# Historical and Recent Breeding of the Western Grebe and Clark's Grebe in a Severely Impaired Ecosystem at Clear Lake, California

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# Historical and recent breeding of the Western Grebe and Clark's Grebe in a severely impaired ecosystem at Clear Lake, California

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    ABSTRACT.—Clear Lake is a large (176.7-km$^2$) natural lake in northern California, USA. An estimated 1000 pairs of Western Grebes (*Aechmophorus occidentalis*) and Clark's Grebes (*A. clarkii*) nested on the lake prior to massive applications of the pesticide dichlorodiphenyldichloroethane (DDD) to kill the Clear Lake gnat (*Chaoborus astictopus*) during 1949–1957. Biomagnification of DDD was implicated as the cause of several mass mortality events of grebes and short-term reproductive failure in the 1950s, although other factors such as mercury (Hg) poisoning may have contributed. Successful nesting resumed in 1960 and increased gradually, with up to 165 nests in 1967 but fewer through 1976. Subsequent surveys revealed up to 390 nests annually during 1992–1995 and up to 2675 nests annually during 1996–2010. We conducted 7–29 nest surveys annually during 2010–2019 and found a mean of 3123 nests per year. The annual number of nests varied dramatically (range 898 to 5936) and was unrelated to water level. The grebes nested at 28 sites in Clear Lake and 9 sites in associated wetlands, with proportionately more nests on Clear Lake and fewer nests in adjacent wetlands during years with low water level. Western Grebes attended 84.9% of the nests and Clark's Grebes attended 15.1%. During years with low water, there were proportionately more open water nests, which were anchored to submergent vegetation farther from shore and in deeper water than marsh nests, which were more densely placed in emergent vegetation closer to shore in shallower water. Brood surveys along the perimeter of the lake at the end of each breeding season revealed considerable variation in the number of young (1–599, $\bar{x} = 153.9$), young per nest (0.00025–0.118, $\bar{x} = 0.04$), and productivity ratio of young to adults (0.0006–0.252, $\bar{x} = 0.07$). Reproductive success was unrelated to water level. Wind-generated waves were a major cause of nest failure, destroying up to 35% of a year's nests. Predation on eggs was also a major cause of nest failure. American Crow (*Corvus brachyrhynchos*) was the dominant predator during the day (84% of predation events), and northern raccoon (*Procyon lotor*) was the dominant predator at night (98% of predation events). Nocturnal predation by mammals occurred most frequently when water level was high because nests were placed closer to shore and were more accessible. The grebes' breeding population has recovered since DDD biomagnification during the 1950s and may be larger due to 2 introduced fish species competing for plankton with benthic larvae of the Clear Lake gnat, which previously transferred large quantities of biomass from aquatic to terrestrial ecosystems during emergence. However, the grebes' reproductive success remains lower at Clear Lake than at several other breeding localities. The bioaccumulation and biomagnification of toxic chemicals and the periodic reductions of prey fish from hypoxic areas of the lake during periods of intense cyanobacterial and algal blooms may reduce reproductive success.

    RESUMEN.—Clear Lake es un lago natural grande (176.7 km$^2$) en el norte de California, EEUU. Se estima que 1000 parejas del achichilique occidental (*Aechmophorus occidentalis*) y achichilique pico naranja (*A. clarkii*) anidaron en el lago antes de las aplicaciones masivas del pesticida diclorodifenildicloroetano (DDD) para matar al díptero de Clear Lake (*Chaoborus astictopus*) durante 1949–1957. La biomagnificación de DDD estuvo implicada como la causa de varios eventos de mortalidad masiva de achichiliques y fallas reproductivas a corto plazo en la década de 1950, aunque otros factores pueden haber contribuido, como el envenenamiento por mercurio (Hg). La anidación exitosa se reanudó en 1960 y aumentó gradualmente, con hasta 165 nidos en 1967 pero menos hasta 1976. Los censos posteriores revelaron hasta 390 nidos anualmente durante 1992–1995 y encontramos durante 1996–2010. Realizamos de 7 a 29 censos de nidos anualmente durante 2010–2019 y encontramos una media de 3123 nidos por año. El número anual de nidos varió drásticamente (rango 898–5936) y no estuvo relacionado con el nivel del agua. Los achichiliques anidaron en 28 sitios en Clear Lake y 9 sitios en humedales asociados, con proporcionalmente más nidos en Clear Lake y menos nidos en humedales adyacentes durante años con bajo nivel de agua. Los achichiliques occidentales asistieron al 84.9% de los nidos y los achichiliques de Clark asistieron al 15.1%. Durante los años con poca agua, hubo proporcionalmente más nidos en aguas abiertas, que estaban anclados a la vegetación sumergida más lejos de la costa en aguas más profundas, que nidos

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de marismas, que estaban más densamente colocados en la vegetación emergente más cerca de la costa en aguas menos profundas. Los censos de cría a lo largo del perímetro del lago al final de cada temporada de reproducción revelaron una variación considerable en el número de crías (1–599, $\bar{x} = 153.9$), crías por nido (0.00025–0.118, $\bar{x} = 0.04$), y una tasa de productividad de jóvenes a adultos (0.0006–0.252, $\bar{x} = 0.07$). El éxito reproductivo no estuvo relacionado con el nivel del agua. Las olas generadas por el viento fueron una de las principales causas de la falla de los nidos, destruyendo hasta el 35% de los nidos de un año. La depredación de los huevos también fue una de las principales causas del fracaso de los nidos. El cuervo americano (*Corvus brachyrhynchos*) fue el depredador dominante durante el día (84% de los eventos de depredación) y el mapache del norte (*Procyon lotor*) fue el depredador dominante durante la noche (98% de los eventos de depredación). La depredación nocturna por mamíferos ocurrió con mayor frecuencia cuando el nivel del agua era alto porque los nidos se colocaron más cerca de la costa y eran más accesibles. La población reproductora de achichiliques se ha recuperado desde la biomagnificación por DDD durante la década de 1950 y puede ser mayor debido a que dos especies de peces introducidas compiten por el plancton con las larvas bentónicas del díptero de Clear Lake, que anteriormente transfirió grandes cantidades de biomasa de los ecosistemas acuáticos a los terrestres durante la emergencia. Sin embargo, el éxito reproductivo de los achichiliques sigue siendo menor que en varias otras localidades de reproducción. La bioacumulación y biomagnificación de sustancias químicas tóxicas y las reducciones periódicas de peces presa de las áreas hipóxicas del lago durante períodos de intensa proliferación de cianobacterias y algas pueden reducir el éxito reproductivo.

Clear Lake, located in Lake County, northern California (38°56′46″ to 39°07′23″N, 122°38′04″ to 122°54′46″W), at an elevation of 402 m above sea level, is considered the oldest lake in North America (Sims 1988). With an area of 176.7 km$^2$ and 114 km of shoreline (Horne and Goldman 1972), it is one of the largest natural lakes in California. Despite its large size, it is relatively shallow, with an average depth of 8.1 m and a maximum depth of 18.4 m (Horne and Goldman 1972). As a consequence of shallow depth and an abundance of nutrients, Clear Lake is a relatively eutrophic lacustrine ecosystem with frequent cyanobacterial and algal blooms occurring during the warm summer months (Goldman and Wetzel 1963, Richerson et al. 1994, Winder et al. 2010). The abundance of nutrients in Clear Lake supports a high biomass of fishes represented by more than 30 species, most of which have been introduced (Thompson et al. 2013). The fishes attract large numbers of piscivorous waterbirds, especially during the winter (Colwell et al. 1997, Cooper 2004), but many waterbirds remain to breed during spring and summer (Wolfe and Norman 1998, Anderson et al. 2008, Shuford 2014, Shuford et al. 2020a, 2020b).

Clear Lake and its associated wetlands are severely impaired by a long history of human activities adversely affecting habitat quality and trophic relationships. Some of the most significant impacts affecting fish and wildlife include the biomagnification of mercury (Hg) from mining activities and acid mine drainage at the Sulphur Bank Mercury Mine, biomagnification of the pesticide dichlorodiphenyldichloroethane (DDD) from massive applications to control populations of the Clear Lake gnat (*Chaoborus astictopus*), habitat loss due to reclamation and modification of wetland habitats, cultural eutrophication from increased nutrient loading, and altered food webs from introductions of numerous species of nonnative fishes (see reviews by Richerson et al. 2000, 2008, Suchanek et al. 2003, Thomson et al. 2013).

The morphologically similar Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*A. clarkii*), hereafter collectively referred to as "grebes," are large piscivorous diving birds that breed colonially on floating nests, often together and occasionally hybridizing, on lakes in western North America (Storer 1965, Ratti 1979, Storer and Nuechterlein 1992, Konter 2011, 2012, LaPorte et al. 2020a, 2020b). Both species nest in Clear Lake. The grebes are ecosystem engineers whose floating nests significantly alter the environment, providing resources for at least 47 other species of vertebrates on Clear Lake (Hayes et al. 2018a). However, the grebes' breeding populations have been severely impacted by human activities. In a research paper provocatively titled "Potential Western Grebe extinction on California lakes," Feerer and Garrett (1977) summarized evidence for a precipitous population decline of the Western Grebe and Clark's Grebe nesting on California lakes, based primarily on data from Clear Lake. The decline was attributed to 3 factors: (1) the excessive application of pesticides to control gnats, (2) a reduction in the food supply due to the introduction of a new species of fish in 1967 to control gnats, and (3) the loss of breeding habitat from the destruction of tule marshes for urban and commercial development.

Despite Feerer and Garrett's (1977) pessimistic predictions of the imminent extirpation

TABLE 1. Summary of historical records of the breeding population (adults), reproductive effort (nests), and reproductive success (young and young:adults) of *Aechmophorus* grebes on Clear Lake, California, during 1938–2010.

| Year | Adults | Nests | Young | Young:adults | Source |
|---|---|---|---|---|---|
| 1938 | 200–300 | — | 20 | — | Moffitt (1938) |
| <1949 | >2000 | — | — | — | Hunt and Bischoff (1960) |
| 1950 | — | many | — | — | Miller (unpublished field notes) |
| 1951 | — | 1 | several | — | Miller (unpublished field notes) |
| 1958 | <50 | 0 | 0 | — | Hunt and Bischoff (1960) |
| 1959 | 60 | 0 | 0 | — | Hunt and Bischoff (1960) |
| 1960 | — | — | 1 | — | Hunt (1962) |
| 1961 | 38 | 36 | 1 | — | Hunt (1962), Herman et al. (1969) |
| 1962 | — | — | 1 | — | Herman et al. (1969) |
| 1963 | — | — | 3 | — | Herman et al. (1969) |
| 1964 | 39 | 0 | 0 | — | Miller (unpublished field notes) |
| 1965 | 74 | 3 | 0 | — | Miller (unpublished field notes) |
| 1966 | — | many | 3 | — | Herman et al. (1969) |
| 1967 | 300 | 165 | 40–60 | — | Herman et al. (1969) |
| 1968 | — | — | 20 | — | Rudd and Herman (1972) |
| 1969 | — | — | 81 | — | Rudd and Herman (1972) |
| 1971 | 410 | — | 205 | 0.50 | Rudd and Herman (1972) |
| 1973 | 400 | 49 | — | — | Feerer and Garrett (1977) |
| 1975 | 200 | 36 | — | — | Feerer and Garrett (1977) |
| 1976 | — | 0 | — | — | Feerer and Garrett (1977) |
| 1992–1995 | 3500 | 150–390 | — | 0.001–0.016 | Elbert and Anderson (1998), Anderson et al. (2008) |
| 1996–2001 | — | 0–2675 | — | 0.04–0.77 | Anderson et al. (2008) |
| 1998 | — | — | 133 | — | Robison et al. (2015) |
| 2000 | — | 2675 | 311 | 0.76 | Robison et al. (2009, 2015) |
| 2001 | — | 925 | 221 | 0.65 | Robison et al. (2009, 2015) |
| 2002 | — | 445 | — | >0.01 | Robison et al. (2009) |
| 2003 | — | 275, 470 | 121, 153 | 0.19, 0.21 | Robison et al. (2009, 2015), Ivey (2004) |
| 2004 | — | 700 | 219 | 0.16 | Robison et al. (2009, 2015) |
| 2005 | — | 2300 | 312 | 0.82 | Robison et al. (2009, 2015) |
| 2006 | — | 800 | 162 | 0.72 | Robison et al. (2009, 2015) |
| 2007 | — | 20 | 20 | 0.0026 | Robison et al. (2009) |
| 2008 | — | 25 | 9 | 0.006 | Robison et al. (2009) |
| 2009 | — | 500 | 37 | 0.022 | Robison et al. (2009, 2015) |
| 2010 | — | — | 94 | — | Robison et al. (2015) |

of breeding grebes on Clear Lake, subsequent studies revealed that the breeding population of grebes on Clear Lake had been gradually increasing (Elbert and Anderson 1998, Anderson et al. 2008, Robison et al. 2015). In this study, we review the history of research on breeding grebes based on a review of the literature, present the results of a 10-year study (2010–2019) on the breeding ecology of grebes, assess the impacts of significant anthropogenic disruptions of the lake's trophic relationships on grebe populations, and discuss the current and potential future threats to the breeding grebes of Clear Lake.

HISTORY OF RESEARCH ON BREEDING GREBES

A summary of historical records of the breeding population (number of adults), reproductive effort (number of nests), and reproductive success (number of young and productivity ratio of young:adults) of grebes on Clear Lake during 1938–2010 is presented in Table 1. Further details of these studies are provided below.

Before 1950

In the earliest account of *Aechmophorus* grebes nesting on Clear Lake, Moffitt (1938) reported that the Western Grebe nested "in numbers" on 16 July 1928 and 4 July 1936, and 200–300 adults with about 20 one-third-grown young were counted on 15 July 1938. It is unknown what portions of Clear Lake were visited.

Research on the *Aechmophorus* grebes of Clear Lake began with a study of their diving and feeding behavior during the summer of 1947, when Lawrence (1949, 1950) noted that nesting occurred during the months of July and

August but provided no further details about the grebes' breeding biology.

## 1950s

The next phase of research focused on the impacts of the pesticide DDD. According to A.H. Miller (*in* Hunt and Bischoff 1960), the grebes' breeding population exceeded 1000 pairs prior to the first large-scale application of DDD to control populations of the Clear Lake gnat in September 1949. A search of Miller's unpublished field notes (available online at eco-reader.berkeley.edu) failed to find any details of his observations prior to 1949, but on 15 July 1950, he observed "many nests" without eggs and "6+" nests with up to 3 eggs at Anderson Marsh. He also noted that grebes were "more common" at Anderson Marsh than in the previous year (1949), indicating that nesting occurred during the first breeding season after the first large-scale application of DDD. The following year, on 6 July 1951, Miller (unpublished field notes) observed a nest with 2 eggs and several small young north of Kelsey Creek, indicating that nesting was successful.

Shortly after the second large-scale application of DDD in September 1954, the mortality of 100 grebes in December 1954 and "more" in March 1955 prompted a study that failed to find any infectious disease (Hunt and Bischoff 1960). The third and final large-scale application of DDD occurred in September 1957, followed by another mortality of 75 grebes in December 1957 (Dolphin 1959, Hunt and Bischoff 1960). Two sick grebes, which exhibited nervous tremors, were collected in 1958, and 5 more grebes were collected in 1959. Lipid samples from these grebes, plus samples from 8 species of fish and 1 species of amphibian, revealed elevated concentrations of DDD (Hunt and Bischoff 1960). Breeding surveys revealed <50 grebes in 1958 and up to 60 grebes in 1959, but no nests were found in areas where they had previously nested and no young were seen on the lake. Several thousand wintering grebes were present in October 1958 (Hunt and Bischoff 1960). Unfortunately, no details were provided for the localities and dates of surveys during the 1950s, except for those of Miller (unpublished field notes), so it is uncertain how frequent or extensive these surveys were. The abrupt reproductive failure of grebes was attributed to DDD poisoning through biomagnification (Hunt and Bischoff 1960). Shortly

thereafter, the plight of Clear Lake's grebes, which represented the first documented case of biomagnification, was introduced to the American public by Rachel Carson (1962) and to the scientific community by Robert L. Rudd (1964).

## 1960s

Breeding surveys of grebes continued sporadically throughout the 1960s. In 1960, one young grebe was reported, but no information was provided on the number of nests (Hunt 1962). In 1961, two separate surveys yielded different results. Herman et al. (1969) reported finding 38 adults and 16 nests on 14 June, but the nests could not be relocated afterward, and no young were seen on the lake. In contrast, Hunt (1962) reported finding 36 nests and 1 young, but most nests were abandoned or destroyed by predators. Hunt (1962) also reported that a collected grebe had lower concentrations of DDD in its tissues than in samples collected during previous years. In 1962, the pesticide methyl parathion was first applied to Clear Lake in another attempt to control populations of the Clear Lake gnat (Cook and Conners 1963). Grebes observed during and after the methyl parathion treatments showed no visible adverse symptoms (Cook and Conners 1963). Because methyl parathion was considerably less toxic and persistent than DDD (Apperson et al. 1976) and was effective in controlling the Clear Lake gnat, it was applied annually until 1975 (Feerer and Garrett 1977, Suchanek et al. 2003). However, its potential toxic effects on grebes were never studied. A single young grebe was found in 1962 and 3 young were reported in 1963 (Herman et al. 1969). A sample of 41 adults and 2 eggs collected during 1959–1963 revealed high levels of DDD (Linn and Stanley 1969). A group of 39 adults were encountered at Long Tule Point on 11 July 1964, but no nests could be found (Miller unpublished field notes). A group of 74 adults and 3 nests, of which only one had eggs, were found at Long Tule Point on 4 July 1965 (Miller unpublished field notes). Many eggs and nests, but only 3 young, were found in 1966, when the lake's breeding population was estimated at 300 individuals (Herman et al. 1969, Rudd and Herman 1972). No details were provided by Hunt (1962), Herman et al. (1969), or Rudd and Herman (1972) for the localities and dates of breeding surveys during the period of 1960–1966, so it is unknown how frequent or extensive the searches were.

A more intensive study of the grebes was conducted during 1967, when monthly aerial censuses of the lake revealed a breeding population of about 300 individuals (Herman et al. 1969). The grebes initiated nest building and egg laying in early May at a single colony at Long Tule Point, where they produced 165 nests, more than 450 eggs, and an estimated 40–60 young (Herman et al. 1969, Rudd and Herman 1972). Laboratory studies of tissue samples from adult grebes collected throughout the year and 89 eggs taken from the colony provided strong evidence that reproduction was still impaired by DDD poisoning, resulting in thinner eggshells and higher-than-normal embryo inviability and hatchling mortality (Herman et al. 1969). Furthermore, evidence from 2 moribund adult female grebes collected in 1968 revealed DDD concentrations in brain and breast muscle tissues that exceeded values considered lethal in other species of birds (Rudd and Herman 1972). Cook (1965) calculated that 4 times more dichlorodiphenyltrichloroethane (DDT) was applied to the watershed during 1949–1964 than DDD applied directly to the lake during 1949–1957, with some DDT runoff into the lake possibly contributing to pesticide poisoning of the grebes (Herman et al. 1969).

In 1967 a small fish, the Mississippi Silverside (*Menidia audens*), was introduced to Clear Lake as a biological control for the Clear Lake gnat (Cooke and Moore 1970). Within 2 years the silverside population appeared to exceed that of all other fish species combined (Cooke 1981), altering the lake's trophic relationships. Rudd and Herman (1972) reported counts of 20 young grebes in 1968 and 81 young in 1969. Although the numbers of adults and nests were not reported, 1969 was the first year in a decade that more than half of mated pairs were accompanied by young. Rudd and Herman (1972) speculated that an unexpectedly dramatic decline of DDD concentrations in the egg lipids of grebes during 1966–1969 was associated with the silverside's introduction, perhaps due to the grebes acquiring a less contaminated diet.

## 1970s

Counts along a 5-mile surface transect in September 1971 revealed a ratio of "almost precisely 1 young bird per mated pair," which was used to estimate that 205 young accompanied 410 adults counted during an aerial survey (Rudd and Herman 1972). Periodic sampling of grebe specimens up until 1973 revealed steadily declining concentrations of DDD in their tissues (Craig and Rudd 1974). "Extensive searches" during 1973–1976, when nesting occurred only at Long Tule Point, revealed 200 pairs with 49 nests in 1973 and 100 pairs with 36 nests in 1975, but low water level precluded nesting in 1976 (Feerer and Garrett 1977). Unfortunately, the number of young were not provided, but mean clutch size decreased from 2.42 in 1967 to 2.10 in 1975, and a small sample of collected eggs revealed that the shells were still abnormally thin due to DDD (Feerer and Garrett 1977). Feerer and Garrett (1977) concluded that grebe populations were declining due to excessive application of pesticides, the introduction of the Mississippi Silverside, and the destruction of breeding habitat. They pessimistically predicted the imminent extirpation of breeding grebes from Clear Lake.

## 1980s

Despite Feerer and Garrett's (1977) dire predictions, no nesting or brood surveys were conducted during the 1980s. As interest in the effects of DDD waned, research shifted toward the effects of Hg biomagnification from local mining activities. The Sulphur Bank Mercury Mine, located along the southeast shore of the Oaks Arm near Clearlake Oaks (Fig. 1), was active during 1872–1957. High concentrations of Hg were first detected in the fishes of Clear Lake in the 1970s (Suchanek et al. 2003). In 1984, a sample of 20 collected grebe specimens revealed high but sublethal levels of Hg in their liver tissues (Littrell 1991).

The Threadfin Shad (*Dorosoma petenense*), another introduced fish first collected in Clear Lake in 1985 (Anderson et al. 1986), subsequently altered the ecosystem's trophic relationships. Like the silverside in the 1960s, the shad's population boomed during 1987–1989 and was accompanied by a dramatic increase in the number of wintering grebes and other piscivorous birds censused during annual Christmas Bird Counts (Colwell et al. 1997). However, both shad and wintering grebe numbers subsequently declined during 1990–1996 (Colwell et al. 1997). Unfortunately, the impact of the shad's population boom and bust on nesting grebe populations was not studied during this period.

## 1990s

Additional grebe specimens collected in 1992 revealed elevated concentrations of Hg in tissues
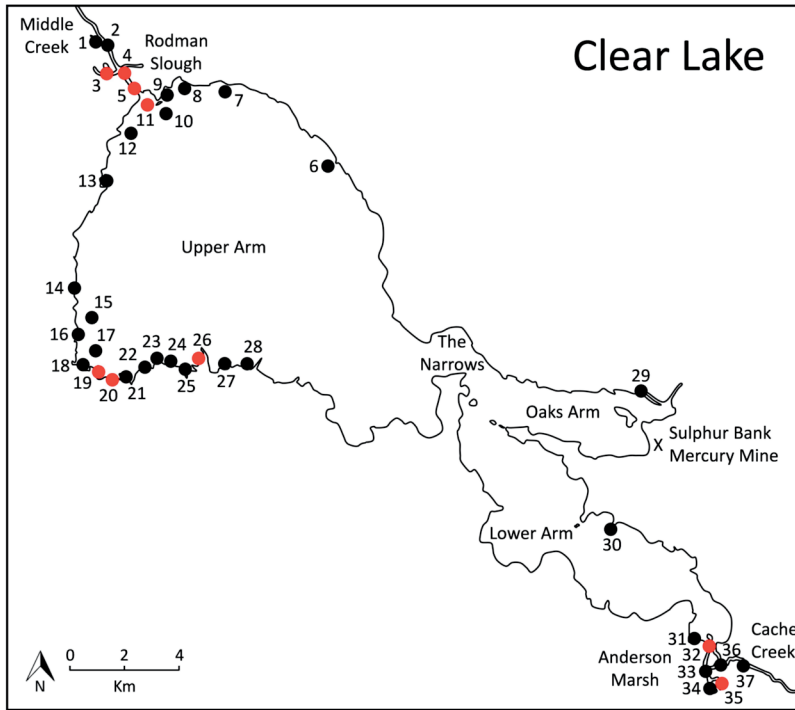
Fig. 1. Locations of 37 colony sites on Clear Lake, California. The number, name, and characteristics of each colony site are given in Table 3. Colony sites averaging >100 nests per year are indicated by a red circle.

(Elbert 1996, Elbert and Anderson 1998) and feathers (Cahill et al. 1997, 1998). Blood biomarkers suggested the grebes suffered from a compromised immune system (Elbert 1996, Elbert and Anderson 1998), but white blood cell counts provided no evidence of infection (Wolfe and Norman 1998).

A long-term monitoring program of breeding grebes was initiated in 1992 by Daniel Anderson and his graduate students from the University of California at Davis (Elbert 1996, Elbert and Anderson 1998). The annual breeding population of Clear Lake during 1992–1995 was estimated at 3500 individuals. The productivity ratios of young to adults, obtained during surveys at the end of the breeding season in September, ranged from 0.001 to 0.16 and were lower than those at Eagle Lake (0.47–0.74) and Tule Lake (0.16–0.48) in northern California. Elbert and Anderson (1998) suggested that factors other than elevated Hg concentrations, such as the biomagnification of other compounds and frequent disturbance from recreational boaters and anglers, could account for the grebes' poor reproductive success. They

suggested that the grebes of Clear Lake represented a sink population with a stable breeding population maintained by recruitment from source populations.

Anderson et al. (2008) conducted 2–5 open water surveys annually and "in some instances low-level aerial photography" during 1991–2001. A map provided the locations of 7 colony sites, including 4 in the Upper Arm, 1 in The Narrows (Fig. 1) between the 3 arms, 1 in the Oaks Arm, and 1 in Anderson Marsh. Because the data were presented graphically, exact values for the number of nests and productivity ratios were not given. Estimates from figures indicate that the number of nests ranged from 150 to 390 during 1992–1995 and from 0 to 2675 during 1996–2001. Productivity ratios ranged from 0.001 to 0.16 during 1992–1995 and from 0.04 to 0.77 during 1996–2001. Complete reproductive failure occurred in 1999 and was attributed to receding water level stranding nests on land. The increase in reproductive effort and success during 1992–2001 was accompanied by a decline in Hg levels in feathers collected during the study.

## 2000s

In 2003, Ivey (2004) conducted aircraft and motorboat surveys, revealing 470 nests, including 350 at Long Tule Point on 5 August (but none on 20 August), 70 at Anderson Marsh (southeast lagoon), 25 at Clearlake Oaks estimated from broods observed during a flight on 10 September (uncertain whether nests were actually observed), and 25 at Rodman Slough and the northwest end of Clear Lake (Fig. 1). Western Grebes outnumbered Clark's Grebes by a ratio of 73 to 27. Surveys along 5 transects in September revealed 153 young with a productivity ratio of 0.21.

Robison et al. (2009, 2015), Robison (2012), and Weems (2012) conducted one or more surveys annually during 1998–2010. The number of nests ranged from 20 in 2007 to 2675 in 2000, the number of young ranged from 9 in 2008 to 312 in 2005, and the productivity ratio ranged from 0.0026 in 2007 to 0.82 in 2005 (Table 1). Based on the sizes of young and their estimated ages, nest initiation was inferred to range from late April to late August. Gericke (2006) studied the effects of anthropogenic disturbance events on grebes in nesting colonies and postnesting staging areas, revealing that the combination of disturbance duration, boat speed, variability of boat speed, and distance to a source of disturbance significantly affected the probability of a response by the grebes.

## 2010s

Ackerman et al. (2015) compared Hg concentrations in grebes and fish sampled at 25 lakes in California in 2012 and 2013. The grebes of Clear Lake ranked seventh highest for Hg in blood, first for Hg in eggs, seventh for Hg in prey fish, and third for Hg in sport fish. At Clear Lake, Hg concentrations in the blood of grebes increased at the end of the breeding season in August and September (Hartman et al. 2017). Humple and Holcomb (2014) and Mills et al. (2016) reported the movements of a few grebes at Clear Lake based on band or satellite transmitter data.

Elsewhere we have published details of our recent grebe research at Clear Lake on copulation behavior (Hayes and Turner 2017), use of nests by other species of vertebrates (Hayes et al. 2018a), nocturnal reproductive activities (Hayes et al. 2018b), and destruction of eggs by males (Hayes et al. 2018c).

## Study Area

Clear Lake comprises 3 major arms (Fig. 1). The Upper Arm is the largest (127 km², 56 km of shoreline) and shallowest (12.2 m max depth), the Oaks Arm is the smallest (12.5 km², 19 km of shoreline, 18.4 m max depth), and the Lower Arm is intermediate in size (37.2 km², 39 km of shoreline, 18.4 m max depth) (Horne and Goldman 1972). Major wetlands associated with the lake include its largest tributary, Rodman Slough, at the northwest end of the lake, and its outlet, Anderson Marsh, at the southeast end of the lake (Fig. 1).

A variety of plant communities border Clear Lake and its associated woodlands. Extensive marshes dominated by tules (*Schoenoplectus* spp.), floating primrose-willow (*Ludwigia peploides*), water smartweed (*Persicaria amphibia*), and cattails (*Typha* spp.) border the northern, western, and southern shores of the Upper Arm and Cache Creek. Smaller patches of marsh occur in Rodman Slough, along the eastern shore of the Upper Arm, and at the east end of the Oaks Arm. Extensive riparian forests dominated by willows (*Salix* spp.), valley oak (*Quercus lobata*), Fremont cottonwood (*Populus fremontii*), and California sycamore (*Platanus racemosa*) border portions of the northern tributaries (Middle Creek and Rodman Slough) and outlets (Anderson Marsh and Cache Creek), and these forests are partially flooded during years with high water levels. Smaller patches of riparian forest associated with small tributaries occur along the southern shore of the Upper Arm. Other sections of the lake are bordered by foothill woodland dominated by blue oak (*Quercus douglasii*) and gray pine (*Pinus sabiniana*), or by chaparral dominated by chamise (*Adenostoma fasciculatum*), manzanita (*Arctostaphylos* spp.), coyote brush (*Baccharis pilularis*), and buckbrush (*Ceanothus* spp.).

Urban development is extensive along the shores of all 3 arms of Clear Lake but is absent at Rodman Slough and most of Cache Creek. The lake is extremely popular for recreational boating and fishing, with dozens or hundreds of recreational motorboats and fewer kayaks and canoes plying the lake daily during fair weather, especially during holiday weekends.

The availability of aquatic habitats in Clear Lake and its associated wetlands is affected by rainfall and its impact on water level. Rainfall occurs mostly during October to May, peaking

in January and occurring only rarely during June to September, especially in July (Suchanek et al. 2008). As a consequence, water level typically peaks during February to April, gradually declines throughout the summer months, and is lowest during October to December (De Leon 2016). Water level varied greatly during the study period (2010–2019), ranging from −0.83 ft Rumsey (0 ft Rumsey = 1318.26 ft above sea level; http://www.lakecountyca.gov/Government /Directory/WaterResources/HydrologicInfo /LevelData/Historical_Water_Levels_of_Clear_ Lake.htm) in 2014 to 10.63 ft Rumsey in 2017 (Fig. 2). These levels were well within the historical extremes of −3.50 ft Rumsey in 1920 and 13.66 ft Rumsey in 1890 (Suchanek et al. 2003, De Leon 2016). High water level allows piscivorous diving birds to enter marshes and swim, forage, and nest farther upstream in channels of tributaries and downstream in the outlet of Clear Lake. When water level recedes below marsh vegetation, piscivorous diving birds are excluded from marshes and shallower areas of tributaries and the outlet. Low water level also reduces the extent of marsh vegetation and facilitates the colonization of mudflats by willows (*Salix* spp.).

## METHODS

### Colony Definitions

The Western Grebe and Clark's Grebe typically nest in colonies (Storer and Nuechterlein 1992, LaPorte 2020a, 2020b). However, the definition of a colony has vexed waterbird biologists for decades (Buckley and Buckley 1980). Lindvall (1976) distinguished between colonial and noncolonial *Aechmophorus* grebes by defining a noncolonial nest as >100 m from the nearest nest. Buckley and Buckley (1980) defined a colony as a given breeding population of animals at a given site for a specific period of time. Gochfeld (1980) defined a colony as a single location supporting breeding birds in sufficiently close proximity to interact socially, and a subcolony as a cluster of birds within a colony that is separated from adjacent clusters by an unused space or habitat discontinuity. Buckley and Buckley (1980) pointed out that a colony is not a fixed point, which is properly termed a colony site.

For the purposes of this study, we arbitrarily defined colony sites as locations where the incipient nests within a colony were separated from the nearest nest of the nearest colony by a gap of at least 400 m or by a minimum swimming distance of 400 m around land or dense aquatic vegetation, even if only one nest was present at the site. We adopted Gochfeld's (1980) definition of a subcolony. Some colonies that began >400 m apart later merged together into larger colonies, which we refer to as supercolonies.

### Nest Surveys

During 2010–2019, we conducted surveys of nesting grebes during 186 days of fieldwork between the dates of 8 April and 3 October, with an average of 18.6 surveys per year (SD = 7.2, range 7 to 29 due to variable funding between years; Table 2). Most surveys were conducted by canoe because many colony sites were located in shallow areas with dense aquatic vegetation, rendering it difficult to navigate in a motorboat. The coordinates of the estimated center of each colony were obtained from Google Earth (http://www.google.com/earth). Some colony sites were observed from land, and several surveys were conducted by motorboat. We repeatedly visited sites where grebes were expected to breed, based on previous reports of breeding sites and newly discovered breeding sites, but because of the long distances between colonies, we usually visited about half of the colony sites per survey and alternated sites during consecutive surveys. Sites where grebes rarely nested were surveyed less frequently than sites where grebes nested more consistently.

During each survey we attempted to count all nests present, regardless of whether or not eggs were present. Potential nests that appeared to be in the incipient stages of construction but were indistinguishable from natural accumulations of vegetation were not counted unless we observed grebes actually constructing them. We often took notes on nests counted in different subsections of a colony to assist with identifying new nests during subsequent surveys. During each survey, all new nests detected were added to the cumulative total number of nests for the year. Counting nests in large and widely dispersed colonies was often difficult, with one observer counting nests on one side of the canoe and a second observer counting nests on the other side of the canoe. Because some distant nests were potentially overlooked and some nests close together may have been counted twice, nest counts of the larger colonies were imprecise
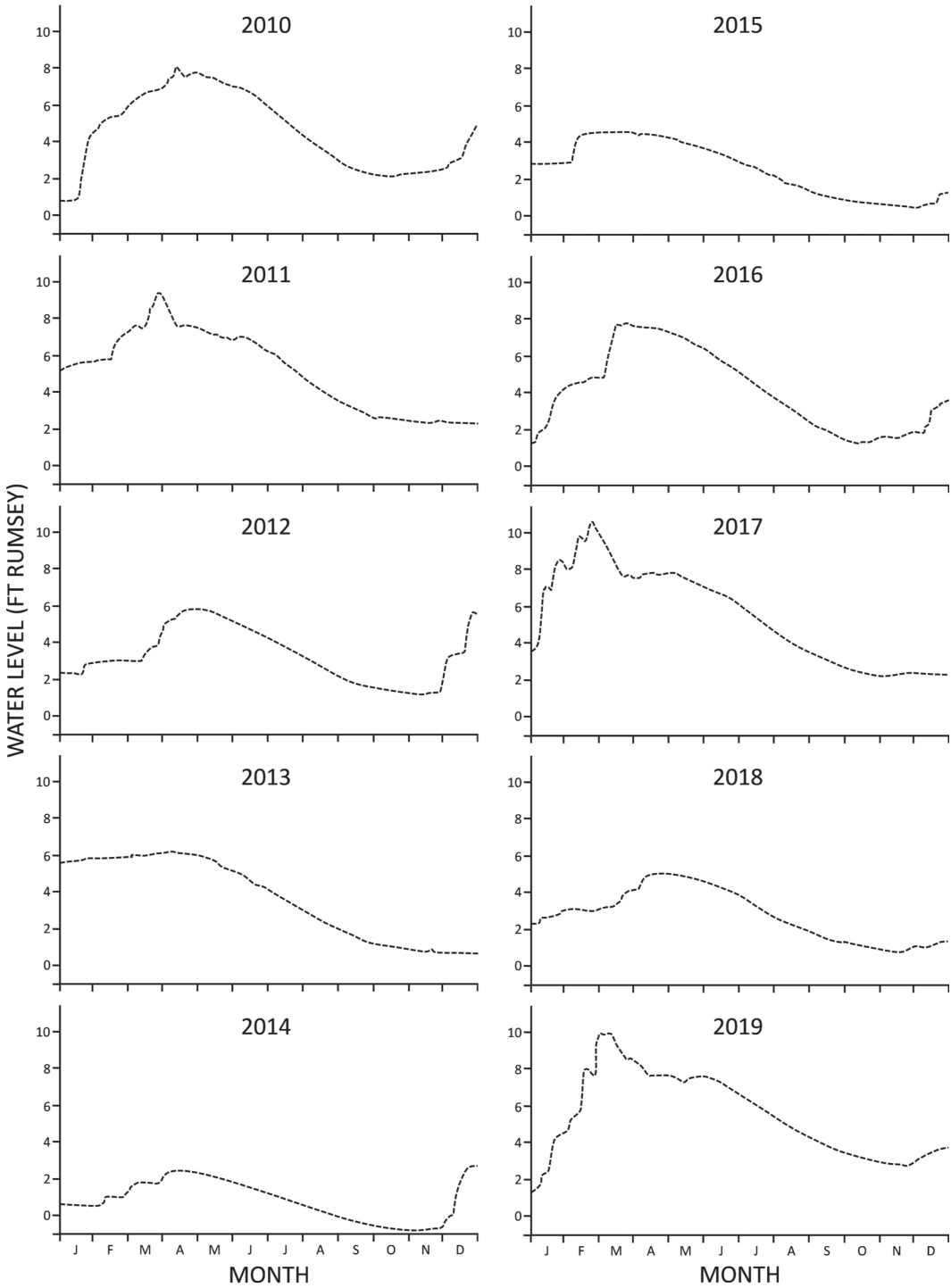
Fig. 2. Annual and seasonal variation in water level (0 ft Rumsey = 1318.26 ft above sea level) at Clear Lake, California, during 2010–2019.

TABLE 2. Annual variation in monitoring effort, number of *Aechmophorus* grebe nests in geographic regions, total number of nests, percentage of nests on Clear Lake, California (adjacent wetlands excluded), and percentage of marsh nests (open water nests excluded).

| Year | Effort (days) | Number of nests | | | | | | Total nests | Clear Lake (%) | Marsh nests (%) |
| | | Rodman Slough | Upper Arm | Oaks Arm | Lower Arm | Anderson Marsh | Cache Creek | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 2010 | 13 | 334 | 369 | 0 | 0 | 440 | 0 | 1143 | 32.3 | 68.4 |
| 2011 | 29 | 1 | 659 | 0 | 405 | 155 | 0 | 1220 | 87.2 | 63.2 |
| 2012 | 29 | 42 | 2224 | 0 | 5 | 113 | 0 | 2384 | 93.5 | 8.3 |
| 2013 | 23 | 202 | 2530 | 0 | 0 | 5 | 0 | 2737 | 92.4 | 2.0 |
| 2014 | 23 | 57 | 5879 | 0 | 0 | 0 | 0 | 5936 | 99.0 | 0.0 |
| 2015 | 15 | 20 | 858 | 8 | 1 | 11 | 0 | 898 | 95.5 | 3.1 |
| 2016 | 16 | 3735 | 206 | 1 | 338 | 703 | 7 | 4990 | 9.2 | 96.4 |
| 2017 | 15 | 2205 | 668 | 0 | 4 | 2198 | 0 | 5075 | 13.2 | 99.7 |
| 2018 | 7 | 355 | 3660 | 0 | 6 | 1 | 0 | 4022 | 91.1 | 4.9 |
| 2019 | 16 | 4 | 167 | 0 | 1516 | 1131 | 11 | 2829 | 27.3 | 79.7 |

estimates. The number of nests counted during a breeding season was used as a measure of reproductive effort.

We attempted to estimate the proportion of nests attended by Western Grebes and Clark's Grebes within selected colonies. Proportions were often based on a single scan of nests within a colony or subsection of a colony, and identification was based on one or both parents within 1 m of a nest. We did not attempt to count the proportion of nests attended by mixed pairs of Western Grebe and Clark's Grebe because it required considerable time to confirm that both species actually attended a nest (e.g., adding material to the nest, incubating eggs, or copulating), and we did not attempt to count the proportion of nests attended by hybrids, whose identification required close observation of bill coloration and facial pattern.

Each nest was classified as either a "marsh nest" if placed among emergent macrophytic vegetation near the shore (e.g., tules, water primrose, willows) or an "open water nest" if placed in open water >1 m from emergent vegetation (Lindvall and Low 1982). For colonies located in open water, we measured the minimum and maximum distances (m) of nests from the shore or emergent vegetation, usually based on measurements from a laser range finder or, in the case of more distant nests, a global positioning system unit.

Late in the 2010 breeding season, when nests appeared to be at a maximum density, we measured clutch size, nearest neighbor distance, density, and water depth of nests at several colonies. Clutch size was determined by counting the number of eggs in each nest. To estimate the number of eggs lost to a wind storm in 2014, mean clutch size was calculated with the inclusion of nests containing no eggs based on the 2 largest colonies combined. Nearest neighbor distance of nests was measured by using either an extendable aluminum pole with graduated markings or a laser range finder. The density of nests was measured by using a transect of known length and width, based on measurements obtained with a laser range finder. The water depth at each nest was measured using an extendable aluminum pole with graduated markings or a nylon line attached to a weight (the line was subsequently measured with the pole). To minimize disturbance of nesting grebes, we did not repeat these measurements during subsequent years.

## Breeding Population Surveys

We conducted a survey of the adult grebe population on Clear Lake from a motorboat during the middle of the breeding season (30 June to 7 August) during 5 of the 10 years (when funding was available) to obtain a minimum estimate of the potential breeding population size and the percent composition of the 2 species. Each survey consisted of a transect along the perimeter of the entire lake, usually 200–300 m from shore, with occasional deviations to inspect flocks of grebes. The distance of the transect was measured with the "Runkeeper" app on a cell phone (runkeeper.com) during 2 surveys ($\bar{x}$ = 108.5 km, SD = 3.5, range 106 to 111 km). We did not enter any tributaries or outlets of the lake, but we entered the major channel between Clear Lake and Clarks Island at Clearlake Oaks (colony site 29 in Fig. 1). We counted all grebes observed on the lake but only identified grebes within 100 m of the motorboat, and we did not count grebes beyond our view in the interior of the Upper Arm of the lake. The proportions of identified Western Grebes and Clark's Grebes were extrapolated for all grebes counted to obtain an estimate of total individuals for each species.

## Brood Surveys

A brood survey to evaluate reproductive success was conducted at the end of each breeding season (13–28 September), based on a fixed-width band transect (Tasker et al. 1984) with a 200-m width along the entire perimeter of the lake, but with occasional deviations to inspect flocks of grebes, and partially across the widest section of the lake. The distance of the transect was measured with the "Runkeeper" app on a cell phone (runkeeper.com) during 4 surveys ($\bar{x}$ = 111.8 km, SD = 9.6, range 100 to 121 km). We counted all adult and young grebes within 100 m of the motorboat. The number of young, young per nest (based on the number of young counted during brood surveys and the number of nests counted throughout the breeding season), and productivity ratio of young to adults were used as measures of reproductive success.

## Water Level

Data on water level (ft Rumsey) during the study period were obtained from the U.S. Geological Survey (http://waterdata.usgs.gov/ca/nwis/uv?site_no=11450000). We used the water level on 1 July (when nesting rapidly accelerates during most years) for each year to examine the effects of water level on (1) proportion of nests on the lake (vs. associated wetlands), (2) proportion of Western Grebes (vs. Clark's Grebes) attending nests, (3) proportion of Western Grebes (vs. Clark's Grebes) counted during midsummer surveys, (4) proportion of marsh nests (vs. open water nests), (5) total number of nests, (6) number of young counted during brood surveys, (7) number of young per nest, and (8) productivity ratio of young to adults during brood surveys.

## Causes of Nest Failure, Injury, and Mortality

We recorded observations on nest failure and attempted to identify causes, including wave action, predation on eggs, chicks, or adults, incidental destruction of eggs by other animals, stranding on land due to lowering water level, and colony abandonment for unknown cause. Nest abandonment due to wind-generated waves was identified by observing nests that had drifted to shore or into very shallow water. Colonies of at least 10 nests were considered abandoned (smaller colonies may have been destroyed by predators) when nesting activities ceased prior to the minimum incubation period of 21 days (Lindvall and Low 1982) without any other suspected cause being identified within 15 days of colony discovery, and were considered not abandoned if nesting activities continued beyond 15 days of colony discovery (some colonies may have initiated nesting >1 week prior to discovery and would therefore have hatched out by the 15th day).

Diurnal predation on grebe eggs was studied by counting the number of predators entering colonies with eggs, the number of predation events on one or more eggs in a nest, and the number of hours spent observing colonies with eggs. Both diurnal and nocturnal predation was studied during 2014–2017 by up to 6 motion-activated cameras (Bushnell Trophy Cam Bone Collector RTAP Night Vision and Bushnell Trophy Cam HD Aggressor No Glow). Each camera was bolted to a U-channel post pushed into bottom sediments and aimed at one or more active nests with one or more eggs. Sampling effort was measured by recording the number of hours from when a grebe first returned to an active nest to the final photo of a grebe in the vicinity of a nest. Intrusions were considered to occur whenever a predator was photographed by a camera, and predation events were considered to occur whenever a predator destroyed,

consumed, or removed one or more eggs from a nest. Incidental destruction of eggs by animals other than predators was identified by examining photographs from motion-activated cameras.

Disturbances by humans were assessed by counting the number of intrusions into active colonies with eggs by motorized watercraft (motorboats, airboats, and jet skis) and paddled watercraft (kayaks and canoes). We divided the number of disturbances by the number of hours spent directly observing colonies with eggs in order to calculate the number of disturbances per hour.

Observations of injured or dead birds were inconsistently recorded before 2016 and were more consistently recorded during 2016–2019. Whenever possible, the causes of injury and mortality were evaluated by direct observation, often documented by photographs.

The potential impact of smoke from wildland fires on reproductive success was evaluated by obtaining data on inhalable particles with diameters $\leq 10$ μm ($PM_{10}$ data) from Lakeport during 2013–2019 (Environmental Protection Agency; http://www.epa.gov/outdoor-air-quality-data).

### Statistical Analyses

Both parametric Pearson correlation coefficients ($r$ statistic) and nonparametric Spearman rank correlation coefficients ($r_s$ statistic; Zar 2010) were calculated to test for significant associations between variables measuring monitoring effort (days of fieldwork), water level, year, location of nests (lake vs. associated wetlands), type of nests (marsh vs. open water nests), species ratio (Western Grebe vs. Clark's Grebe), reproductive effort (number of nests), and reproductive success (number of young, number of young per nest, and productivity ratio of young to adults). Because of a small sample size of 10 years and nonnormal monotonic distributions for some variables, only the more conservative nonparametric Spearman rank correlation coefficients are provided except for one case in which both are provided because there was a difference in the significance between the 2 tests. A Mann–Whitney $U$ test ($U$ statistic; Zar 2010) was used to test for differences in nearest neighbor distances between marsh nests and open water nests. Statistical tests were computed with Statistix 10 software with 2-tailed probabilities and $\alpha = 0.05$ (Anonymous 2013).

Because $P$ values conflate effect size and sample size, and a sample size of 10 yields significant correlations only for very large effects ($r$ or $r_s >$ 0.58; Zar 2010), we highlight effect sizes for all significant statistical test results. Effect sizes are more meaningful and can be readily compared among different data sets and different studies (Cohen 1988, Hojat and Xu 2004, Nakagawa and Cuthill 2007). For correlation coefficients ($r$ or $r_s$), values of ~0.1, ~0.3, and >0.5 loosely correspond to small, medium, and large effects, respectively (Cohen 1988). The same interpretation applies to $r$ from the Mann–Whitney $U$ test, with $r$ calculated as $z / \sqrt{N}$ (Field 2013).

### Results

#### Number of Grebe Nests and Clutch Size

The number of grebe nests per year varied greatly from 898 in 2015 to 5936 in 2014, with a mean of 3123.4 (SD = 1804.0, $n = 10$ years; Table 2). The number of grebe nests was not correlated with year ($r_s = 0.54$, $P = 0.10$, $n =$ 10 years) or water level ($r_s = -0.10$, $P = 0.79$, $n = 10$ years).

The maximum mean clutch size in the 2 largest colonies in 2010 ranged from 2.29 (SD = 0.94, range 1 to 5, $n = 76$ nests) at Rodman Slough South to 2.37 (SD = 1.09, range 1 to 7, $n = 294$) at Anderson Marsh Southeast on 6 August 2010.

#### Colony Sites, Persistence, and Size

Nesting colonies of grebes occurred at 37 sites and were concentrated at Rodman Slough (5 sites), along the northwestern shore (7 sites) and southwestern shore (15 sites) of the Upper Arm, at the southeastern end of the Lower Arm (2 sites), and in Anderson Marsh (4 sites) (Fig. 1, Table 3). A few nests were constructed during 1 or 2 years only along the east shore of the Upper Arm (1 site), at the east end of the Oaks Arm (1 site), in the middle section of the Lower Arm (1 site), and in Cache Creek (2 sites) (Fig. 1, Table 3).

Nesting occurred during >5 years at only 10 colony sites, and during all 10 years at only 3 colony sites: Rodman Slough South, West of Tule Island, and Twin Coves West (Table 3). West of Tule Island was the only colony site averaging >1000 nests per year ($\bar{x} = 1011.6$; Table 3). During some years 2 subcolonies formed independently at distances >400 m apart at West of Tule Island, and they were divided by a deeper channel south of Rodman Slough. But during other years, a colony on one

TABLE 3. Characteristics of *Aechmophorus* grebe colony sites at Clear Lake, California, and associated wetlands, including site number corresponding with Fig. 1, coordinates (decimal degrees north, west), years active, number of nests per year, percentage of marsh nests, and distance of grebe nests from shore or emergent vegetation. Supercolonies, which occasionally form by the merger of 2 or more colonies, are indicated by superscripted letters.

| Colony | Coordinates | Years active | Number of nests per year | | | Marsh nests (%) | Distance from shore (m) |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | | | Mean | SD | Range | | |
| Rodman Slough tributaries | | | | | | | |
| 1. Middle Creek Marsh | 39.1353, −122.9027 | 1 | 1.1 | 3.5 | 0–11 | 100 | 0 |
| 2. Rookery Channel | 39.1341, −122.8990 | 1 | 0.2 | 0.6 | 0–2 | 100 | 0 |
| 3. Rodman Slough Northwest[a] | 39.1277, −122.8986 | 2 | 424.2 | 894.5 | 0–2163 | 100 | 0 |
| 4. Rodman Slough North[a] | 39.1261, −122.8940 | 6 | 113.1 | 263.5 | 0–844 | 81.5 | 0–42 |
| 5. Rodman Slough South[a] | 39.1209, −122.8895 | 10 | 156.9 | 259.0 | 1–799 | 84.0 | 0–69 |
| Clear Lake: Upper Arm | | | | | | | |
| 6. Lucerne | 39.0923, −122.8061 | 2 | 1.3 | 3.8 | 0–12 | 0 | 225–500 |
| 7. Nice East | 39.1190, −122.8499 | 2 | 0.3 | 0.7 | 0–2 | 0 | 70–565 |
| 8. Nice West[b] | 39.1214, −122.8689 | 4 | 29.0 | 65.8 | 0–212 | 0 | 30–683 |
| 9. Northeast of Tule Island[b] | 39.1172, −122.8748 | 3 | 39.2 | 112.2 | 0–357 | 0 | 0–426 |
| 10. South of Tule Island[b] | 39.1109, −122.8737 | 2 | 4.0 | 8.6 | 0–23 | 0 | 473–578 |
| 11. West of Tule Island[b] | 39.1149, −122.8842 | 10 | 1011.6 | 1462.1 | 3–4721 | 0.2 | 0–1100 |
| 12. Lyons Creek[b] | 39.1050, −122.8919 | 3 | 99.8 | 202.0 | 0–518 | 0 | 160–1000 |
| 13. Rocky Point | 39.0881, −122.9003 | 2 | 1.3 | 3.8 | 0–12 | 0 | 59–90 |
| 14. Rumsey Bay | 39.0546, −122.9139 | 1 | 0.1 | 0.3 | 0–1 | 0 | 68 |
| 15. Library Park | 39.0453, −122.9109 | 1 | 0.1 | 0.3 | 0–1 | 0 | 500 |
| 16. Willow Point | 39.0391, −122.9121 | 4 | 3.2 | 8.4 | 0–27 | 0 | 14–207 |
| 17. Shoal | 39.0323, −122.9059 | 2 | 13.5 | 29.5 | 0–84 | 0 | 300–650 |
| 18. Manning Creek | 39.0280, −122.9099 | 7 | 94.5 | 144.2 | 0–427 | 0.2 | 0–416 |
| 19. Twin Coves West[c] | 39.0262, −122.9027 | 10 | 268.8 | 435.6 | 2–1329 | 53.6 | 0–307 |
| 20. Twin Coves East[c] | 39.0243, −122.8977 | 7 | 133.2 | 273.8 | 0–866 | 4.6 | 0–350 |
| 21. Rumsey Slough | 39.0253, −122.8916 | 6 | 15.1 | 29.0 | 0–94 | 7.9 | 0–470 |
| 22. Lands End | 39.0278, −122.8849 | 2 | 0.4 | 1.0 | 0–3 | 33.3 | 0–127 |
| 23. Holiday Cove | 39.0293, −122.8792 | 1 | 0.2 | 0.6 | 0–2 | 100 | 0 |
| 24. Adobe Creek | 39.0298, −122.8747 | 4 | 6.4 | 15.2 | 0–49 | 10.9 | 0–162 |
| 25. McGaugh Slough | 39.0277, −122.8671 | 1 | 0.2 | 0.6 | 0–2 | 100 | 0 |
| 26. Long Tule Point | 39.0305, −122.8610 | 6 | 109.8 | 211.6 | 0–513 | 12.9 | 0–150 |
| 27. Corinthian Bay | 39.0284, −122.8508 | 5 | 5.7 | 13.6 | 0–44 | 43.9 | 0–100 |
| 28. Quercus Point | 39.0294, −122.8403 | 2 | 2.8 | 7.9 | 0–25 | 0 | 68–295 |
| Clear Lake: Oaks Arm | | | | | | | |
| 29. Clearlake Oaks | 39.0201, −122.6754 | 2 | 0.9 | 2.5 | 0–8 | 100 | 0 |
| Clear Lake: Lower Arm | | | | | | | |
| 30. Gooseneck Point | 38.9758, −122.6872 | 1 | 0.1 | 0.3 | 0–1 | 0 | 20 |
| 31. Sunrise Shores | 38.9403, −122.6527 | 5 | 67.0 | 142.7 | 0–405 | 100 | 0 |
| 32. Indian Island[d] | 38.9367, −122.6453 | 5 | 160.7 | 477.0 | 0–1516 | 75.5 | 0–104 |

Table 3. Continued.

| Colony | Coordinates | Years active | Number of nests per year | | | Marsh nests (%) | Distances (m) from shore |
|---|---|---|---|---|---|---|---|
| | | | Mean | SD | Range | | |
| Outlets | | | | | | | |
| 33. Anderson Marsh North[d] | 38.9282, −122.6473 | 7 | 30.4 | 48.1 | 0–142 | 95.7 | 0–49 |
| 34. Anderson Marsh Southwest[e] | 38.9240, −122.6435 | 5 | 58.8 | 83.5 | 0–233 | 89.6 | 0–43 |
| 35. Anderson Marsh Southeast[e] | 38.9235, −122.6401 | 6 | 660.7 | 386.5 | 0–2054 | 100 | 0 |
| 36. Cache Creek West | 38.9311, −122.6378 | 1 | 1.1 | 3.5 | 0–11 | 0 | 13–27 |
| 37. Cache Creek East | 38.9293, −122.6299 | 1 | 0.7 | 2.2 | 0–7 | 100 | 0 |

side of the channel expanded gradually to the other side, so we have considered West of Tule Island a single colony site. The colony site with the second highest number of nests was Anderson Marsh Southeast ($\bar{x}$ = 660.7 nests), followed by Rodman Slough Northwest ($\bar{x}$ = 424.2) and Twin Coves West ($\bar{x}$ = 268.8; Table 3). Nesting occurred during only 1 or 2 years at 18 of 37 colony sites (Table 3).

The number of nests in each colony varied greatly (Table 3). The largest colony comprised 4721 nests at West of Tule Island in 2014, but it was an arbitrarily defined subset of a super-colony comprising 5587 nests scattered 3 km across the north end of the Upper Arm, from the Lyons Creek colony site along the west shore to the Nice East colony site along the east shore. Other large supercolonies included 3722 nests at Rodman Slough in 2016, 2184 nests in Anderson Marsh in 2017, and 1606 nests at Indian Island and Anderson Marsh in 2019.

The distribution of nests and number of nests at colony sites were strongly affected by water level, which was negatively correlated with the proportion of nests on Clear Lake compared with its associated wetlands ($r_s$ = −0.77, $P$ = 0.014, $n$ = 10 years; large effect size; Fig. 3). During low-water years, proportionately more nests were located on Clear Lake, and during high-water years proportionately more nests were located in channels of the tributaries and outlets (Fig. 3, Table 2).

Seasonal Variation in Nesting

The initiation of nesting was highly variable among years (Fig. 4). Nest construction usually began from late May to the middle of June (Fig. 4), and egg laying usually began during the second half of June. Nesting began much earlier during 2 years. In 2016, the first nests with eggs were reported at Rodman Slough Northwest on 9 May (Kraig Jillson personal communication), and the first chicks were reported during the last week of May (Faith Rigolosi personal communication), well before we began our surveys on 10 June. In 2017, we found 174 nests with up to 5 eggs in individual nests at Rodman Slough Northwest on 30 April. However, about 2000 nests, many with eggs, were found at Anderson Marsh Southeast when we first checked the colony site a week later on 7 May. Furthermore, 2 small chicks were observed nearby on the previous day (6 May) by Tom McFarling (personal communication), indicating that egg laying must
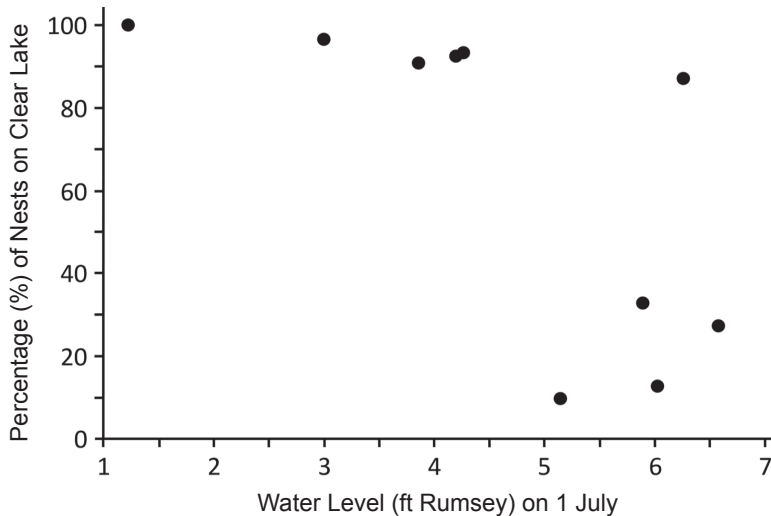
Fig. 3. Relationship between the percentage (%) of grebe nests on Clear Lake, California (vs. in associated wetlands of tributaries and outlets), and water level (ft Rumsey on 1 July) in each breeding season from 2010 to 2019.

have commenced by 17 April at the latest but probably earlier, based on a minimum incubation period of 21 days (Lindvall and Low 1982). The latest documented start of the breeding season occurred during 2012, when no nests were found on 3 June, 3 nests but no eggs were found on 10 June, and 46 nests but only 1 egg on 22 June.

The number of new nests found on the lake normally peaked during July or August and declined precipitously in late August and September (Fig. 4). The longest breeding season occurred during 2017, with more than 4 continuous months of nesting activity at Anderson Marsh Southwest. The latest breeding activity occurred on 3 October 2010, when at least 11 of 14 nests with eggs were attended by incubating grebes at Northeast of Tule Island. No nests were found when the colony site was scrutinized with a telescope from land on 7 October.

Because we could not pinpoint the first dates of nest initiation or egg laying, we did not attempt to statistically analyze the relationship between seasonal variation in nesting activities and water level. Nevertheless, seasonal variation in nesting activities did not appear to be associated with water level. For example, nesting began earliest during a high-water year in 2017, but began no earlier than usual during the high-water years of 2011 and 2019, and nesting during the low-water year of 2014 peaked much earlier than during the high-water year of 2011 (Figs. 2, 4).

## Grebe Species Ratios

Western Grebes and Clark's Grebes nested together in mixed species colonies, although Clark's Grebes were sometimes absent in small colonies of up to 44 nests. The ratio of nests attended by Western Grebes and Clark's Grebes varied greatly during the study period, ranging from 96.3 to 3.7 in 2011 to 59.4 to 40.6 in 2015, with an overall ratio of 84.9 to 15.1 when data from all years were combined ($n = 4465$ nests; Table 4). The proportion of Western Grebes (vs. Clark's Grebes) attending nests was unrelated to water level ($r_s = 0.20$, $P = 0.56$, $n = 10$ years). Our 2015 data, which had the lowest number of nests (Table 2) and the lowest ratio of Western Grebes to Clark's Grebes (Table 4), are biased because we neglected to obtain a ratio of species attending nests at a colony of 293 nests with a much smaller proportion of Clark's Grebes at West of Tule Island in July. When data from 2015 are excluded, the overall ratio of Western Grebes to Clark's Grebes attending nests is 85.5 to 14.5 ($n = 4369$ nests). We documented small numbers of mixed pairs and hybrids attending nests, but we estimate that the 2 groups made up <3% of all nests.

The ratios of adult Western Grebes to Clark's Grebes obtained during midsummer population surveys ranged from 90.6 to 9.4 in 2019 to 72.8 to 27.2 in 2016 (Table 4). The ratios of Western Grebes to Clark's Grebes attending nests varied
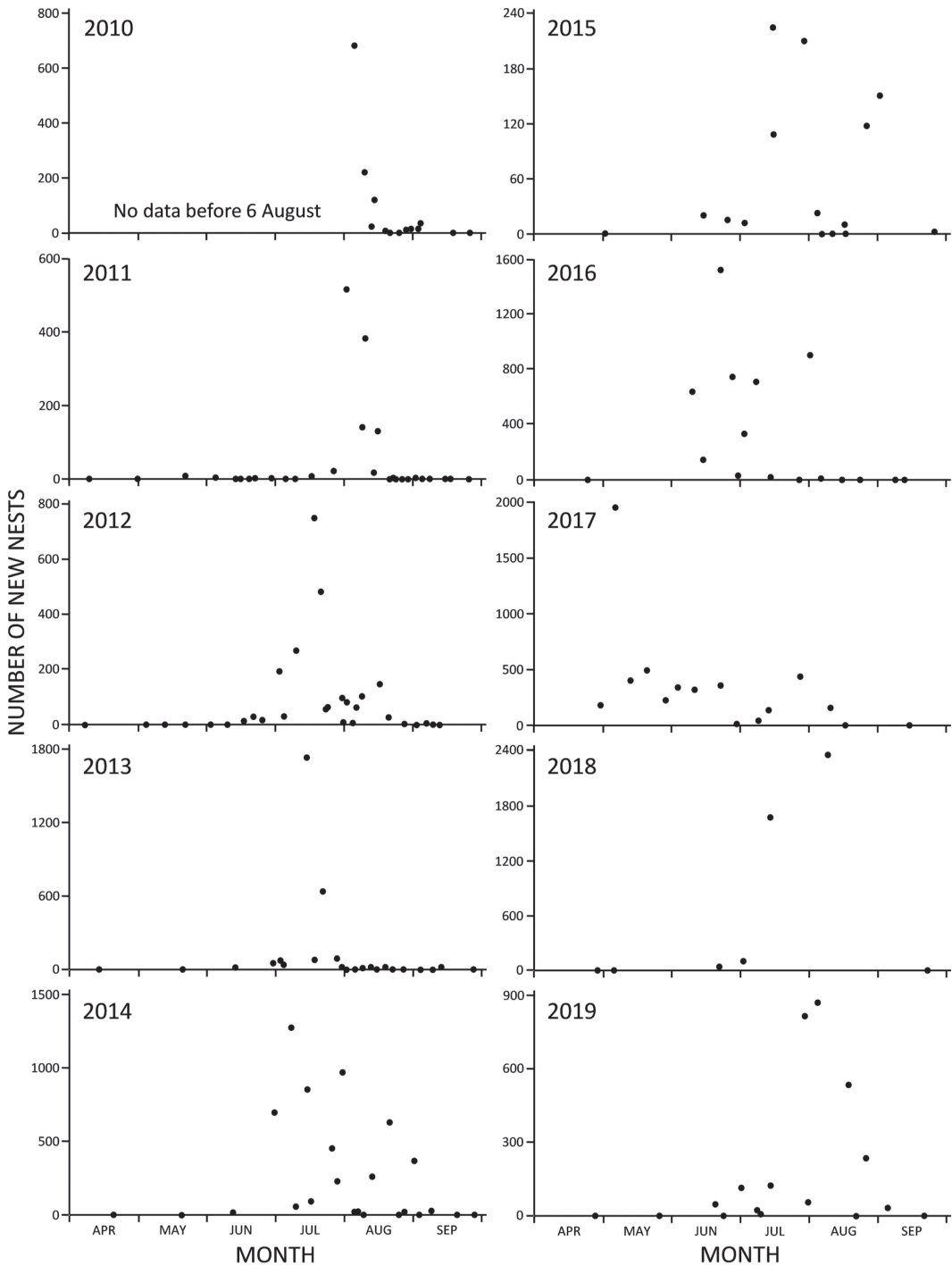
Fig. 4. Annual and seasonal variation in the number of new grebe nests detected during each day of fieldwork at Clear Lake, California, during the 2010–2019 breeding seasons.

TABLE 4. Numbers and percentages (in parentheses) of Western Grebes and Clark's Grebes attending nests and observed throughout Clear Lake, California, during midsummer population surveys.

| Year | Attending nests | | | Observed throughout Clear Lake | | |
|---|---|---|---|---|---|---|
| | Nests sampled | Western Grebe (%) | Clark's Grebe (%) | Total grebes | Western Grebe (%) | Clark's Grebe (%) |
| 2010 | 431 | 400 (92.8) | 31 (7.2) | — | — | — |
| 2011 | 681 | 656 (96.3) | 25 (3.7) | — | — | — |
| 2012 | 76 | 65 (85.5) | 11 (14.5) | 7760 | 6487 (83.6) | 1273 (16.4) |
| 2013 | 889 | 838 (94.3) | 51 (5.7) | 8250 | 6238 (75.6) | 2012 (24.4) |
| 2014 | 450 | 395 (87.8) | 55 (12.2) | — | — | — |
| 2015 | 96 | 57 (59.4) | 39 (40.6) | 5077 | 3991 (78.6) | 1086 (21.4) |
| 2016 | 640 | 445 (69.5) | 195 (30.5) | 3236 | 2356 (72.8) | 880 (27.2) |
| 2017 | 249 | 174 (69.9) | 75 (30.1) | — | — | — |
| 2018 | 510 | 391 (76.7) | 119 (23.3) | — | — | — |
| 2019 | 443 | 372 (84.0) | 71 (16.0) | 2364 | 2142 (90.6) | 222 (9.4) |
| TOTAL | 4465 | 3793 (84.9) | 672 (15.1) | 26,687 | 21,214 (79.5) | 5473 (20.5) |

more and was not correlated with the ratios of adult Western Grebes to Clark's Grebes counted during midsummer population surveys ($r_s = 0.10$, $P = 0.78$, $n = 5$ years). The ratio of Western Grebes to Clark's Grebes during all 5 years of midsummer population surveys combined was 79.5 to 20.5 ($n = 26,687$ grebes; Table 4).

## Types of Grebe Nests

Marsh nests (Fig. 5A) were attached to emergent vegetation along the shore, including tules, water smartweed, water primrose, and willows. A few nests classified as marsh nests were attached to wooden structures anchored to the substrate, floating pieces of wood, wire mesh connecting beams of a wooden structure, or buoys (Fig. 6A–C). Open water nests (Fig. 5B) were anchored to submerged vegetation, mostly pondweed (*Stuckenia* spp.) and coon's tail (*Ceratophyllum demersum*), in open water up to 1.1 km from shore (Table 3). The proportions of marsh nests and open water nests varied greatly among the colonies, with marsh nests more prevalent along narrow channels of tributaries and outlets, and open nests more prevalent in lagoons along the shore of Clear Lake (Tables 2–3). The proportion of marsh nests was significantly correlated with water level ($r_s = 0.81$, $P = 0.007$, $n = 10$ years; large effect size). During high-water years, more marsh nests were constructed, and during low-water years, more open water nests were constructed (Fig. 7, Table 2) because less marsh vegetation was available. During 2014, when water level was lowest, nearly all grebe nests were open water nests (Fig. 7, Table 2) because all marsh vegetation was above the water level, precluding nesting.

Mean nearest neighbor distance was shorter between marsh nests ($\bar{x} = 3.1$ m, SD = 1.8, range 1 to 13 m, $n = 168$ in 2 colonies) than between open water nests ($\bar{x} = 60.0$ m, SD = 54.1, range 3 to 200 m, $n = 20$ in 2 colonies) ($U = 144$, $P < 0.001$; $r = 0.49$, large effect size). Mean nearest neighbor distance in colonies with marsh nests ranged from 2.9 m (SD = 0.8, range 1.7 to 5.2 m, $n = 61$ of 440 nests) at Anderson Marsh Southeast to 3.2 m (SD = 2.1, range 1.0 to 13.0, $n = 107$ of 334 nests) at Rodman Slough South. In colonies with open water nests, mean nearest neighbor distances ranged from 33.9 m (SD = 35.7, range 3 to 130 m, $n = 12$ nests) at Twin Coves West to 96.5 m (SD = 58.9, range 60 to 200 m, $n = 8$ nests) in a subset of a larger colony at West of Tule Island.
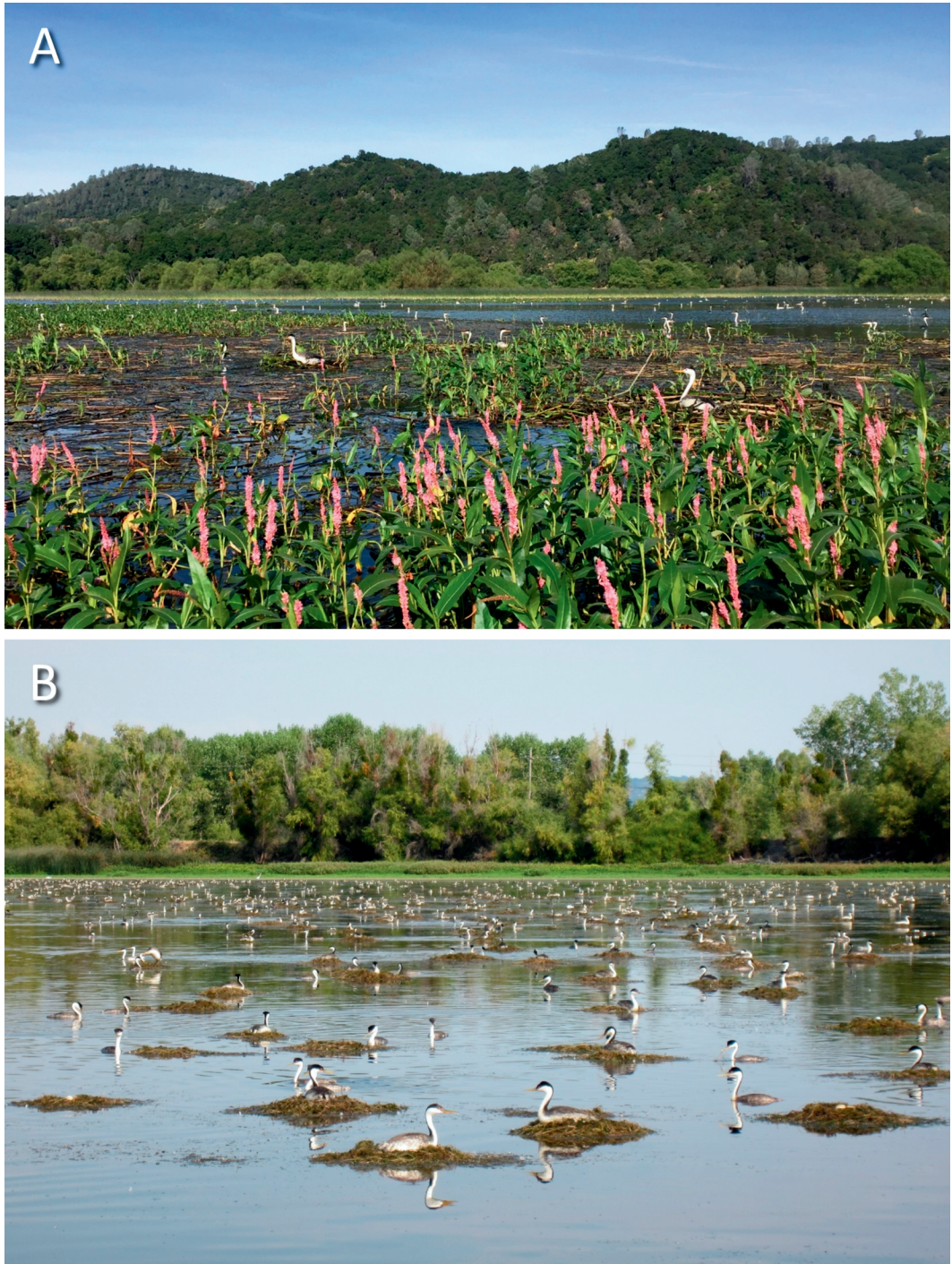
Fig. 5. Types of grebe nests. **A,** Marsh nests at Anderson Marsh Southeast on 30 May 2017. **B,** Open water nests at West of Tule Island on 17 July 2014. Photos by Floyd E. Hayes.
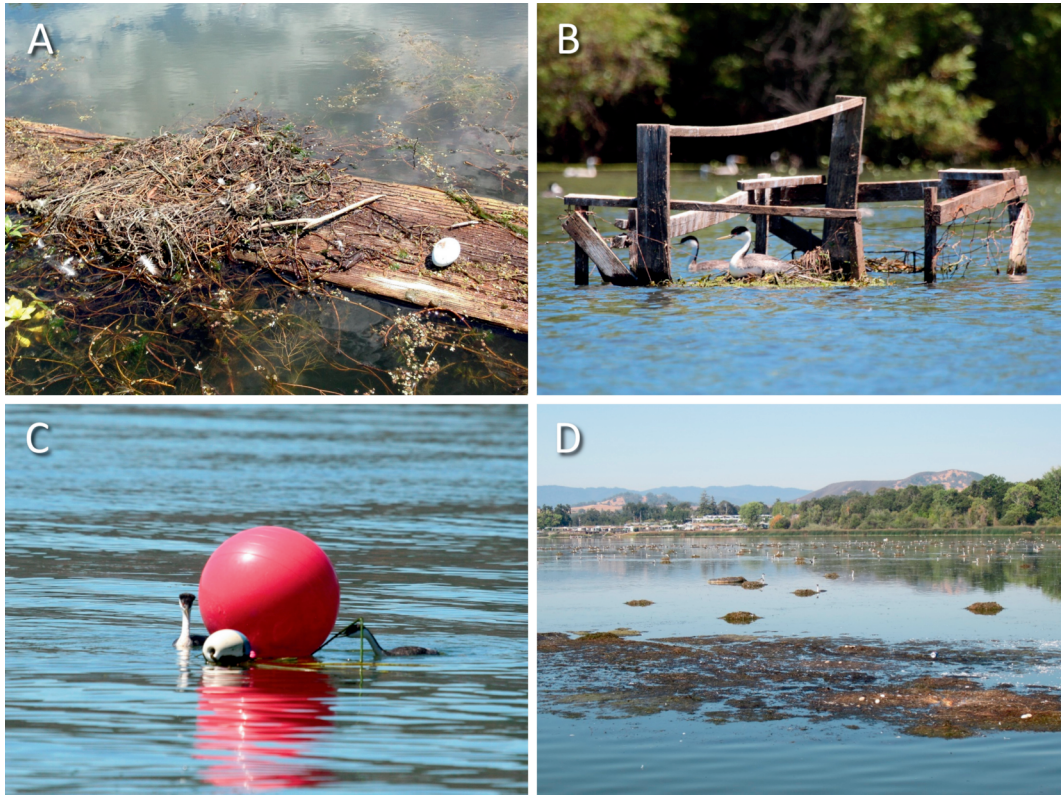
Fig. 6. Unusual grebe nests. *A,* Nest on a floating board at Rodman Slough North on 30 July 2015. *B,* Nest on wire mesh of a wooden structure at Rodman Slough Northwest on 23 June 2017. *C,* Nest on a buoy at Gooseneck Point on 24 July 2012. *D,* Nest stranded on a mudflat at West of Tule Island on 14 August 2014. Photos by Floyd E. Hayes.
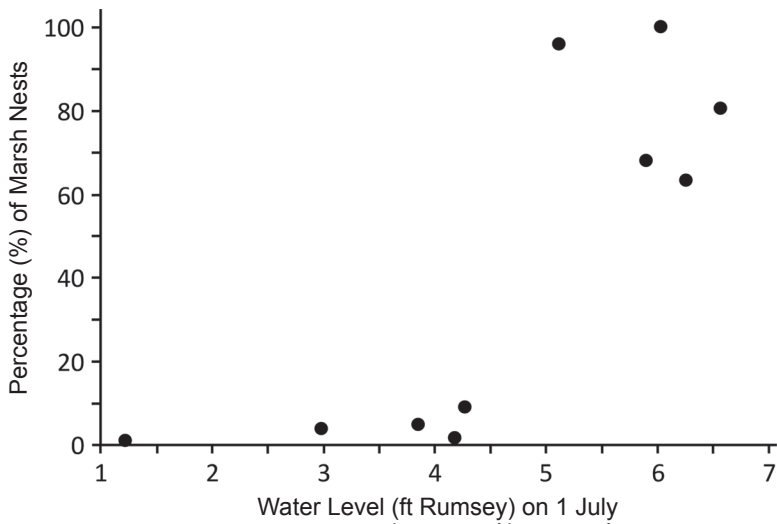


Fig. 7. Relationship between the percentage (%) of marsh nests (vs. open water nests) and water level (ft Rumsey on 1 July) in each breeding season from 2010 to 2019.

TABLE 5. Number of young and adult *Aechmophorus* grebes, number of young per nest, and productivity ratio of young to adults at Clear Lake, California. The numbers of young and adults are based on brood surveys at the end of the breeding season, and the number of nests is based on the total number of nests during the year.

| Year | Young | Adults | Young:nest | Young:adults |
|---|---|---|---|---|
| 2010 | 121 | 2694 | 0.106 | 0.045 |
| 2011 | 10 | 2245 | 0.008 | 0.004 |
| 2012 | 125 | 3828 | 0.052 | 0.033 |
| 2013 | 44 | 1630 | 0.017 | 0.027 |
| 2014 | 176 | 1115 | 0.030 | 0.158 |
| 2015 | 2 | 730 | 0.002 | 0.003 |
| 2016 | 353 | 3131 | 0.071 | 0.113 |
| 2017 | 599 | 2374 | 0.118 | 0.252 |
| 2018 | 1 | 1692 | 0.00025 | 0.0006 |
| 2019 | 108 | 2746 | 0.038 | 0.039 |

The density of nests was relatively high in colonies with marsh nests, ranging from 339.4 nests/ha (0.66 ha surveyed) at Anderson Marsh Southeast to 432.5 nests/ha (0.40 ha surveyed) at Rodman Slough South. The density of nests was relatively low in colonies with open water nests, ranging from 51.9 nests/ha (1.75 ha surveyed) at West of Tule Island to 83.3 nests/ha (0.18 ha surveyed) at Nice West.

Marsh nests were placed in shallower water ($\bar{x}$ = 0.64, SD = 0.20, range 0.29 to 1.06 m, $n$ = 154 nests in 2 colonies) than open water nests ($\bar{x}$ = 1.61 m, SD = 0.41, range 0.97 to 2.30 m, $n$ = 20 nests in 2 colonies) ($U$ = 5.5, $P$ < 0.001; $r$ = 0.55, large effect size). Mean water depths of nests in colonies with marsh nests ranged from 0.44 m (SD = 0.06, range 0.29 to 0.62 m, $n$ = 62 nests) at Anderson Marsh Southeast to 0.78 m (SD = 0.14, range 0.47 to 1.06 m, $n$ = 92 nests) at Rodman Slough South. Water depths of open water nests were more difficult to measure due to wind blowing the canoe, so fewer measurements were taken. Mean water depths ranged from 1.19 m (SD = 0.15, range 0.97 to 1.47 m, $n$ = 8 nests) in a nearshore subset of a colony 18–260 m from shore at West of Tule Island to 1.89 m (SD = 0.27, range 1.5 to 2.3 m, $n$ = 12 nests) in a colony 60–185 m from shore at Twin Coves West to 3.17 m (SD = 0.06, range 3.1 to 3.2 m, $n$ = 3 nests, excluded from the statistical testing above) in the 3 most distant nests about 900–950 m from shore at West of Tule Island. Water depths of nests gradually decreased during the incubation period because water level declined steadily during the breeding season (Fig. 2), sometimes resulting in active nests becoming stranded on land and abandoned by the grebes. Although the deepest water we measured for a nest was 3.1 m, some of the nests we observed in subsequent years (up to 1.1 km from shore) may have been in deeper water.

Some incomplete nests did not appear to be serious attempts at breeding, especially toward the end of the breeding season. For example, on 13 September 2013 we found many small clumps of floating vegetation in the northeast section of the Upper Arm, including 12 clumps resembling incipient nests to which pairs of grebes were busily adding vegetation. The incipient nests were scattered across 2 km of the lake, about 225–450 m from shore near Lucerne. Given the early stage of nest construction, absence of eggs or copulation, exposed position of the nests in deep water, and lateness of the breeding season, we suspected that the sight of small nest-sized clumps of vegetation temporarily stimulated the grebes to add vegetation to them.

Breeding Population Size and Productivity

The number of adult grebes counted during midsummer population surveys on Clear Lake (associated wetlands excluded) varied greatly from 2364 to 8250, with a mean of 5337.4 (SD = 2630.4, $n$ = 5 years; Table 4). The number of adult grebes was not correlated with water level ($r_s$ = −0.70, $P$ = 0.23, $n$ = 5 years), total number of grebe nests ($r_s$ = −0.50, $P$ = 0.45, $n$ = 5 years), or number of grebe nests on Clear Lake only ($r_s$ = 0.50, $P$ = 0.35, $n$ = 5 years).

The number of young observed during brood surveys at the end of the breeding season varied dramatically from 1 to 599, with a mean of 153.9 (SD = 189.0, $n$ = 10 years; Table 5), and was not significantly correlated with the number of nests ($r_s$ = 0.58, $P$ = 0.08, $n$ = 10 years) or water level ($r_s$ = 0.20, $P$ = 0.56, $n$ = 10 years). The number of young per nest also varied dramatically from 0.00025 to 0.118, with a mean of

0.04 (SD = 0.04, $n$ = 10 years; Table 5), and was strongly correlated with the number of young ($r_s$ = 0.88, $P$ = 0.001, $n$ = 10 years; large effect size), but was not significantly correlated with the number of nests ($r_s$ = 0.26, $P$ = 0.45, $n$ = 10 years) or water level ($r_s$ = 0.47, $P$ = 0.17, $n$ = 10 years). The productivity ratio during brood counts also varied dramatically from 0.0006 to 0.252, with a mean of 0.07 (SD = 0.08; Table 5), and was strongly correlated with the number of young ($r_s$ = 0.95, $P$ < 0.001, $n$ = 10 years; large effect size) and the number of young per nest ($r_s$ = 0.85, $P$ = 0.003, $n$ = 10 years; large effect size) but was not significantly correlated with the number of nests ($r_s$ = 0.60, $P$ = 0.07; however, $r$ = 0.75, $P$ = 0.01, $n$ = 10 years; large effect size) or water level ($r_s$ = 0.22, $P$ = 0.51, $n$ = 10 years).

### Natural Causes of Nest Failure

Destruction of open water nests by wind-generated waves was a major cause of nest failure. The waves detach nests from submergent vegetation and blow the nests into very shallow water or ashore where they are abandoned by the grebes even when eggs are present. We observed indirect evidence of this occurring during 2010–2015 and in 2019, but not during the high water years of 2016–2017, when few open water nests were constructed, or in 2018, when few surveys were conducted (Fig. 2, Table 2). For example, about 200 of 247 nests were blown into shallow water at Long Tule Point between 11 and 14 August 2011 (Fig. 8), representing about 16% of the year's nests, and about 100 of 148 nests blew ashore at Twin Coves East between 29 July and 6 August 2013, representing about 4% of the year's nests. Direct evidence of nest destruction by waves was obtained by motion-activated cameras, which photographed multiple nests drifting toward shore during 10–11 August 2014, when at least 1000 of about 3500 active nests, with an estimated 2030 eggs (based on 2.03 eggs per nest at the 2 largest colonies in 2010; see methods), blew ashore at West of Tule Island, Northeast of Tule Island, and Nice West, representing about 17% of the year's nests. More drifting nests were photographed by motion-activated cameras on 18 July 2015, when most, if not all, of 318 nests were blown ashore at West of Tule Island, representing about 35% of the year's nests. On 2 occasions, we directly observed drifting nests: one abandoned and empty nest drifted a few

hundred meters upstream in Rodman Slough on 5 August 2012, and another with 2 eggs incubated by a Clark's Grebe drifted about 100 m upstream in Rodman Slough and was abandoned by the adult when the nest drifted underneath a bridge on 10 August 2014. We did not observe any evidence of marsh nests destroyed by waves.

Predation was also a major cause of nest failure. During daylight, predation events were detected at a much greater rate by direct observation (0.33/h; $n$ = 301.5 h) than during monitoring by motion-activated cameras (0.0016/h; $n$ = 6650 h; Table 6), presumably because many nests could be observed simultaneously during direct observation, whereas each camera was focused on only one or a few nests. Four species of birds preyed upon grebe eggs, but only during the day (Table 6). In the analysis discussed below, which compared the frequency of predation among different bird species, data from direct observations and camera monitoring were combined. The American Crow (*Corvus brachyrhynchos*) was the major diurnal predator of grebe eggs, preying on eggs during 33% of intrusions and accounting for 84% of predation events (Fig. 9C, Table 6). In 2014 we obtained indirect evidence of the extent of crow predation on eggs at the West of Tule Island colony. On 2 July, 19 days after the first 2 nests were found, we spotted a crow carrying a grebe egg to a muddy beach east of the mouth of Rodman Slough, where it was consumed. The beach was littered with the cracked remains of 72 eggs, presumably consumed by crows, when 549 nests were within 700 m in the subcolony east of the channel south of Rodman Slough (additional nests were present >1000 m away in a subcolony west of the channel), indicating a minimum predation of 0.13 eggs per nest. The number of cracked eggs on the beach increased to 101 on 8 July, when 1711 nests were present in the subcolony, amounting to a predation rate of 0.06 eggs per nest. The number of cracked eggs on the beach declined during 6 subsequent visits in July despite a dramatic increase in the number of grebe nests, suggesting that the rate of egg predation was greatest during the early period of colony formation. The California Gull (*Larus californicus*) entered grebe colonies more frequently than crows, representing 64% of intrusions by all predators combined and accounting for 8% of predation events, but only 1.5% of intrusions resulted in predation (Fig. 9A, Table 6), demonstrating that grebe eggs were seldom
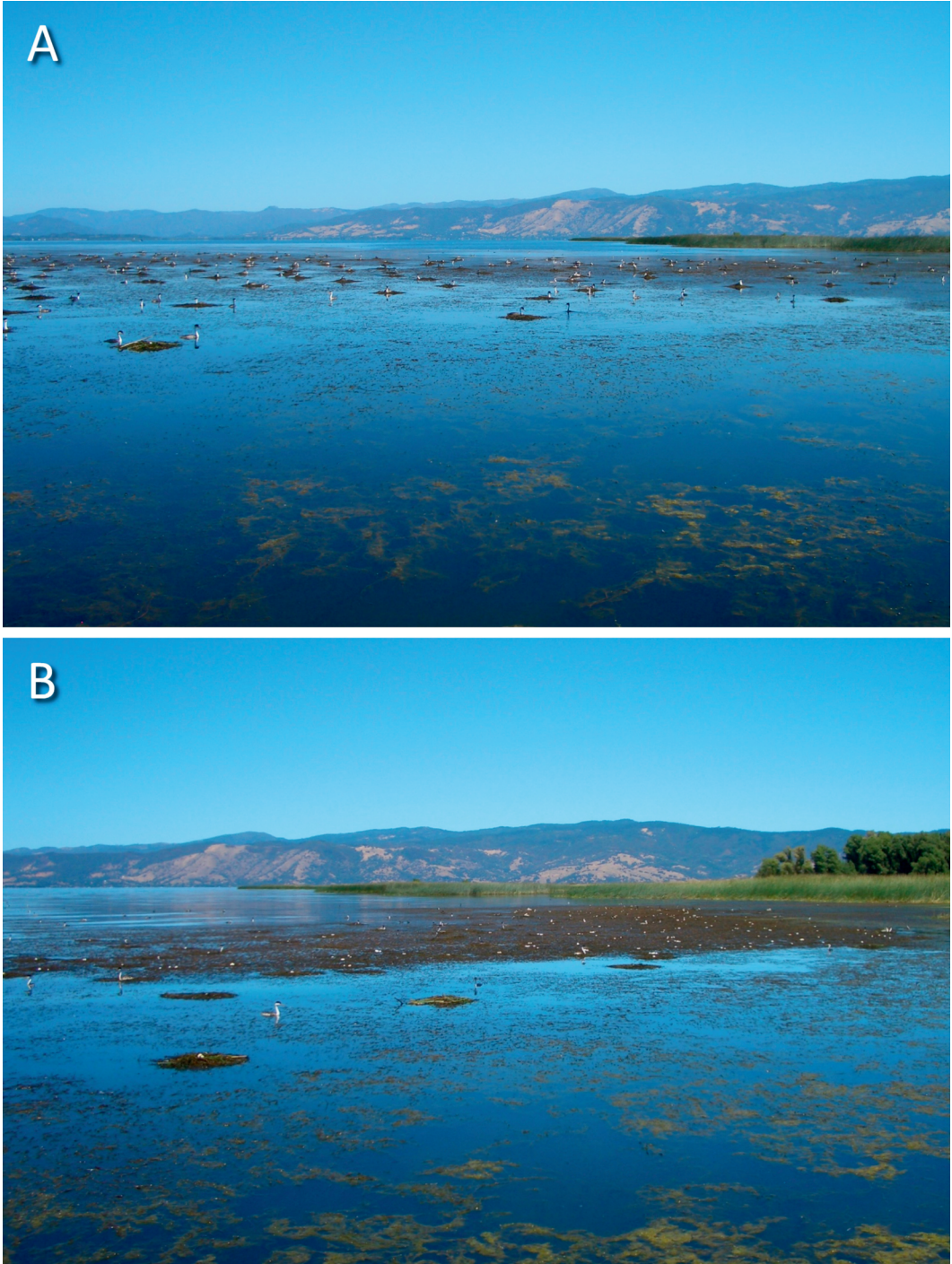
Fig. 8. Consequences of a windstorm on Clear Lake, California. *A,* Active open water grebe nests at Long Tule Point on 11 August 2011. *B,* The same nests, most abandoned, in shallow water on 14 August 2011 after a windstorm. Photos by Floyd E. Hayes.

TABLE 6. Number of intrusions and predation events at grebe nests during the day (direct observations/camera monitoring) and night (camera monitoring only), based on 301.5 hours of direct observations during 2010–2019 and 11,309 hours of day and night monitoring by motion-activated cameras during 2014–2017. Data updated from Hayes et al. (2018a).

| Species | Day | | Night | |
|---|---|---|---|---|
| | Intrusions | Predations | Intrusions | Predations |
| Ring-billed Gull | 49/0 | 4/0 | 0 | 0 |
| California Gull | 601/1 | 9/0 | 0 | 0 |
| American Crow | 247/20 | 82/10 | 0 | 0 |
| Common Raven | 10/0 | 2/0 | 0 | 0 |
| Northern raccoon | 0/0 | 0/0 | 65 | 42 |
| American mink | 0/1 | 0/1 | 3 | 1 |
| Northern river otter | 18/1 | 1/0 | 0 | 0 |

targeted for predation. The Ring-billed Gull (*Larus delawarensis*) accounted for 4% of predation events, and 8% of intrusions resulted in predation (Table 6). The Common Raven (*Corvus corax*) accounted for only 2% of predation events but preyed upon eggs during 20% of intrusions (Table 6). On a few occasions individuals of both grebe species successfully chased away California Gulls, American Crows, and Common Ravens from their nests.

Three species of mammals preyed upon grebe eggs, mostly at night (Table 6). The northern raccoon (*Procyon lotor*) was the major mammalian predator, accounting for 96% of intrusions by predators and 98% of egg predation events at night (Fig. 9D, Table 6). The American mink (*Neovison vison*) accounted for the remaining 4% of intrusions by predators and 2% of egg predation events at night, plus 0.1% of intrusions and 0.9% of all bird and mammal predation events combined during daylight (Fig. 9E, Table 6). Although northern river otters (*Lontra canadensis*) occasionally entered colonies, accounting for 2% of diurnal intrusions by bird and mammal predators combined, we never observed predation on eggs but once heard an otter crunching eggs in a nest hidden by tules and subsequently confirmed that 4 eggs were smashed in a nest. The northern river otter accounted for 0.9% of egg predation events by birds and mammals combined during daylight (Table 6). A camera once photographed an otter only 0.1–0.2 m from an active grebe nest, but it did not eat the single egg inside the nest. When approached by otters, nearby nesting grebes abandoned their nests and swam toward open water. We never observed or photographed a grebe chasing away a mammalian predator.

The rates of nocturnal intrusion and egg predation per camera hour (unadjusted for day vs. night) by mammals were greatest when water level was high and proportionately more nests were placed in emergent vegetation near the shore rather than in open water. During 2014, when water level was low (Fig. 2) and zero nests were placed in emergent vegetation near the shore (Table 2), we recorded one intrusion per 367 camera hours and one predation event per 514 camera hours. During 2015, when water level was slightly higher (Fig. 2) with 3.1% of nests placed in emergent vegetation near the shore (Table 2), we recorded just one intrusion and no predation during 1937 camera hours. But in 2017, when water level was much higher (Fig. 2) and 99.7% of nests were placed in emergent vegetation near the shore (Table 2), we recorded one intrusion per 97 camera hours and one predation event per 165 camera hours.

We observed 2 instances of predation on small chicks within a large colony. Both times, a Ring-billed Gull flew off with a chick and swallowed it while flying (Fig. 9B), but we were uncertain whether the gulls took the chicks from the nests or the water. On a few occasions, we observed 2 potential avian predators, the Bald Eagle (*Haliaeetus leucocephalus*) and Peregrine Falcon (*Falco peregrinus*), flying over active grebe colonies. Although both species are known to prey on adult grebes (Munro 1938, Knight et al. 1990, Barnes 2011), we observed only one attempted predation, when a diving Peregrine Falcon came within 1 m of capturing an incubating adult grebe, which eluded capture by jumping off its nest and diving underwater.

Some nests were apparently abandoned due to predation on adult grebes. Of 30 dead adults encountered during 2016–2019, at least 5 (16.7%) appeared to have died by predation, based on partial consumption of the head, neck, or both (Fig. 9F). Other partially consumed adults were noted, but not quantified, during 2012–2015. The partially consumed adults were usually on
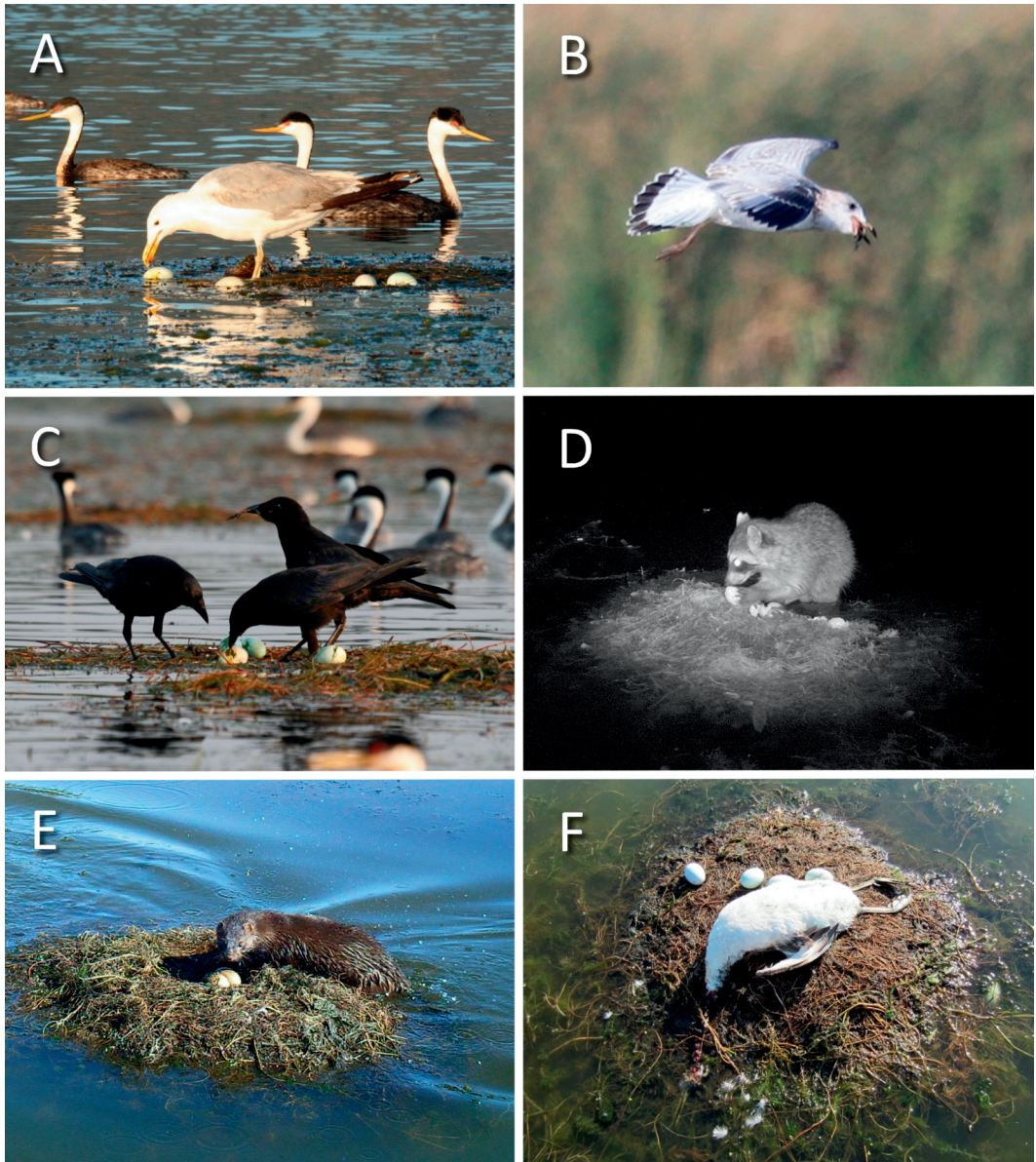
Fig. 9. Predation on grebes. ***A,*** Predation on eggs by a California Gull at West of Tule Island on 31 July 2012. ***B,*** Predation on a chick by a Ring-billed Gull at West of Tule Island on 28 August 2014. ***C,*** Predation on eggs by American Crows at Long Tule Point on 10 July 2012. ***D,*** Predation on eggs by a northern raccoon at West of Tule Island on 5 September 2014. ***E,*** Predation on eggs by an American mink at West of Tule Island on 31 August 2014. ***F,*** Predation on an adult but not the eggs by an unknown predator at West of Tule Island on 14 August 2014. Photos by Floyd E. Hayes.

a nest, often with intact eggs, but were sometimes floating in the water beside the nest. We never observed or photographed predation on an adult grebe.

Our cameras documented 4 incidents of intentional egg destruction (eggs smashed or expelled from nest) by Western Grebes and 3 by Clark's Grebes. All incidents were perpetrated by males, based on their notably longer and stouter bills (Ratti and McCabe 1983, Storer and Nuechterlein 1985, 1992, Hartman et al. 2016). Five incidents occurred at 3 recently vacated nests in
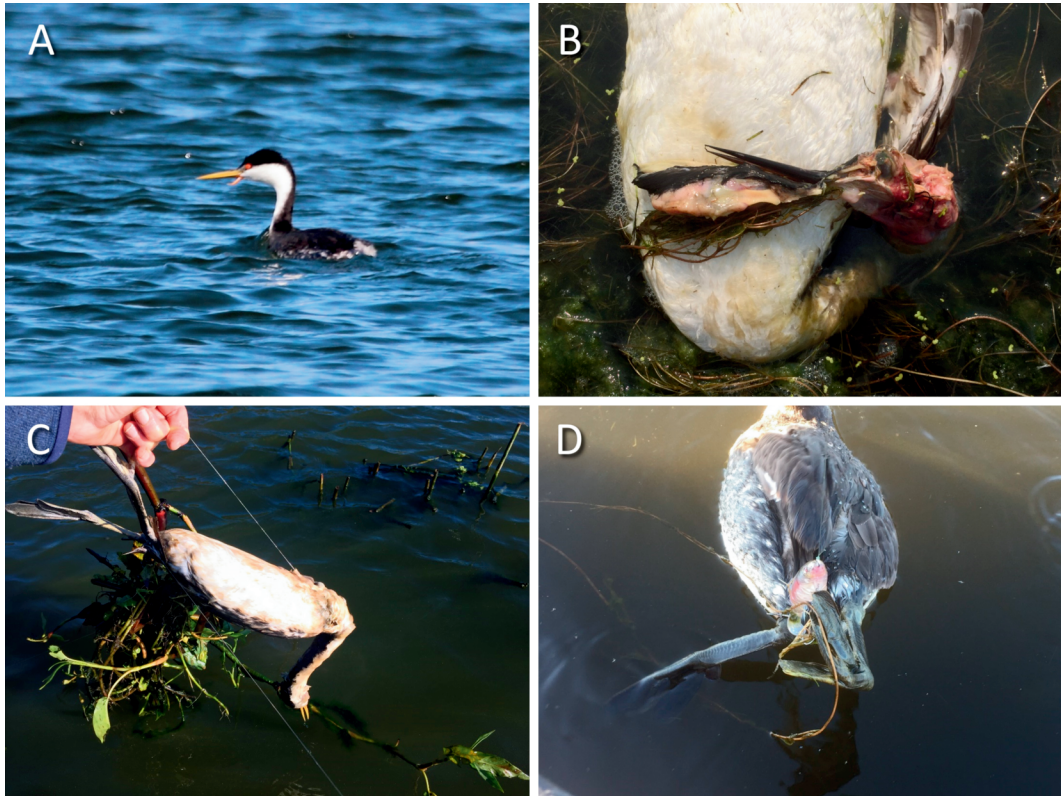
Fig. 10. Injuries of grebes. **A,** Western Grebe with a sublingual oral fistula at Clear Lake, California, on 13 September 2016. **B,** Western Grebe probably fatally struck by a motorboat at Lakeport on 10 August 2018. **C,** Clark's Grebe fatally entangled in fishing gear at Anderson Marsh Southeast on 11 June 2017. **D,** Live Western Grebe with both legs hooked in a fishing lure at Lakeport on 15 July 2018. Photos by Floyd E. Hayes.

which the previous eggs had been destroyed by mammalian predators. Two incidents occurred at nests with an unknown history.

On 3 occasions our cameras documented the destruction of eggs by the incidental activities of other animal species. Motion-activated cameras revealed a vigorously thrashing pair of spawning Common Carp (*Cyprinus carpio*) crushing 1 of 2 eggs in an attended nest, a Pond Slider (*Trachemys scripta*) knocking an egg out of an unattended nest, and another Pond Slider and 2 Western Pond Turtles (*Actinemys marmorata*) crushing 2 Western Grebe eggs in an unattended nest.

Illness or injury may have resulted in some nest failures. Of 30 dead adults encountered during 2016–2019, twenty-two (73%) lacked any external evidence of trauma. We photographed a swimming Western Grebe with its tongue protruding through an opening in its throat (Fig. 10A), a rare condition of unknown etiology, but thought to be natural, referred to as a sublingual oral fistula.

We observed only one incident of nest abandonment due to stranding on land as the water level receded. In 2014, when water level was lowest, several nests were stranded on a mudflat about 200–300 m from shore at West of Tule Island (Fig. 6D).

Entire colonies were sometimes abandoned for no apparent reason. These events occurred within 15 days of colony discovery in 8.5% of colonies ($n = 71$) of 10 or more nests that were surveyed for at least 15 days. Nesting at a colony site sometimes reoccurred after initial abandonment, especially in small colonies. The most spectacular example of abandonment and renesting occurred at Anderson Marsh Southeast in 2019, when the number of nests increased from 4 on 27 May to 153 on 2 July, decreased to 0 on 9 and 15 July, and increased a second time from 84 on 30 July to 754 on 19 August.

Anthropogenic Causes of Nest Failure

Human activities may have caused abandonment of some nests. We observed 30 intrusions of motorized watercraft (motorboats, airboats, and jet skis) into colonies with eggs, for a rate of 0.1/h, and 14 entries of paddled watercraft (kayaks and canoes, excluding our own canoe) into colonies, for a rate of 0.05/h ($n = 301.5$ h). The large wakes created by motorized watercraft often caused nests to bob up and down in the water, but we observed only one instance of an egg actually rolling out of a nest, when a motorboat passed within 1 m of 2 nests (the other nest with 4 eggs was unaffected). We never observed any direct strikes by watercraft on adult grebes or grebe nests. However, one adult near a colony probably died from collision with the propeller of a motorboat, based on the cranium and attached skin and feathers of the head being cleanly split from one end to the other (Fig. 10B), accounting for 3.3% of observed adult mortality during 2016–2019. Two adults (5.7%) in grebe colonies died from entanglement in fishing line (Fig. 10C), accounting for 5.7% of observed adult mortality during 2016–2019. Some eggs were collected by researchers to study Hg concentrations in 2012 and 2013 (Ackerman et al. 2015).

We encountered 2 living adult Western Grebes entangled in fishing gear: 2 fish hooks on a lure were deeply embedded in both legs of one grebe (Fig. 10D), and a leg of the other grebe was entangled in fishing line. Both birds were successfully disentangled and released. One swimming Western Grebe consistently pointed its head skyward during a period of about 15 min and may have had a fish hook embedded inside its throat or neck, preventing it from lowering its head.

There was no evidence that our visits to the breeding colonies negatively impacted reproductive effort or reproductive success. The number of days of our monitoring effort per breeding season, which varied by more than 4-fold, was not significantly correlated with the number of nests ($r_s = -0.01$, $P = 1.0$, $n = 10$ years), number of young ($r_s = 0.18$, $P = 0.61$, $n = 10$ years), number of young per nest ($r_s = -0.02$, $P = 0.95$, $n = 10$ years), or the productivity ratio ($r_s = 0.06$, $P = 0.86$, $n = 10$ years).

Smoke generated by nearby wildland fires of anthropogenic origin may have contributed to the extremely low reproductive success of grebes in 2015 and 2018, when the number of young,

young per nest, and productivity ratio were the lowest (Table 5). The mean $PM_{10}$ at Lakeport during 2013–2019 was 10.5 μg/m$^3$ (SD = 12.0, range 0 to 176, $n = 421$). The highest $PM_{10}$ value during the grebes' breeding season occurred during 12–16 August 2015, when the $PM_{10}$ rose to 61 μg/m$^3$ during the Rocky Fire (29 July–14 August), which burned within 6 km of the Oaks Arm of the lake, and the smaller Jerusalem Fire (9–25 August). Although we found 23 new grebe nests on 5 August, no new nests were found on 7 or 12 August, but 9 new nests were found on 17 August. The $PM_{10}$ rose to 45 μg/m$^3$ during 6–12 August 2018, when the Mendocino Complex Fire (formed by merger of River Fire and Ranch Fire) burned within 3 km of the Upper Arm of the lake from 27 July to 18 September. On 10 August, while the smoke was still thick over Clear Lake, we counted 2665 nests, mostly at the north end of the lake and its largest tributary; many of the nests were active, with the grebes engaged in nest construction, copulation, and incubation.

## Discussion

### Number of Grebe Nests

Nest counts provide the most accurate method of measuring reproductive effort in colonial waterbirds (Hutchinson 1980). Nevertheless, 3 factors potentially affect the accuracy of grebe nest counts at Clear Lake and render it difficult to compare historical data with this study. First, our observations reveal that grebes nest in many more marshes, lagoons, and channels of Clear Lake and associated wetlands than previously recognized. Most (if not all) historical reports of nest surveys were probably based on surveys in fewer areas. For example, the lack of previous reports of nests in channels of upper Rodman Slough (>1 km upstream from Clear Lake), where we often encountered nesting grebes during high-water years, suggests that those channels may never have been searched. Second, frequent site visits are required to obtain accurate counts because floating nest platforms may be detected within hours of their initial construction and may disappear within a few days once abandoned, especially open water nests vulnerable to wave action. Because 1–2 weeks often elapsed between our visits to colony sites, our nest counts should be considered conservative, especially during 2010, when surveys did not begin until 6 August, and in 2018, when

only 7 surveys were conducted (Table 2) due to a paucity of funding. Most (if not all) historical reports of nest surveys were probably based on fewer visits. And third, nests are often hidden in aquatic vegetation, rendering it difficult to approach and detect marsh nests from a motorboat, which was probably used in most (if not all) historical surveys. Marsh nests are more easily overlooked than open water nests, even from a canoe or kayak, and some marsh nests during both historical and recent surveys undoubtedly escaped detection.

Unfortunately, few data are available on the number of breeding grebes before the first application of DDD on Clear Lake in 1949, with a single reference claiming that the breeding population exceeded 1000 pairs (Miller *in* Hunt and Bischoff 1960). Although it remains uncertain how extensive subsequent searches were during 1950–1976 (Miller unpublished field notes; Hunt and Bischoff 1960, Hunt 1962, Herman et al. 1969, Rudd and Herman 1972, Feerer and Garrett 1977), the maximum annual count of 165 nests during this multidecadal period strongly implies that the breeding population was genuinely low compared with subsequent annual counts of up to 390 nests during 1992–1995 (Elbert and Anderson 1998, Anderson et al. 2008), up to 2675 nests during 1996–2010 (Anderson et al. 2008, Robison et al. 2009, 2015), and up to 5936 nests during 2010–2019 (this study). The gradually increasing number of grebe nests during the past 6 decades indicates that the local breeding grebe population has fully recovered from the last massive DDD application in 1957.

Our mean annual count of 3123 nests during 2010–2019 suggests that the current breeding population of grebes may be substantially larger than the estimated historical breeding population of >1000 pairs prior to 1949 (Miller *in* Hunt and Bischoff 1960). One possible explanation is that the loss of suitable breeding habitat in other parts of California (Ivey 2004) and elsewhere (Donnelly et al. 2020) may have concentrated more breeding grebes in Clear Lake. Another possible explanation is that the fish biomass of Clear Lake likely increased due to increased eutrophication, which is thought to explain increased breeding populations of the Great Crested Grebe (*Podiceps cristatus*) in Switzerland (Keller and Korner-Nievergelt 2019), and due to the introduction of new fish species, which compete for plankton with larval Clear

Lake gnats (David Woodward personal communication). Prior to the massive applications of DDD during 1949–1957, an estimated 531–712 billion larval Clear Lake gnats emerged annually from the bottom of the Upper Arm alone during the summers of 1939 and 1940, transferring an estimated 266–356 tons of biomass from aquatic to terrestrial ecosystems (Lindquist and Deonier 1942). The benthic larvae of the gnat are similarly abundant in the 2 lower arms of the lake (Lindquist and Deonier 1943), indicating an even greater transfer of biomass from the lake to terrestrial ecosystems. The gnat's population was effectively reduced by massive applications of DDD during 1949–1957 and methyl parathion during 1962–1975, but its population has never recovered. Colwell et al. (1997) demonstrated declines in gnat abundance following the introduction of the Mississippi Silverside in 1967 and Threadfin Shad in 1985. The fish presumably compete with the larval gnats for plankton. With proportionately less plankton biomass being converted into gnat biomass and exiting the aquatic ecosystem during emergence, proportionately more plankton biomass is converted into fish biomass, which becomes available to piscivorous birds.

The causes of dramatic annual variation in reproductive effort are uncertain. No long-term trend occurred during our study period, and the number of grebe nests was not correlated with water level. Because dramatic fluctuations in the breeding populations of other piscivorous birds, specifically cormorants and herons, occurred before and during our study period (Hayes et al. in preparation), we suspect that the abundance of the grebes' food supply may have a direct effect on reproductive effort. Annual fluctuations in fish abundance have been documented for Clear Lake (Winder et al. 2010, Thomson et al. 2013) and have been correlated with populations of wintering piscivorous birds (Colwell et al. 1997), but no recent fish population data are available to compare with the number of grebe nests. Fish abundance is affected by periodic mass mortalities of fish populations, which have been attributed to cold spells during winter (Thomson et al. 2013) and hypoxia caused by cyanobacterial and algal blooms during summer (Feyrer et al. 2020, Stang 2020, Cortés et al. 2021). Fluctuations in the abundance and age class distribution (body sizes) of fish prey potentially affect the population size and reproductive effort of piscivorous

freshwater birds (Keller and Korner-Nievergelt 2019).

## Colony Sites, Persistence, and Size

Prior to this study, only a few colony sites had been identified. Anderson et al. (2008) mapped 7 colony sites observed during 1991–2001, but 3 of these were in locations where we never observed nesting: just south of Rocky Point in the Upper Arm, at the north tip of Buckingham Point in The Narrows between the 3 arms of the lake, and east of Rattlesnake Island in the Oaks Arm. Our documentation of nesting at 37 sites vastly exceeds all previous studies and provides a basis for future comparisons. The use of some colony sites may be increasing in frequency. For example, nesting occurred only twice at Rodman Slough during 1992–2009 (Robison et al. 2009), but we recorded nesting every year during 2010–2019.

Water level clearly affected the distribution of nests. During low-water years, most nests were located on Clear Lake because of insufficient water level in channels of the tributaries and outlets, and during high-water years most of the nests were located in channels of the tributaries and outlets. The upper Rodman Slough and Anderson Marsh colonies were used only during years with sufficiently high water level, and no nesting occurred in the Lower Arm of Clear Lake or in adjacent wetlands of Anderson Marsh and Cache Creek during 2014, when water level was lowest (Fig. 2, Table 2).

## Seasonal Variation in Nesting

The phenology of nesting grebes in California is poorly known. Based on the sizes of young and their estimated ages, Robison et al. (2015) inferred that nest initiation at Clear Lake ranged from late April to late August. Our study reveals a greater range of nest initiation dates and considerable variation in the phenology of nesting with no obvious explanation. Nest initiation usually begins from late May to the middle of June but occurs in April during some years, with egg laying by 17 April or earlier. Nest initiation typically ceases during August but can extend into September, with eggs still being incubated as late as 3 October.

## Grebe Species Ratios

In recent decades, Western Grebes always outnumbered Clark's Grebes on Clear Lake. The proportion of Western Grebes at the end of each breeding season did not change during the period of 1998–2019 ($r_s = -0.04$, $P = 0.86$, $n = 18$ years), based on data from Robison (2012) for 1998–2009 and this study for 2010–2019. However, Feerer (1977) reported that Western Grebes made up only 40% of the breeding population in 1975, although his sample size of 152 adults was rather small. Is it possible that Feerer (1977) transposed his percentages for Western Grebe and Clark's Grebe? Storer and Nuechterlein (1985) and Livezey and Storer (1992) analyzed plumage and morphological characters in 111 adult grebes collected by Steven Herman from Clear Lake during 1967–1979 but did not provide the number of each species collected during the breeding season. An examination of the online catalog for their specimens in the University of Michigan Museum of Zoology (portal.vertnet.org) collected during the months of May–August revealed that Western Grebes comprised 64.4% of the breeding population, which is more consistent with the proportion of Western Grebes during 1998–2019, but the sample size is very small ($n = 45$). These data suggest that the proportion of Western Grebes may have increased slightly during the past half century, but the data prior to 1998 are insufficient to warrant any conclusion.

## Types of Grebe Nests

The distinction between marsh nests and open water nests among *Aechmophorus* grebes was first described by Lindvall and Low (1982), who reported that 54% of nests at Bear River Migratory Bird Refuge in Utah were in "emergent vegetation" (marsh nests), 41% were in "open water" (open water nests), and 5% were "dry-land nests." The proportions of marsh nests and open water nests at Clear Lake and associated wetlands varied greatly among colony sites and years, and were highly correlated with water level, with open water nests more prevalent during low water level. We never observed active dry-land nests described by others (Nero et al. 1958, Nero 1959, Lindvall and Low 1982, Santolo 2021), although a few nests became stranded on dry land and were abandoned by the grebes as water level declined.

## Breeding Population Size and Productivity

Estimating the breeding population size of grebes on Clear Lake and its associated wetlands is difficult. Nest counts do not accurately reflect the number of breeding pairs because some nests

are abandoned before eggs are laid and others are reused multiple times, presumably by pairs whose initial nest(s) failed, because a nest is a resource that requires considerable energy to construct and maintain (Hayes and Turner 2017, Hayes et al. 2018a, 2018b, 2018c). The midsummer population surveys along relatively standardized transects on Clear Lake are also inaccurate for estimating the number of breeding pairs because we could not enter the shallower and narrower channels and lagoons of Rodman Slough and Anderson Marsh in a motorboat to count the hundreds or thousands of grebes nesting in those areas during most years (Table 2). For example, during 2016 and 2019 the number of nests on Clear Lake and associated wetlands exceeded the number of grebes counted on the lake during midsummer (Tables 2, 4). Aerial surveys from low-flying aircraft have been used to estimate the breeding population of Clear Lake (Herman et al. 1969, Ivey 2004, Robison et al. 2009) and may be more accurate. Aerial surveys from a slower-flying drone may be even more effective and have been used to count Western Grebe nests elsewhere (Lachman et al. 2020, McKellar et al. 2021), but no such surveys have been conducted on Clear Lake.

Reproductive effort (number of nests) was not correlated with any of the 3 measures of reproductive success (number of young, number of young per nest, and productivity ratio) due to annual variability in nesting success, with more young per nest produced during some years than in other years. All 3 measures of reproductive success were strongly correlated. The number of young and the number of young per nest are dependent on the length of the transect during the brood survey, which varied from 100–121 km. The productivity ratio is independent of the length of the transect but is potentially biased by the departure from the lake of breeding adults who failed to reproduce and the arrival on the lake of nonbreeding adults from other localities. All 3 measurements of reproductive success assume that all young were hatched on Clear Lake or its associated wetlands and did not immigrate from another breeding colony (short flights begin at the age of 70 days; LaPorte et al. 2014). Reproductive success varied dramatically and was not correlated with water level.

The productivity ratio has been used since 1992 as a measure of reproductive success on Clear Lake by several studies (Elbert 1996, Elbert and Anderson 1998, Ivey 2004, Anderson et al. 2008, Robison et al. 2009, 2015), facilitating comparisons among studies. The long-term trend since 1992 has been nonsignificant ($r_s = -0.26$, $P = 0.22$, $n = 23$ years). However, the productivity ratio was relatively high during 2000–2006 (Table 1), when prey fish were abundant (Anderson et al. 2008). Productivity ratios at Clear Lake are unusually low, with a mean of 0.20 during 2000–2019, compared with other localities such as Eagle Lake (0.21–0.82 during 1992–1998, 2000–2001) and Tule Lake (0.34–0.48 during 1992–1994) in California (Elbert and Anderson 1998, Anderson et al. 2008), and Delta Marsh in Manitoba (0.39–0.88 during the 1970s and 2009–2010; LaPorte et al. 2014).

Natural Causes of Nest Failure

Wind-generated waves were the major cause of nest failure, destroying up to 35% of a year's nests. A study of nesting Western Grebes at Lake Christina, Minnesota, similarly revealed that windstorms were the leading cause of nest failure, destroying up to 38% of nests (Allen et al. 2008). The loss of nests to wind-generated waves is greater during periods of drought when water level is low and the grebes are forced to construct open water nests, which are more vulnerable than marsh nests sheltered within emergent vegetation.

Although egg predation was a major cause of nest failure, it is difficult to estimate the proportion of nests whose eggs were consumed by predators. The American Crow was the dominant predator of eggs during the day, and the northern raccoon was the dominant predator of eggs at night. Both of these predators are human commensals with increasing populations (Marzluff et al. 2001, Prange et al. 2003). Our observations in 2014 of cracked eggs on a beach presumably deposited by foraging crows revealed a minimum predation of 0.13 eggs per nest during the first 3 weeks of colony formation followed by a subsequent decline, perhaps due to adult grebes more consistently attending and defending their eggs as incubation progressed. We often observed crows feeding directly on eggs in a nest without carrying them away, and some eggs may have been carried elsewhere, indicating that our estimate of predation by crows is conservative.

The intentional destruction of eggs by male grebes is a minor cause of nest failure. The eggs may have been destroyed to usurp nests or to prevent brood parasitism or cuckoldry (Hayes et

al. 2018c). Unintentional destruction may also occur when eggs are knocked off of nests when incubating grebes hastily depart in response to the approach of watercraft or a potential predator.

We documented only a few cases of incidental destruction of grebe eggs by spawning Common Carp and basking Western Pond Turtles and Pond Sliders, usually eggs in already-abandoned nests. Because many species of vertebrates exploit the nests of grebes for egg dumping, predation, scavenging, resting, and foraging (Hayes et al. 2018a), incidental destruction of eggs likely occurs more frequently than our limited data suggest. Destruction of nests by the Common Carp was considered the second highest cause of nest failure in Western Grebes at a marsh in Manitoba, Canada, but that result was limited to a single colony during a single year (LaPorte et al. 2014). Elsewhere we reported the use of grebe nests at Clear Lake by 47 species of vertebrates (Hayes et al. 2018a). In 2019 we added a new species: a Great-tailed Grackle (*Quiscalus mexicanus*) foraging for invertebrates on a grebe nest.

Little is known about illnesses in grebes, which may be of natural or anthropogenic etiology (Storer and Nuechterlein 1992, LaPorte et al. 2020a, 2020b). We documented one instance of a sublingual oral fistula, which is characterized by the tongue protruding through an opening in the throat. This condition is rarely reported in birds and has not been previously reported for any grebe. Suggested causes include genetic abnormalities, nutritional deficiencies, infections, ectoparasites, trauma from injuries such as bill insertion during food exchange, aggression, and kleptoparastitism (Hayes et al. 1986, Castro and Taylor 2001, Reynolds et al. 2009, Hughes et al. 2013). Birds with sublingual oral fistulas have been observed nesting (Low et al. 2007, Reynolds et al. 2009, Greño et al. 2017), indicating that the condition does not necessarily preclude reproduction.

Abandonment of nests and entire colonies often occurred for unknown cause. Small colonies may be abandoned after raids by avian or mammalian predators. Larger colonies are presumably less likely to be abandoned after predation due to the smaller proportion of nests affected. Colonies may also be abandoned when populations of prey fish disperse from the colonies when the water becomes increasingly hypoxic due to cyanobacterial and algal blooms (Feyrer et al. 2020, Stang 2020, Cortés et al.

2021) and foraging for prey in areas increasingly distant from the colonies becomes energetically infeasible. However, the reproductive success of grebes was much higher in 2017, when hypoxia was severe, than in 2018, when hypoxia was less severe (Table 5; Feyrer et al. 2020).

### Anthropogenic Causes of Nest Failure

Clear Lake has been heavily contaminated by chemical pollutants (Suchanek et al. 2003). Reproductive failure of the grebes of Clear Lake during the 1950s and the slow reproductive recovery during the 1960s and early 1970s was consistently attributed to biomagnification of DDD, based on elevated DDD concentrations in plankton, higher concentrations in fishes, and even higher concentrations in grebes (Dolphin 1959, Hunt and Bischoff 1960, Hunt 1962, Herman et al. 1969, Linn and Stanley 1969, Rudd and Herman 1972). However, Suchanek et al. (2003) pointed out that the last major mining of mercury at the Sulphur Bank Mercury Mine occurred during the 1950s and suggested that biomagnification of Hg during this period may also have been a contributing factor, either additively or synergistically. Elevated Hg concentrations have been documented in the eggs, tissues, and feathers of the grebes of Clear Lake since 1984 (Littrell 1991, Elbert 1996, Cahill et al. 1997, 1998, Elbert and Anderson 1998, Wolfe and Norman 1998) and as recently as 2012–2013 (Ackerman et al. 2015, Hartman et al. 2017), and Hg levels may have been much higher during the 1950s. Although no study has linked Hg concentrations to reproductive failure in grebes, Hg biomagnification adversely affects reproduction in other species of birds (Burger and Gochfeld 1997). Feerer and Garrett (1977) suggested that annual applications of the pesticide methyl parathion during 1962–1975 may have contributed to the reproductive failure of the grebes. Although "many Western Grebes observed during and after the methyl parathion treatments of 1962 showed no visible adverse symptoms" (Cook and Conners 1963), the impact of methyl parathion bioaccumulation in grebes has not been rigorously studied. Bennett et al. (1991) documented adverse impacts of methyl parathion bioaccumulation on the reproduction of the Mallard (*Anas platyrhynchos*). A variety of other herbicides and pesticides have been and continue to be applied in the aquatic and adjacent terrestrial ecosystems of Clear Lake (Suchanek et al. 2003), but their potential

synergistic impacts on the reproduction of grebes are unknown.

Feerer and Garrett (1977) suggested that the loss of breeding habitat from the destruction of tule marshes for urban and commercial development contributed to the decline of nesting grebes at Clear Lake. Although about 85% of Clear Lake's natural wetland habitats have been destroyed (Richerson et al. 1994, Suchanek et al. 2003), our data reveal that many colony sites with tule marshes used by nesting grebes are not used annually, suggesting that a surplus of suitable marsh habitat is available and does not limit the reproduction of grebes.

The introduction of new species of fishes has dramatically altered the trophic relationships of Clear Lake (Thomson et al. 2013). The introduced Common Carp vigorously thrashes at the surface during spawning, and such activity is considered the second highest cause of nest failure in Western Grebes at a marsh in Manitoba, Canada (LaPorte et al. 2014); however, we documented only one such incident on Clear Lake with a motion-activated camera. Feerer and Garrett (1977) suggested that the introduction in 1967 of the Mississippi Silverside, which quickly became the most abundant species of fish in the lake (Cook 1981), contributed to the decline of nesting grebes by competing with the grebes' preferred prey fish. However, the number of nesting grebes has steadily increased since the Mississippi Silverside's introduction, perhaps due to the silverside competing with the Clear Lake gnat for plankton and increasing the lake's biomass by suppressing the export of biomass from aquatic to terrestrial ecosystems when the gnats mature.

We rarely observed grebe nests impacted directly by the waves created by motorized watercraft and never observed any direct strikes on nests by watercraft, primarily because the grebes prefer nesting in areas with extensive submergent or emergent vegetation, which are generally avoided by humans in motorboats. Nevertheless, such incidents undoubtedly occur more often than our limited observations suggest and more often than has been observed in the past. For example, 85% of the grebe nests on Clear Lake were destroyed by airboats in 2002 (Robison et al. 2009). Grebes foraging or loafing in open water are adept at avoiding approaching motorboats, but our photographic evidence of a dead adult likely killed by the propeller of a motorboat indicates that lethal collisions do occur.

Entanglement in fishing gear is a well-known hazard for waterbirds (Ryan 2018), and the entanglement of a breeding adult is a potential cause of nest failure. We observed 4 instances, of which 2 were fatal and the other 2 likely would have been fatal without intervention. Humple and Holcomb (2014) reported a banded Clark's Grebe that died in Clear Lake "in an apparent fishing interaction." Entanglement of Western Grebes and Clark's Grebes in fishing gear has been reported elsewhere (Chatwin 1956, Arnold 1994, Moore et al. 2009).

Smoke from nearby wildland fires of anthropogenic origin may have contributed to the extremely low reproductive success of grebes in 2015 and 2018. Our observations indicate that the grebes did not cease breeding activities during the fires. The potential impact of smoke generated by wildland fires on the reproductive success of waterbirds is poorly known. Although the chicks of wading birds in a mixed-species rookery in the Everglades initially survived intense smoke inhalation from a fire (Epanchin et al. 2002), no follow-up studies were conducted. Excessive smoke inhalation in birds is known to reduce egg production and increase susceptibility to respiratory infections, often resulting in delayed mortality up to 4 weeks later (Morris et al. 1986, Simone-Freilicher 2008, Kinne et al. 2010). Developing chicks may be more susceptible than adults to the adverse health effects of smoke inhalation from wildland fires.

Conclusions and Recommendations

Although Clear Lake's breeding population of grebes has recovered since DDD biomagnification during the 1950s, reproductive success remains inexplicably lower than at 4 other lakes (Almanor, Antelope, Davis, and Eagle) in northeastern California (Elbert and Anderson 1998, Plumas Audubon Society unpublished data for 2010–2019 breeding seasons). Nest failure is caused primarily by natural factors, especially wind-generated waves and predation. Direct anthropogenic causes of nest failure, such as the destruction of nests by waves generated by motorized watercraft, collisions with motorized watercraft, and entanglement in fishing gear, are relatively minor. The natural and direct anthropogenic causes of nest failure documented at Clear Lake presumably occur at similar rates at other breeding localities. If so, what is different about Clear Lake? We suggest that 2 factors

somewhat unique to Clear Lake may reduce reproductive success: (1) bioaccumulation and biomagnification of toxic chemicals and (2) periodic reductions in availability of prey fish.

The development of grebe eggs and young may be impaired by the synergistic effects of a cocktail of bioaccumulated and biomagnified chemicals from pesticides, herbicides, fertilizers, and acid mine drainage, as suggested by Elbert and Anderson (1998). These chemicals occur at high levels in Clear Lake (Richerson et al. 1994, Suchanek et al. 2003). Previous studies have focused on the impact of only 2 chemical contaminants on Clear Lake's grebes. The first, DDD, has not been applied to the lake in >60 years, and its concentrations in grebe tissues had substantially declined when DDD was last measured in the 1970s (Craig and Rudd 1974). The second, Hg, still lingers in the lake from acid mine drainage (Suchanek et al. 2008). Studies as recently as 2012 and 2013 revealed that higher concentrations of Hg occur in the blood of grebes at Clear Lake than those at Eagle Lake and Tule Lake, and Hg concentrations increase during the breeding season (Ackerman et al. 2015, Hartman et al. 2017). A variety of herbicides are frequently applied to Clear Lake in an effort to control algal blooms and invasive aquatic plants, including copper sulfate (since 1994) and fluridone (since 1996) (Suchanek et al. 2003, Siemering 2005, Richerson et al. 2008, Siemering et al. 2008). High concentrations of copper sulfate reduce eggshell thickness and egg production in birds (Griminger 1977, Stevenson et al. 1983, Almansour 2006), but its effects on grebes have not been studied. Fluridone is allegedly harmless to wildlife (Arnold 1979), but its potential effects on birds have not been rigorously studied. The health of developing grebe eggs and young should be studied and compared at different breeding localities. More importantly, the remediation of toxic chemicals in Clear Lake should continue.

Periodic reductions in the grebes' food supply may have a direct effect on reproductive success. Clear Lake is a highly eutrophic ecosystem (Richerson et al. 1994). The relatively high concentrations of nutrients support a correspondingly high biomass of plankton, invertebrates, fishes, and piscivorous birds. However, intense cyanobacterial and algal blooms, which occur naturally but are enhanced by anthropogenic nutrient inputs, frequently occur during summer in lagoons and channels with reduced water circulation (Richerson et al. 1994). The hypoxic conditions associated with such blooms displace fish populations and occasionally cause mass mortality of fishes (Feyrer et al. 2020, Stang 2020). The potential linkage between food supply and reproductive success in grebes should be further investigated.

The water level of Clear Lake is dependent on precipitation, but it is managed to some extent by humans (De Leon 2016). Maintaining high water levels is beneficial to the grebes. Although water level was not significantly correlated with reproductive effort or success, a greater proportion of grebes construct marsh nests in the associated wetlands of Clear Lake during periods of high water level, where they are less vulnerable to wind-generated waves and disturbance by humans in motorized watercraft.

Our data on the nesting ecology of the grebes of Clear Lake provide a historical benchmark for future comparisons. The future of Clear Lake's lacustrine ecosystem is uncertain. Changes are inevitable and difficult to predict. For example, a potential future threat is the introduction of the freshwater zebra mussel (*Dreissena polymorpha*) or quagga mussel (*D. rostriformis bugensis*). Both species are rapidly spreading across North America and dramatically altering the trophic relationships of aquatic ecosystems (MacIsaac 1996, Nalepa and Schloesser 2014, Karatayev et al. 2015). The potential effects of introduced mussels on the breeding grebes of Clear Lake are difficult to predict. Future monitoring of the grebes' nesting activities will be vital to document the impact of any future ecosystem changes.

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