort and success were unaffected by Hg. Hg concentrations in the feathers of another piscivorous bird at Clear Lake, the Western Grebe, declined precipitously from 1967–1969 to 1992, but marked fluctuations occurred in the feathers of the Western Grebe and another piscivorous bird, the Osprey (*Pandion haliaetus*), during 1992–2006,

perhaps due to population fluctuations of their fish prey (Anderson et al. 2008; Eagles-Smith et al. 2008). Hg is presumably declining in cormorants and herons at the lake and is unlikely to have contributed to the decline of breeding Double-crested Cormorants and Great Blue Herons since 1993.

Habitat loss may have reduced the carrying capacity of breeding cormorants and herons. An estimated 85% of the natural wetlands of Clear Lake have been destroyed (Richerson et al. 1994; Suchanek et al. 2003), but we are unaware of any major wetland losses in recent decades. At Clear Lake, cormorants and herons depend on tall, broad-leaved trees for nesting, but no major loss of trees has occurred at any of the 10 colony sites. Thus, habitat loss is unlikely to have contributed to the recent declines since 1993 of breeding Double-crested Cormorants and Great Blue Herons.

Population fluctuations of fish species preyed upon by cormorants and herons potentially affect the

breeding populations. Several dramatic fluctuations in fish populations in Clear Lake have been documented, driven in part by the introduction of exotic species and cold winter temperatures during some years (Eagles-Smith 2008; Thompson et al. 2014). It is possible that the high numbers of nesting Double-crested Cormorant and Great Blue Heron on Clear Lake during 1993–1994 (Wolfe and Norman 1998) were the consequence of a population spike of their fish prey. The Mississippi Silverside (*Menidia audens*) and Threadfin Shad (*Dorosoma petenense*) are small, introduced species that could be a large component of the diet of these birds. Populations of these two abundant fish species, however, were relatively low during 1993–1994 (Eagles-Smith et al. 2008). Unfortunately, no published data are available on their populations since 2004, so we cannot assess the impact of fluctuating fish populations on breeding populations of cormorants and herons.

Cyanobacterial and algal blooms occur frequently during the warm summer months on Clear Lake (Smith et al. 2023) and can affect the spatial distribution of fish populations, especially during episodes of hypoxia. Several studies have documented the avoidance of hypoxia by fish at Clear Lake (Feyrer et al. 2020; Stang 2020; Cortés et al. 2021), which could reduce the availability of fish for piscivorous birds if they move farther from a colony, increasing the energetic expense of foraging. Hypoxia may explain why grebes occasionally abandon their colonies at Clear Lake (Hayes et al. 2022), but the breeding season of cormorants and herons at Clear Lake peaks in April and early May, with most nestlings fledging by the end of May, usually before hypoxic conditions occur.

Fluctuating water levels may affect the distribution of nesting colonies and reproductive effort. Lower water levels exacerbate cyanobacterial and algal blooms, creating more hypoxic conditions as discussed above. Lower water levels may also concentrate fish and other aquatic prey, however, which may be captured more efficiently, potentially increasing the number of nesting pairs. At Clear Lake, colonies of the Western Grebe and Clark's Grebe, which construct floating nests, are more likely to nest in marshes, especially in associated wetlands, when the water level is high, but the number of nests per breeding season was unrelated to water level (Hayes et al. 2022). The breeding season of cormorants and herons at Clear Lake coincides with relatively high-water levels, which decline as the breeding season progresses. Our data demonstrate that the number of cormorant and heron nests was unrelated to water level.

Undetected natural or anthropogenic disturbances may adversely affect the reproductive effort and success of cormorants and herons. Increases in the volatility or amount of rainfall adversely affects reproductive effort of herons in the San Francisco Bay area (Kelly and Condeso 2014) and likely impact their breeding in Clear

Lake as well. Several species of birds and mammals prey on the eggs or nestlings of herons and cormorants in the San Francisco Bay area, where the Common Raven (*Corvus corax*) is the dominant predator (Hothem and Hatch 2004; Kelly et al. 2005, 2007; Brussee et al. 2016; Carle et al. 2017). Although we never observed predation on eggs or nestlings of breeding cormorants or herons at Clear Lake, the American Crow (*Corvus brachyrhynchos*) is the dominant diurnal predator and the Northern Raccoon (*Procyon lotor*) is the dominant nocturnal predator of Western Grebe and Clark's Grebe eggs at Clear Lake (Hayes et al. 2022). The raven, crow, and raccoon are human commensals with increasing populations (Marzluff et al. 2001; Kelly et al. 2002; Prange et al. 2003) and may adversely affect reproductive effort and success of cormorants and herons. Frequent disturbances or even shooting by humans could also reduce breeding populations, although we are unaware of any such incidents.

In conclusion, the apparent decline in breeding populations of Double-crested Cormorant and Great Blue Heron since 1993 is difficult to understand. Our data represent a historical baseline for future comparisons. Future monitoring of breeding cormorants and herons, as well as their habitat and prey, is needed to better understand long-term trends and the environmental drivers of change in their breeding populations, especially when new threats emerge, such as the introduction of freshwater mussels (MacIsaac 1996; Nalepa and Schloesser 2014; Karatayev et al. 2015). Such monitoring should occur on an annual basis, preferably more than once per breeding season to determine the dates when nesting peaks. For example, our repeated surveys during some years suggest that the number of nests peaks by mid-April for the Great Blue Heron, by mid-May for the Great Egret, and by late May for the Black-crowned Night-Heron, with interannual variation. Given the challenges of counting nests from the shore or watercraft, videos taken by unmanned aerial systems (often referred to as drones) could be used to supplement counts of nests (Barr et al. 2018; Jones et al. 2020; Prosser et al. 2022).

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FLOYD HAYES is a Professor of Biology at Pacific Union College, Angwin, California. He previously worked for a year as a primary school teacher in Micronesia, 3 y in the U.S. Peace Corps as a Vertebrate Biologist at the National Museum of Natural History of Paraguay, 9 y as a Biology Professor at the University of the Southern Caribbean and University of the West Indies in Trinidad, and 1 y as a Wildlife Biologist at the Division of Fish and Wildlife in the U.S. Virgin Islands. He has published research on a variety of invertebrates and vertebrates based on field work in 18 countries. (Photographed by Jessica Edens).



BRYAN MCINTOSH is a graduate of Humboldt State University (now Cal Poly Humboldt) in General Biology and Zoology, with a major interest in field ornithology and photography. The combination of these two is his primary focus as a developing photonaturalist. Some of this work can be seen at: <https://bryanm95451.wixsite.com/mysite>. (Photographed by Floyd Hayes).



DOUG WEIDEMANN is a Molecular Biology Research Technician. His work mainly focuses on understanding gene expression regulation, in particular RNA dynamics. Doug has also worked on a variety of ecology, wildlife biology, and evolutionary biology bird studies, including studying grebes, cormorants, and herons at Clear Lake, California. (Photographed by Floyd Hayes).



BRAD BARNWELL grew up in southern California and graduated from the University of Oregon, Corvallis, with a Parks and Recreation degree. After 5 y in the U.S. Coast Guard and two summers working in Colorado for the U.S. National Park Service, he moved to Lakeport, California, in 1982. He served on the Board of Directors for the Lake County Land Trust and Clear Lake State Park Interpretive Association. As a member of the Redbud Audubon Society, Brad often led hikes and gave presentations, and assisted with a study on the grebes of Clear Lake. Since retiring in 2005, he often observes and photographs birds and wildlife and leads bird walks for the Land Trust, Clear Lake State Park, and Redbud Audubon Society. (Photographed by Brad Barnwell).



DONNA MACKIEWICZ is an avid naturalist with a passion for birding and environmental education. She served as a National Audubon Society board member for 40 y, sponsoring four winning Presidential Environmental Youth Award projects with students in EPA Region 6, and currently serves as president of the Redbud Audubon Society. Currently a member of the Blue Ribbon Committee for the Rehabilitation of Clear Lake, her work on the Socio-economic Committee keeps her focused on the long term brighter future for Clear Lake. (Photographed by Roberta Lyons).

APPENDIX

APPENDIX TABLE. Survey dates and number of nests at each colony site where each cormorant and heron species was detected breeding during 2006–2024, and in sites (indicated with asterisk) where breeding was detected during 1993–2000 by others but not during 2006–2024.

Double-crested Cormorant (<i>Nannopterum auritum</i>)	
Upper Rodman Slough	2010 – 28 March, 0; 02 May, 0
2011 – 03 March, 20; 10 April, 53; 22 May, 35	2011 – 20 March, 0; 10 April, 0; 22 May, 0
2012 – 08 April, 32; 22 May, 23	2012 – 08 April, 0; 05 May, 0
2013 – 14 April, 38	2013 – 14 April, 0
2014 – 20 April, 6	2014 – 20 April, 0
2016 – 24 April, 51	2015 – 02 May, 0
2017 – 30 April, 21	2016 – 24 April, 0
2018 – 29 April, 3	2017 – 30 April, 22
2019 – 28 April, 0	2018 – 12 April, 0; 06 May, 2
2024 – 21 March, 0; 11 April, 0	2019 – 18 April, 0; 27 May, 4
	2024 – 11 April, 0
Reeves Point	Clearlake Oaks Wetlands
2006 – 22 April, 100	2020 – 26 March, 0; 30 April, 22
2008 – 26 April, 2	2021 – 02 March, 24; 03 March, present
2009 – 25 April, 3	2022 – 03 March, 0; 15 March, 25
2010 – 28 March, 0; 24 April, 0	2023 – 12 January, 12; 14 January 20; 01 February, 21
2011 – 10 April, 0	2024 – 01 January, 15; 01 February, 28; 01 March, 30;
2012 – 13 May, 0	01 April, 40; 30 April, present
2014 – 20 April, 0; 20 May, 0	
2018 – 29 April, 50	
2019 – 28 April, 41	
2024 – 21 March, 30	
	Great Blue Heron (<i>Ardea herodias</i>)
Long Tule Point	Upper Rodman Slough
2006 – 22 April, 0	2011 – 03 March, 27; 10 April, 46; 22 May, 33
2008 – 26 April, 0	2012 – 08 April, 50; 22 May, 10
2009 – 12, 25 April, 0	2013 – 14 April, 23
2010 – 28 March, 0; 24 April, 0	2014 – 20 April, 16
2011 – 20 March, 0; 10 April, 0; 22 May, 0	2016 – 24 April, 42
2012 – 08 April, 0; 13 May, 0	2017 – 30 April, 19
2013 – 14 April, 0	2018 – 29 April, 12
2014 – 20 April, 0	2019 – 28 April, 7
2015 – 02 May, 0	2024 – 21 March, 0; 11 April, 0
2016 – 24 April, 0	
2017 – 30 April, 25	Lyons Creek
2018 – 29 April, 20	2024 – 14 April, 15
2019 – 28 April, 29	
2024 – 21 March, 31	
	Reeves Point
Quercus Point*	2006 – 22 April, 10
2006 – 22 April, 0	2008 – 26 April, 1
2008 – 26 April, 0	2009 – 25 April, 0
2009 – 25 April, 0	2010 – 28 March, 0; 24 April, 0
2010 – 24 April, 0	2011 – 10 April, 0
2011 – 10 April, 0	2012 – 13 May, 0
2024 – 21 March, 0	2014 – 20 April, 0; 20 May, 0
	2018 – 29 April, 7
Cache Creek	2019 – 28 April, 9
2009 – 05, 26 April, 0	2024 – 21 March, 13

Long Tule Point

2006 – 22 April, 20
 2008 – 26 April, 12
 2009 – 12 April, 57
 2010 – 28 March, 85; 24 April, present
 2011 – 20 March, 71; 10 April, 84; 22 May, 24
 2012 – 08 April, 84; 13 May, present
 2013 – 14 April, 61
 2014 – 20 April, 25
 2015 – 02 May, 27
 2016 – 24 April, 8
 2017 – 30 April, 10
 2018 – 29 April, 1
 2019 – 28 April, 3
 2024 – 21 March, 8

Quercus Point

2006 – 22 April, 0
 2008 – 26 April, 2
 2009 – 25 April, 0
 2010 – 24 April, 5
 2011 – 10 April, 2
 2024 – 21 March, 0

Kelsey Creek

2021 – 6, 11 April, 1
 2022 – 12, 14, 20 March, 1
 2023 – 9, 20 February, 1; 24, 27 March, 1; 24 April, 1;
 13, 16, 18, 25, 27 May, 1; 1 June, 1
 2024 – 6, 15 January, 1; 9 February, 3; 12 February,
 5; 25 February, 7; 25, 31 March, 7; 11, 15 April, 7;
 25 April, 8

Cache Creek

2009 – 05 April, 19; 26 April, present
 2010 – 28 March, 52; 02 May, present
 2011 – 20 March, 53; 10 April, 52; 22 May, 13
 2012 – 08 April, 57; 05 May, present
 2013 – 14 April, 22
 2014 – 20 April, 11
 2015 – 02 May, 25
 2016 – 24 April, 44
 2017 – 30 April, 41
 2018 – 12 April, 19; 06 May, 27
 2019 – 18 April, 8; 27 May, 6
 2024 – 11 April, 35

Clearlake Oaks Wetlands

2020 – 26 March, 6; 30 April, present
 2021 – 02 March, present; 03 March, 7
 2022 – 03 March, 8; 15 March, present
 2023 – 12, 14 January, 12; 1 February, 14
 2024 – 01 January, 0; 01 February, 0; 01 March, 12;
 01 April, present; 30 April, 12

Great Egret (*Ardea alba*)

Upper Rodman Slough

2011 – 03 March, 0; 10 April, 7; 22 May, 9
 2012 – 08 April, 0; 22 May, 1
 2013 – 14 April, 0
 2014 – 20 April, 0
 2016 – 24 April, 15
 2017 – 30 April, 8
 2018 – 29 April, 1
 2019 – 28 April, 0
 2024 – 21 March, 0; 11 April, 0

Lower Rodman Slough

2011 – 03 March, 0; 10 April, 3; 22 May, 3
 2012 – 08 April, 0; 22 May, 5
 2013 – 14 April, 3
 2014 – 20 April, 16
 2016 – 24 April, 0
 2017 – 30 April, 0
 2018 – 29 April, 0
 2019 – 28 April, 0
 2024 – 21 March, 0; 11 April, 0

Reeves Point

2006 – 22 April, 0
 2008 – 26 April, 0
 2009 – 25 April, 0
 2010 – 28 March, 0; 24 April, 0
 2011 – 10 April, 0
 2012 – 13 May, 0
 2014 – 20 April, 0; 20 May, 0
 2018 – 29 April, 6
 2019 – 28 April, 7
 2024 – 21 March, 0

Quercus Point

2006 – 22 April, 0
 2008 – 26 April, 0
 2009 – 25 April, 1
 2010 – 24 April, 0
 2011 – 10 April, 0
 2024 – 21 March, 0

Cache Creek

2009 – 05, 26 April, 1
 2010 – 28 March, 2; 02 May, 7
 2011 – 20 March, 0; 10 April, 9; 22 May, 11
 2012 – 08 April, 2; 05 May, 4
 2013 – 14 April, 14
 2014 – 20 April, 5
 2015 – 02 May, 4
 2016 – 24 April, 6
 2017 – 30 April, 10

2018 – 12 April, 20; 06 May, present
 2019 – 18 April, 1; 27 May, 2
 2024 – 11 April, 35

Clearlake Oaks Wetlands

2020 – 26 March, 0; 30 April, 0
 2021 – 03 March, 0
 2022 – 03 March, 0; 15 March, 0
 2023 – 12, 14 January, 0; 1 February, 0
 2024 – 01 January, 0; 01 February, 0; 01 March, 5; 01, 30 April, present

2012 – 13 May, 0
 2014 – 20 April, 0; 20 May, 0
 2018 – 29 April, 0
 2019 – 28 April, 5
 2024 – 21 March, 0

Quercus Point*

2006 – 22 April, 0
 2008 – 26 April, 0
 2009 – 25 April, 0
 2010 – 24 April, 0
 2011 – 10 April, 0
 2024 – 21 March, 0

Black-crowned Night-Heron (*Nycticorax nycticorax*)

Willow Point

2009 – 17 May, 34
 2010 – 6 June, 41
 2011 – 20 March, 0; 10 April, 0; 22 May, 41
 2012 – 10 June, 41
 2013 – 14 April, 0; 21 May, present; 14 June, 96
 2014 – 20 April, 0; 20 May, 49
 2015 – 2 May, 36
 2016 – 24 April, 102
 2017 – 30 April, 0
 2018 – 29 April, 0
 2019 – 28 April, 0
 2024 – 11 April, 94; 14 April, 95

Reeves Point

2006 – 22 April, 0
 2008 – 26 April, 0
 2009 – 25 April, 0
 2010 – 28 March, 0; 24 April, 0
 2011 – 10 April, 0

Cache Creek

2009 – 05, 26 April, 0
 2010 – 28 March, 0; 02 May, 0
 2011 – 20 March, 0; 10 April, 0; 22 May, 0
 2012 – 08 April, 0; 05 May, 4
 2013 – 14 April, 0
 2014 – 20 April, 0
 2015 – 02 May, 0
 2016 – 24 April, 0
 2017 – 30 April, 0
 2018 – 12 April, 0; 06 May, 0
 2019 – 18 April, 0; 27 May, 5
 2024 – 11 April, 0

Clearlake Oaks Wetlands

2020 – 26 March, 0; 30 April, 0
 2021 – 03 March, 0
 2022 – 03 March, 0; 15 March, 0
 2023 – 12, 14 January, 0; 1 February, 0
 2024 – 01 January, 0; 01 February, 0; 01 March, 0; 01, 30 April, 8
