Lake elevation and reproductive success in Western and Clark's grebes at two northern California lakes

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CONTENTS

LIST OF FIGURES

LIST OF TABLES

Abstract. Degradation and loss of wetlands throughout the world has lead to increased concern for conservation and management of wetlands and wetland-dependent bird species. Of particular concern are lacustrine wetland ecosystems where water level is increasingly regulated for human benefit. As a result, artificial water level fluctuations serve as a dominant ecological force affecting habitat-selection and life-history events of wetland-dependent waterbirds. Despite a growing knowledge base in this area, little is known about how hydroperiod changes affect the reproductive success of over-water nesting birds. Using an information-theoretic approach, we analyzed a long-term dataset to assess the relationship between lake elevation changes and the reproductive success of two wetland-dependent, over-water nesting birds, Western and Clark's Grebes (*Aechmophorus occidentalis* and *A. clarkii*). Several reproductive indices were developed and analyzed, each summarizing separate aspects of avian reproductive ecology. Models containing only lake elevation parameters received the most support and explained the most variation of two of our reproductive indices: Productivity ($YY \cdot Ad^{-1}$) and Breeding Adult Ratio (Ad with $YY \cdot (Total\ Ad)^{-1}$). Alternatively, lake elevation appeared to have no explanatory power for Average Brood Size ($YY \cdot Pair^{-1}$). Our results indicate that lake elevation is an important factor affecting a lake's population level reproductive success, but is not a determinant of individual nest fate. These findings underscore the need for careful consideration of over-water nesting bird ecology in managed wetlands, in that changes in lake elevation have the potential to influence the annual reproductive output of an entire lake's population of Western and Clark's Grebes.

INTRODUCTION

In the United States most threatened and endangered species are dependent upon wetland ecosystems for at least part of their life cycles (Niering 1988, Laubhan and Fredrickson 1993, Tori et al. 2002). Wetlands are a critical habitat for an estimated one-third of North American bird species and are particularly important for waterbirds, serving as staging areas, feeding grounds, refugia from predators, and nesting areas (Wharton et al. 1982, Kushlan 1989, Tori et al. 2002).

Due to increasing urban and agricultural development, an average of 50% of historic wetland habitat has been lost both worldwide and in the United States (Fraser and Keddy 2005, Mitsch and Gosselink 1993). Some regions in the continental United States presently contain only 9% of historic wetlands (Mitsch and Gosselink 1993, Ward et al. 2010). Those wetlands that remain generally occur in small tracts and have undergone drastic human-induced alterations and degradation (Laubhan and Fredrickson 1993, Tori et al. 2002, Fraser and Keddy 2005). As a result, wetland management is a key focus of waterbird management (Ma et al. 2010).

Lacustrine wetlands in particular present a wildlife management challenge due to the increasing regulation of lake levels for the purposes of flood control, hydroelectric power generation, and irrigation (Wantzen et al. 2008). Such regulation has resulted in alteration of wetland function and subsequent declines in wildlife biodiversity (Laubhan and Fredrickson 1993). In an attempt to improve management practices, recent research has focused on aspects of lacustrine wetland biology impacted by regulation (Leira and Cantonati 2008, Ma et al. 2010). Variables such as habitat area, vegetation cover, connectivity, food abundance, and shoreline development have been considered (Ma et al. 2010). Although all lakes differ in respect to overall size, bathymetry, and the factors mentioned above, wetland ecosystems are governed primarily by the quantity and quality of water within the system as well as the intra- and inter-annual variation of this resource (Mitsch and Gosselink 1993, Coops et al. 2003). Variability in hyrdoperiod is essential for the maintenance of productive wetland ecosystems but extreme artificial fluctuations, such as those resulting from water management, may adversely affect natural wetland processes and wetland-dependent bird species.

Water level fluctuation has been discussed in the literature as affecting wetland-dependent bird species in a variety of ways. Anecdotal and quantitative accounts have linked changes in avian diversity and abundance to water level variation (Moseley 1930, Taft et al. 2002, Tozer et al. 2010). The effect of water depth on foraging location and niche partitioning of wetland-dependent bird species has received ample attention, especially for waterfowl (Pöysä 1983, Barnes and Nudds 1990, Colwell and Taft 2000). The effect of water level variation on the reproductive success of various waterbird species has also been investigated. This topic has been explored in the ecological context of wading waterbirds (Cézilly et al. 1995, Ivey and Dugger 2008), dabbling waterbirds (Moreno-Matiella and Anderson 2005), diving waterbirds (Mudge and Talbot 1993, DeSorbo et al. 2007), and passerines (Baiser et al. 2008). Patterns of water level fluctuation have been demonstrated to be the primary determinant of breeding initiation and success in some bird species (Kushlan 1989). Very few studies, however, have sought to determine how these phenomena affect aspects of nesting ecology and reproductive success of over-water nesting birds, a group of avian taxa that are particularly sensitive to changes in water level (Paillisson et al. 2006). Additionally, datasets tracking long-term population trends of wetland-dependent waterbirds are scarce (Ward et al. 2010), indicating the need for further investigation, especially in the form of long-term studies (Leira and Cantonati 2008, Ma et al. 2010, Ward et al. 2010).

Western and Clark's Grebes (*Aechmophorus occidentalis* and *A. clarkii*) are particularly interesting for investigating the effects of lake elevation on reproductive success in that both species are over-water nesting, wetland-dependent waterbirds. These species migrate inland from their wintering grounds on the Pacific coast of North America to breed in reservoirs and lakes throughout central and western North America from Canada to Mexico (Storer and Nuechterlein 1992). They build floating nest structures and anchor them to emergent wetland vegetation and other floating substrates. Nests are constructed of either submergent or emergent wetland vegetation (Nuechterlein 1975, Storer and Nuechterlein 1992). Wetlands containing a minimum of 25cm of water are preferentially chosen for nest placement (Nuectherlein 1975, Short 1984, Storer and Nuechterlein 1992). Although Western and Clark's Grebes have been recorded as nesting on land such accounts are rare and likely the result of recent extreme changes in lake elevation (Nero and Bard 1958, Lindvall and Low 1982).

Due to their over-water nesting behavior, preferential selection of nesting areas with a minimum water depth, and use of wetland vegetation for nesting material, water level fluctuation has been suggested as a potential factor limiting reproductive success of these species (Feerer and Garrett 1977, Lindvall and Low 1982, Parmelee and Parmelee 1997, Riensche et al. 2009). In Saskatchewan, nests that had been stranded due to a recent change in water level were believed to have experienced “extremely low” levels of nest success (Nero and Bard 1958). Davis (1961) asserted that inter-annual variation in water levels in northern Colorado prevented pairs in small Western Grebe colonies from nesting at sites occupied the prior year. It was also indicated that grebes only nested at these locations when water levels were “high enough” for a sustained period of time (Davis 1961). Feerer and Garret (1977) noted that chronic low water levels at Clear Lake, California, during the 1976 nesting season precluded grebes from nesting at this lake. Their work at Eagle Lake, California, also indicated that unstable water levels resulted in loss of wetland nesting habitat. The authors implicated these unstable water levels as being one of the major factors causing population declines of these species throughout their range. More recently, a 38cm drop in water level at one grebe colony in the Bear River Migratory Refuge, Utah, was observed to occur in less than three weeks. Investigators at this site noted that 25% of nests were abandoned following the event (Lindvall and Low 1982). In 1995, investigators observed an initiation of courtship behavior following a rise in water level and subsequent growth of nesting vegetation at a colony site located on Lake Mead, Nevada (Parmelee and Parmelee 1997). The authors indicated that these abiotic factors likely influenced the initiation of these behaviors.

Despite these accounts, to date no formal or long-term quantification of the effect of fluctuating water levels at breeding lakes (lake elevation change) on the reproductive success of Western and Clark’s Grebes exists, yet the maintenance of stable water levels long enough to complete hatching has been identified as critical for ensuring nest success for these species (Ivey 2004, Riensche et al. 2009). This recommendation is based on information that is largely anecdotal and temporally limited in scope.

To better understand the relationship between lake elevation and grebe reproductive ecology, we investigated the effect inter-annual lake elevation changes have on the reproductive success of Western and Clark’s Grebes. The goal of our study was to gain insight into the abiotic factors affecting grebe nesting ecology and to aid in the establishment of wetland management practices for these species. To accomplish this goal, we collected reproductive data at two northern California lakes- Clear Lake and Eagle Lake- from 1997-2010. These study sites were chosen based on their significant contributions to the nesting population of Western and Clark's Grebes in California (Ivey 2004). In addition, each location represents a lake system in which natural fluctuations in lake elevation have been altered or regulated for human benefit (Gester 1962, Suchanek et al. 2003).

STUDY SITES

Clear and Eagle Lake are important nesting areas for Western and Clark's Grebes. They are located in Northern California, a region which is estimated to contain approximately 5.6% of the global breeding population of *Aechmophorus* Grebes (Ivey 2004). More locally these sites account for an appreciable proportion of the Intermountain West breeding population of these two species; Eagle Lake normally comprises 22% of this population, while Clear Lake comprises nearly 13% (Ivey 2004).

Clear Lake. Clear Lake is located approximately 402m above mean sea level in the southeast region of the North Coast Range of California (Figure 1) (Suchanek et al. 2003). The Clear Lake basin has been highly impacted since European settlement. Originally, mixed oak woodland, coniferous forest, and chaparral habitat dominated the landscape (Suchanek et al. 2003, Gericke 2006). Currently, the area around Clear Lake is extensively developed, supporting agricultural production and numerous urban areas (Suchanek et al. 2003). As a result of this development, 85% of the lake's original 3642 hectares of wetland habitat has been lost (Suchanek et al. 2003, Gericke 2006). Flooded emergent wetland vegetation now totals only 607ha, with the largest stands existing in only three main areas of the lake (Suchanek et al. 2003).

Hydrology of the lake was also impacted by European settlement. The lake's watershed consists of 13 separate inlets, most of which flow into the northwest portion of the lake, and a single outlet, Cache Creek, located on the southeast portion of the lake (Figure 2) (Suchanek et al. 2003, Gericke 2006). Construction of Cache Creek Dam was completed in 1914 for the purpose of diverting lake water to Yolo County, California (Suchanek et al. 2003, Lundquist and Smythe 2010). Both the water rights to use Clear Lake water and the dam are owned and

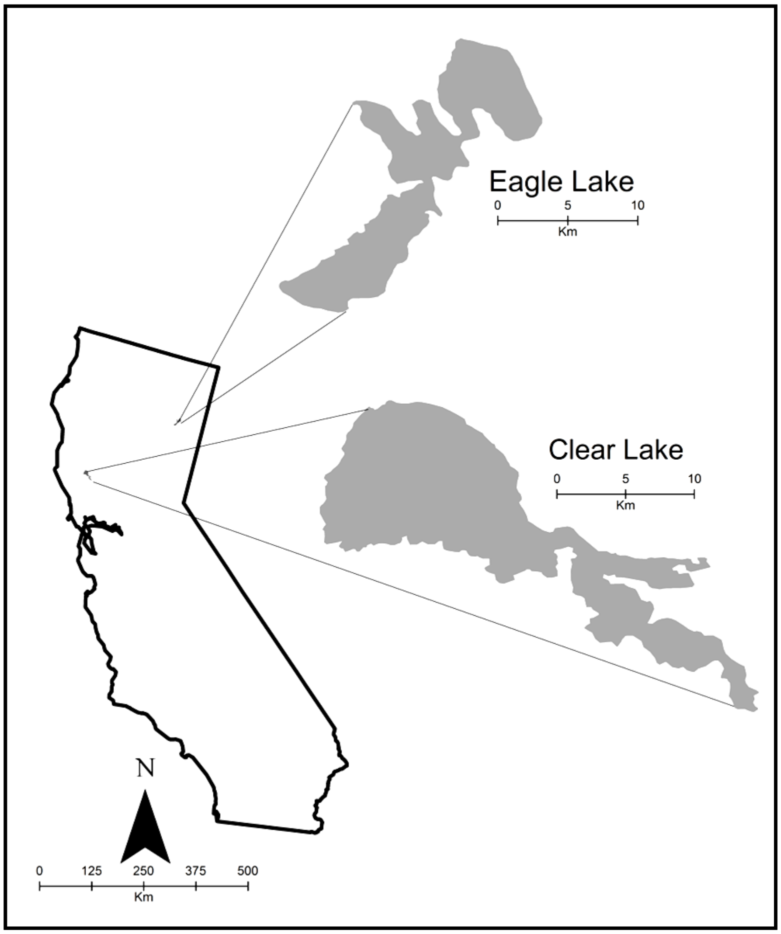

FIGURE 1. Study locations. Clear and Eagle Lakes, California.

operated by the Yolo County Flood Control and Water Conservation District (Lundquist and Smythe 2010).

Although the lake serves primarily as an agricultural irrigation reservoir for Yolo County, lake elevation is also managed for the purposes of flood prevention and lake recreation (Richerson et al. 1994, Lundquist and Smythe 2010). In order to balance these three aspects of lake elevation management, operation of the dam is outlined in two court decrees, the Gopcevic Decree of 1920 and the Solano Decree of 1978 (Richerson et al. 1994, Lundquist and Smythe 2010). The Gopcevic Decree outlines how lake elevation is to be managed during the winter months; maintaining a maximum lake elevation to prevent flooding (Richerson et al. 1994). The Solano Decree outlines dam operation during the summer months by maintaining summer lake levels between 403.9 and 405.3m above mean sea level (Richerson et al. 1994, Lundquist and

Smythe 2010). Annual outflow to Yolo County is determined by lake elevation on 1 May. If Clear Lake reaches an elevation of 404.5m on this date, 185 million m^3 of water is available for diversion to Yolo County. No water is diverted from the lake if the 1 May lake elevation is below 402.8m (Lundquist and Smythe 2010). The bathymetry of Clear Lake is illustrated in Figure 2.

Eagle Lake. Eagle Lake is located 1557m above mean sea level in northeastern California (Figure 1). The lake is situated in a geologic transitional zone where the Modoc Plateau, Southern Cascade, Sierra Nevada, and Great Basin geomorphic provinces converge (Gester 1962). As a result of the varied geology, the lakeshore supports a variety of vegetation communities including those dominated by juniper and sagebrush scrub, mixed conifer and pine forest, and mountain mahogany (Koplin 1980). Flooded emergent wetland vegetation exists in four separate stands, the largest located in the lake's north basin and three smaller stands exist in the central basin (Wright-Myers and Bogiatto 2007). Today, the lakeshore remains largely undeveloped and 80% of the land surrounding the lake is managed by the United States Forest Service and Bureau of Land Management (Shaw 1998).

The lake's current hydrology is complicated by both the geology of the area and historic attempts to divert lake-water for human uses. Eagle Lake was naturally a closed drainage system consisting of one major inlet, two smaller tributaries, and no natural surface-water outlet (Gester 1962, United States Department of the Interior 2010). Groundwater seepage through the porous volcanic rock surrounding the lake contributed to inflow and outflow of water to the lake basin, and was the sole source of historical outflow (United States Department of the Interior 2010). As a result of this closed system, annual lake elevation is highly variable and fluctuates with annual run-off, precipitation, and groundwater-flow amounts (Gester 1962, Dolcini 1972, United States Department of the Interior 2010).

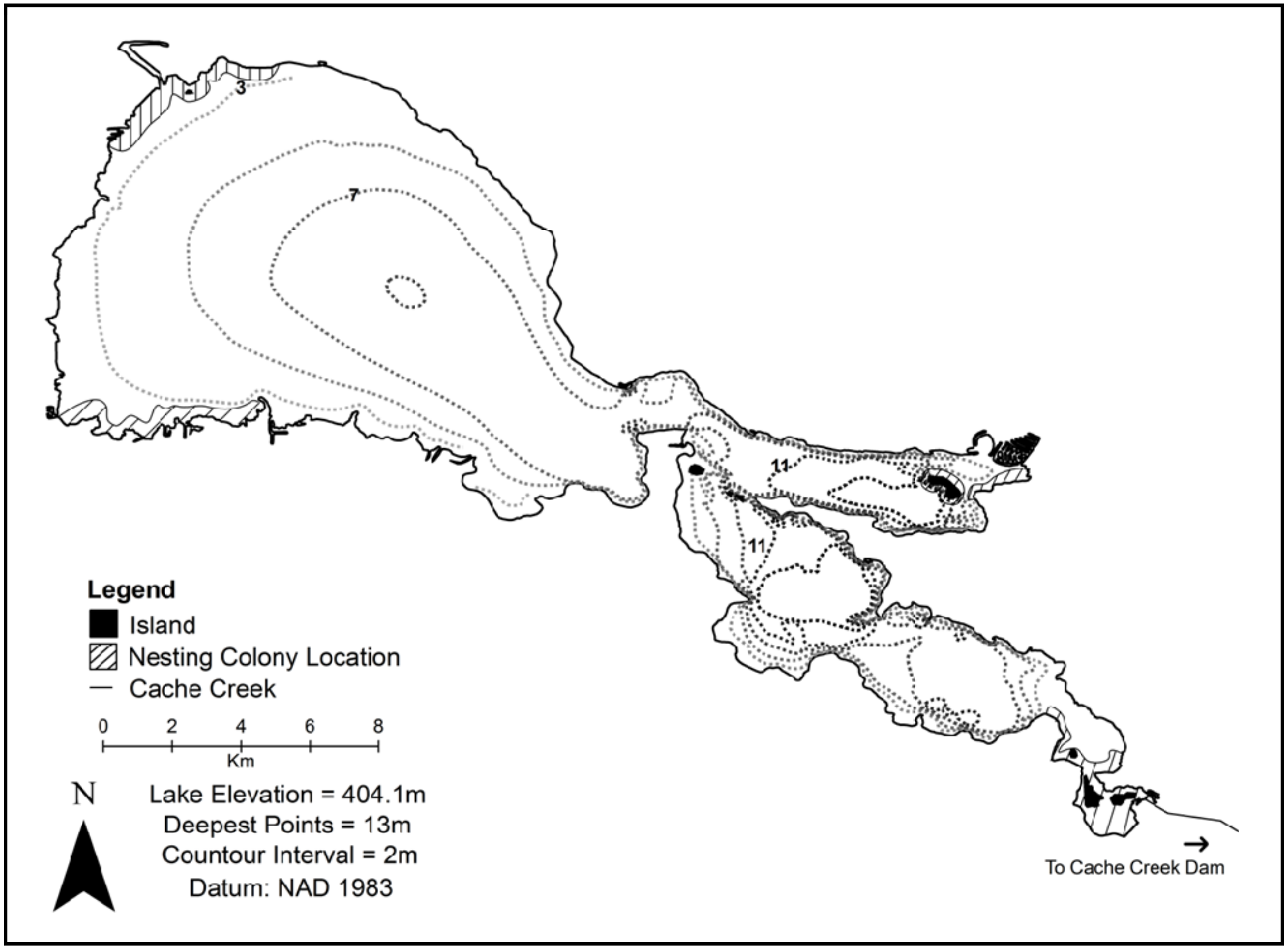

FIGURE 2. Bathymetric map of Clear Lake, California, USA. Not all nesting colony locations were occupied every nesting season. These locations represent sites observed to host grebe nesting colonies at some point between 1997-2010.

In 1923, construction was completed on a 2225m tunnel in the lake's southern basin for the purpose of diverting water from Eagle Lake to more arid areas located to the southeast (Figure 3) (Gester 1962, Dolcini 1972, Huntsinger and Maslin 1976, Rich 2009, United States Department of the Interior 2010). Initial drainage through the tunnel totaled approximately 382 million m^3 between 1923 and 1935 (Gester 1962, Rich 2009). This contributed to a 9.1m drop in lake elevation, although drought was implicated as the main cause of decline (Gester 1962, Rich 2009). Concerns over low lake levels prompted an investigation by the California Department of Water Resources into alternative plans for controlling outflow through the tunnel (Dolcini 1972).

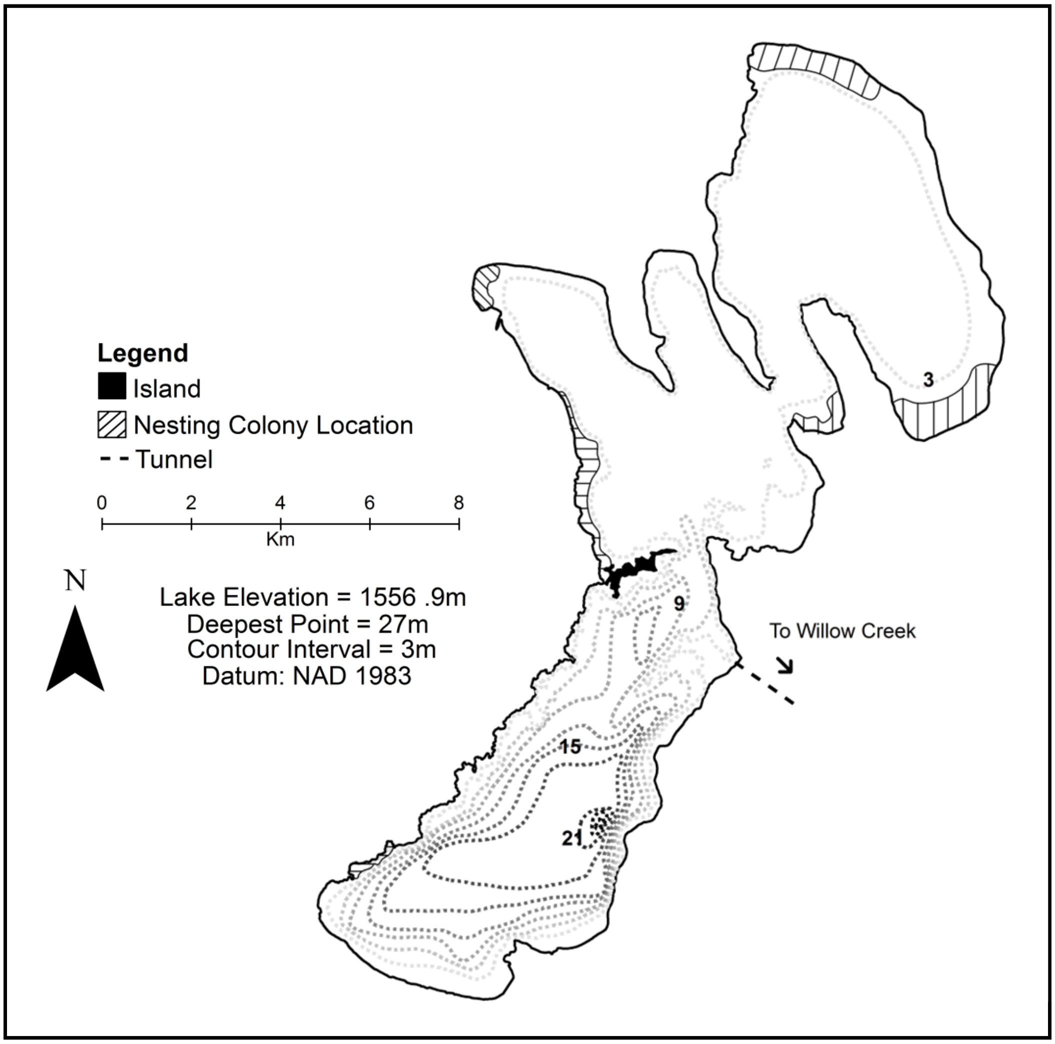

FIGURE 3. Bathymetric map of Eagle Lake, California, USA. Not all nesting colony locations were occupied every nesting season. These locations represent sites observed to host grebe nesting colonies at some point between 1997-2010.

The investigation considered several alternative procedures for operation of the tunnel and attempted to balance the needs of both wildlife and water users. The 1972 investigative report concluded that the best option for strict fish and wildlife management, especially for nesting grebes and their prey fish species, would be to control outflow through the tunnel, maintaining lake elevation at or above 1554m (Dolcini 1972). The basis for this recommendation was that extent of flooded emergent wetland vegetation varies with lake elevation; extending up to 300m from shore at high elevations to exposing unproductive alkaline soils at elevations below 1554m, resulting in the degradation of littoral zone vegetation (Dolcini 1972, Wright-Myers and Bogiatto 2007, R.E. Weems, pers. obs.). This is particularly evident in the lake's shallower north basin where the largest stand of grebe nesting vegetation is located (Figure 3) (Dolcini 1972, Wright-Myers and Bogiatto 2007, R.E. Weems, pers. obs.). Despite the benefit to wildlife, the report indicated that maintenance of lake elevation above 1554m would be detrimental to local development around the lake (Dolcini 1972). To prevent flooding, accommodate the desires of water users, and provide the most benefit to local fish and wildlife resources, the report ultimately concluded the best alternative would be to construct a plug in the tunnel equipped with a control valve to allow for operational flexibility (Dolcini 1972).

Following the recommendation of the 1972 investigative report, the United States Bureau of Land Management constructed a plug into which a 20.3cm pipe was inserted in order to decrease surface-water outflow from the lake (United States Department of the Interior 2010). Currently, surface water only flows directly through the pipe when lake elevation is sufficiently high to reach the tunnel. Because direct outflow through the tunnel is dependent on lake elevation, outflow of lake-water into the pipe is variable and can account for >1%, or 1.3 million $m^3 \cdot yr^{-1}$, to <9%, 8 million $m^3 \cdot yr^{-1}$, of the total annual lake outflow (Raymond Vail and Associates 1979, United States Department of the Interior 2010). Estimates indicate that for every 0.3m rise in lake elevation, there is a resultant 0.02 $m^3 \cdot s^{-1}$ increase in flow through the tunnel (Raymond Vail and Associates 1979). Water flowing through the tunnel when lake levels are too low to reach the inlet is presumed to be the result of groundwater seepage (United States Department of the Interior 2010). This groundwater originates from the lake itself and is the result of the tunnel intersecting an area of excessive seepage approximately 91m from the lake shore (Rich 2009, United States Department of the Interior 2010). The affect this seepage exerts on lake elevation and Eagle Lake wildlife is, at present, unclear (Rich 2009, United States Department of the Interior 2010).

Currently, the biotic and abiotic factors that determine nest initiation and completion for Western and Clark’s Grebes remain unknown (Parmelee and Parmelee 1997). Investigating and identifying the habitat characteristics that affect reproductive success for these species is crucial to their conservation and management. In addition, incorporating individual species’ ecology and life-history characteristics into a management plan is critical to the principle of integrated wetland management, an approach that attempts to maximize the benefit of management to an entire community of species using a wetland (Laubhan and Fredrickson 1993). Because grebes require not only shallower flooded wetland habitat for nesting, but also deep open-water for foraging, grebe-oriented wetland management has the potential to benefit numerous wetland-dependent species (Storer and Neuchterlein 1992, Laubhan and Fredrickson 1993). Lastly, studies on the possible effect of lake elevation on over-water nesting species’ reproductive success are rare. This study therefore aids in identifying those habitat characteristics that are most crucial to Western and Clark’s Grebe nesting initiation, while providing insight into variables of successful management for not only these, but other wetland-dependent and over-water nesting species as well.

METHODS

STUDY SITES

Data were collected at Clear Lake, Lake County, California (39°00’N and 122°45’W) and Eagle Lake, Lassen County, California (40°38’N and 120°44 ’W) (Figure 1). Consistent monitoring and data collection of Western and Clark’s Grebe breeding effort was conducted at these locations from 1997 to 2010. These sites were chosen based on their significant contributions to the breeding population of *Aechmophorus* Grebes.

SURVEY TIMING

Western and Clark's Grebes were monitored annually during the breeding season at both Clear and Eagles Lakes. Surveys were conducted from June to October each year from 1997- 2010, with the exception of 2005 in which no reproductive data were collected at Eagle Lake. Initiation of nesting was site-dependent and varied from year to year. Due to this variation, each lake was initially visited to determine breeding phenology and synchrony. These observations were used to determine the timing of subsequent nesting and productivity surveys. Further details on surveys are outlined by Elbert (1996), Elbert and Anderson (1998), and Anderson et al. (2008).

NESTING SURVEYS

Nesting surveys were conducted to determine estimates of colony sizes. These nesting colony surveys were conducted most often from a boat and less frequently from aircraft. When conducted by boat, observations were made from outside the colony to minimize disturbance. Timing of subsequent brood surveys was based on observations of nesting-commencement dates and chick-maturation rates.

BROOD SURVEYS

Western and Clark's Grebes have an average incubation period of 23 days (Bent 1919, Gould 1974, Lindvall & Low 1982, Shaw 1998) and an eight-week brood rearing period (Storer and Nuechterlein 1992). In a study by Ratti (1979), captive chicks of both species began transitioning to adult morphological characteristics between 40 and 80 days after hatching. Based on this information, brood surveys were timed for approximately 42 days after initiation of nesting, thus ensuring clear distinction between chicks and adults during the surveys.

Brood surveys were conducted by outboard motorboat. Pelagic-strip transects were run in each basin at both Clear and Eagle Lakes. While on transect, two observers recorded observations from opposite sides of the boat. All birds within 200m of each side of the boat were recorded. Data recorded included species of observed grebes, pair status (single adult or pair), and whether or not chicks were present or absent. When it was not possible to accurately identify species, the bird was classified to genus. If grebe chicks were present, brood size and approximate age were recorded. Chicks were aged as a percentage of adult size as described in Elbert (1996) and Elbert and Anderson (1998). Surveys were conducted between 0900 and 1600 hours and only during calm water conditions.

REPRODUCTIVE INDICES

Data collected from annual brood surveys were summarized into three reproductive indices for this study. These indices allowed separate measures of Western and Clark's Grebe annual reproductive success to be analyzed.

(1) Productivity was defined as the ratio of the total number of chicks to the total number of adults observed in the sample ($YY \cdot Ad^{-1}$). This measure indicated the proportion of young of the year present in the population sample. (2) Breeding Adult Ratio was calculated as the ratio of adults observed with chicks to the total number of adults observed in the sample ($Ad\ w/YY \cdot [Total\ Ad]^{-1}$). This metric provided an estimate of the proportion of breeding birds in the sample population. (3) Average Brood Size was defined as the number of chicks per successful pair in the sample ($YY \cdot Pair^{-1}$). This index was calculated by dividing the total number of chicks observed with paired adults by the total number of pairs observed with chicks, thus providing an estimate of annual average brood size.

LAKE ELEVATION DATA

Lake elevation data for the period of study was requested from local agencies. Eagle Lake data were collected and provided by Lassen County Public Works (Joel Rathje, pers. comm.). Lake elevation was measured on a monthly basis at this location, but collection dates were not consistent across months, and in certain months no lake elevation data were collected. The lake elevation data used in our analysis were based on the month grebes were determined to be nesting at this location. These data were available for all years, with the exception of 2006 when no elevation data were collected by the agency during the grebe breeding season.

Clear Lake elevation data were collected daily by the United States Geologic Survey (Rockwell et al. 1998, Hayes et al. 1999, Webster et al. 2000, Anderson et al. 2001, Rockwell et al. 2002, Smithson et al. 2003, Friebel et al. 2004, Webster et al. 2005, United States Geological

Survey 2006-2011). Daily mean water level was recorded in reference to the “Rumsey gauge,” a location-specific measurement developed in 1872 (Richerson et al. 1994). This gauge, measuring lake level in feet, is used to determine outflow through Cache Creek Dam for agricultural irrigation in Yolo County, California (Lundquist and Smythe 2010). A value of 0.0 Rumsey is equivalent to a lake elevation of 401.8 meters above mean sea level. Clear Lake is considered “full” when it reaches 7.56 Rumsey; equivalent to 404.2 meters above sea level (Tom Smythe, Lake County Department of Public Works, pers. comm.). Rumsey measurements were converted to lake elevation based on the following formula: E_t = (1318.26ft + R) x 0.3048; where E_t is the lake elevation at time t, R is the Rumsey measurement at time t, and 0.3048 is the feet to meters conversion factor.

Clear Lake elevation data used in our analysis were selected based on nest initiation dates. Nest initiation dates which were determined by performing a back-calculation based on estimated chick ages at the time of brood surveys. The estimated age of the chick, measured in days, was added to the 23-day average incubation period; these values were subtracted from the Julian dates of the brood surveys. This provided a precise estimate of nest initiation date. Because mean water levels were collected daily at Clear Lake, the lake elevation measurement taken the day of estimated nest initiation was used in our analysis.

LAKE ELEVATION INDICES

Because lake elevations between Clear and Eagle Lakes differed based on their elevation above mean sea level, two indices of lake elevation were calculated. These indices standardized changes in yearly lake elevation, allowing meaningful comparisons between the two study sites.

Residual Lake Elevation (RLE) was calculated as the difference between the yearly nesting lake elevation (measured as described above) and the mean nesting lake elevation for the study period, 1997-2010. This index provided an absolute measure of lake elevation change at each location, scaling changes in yearly nesting lake elevation to the study period mean. Mean nesting lake elevation was determined independently for each location. In years where lake elevation was higher than the mean, positive residual lake elevations were produced, whereas years in which lake elevation was lower produced negative residual values.

The second lake elevation index was the Standard Normal Deviate of Lake Elevation (SNDLE). This value was calculated independently for each location by dividing the yearly RLE value by the standard deviation from mean lake elevation. The standard deviation from mean lake elevation was also determined independently for each location. This index provided a relative measure of lake elevation change at each location for the study period. Again, years where lake elevation was higher than the mean for the study period produced positive values; years when lake elevation was lower produced negative values.

STATISTICAL ANALYSES

An information-theoretic approach was used to assess the relationship between lake elevation at time of nest-initiation and grebe reproductive effort (Burnham and Anderson 2002). We hypothesized that reproductive success would be negatively affected by decreases in lake elevation. Three sets of *a*-priori mixed models were constructed for comparison. These models were based on our field observations, knowledge of lake hydrology, and elevation trends at each study site during the study period. Observations over the study-period indicated a decrease in reproductive success in years where there was a decrease in lake elevation from the prior year (Figures 4 and 5). Based on these criteria, both indices of Lake Elevation (RLE and SNDLE), Lake, and Year were combined in biologically meaningful combinations to form sets of mixed models of reproductive success, with Lake treated as a Random Effect (Skinner and Holmes 2003). Year and Lake were included to determine whether there were changes in our reproductive indices that could not be attributed to lake elevation.

The three model-sets were constructed based on the reproductive index under consideration and included all relevant interactions among variables. The first set of models analyzed the relationship between Productivity ($YY \cdot Ad^{-1}$) and the variables mentioned above, the second analyzed these relationships using the Breeding Adult Ratio ($Ad\ w/YY \cdot [Total\ Ad]^{-1}$), and the last analyzed the relationship between these variables and Average Brood Size ($YY \cdot Pair^{-1}$). Each set consisted of 17 candidate models for consideration.

Candidate models were ranked based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c) (Burnham and Anderson 2002) using JMP® Version 9.0 (SAS Institute 2010). Given the data, the top model in each set of candidate models was determined based on the lowest AIC_c value (Table 1). All other models in the set of candidate models were then ranked by the difference between the AIC_c value for the model under consideration and the AIC_c value for the top model (ΔAIC_c). In addition to ΔAIC_c values, "Akaike weights" (w_i) and "evidence ratios" (Burnham and Anderson 2002), as well as Adjusted R^2 values, provided criteria for further model comparison. Akaike weights were computed independently for each set of candidate models and comparisons of these values were only made within each defined set of models (Burnham and Anderson 2002). Models with the largest w_i values were considered more plausible for our data set. Evidence ratios were computed as described in Burnham and Anderson (2002). These values were also computed and compared independently for each set of candidate models. Models with higher evidence ratios were considered to have less support than those with lower values (Burnham and Anderson 2002). Adjusted R^2 values were generated for each model in JMP® 9 (SAS Institute 2010). Models that had the highest Adjusted R^2 values were considered to explain the most variation of our data, and along with all other criteria considered, were favored. Adjusted R^2 values were not the main criteria for comparison, however, because it is assumed that many other factors, both biotic and abiotic, affect the reproductive indices measured in our study.

During model comparison, subsequent models were considered to have substantial support only if their AIC_c values fell between 0 to 2 ΔAIC_c of the top model, and the inclusion of additional parameters was justified by resulting in an increase in the amount of variation explained by the new model, as measured by the Adjusted R^2 value in this case (Burnham and Anderson 2002, Arnold 2010). When the addition of a single variable resulted in an AIC_c value

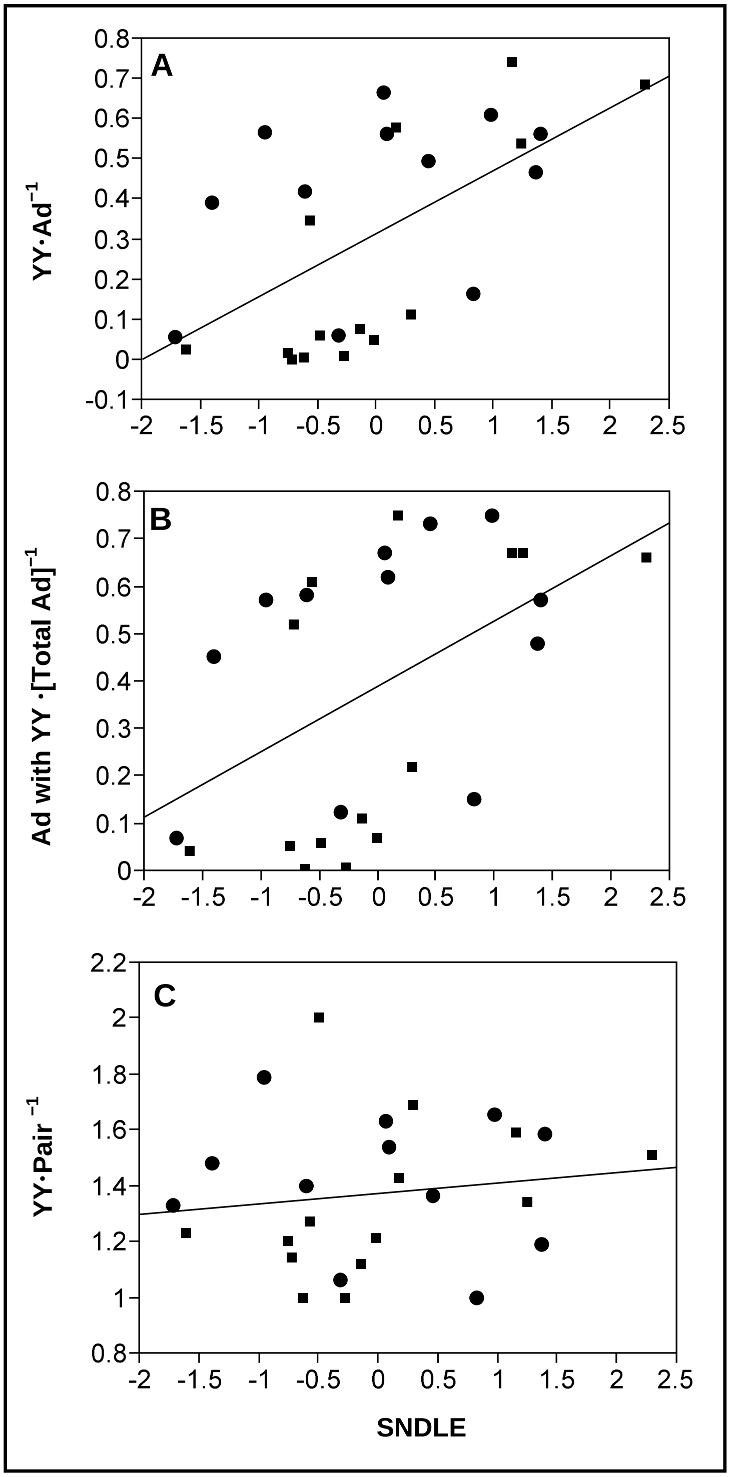

FIGURE 4. Relationship between three indices of reproductive success **A.** Productivity (YY·Ad^{-1}), **B.** Breeding Adult Ratio (Ad with-YY·[Total Ad]$^{-1}$), and **C.** Average Brood Size and Standard Normal Deviate of Lake Elevation (SNDLE). Squares represent Clear Lake data and circles represent Eagle Lake data.

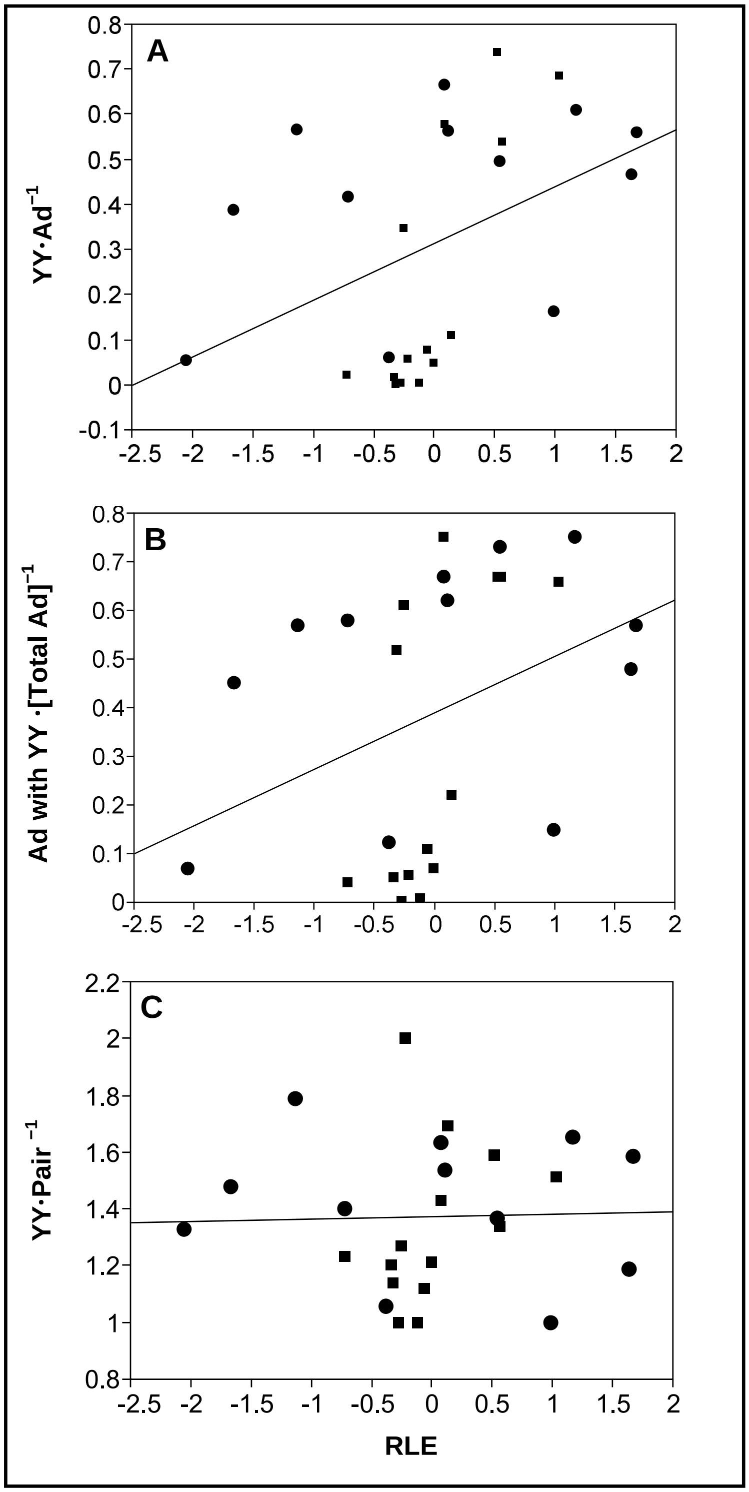

FIGURE 5. Relationship between three indices of reproductive success **A.** Productivity (YY·Ad^{-1}), **B.** Breeding Adult Ratio (Ad with-YY·[Total Ad]$^{-1}$), and **C.** Average Brood Size and Residual Lake Elevation (RLE). Squares represent Clear Lake data and circles represent Eagle Lake data.

within 2 ΔAIC_c of the top model, but there was no increase in the amount of variation explained, this additional variable was considered to be ecologically uninformative and thus the model was not considered competitive (Arnold 2010). All subsequent models were considered to have little support if their ΔAIC_c values fell between 4 and 7, and virtually no support if their ΔAIC_c values were □10 (Burnham and Anderson 2002).

In order to further guard against the consideration of non-competitive models, only models that fell within a 95% credibility set of candidate models were analyzed as described in Burnham and Anderson (2002) and Symonds and Moussalli (2011). This method ensured an approximately 95% chance that one of the models in the set was the best model, given the data and the set of models under consideration. Models included in this 95% credibility set can be found in Table 1. Once defined, these models were averaged in order to gain parameter estimates, measurements of standard error, 85% confidence limits (as suggested in Arnold (2010)), and measures of variable importance (Table 2). In addition, model averaging was employed as a solution for any model selection uncertainty that arose due to Akaike weights of the best approximating models being ≤ 0.9 (Burnham and Anderson 2002, Arnold 2010, Symonds and Moussalli 2011).

RESULTS

Nesting lake elevation measurements differed markedly between the two study locations. Clear Lake nesting elevations were highly variable between years throughout the study-period; ranging from a low of 402.4m above mean sea-level, measured in 1999, to a high of 404.1m above mean sea-level in 2005 (Figure 6). Average nesting lake elevation for this location was 403.1m above mean sea-level. Eagle Lake nesting lake elevation showed a relatively steady decline throughout the study-period. High lake elevation for the study-period occurred in 1998, measuring 1556.9m above mean sea-level; low lake elevation measured 1553.2m above mean sea-level in 2010. The average nesting lake elevation for the study period was 1555.2m above mean sea-level at this location (Figure 6). Seven years of the 14 year study-period had RLE and SNDLE measures

TABLE 1. 95% credibility sets (those models whose cumulative Akaike weights (acc w_i) were $\leq$ 0.95) for three different model-sets including factors affecting **A.** Productivity ($YY \cdot Ad^{-1}$), **B.** Breeding Adult Ratio (Ad w/$YY \cdot [\text{Total Ad}]^{-1}$), and **C.** Average Brood Size ($YY \cdot Pair^{-1}$) of Western and Clark's Grebes at Clear and Eagle Lakes, California, 1997-2010. Each model-set was ranked according to Akaike's Information Criterion adjusted for small sample sizes (AIC_c). The AIC_c value, number of parameters (K), ΔAIC_c, AIC_c weights (w_i), cumulative Akaike weights (acc w_i), Evidence Ratios, and Adjusted R^2 values are also reported for all models in each set.

Model[a]	K	AIC_c	ΔAIC_c	w_i	acc w_i	Evidence Ratio	Adjusted R^2
A. *Productivity ($YY \cdot Ad^{-1}$)*							
SNDLE	3	-0.29	0.00	0.71	0.71		0.32
Year, SNDLE	4	2.42	2.71	0.18	0.89	3.87	0.29
Year, SNDLE, Year x SNDLE	5	5.20	5.49	0.05	0.94	15.56	0.27
B. *Breeding Adult Ratio (Ad w/$YY \cdot [\text{Total Ad}]^{-1}$)*							
SNDLE	3	7.13	0.00	0.49	0.49		0.21
Year, SNDLE	4	9.02	1.89	0.19	0.68	2.57	0.20
RLE	3	10.49	3.36	0.09	0.77	5.36	0.09
Year	3	10.77	3.64	0.08	0.85	6.18	0.09
Intercept Only Model	2	11.83	4.70	0.05	0.90	10.50	0.00
Year, RLE	4	12.08	4.95	0.04	0.94	11.87	0.10
C. *Average Brood Size ($YY \cdot Pair^{-1}$)*							
Intercept Only Model	2	6.97	0.00	0.47	0.47		0.00
Year	3	8.66	1.69	0.20	0.67	2.34	0.00
SNDLE	3	9.79	2.82	0.12	0.79	4.09	0.00
RLE	3	10.30	3.33	0.09	0.88	5.29	0.00
Year, RLE	4	11.85	4.88	0.04	0.92	11.46	0.00

[a] SNDLE= Standard Normal Deviate of Lake Elevation, RLE= Residual Lake Elevation

TABLE 2. Model-averaged parameter estimates predicting Western and Clark's Grebe reproductive success at Clear and Eagle Lakes, California, USA, 1997-2010. Only those reproductive indices found to be affected by lake elevation are included.

Variable[a]	Estimate	SE	Lower 85% CI	Upper 85% CI	Importance
$YY{\cdot}Ad^{-1}$					
Intercept	-1.47	7.49	-12.26	9.32	0.94
SNDLE	0.16	0.05	0.90	1.02	0.94
Year	0.04	0.04	-0.02	0.09	0.23
Year x SNDLE	-0.01	0.01	-0.02	0.00	0.05
Ad w/$YY{\cdot}[Total\ Ad]^{-1}$					
Intercept	11.07	19.11	-16.45	38.59	0.94
SNDLE	0.13	0.05	0.06	0.20	0.68
Year	-0.02	0.02	-0.05	0.01	0.31
RLE	0.09	0.07	-0.01	0.19	0.13

[a] $YY{\cdot}Ad^{-1}$= Productivity, Ad w/$YY{\cdot}[Total\ Ad]^{-1}$= Breeding Adult Ratio,
SNDLE= Standard Normal Deviate of Lake Elevation, RLE= Residual Lake Elevation

below zero at Clear Lake, whereas six years of the 13 year study-period had RLE and SNDLE measures below zero at Eagle Lake (Figures 7 and 8).

Reproductive indices also differed between study sites. Eight of 14 years had Productivity ($YY{\cdot}Ad^{-1}$) estimates $\leq$ 0.1 at Clear Lake, whereas only two of 13 years had Productivity estimates of $\leq$ 0.1 at Eagle Lake (Figure 9). The Breeding Adult Ratio (Ad w/$YY{\cdot}[Total\ Ad]^{-1}$) indicated a similar trend with again eight of the 14 years having estimates of $\leq$0.1 at Clear Lake, and only one year of 13 having an estimate of $\leq$ 0.1at Eagle Lake (Figure 10). The Average Brood Size ($YY{\cdot}Pair^{-1}$) was less variable between study sites and ranged between 1.0 and 2.0 at Clear Lake and 1 to 1.79 at Eagle Lake (Figure 11, Table 3). For summary statistics of all reproductive indices by site, please see Table 3.

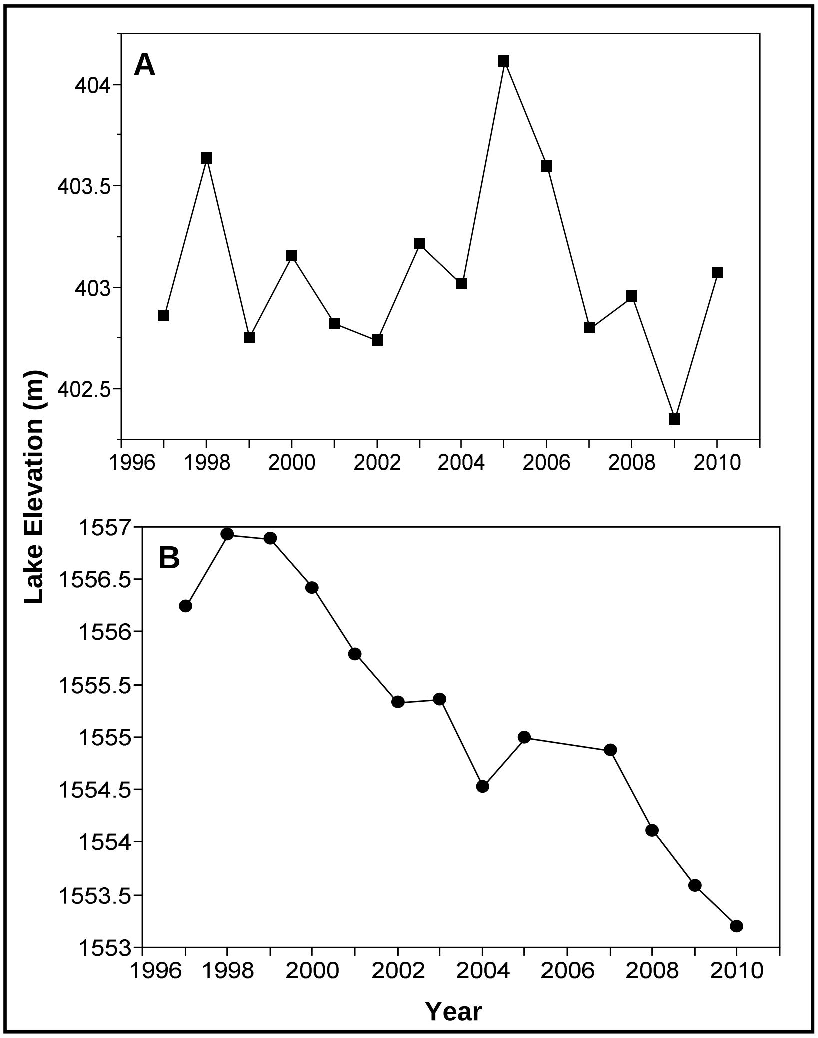

FIGURE 6. Fourteen year trend (1997-2010) in Lake Elevation at **A:** Clear Lake (squares) and **B:** Eagle Lake (circles)

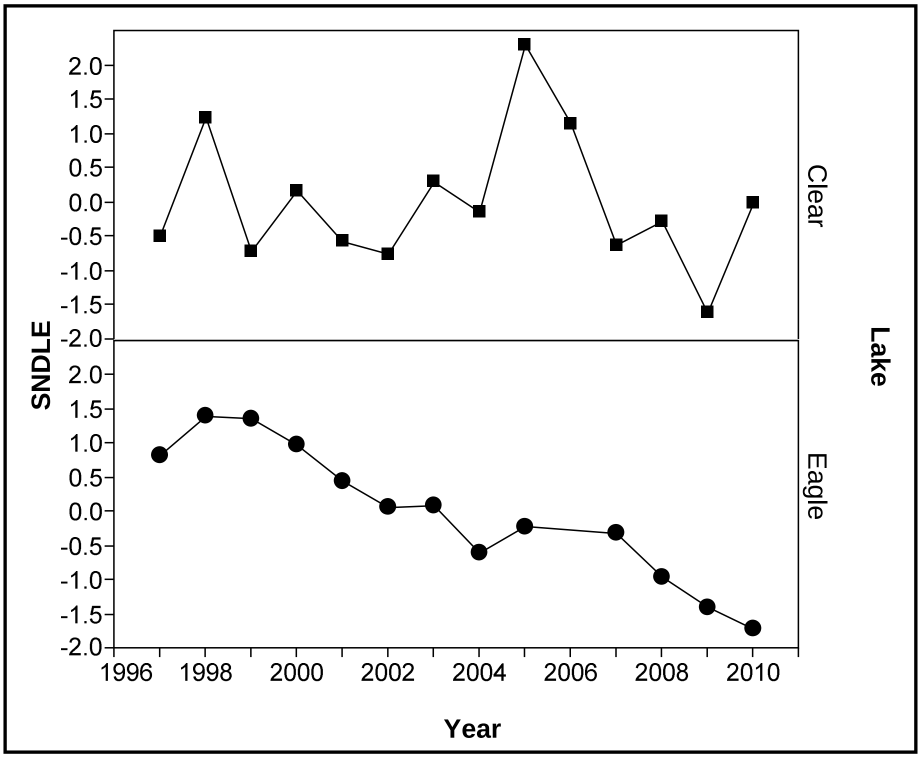

FIGURE 7. Trend in Standard Normal Deviate of Lake Elevation (SNDLE) at Clear and Eagle Lakes, California, USA.

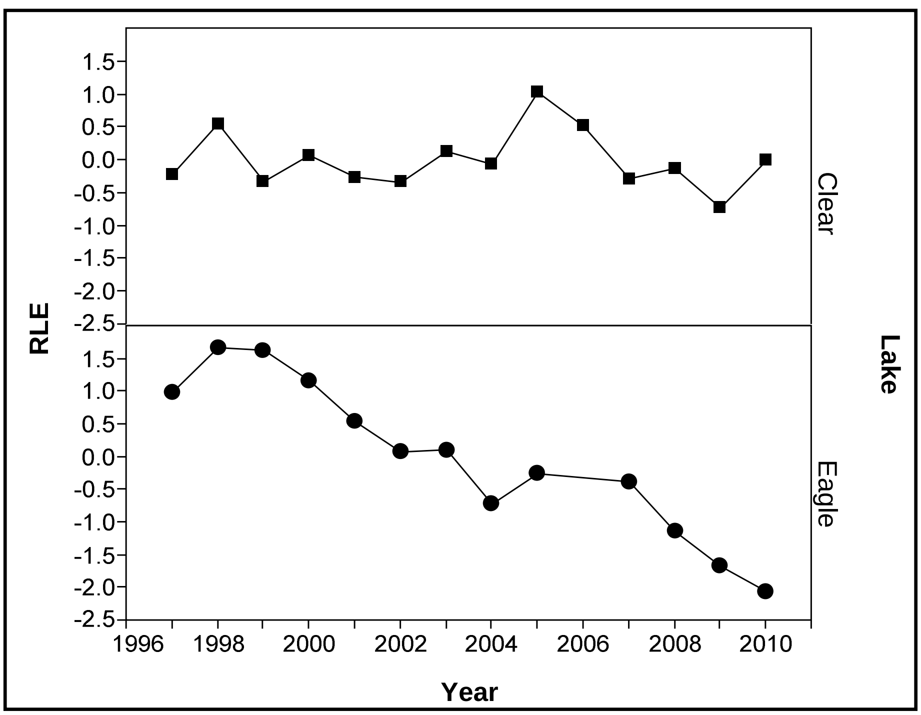

FIGURE 8. Trend in Residual Lake Elevation (RLE) at Clear and Eagle Lakes, California, USA.

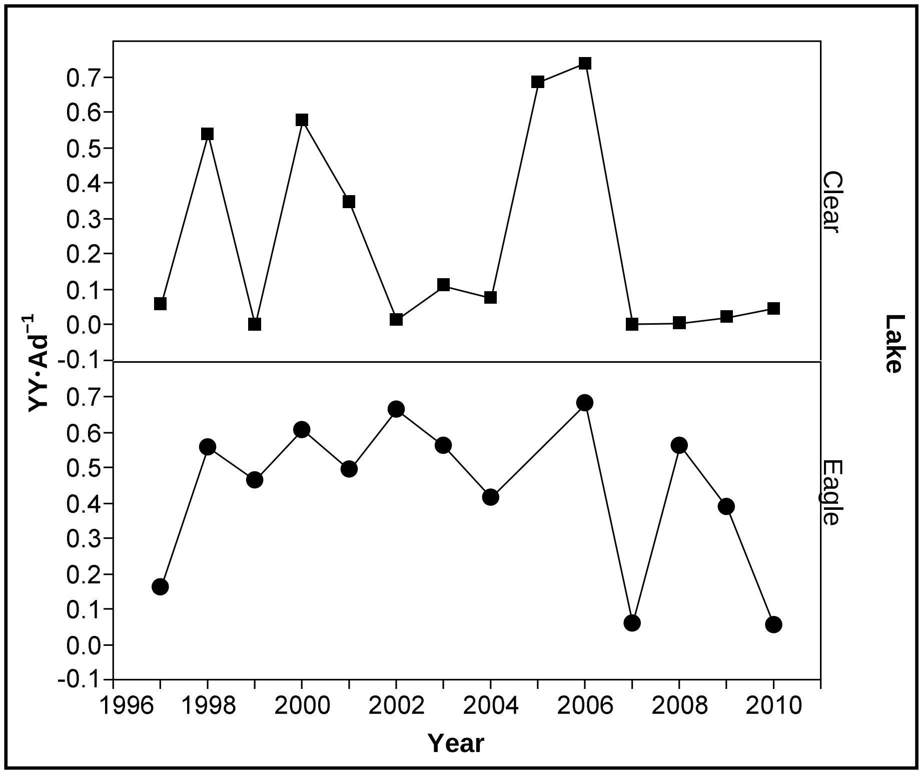

FIGURE 9. Trend in Productivity (YY·AD^{-1}) at Clear and Eagle Lakes, California, USA.

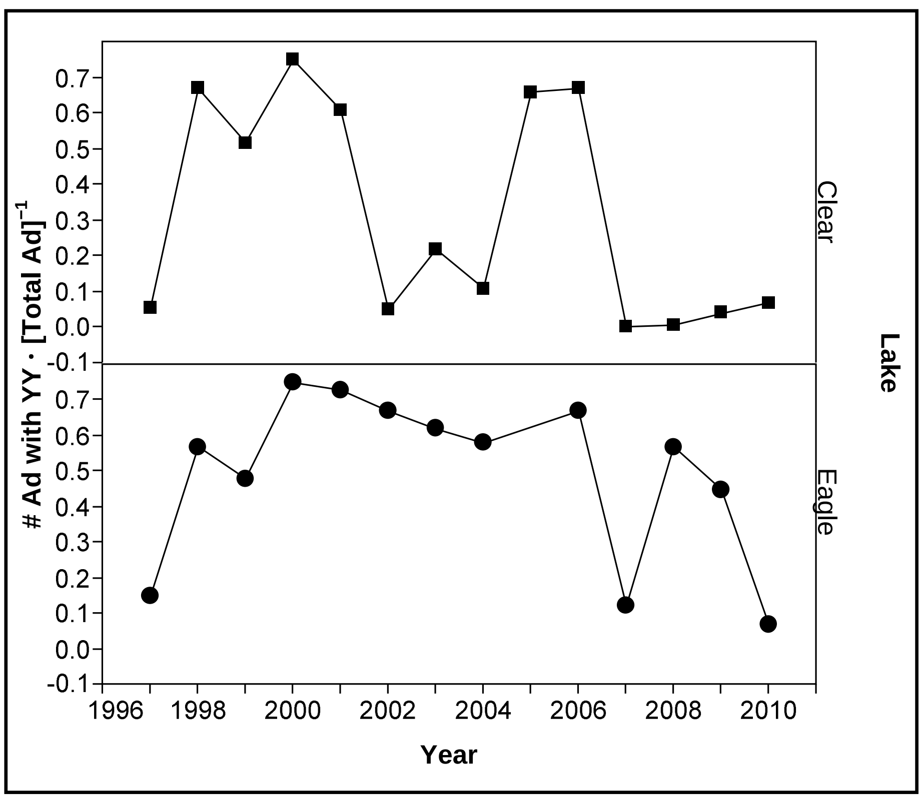

FIGURE10. Trend in Breeding Adult Ratio (Ad w/YY·[Total Ad]$^{-}$)^{1} at Clear and Eagle Lakes, California, USA.

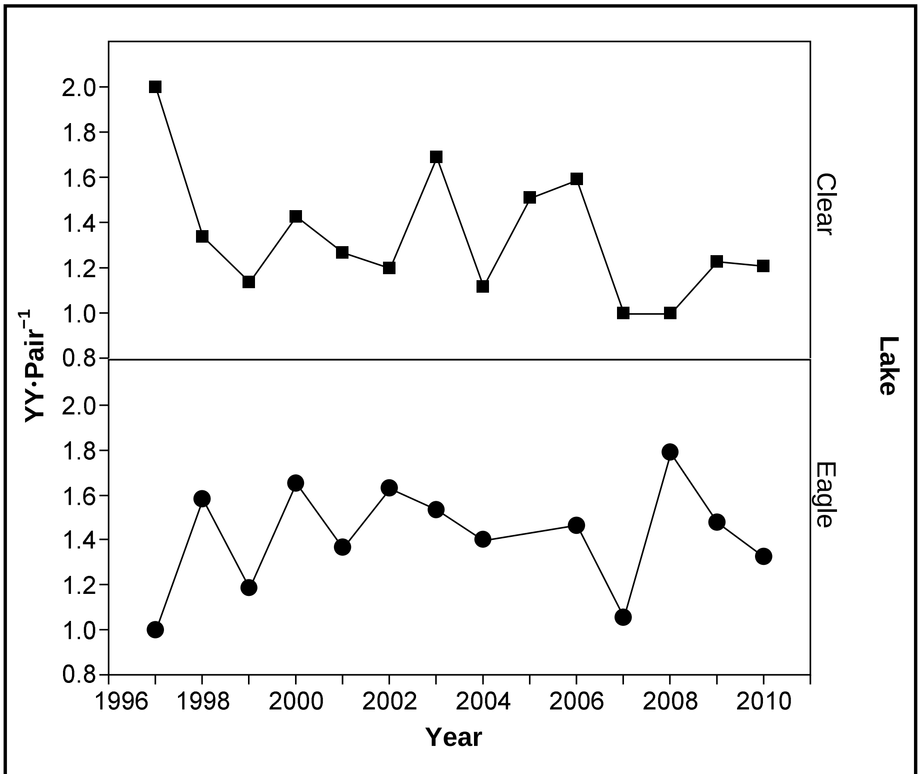

FIGURE 11. Trend in Average Brood Size (YY·Pair^{-})^{1} at Clear and Eagle Lakes, California, USA.

TABLE 3. Summary statistics of reproductive indices.

Lake	Productivity ($YY \cdot Ad^{-1}$)	Ad w/YY·[Total Ad]$^{-1}$	YY·Pair^{-1}
Clear Lake			
Mean	0.23	0.32	1.34
Std. Dev.	0.28	0.23	0.28
Std. Error	0.07	0.08	0.07
Maximum	0.74	0.75	2
Minimum	0.001	0.003	1
95% CI	0.08-0.37	0.20-0.44	1.19-1.48
Eagle Lake			
Mean	0.44	0.49	1.42
Std. Dev.	0.22	0.23	0.23
Std. Error	0.06	0.06	0.06
Maximum	0.68	0.75	1.79
Minimum	0.05	0.07	1
95% CI	0.32-0.56	0.36-0.62	1.29-1.55

The best approximating models for both Productivity (YY·Ad^{-1}) and Breeding Adult Ratio (Ad w/YY·[Total Ad]$^{-1}$) contained SNDLE as the only explanatory variable, with each model having a 71% and 49% probability of being the best model, respectively (Table 1). These models were 3.87 and 2.57 times more likely than the next best approximating models in the candidate set, which for both sets of models contained Year as the only additional explanatory variable. The best models also explained the largest proportion of variation of these data, as measured by the Adjusted R^2 value when compared to other models within the 95% credibility set. The model predicting Productivity (YY·Ad^{-1}) explained 32% of the data variation, the model predicting Breeding Adult Ratio (Ad w/YY·[Total Ad]$^{-1}$) accounted for 21% (Table 1).

Indices of change in nesting lake elevation, RLE and SNDLE, displayed no explanatory power for the Average Brood Size (YY·Pair^{-}1) reproductive index. The set of candidate models indicated that the intercept-only model was the best approximating model based on calculated

Akaike weights and evidence ratios. Further, all models in the candidate set had Adjusted R^2 values of zero (Table 1).

Due to model selection uncertainty arising from Akaike weights of <0.9, model averaging was employed. For the credibility set of models predicting Productivity (YY·Ad^{-1}), two variables (Year and Year x SNDLE) had model-average 85% confidence intervals that included zero, indicating that these parameters contain no biological information in predicting this response. For models predicting Ad w/YY·[Total Ad]$^{-1}$, two variables (Year and RLE) had model-averaged 85% confidence intervals that included zero, again indicating their lack of explanatory power. Model averaging provided further support for the importance of SNDLE in predicting these two measures of reproductive success. This variable had the highest importance value in both the Productivity (YY·Ad^{-1}) and Ad w/YY·[Total Ad]$^{-1}$ models, producing values of 0.94 and 0.68 respectively (Table 2).

DISCUSSION

Lake elevation was the single most important factor affecting population-level reproductive success of both Western and Clark's Grebe's at our study sites. In particular, Standard Normal Deviate of Lake Elevation (SNDLE) contained the most predictive power in estimating both Productivity (YY·Ad^{-1}) and the Breeding Adult Ratio (Ad w/YY·[Total Ad]$^{-1}$), and was positively correlated with both measures (Table 1, Figure 4). Interestingly, SNDLE had no predictive power, and displayed no correlation with the Average Brood Size (YY·$Pair^{-1}$) parameter (Figure 4). Analysis of our reproductive indices and Residual Lake Elevation (RLE) indicated similar relationships (Figure 5). These results indicate that annual changes in lake elevation have little to no effect in determining the fate of individual nests, but that declines in lake elevation have a negative impact on each lake's overall potential breeding population.

The effect that lake elevation change has at a population-level is likely a function of habitat availability. Western and Clark's Grebes are over-water nesting species, utilizing littoral zone wetlands as nesting locations (Storer and Nuechterlein 1992). At both Clear and Eagle Lakes, this habitat is coincident with grebe nesting colony locations and is located in the shallowest portions of the lake (Figures 2 and 3). As a result of the shallow bathymetry at which this habitat occurs, it is susceptible to changes in hydroperiod. Hydrologic conditions can affect entire wetland plant communities, resulting in changes in the total biomass, presence/absence of species, seedling establishment during drawdown, and the degree of openness (open-, hemi-, or closed-marsh) (Owen 1999, Miller and Zedler 2003, Ward et al. 2010). Additionally, due to their shallow and variable nature, these locations are likely to become inaccessible to nesting grebes as lake elevations decline (Wantzen et al. 2008). This effect was demonstrated in a recent study at Eagle Lake in which the extent of wetland vegetation varied with water level (Wright-Myers and Bogiatto 2007). Certain wetland areas containing preferred plant species were no longer available to overwater-nesting waterfowl at low water levels, resulting in the increased importance of individual stands of emergent vegetation to nesting birds and a decrease in overall habitat availability (Wright-Myers and Bogiatto 2007). Our study indicates that this phenomenon results in a threshold on the proportion of the population that is able to successfully nest.

Habitat quality is likely also affected by changes in lake elevation and may be another variable exerting a population-level effect on nesting grebes. Ward et al. (2010) suggest that changes in hydrology affect marsh habitat structure. Further, habitat structure was the parameter with the most predictive power for population declines in 10 of their 12 focal species. Western and Clark’s Grebe nest success is also impacted by habitat structure. High winds and wakes from recreational boats have been observed to increase vulnerability and rates of nest abandonment for these species, accounting for as much as 69% of nest failures in a given season (Koplin 1980, Nuechterlein 1975, Allen et al. 2008a). Allen et al. (2008b) found that littoral-zone vegetation helped to attenuate these forms of wave-action at artificial grebe nests, with denser stands of emergent vegetation having a greater ability to do so. Additionally, artificial grebe nest-sites located further from the edge of a colony and further from open-water were found to have a greater degree of wave attenuation and a significantly lower rate of sinking than those that were not. These results, when viewed in the context of our findings and those of other studies, suggest that as lake elevation decreases, grebes can likely only gain access to wetland vegetation that is closer to open-water and wetland edges (Dolcini 1972, Paton 1994, Wright-

Myers and Bogiatto 2007). Because both winds and boat wakes are common occurrences at Clear and Eagle Lakes, nests placed in this lower quality habitat would be more susceptible to wave action and resultant nest failure.

The lack of effect of lake elevation change on Average Brood Size was unexpected. We had predicted that lake elevation and brood size would be positively correlated. Our hypothesis was based on the prediction that mammalian predation rates would be higher for grebe nests located in shallow water (Lokemoen 1966, Picman et al. 1993, Hoover 2006, Myers and Bogiatto 2007). This may yet be true, but predation may have a population-level effect. For example, instead of simply reducing the number of eggs in a clutch, and thus the size of the resultant brood, it is more likely that predation-events result in the consumption of all eggs present or the abandonment of a nest or sub-colony entirely (Lokemoen 1966, Paton 1994). This effect would not have been measured in the Average Brood Size index as it was defined for our study. Additionally, predation is likely strongly correlated with habitat quality (Lokemoen 1966). As lake elevation is reduced, the amount of edge habitat increases, increasing the probability for edge-related predation events and resulting in a decrease in nest success (Paton 1994). Edge-effects in wetland habitats have been assumed to be more significant than those in terrestrial habitats due to the marked contrast between the patch and the surrounding matrix (Angelstam 1986, Batáry and Báldi 2004). If edge effects did have an increased effect with lower lake elevations, this phenomenon would have the potential to create an additive or synergistic population-level effect among habitat availability, habitat quality, and predation rates (Picman et al. 1993).

Kushlan (1989) suggests that avian populations utilizing variable-depth wetlands are able to accommodate to some degree of change in lake elevation. Observations from our study and other Western and Clark's Grebes studies indicate that this is true for Western and Clark's Grebes as well. At both Clear and Eagle Lake, grebes were observed to delay nesting when wetland conditions were not ideal and in certain years they were observed nesting as late as October (R.E. Weems, pers. obs.). Parmelee and Parmelee (1997) observed similar behavior at Lake Mead, Nevada, where grebes were observed to immediately begin nesting once dry habitat became inundated. Grebes were also observed nesting into late December at this location

(Parmelee and Parmelee 1997). Delay of nest-initiation may be an important strategy to overcome changes in habitat availability or other factors that are used as cues for these species.

Although these species do possess a certain degree of plasticity, there are limits to which this is a successful strategy. For example, timing of nest initiation has been demonstrated to negatively affect nest success and result in population instability (Kushlan 1989). In addition, there are limits to which an organism is able to accommodate change, especially when conditions are greatly deviant from normal (Kushlan 1989). The recent low lake levels and continued lake elevation declines at Clear and Eagle Lakes may represent such an example (Figure 6). The lowest lake elevation on record for Eagle Lake was 1552m above mean sea-level (Dolcini 1972). Nesting lake elevation in 2010 measured 1553.2m above mean sea-level, indicating a 3.7m decline from the study period high (Figure 6). This change occurred in a period of only 12 years. Prior research at Eagle Lake has demonstrated that as lake elevation declines below 1554.5m, the amount of littoral vegetation is reduced, unproductive alkaline soils are exposed, and the population of tui chub (*Gila bicolor*), a dominant grebe prey species at Eagle Lake, begin to decline (Dolcini 1972). Eagle Lake elevation has been at or below this level since 2008 (Figure 6). From 2007-2010, nesting lake elevation was below the study period average of 403.1m at Clear Lake (Figure 5). These changes in lake elevation represent a great and prolonged deviation from what could be considered normal for these locations.

CONSERVATION IMPLICATIONS

It is to be expected that in a dynamic habitat, such as a wetland, habitat suitability for nesting birds will vary (Ward et al. 2010). Further, it follows that species dependent on variable habitats for important life-history events will undergo population fluctuations and changes in reproductive success (Kushlan et al. 1989, Ward et al. 2010). What is important from a management perspective is the duration and severity of such fluctuations and the added human-induced impact. Lake elevation at each of our study locations is artificially regulated to a certain degree for human benefit (Lundquist and Smythe 2010, United States Department of the Interior 2010). In fact, naturally fluctuating lakes in North America and Europe are increasingly rare (Wantzen et al. 2008). Our results indicate that when inter-annual lake elevations fluctuate widely, over short time periods, Western and Clark's Grebe population-level reproductive success is negatively affected. Therefore, we recommend that lake managers consider the habitat requirements of over-water nesting bird species when conducting lake elevation draw-downs, allowing for optimal habitat availability during the peak nesting season. This recommendation is particularly important during periods of drought, as was experienced in California in 2007-2009, when habitat was already naturally limited (State of California et al. 2010). We do not, however, recommend strict stabilization of water levels since periodic fluctuations in wetlands are required for the maintenance of wetland plant communities that wetland-adapted avian populations depend upon (Kushlan 1989, Mitsch and Gosselink 1993).

FUTURE RESEARCH

As indicated by the Adjusted R^2 values associated with our best models, lake elevation is not the only factor affecting the reproductive success of Western and Clark's Grebes (Table 1). Anthropogenic disturbance has been suggested as being a potential limiting factor in the nesting success of these and other colonially nesting waterbird species (Lindvall and Low 1982, Vos et al. 1985, Rodgers and Smith 1995, Gericke 2006, Desorbo et al. 2007). Further investigation into the impacts of human disturbance on nesting grebes in the form of long-term studies would be advantageous. Food abundance is likely to be another factor affecting population-level reproductive effort and average brood size for these species (Allen et al. 2007). At Clear Lake, Thredfin Shad (*Dorosoma petenense*) have been shown to display large fluctuations in population. These fluctuations have been demonstrated to be strongly correlated with piscivorous-bird numbers (Colwell et al. 1997). Studies investigating the effect of food resources on Western and Clark's Grebe reproductive success would also be informative. Additionally, this factor may help to discern between population- level and individual-nest success rates. We recommend that these investigations take place on both the breeding grounds and the Pacific Coast wintering grounds. Lastly, studies investigating the precise effect that lake elevation has on habitat availability, habitat quality, and predation rates on the breeding grounds would help to determine whether these factors exert an additive or synergistic effect on population-level reproductive success. Further, this could allow for precise lake elevation guidelines to be developed and help to inform optimum habitat availability requirements for these species.

It remains true that the specific, proximal biotic and abiotic factors affecting reproductive success of these species are still largely unknown. It is clear that there are multiple variables that affect Western and Clark's Grebe reproductive success. Detailed investigations into the factors mentioned above will be crucial to the informed population management of these unique and charismatic birds.

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LITERATURE CITED

Allen, J.H., G.L. Nuechterlein, and D. Buitron. 2007. Resident non-game waterbird use following biomanipulation of a shallow lake. Journal of Wildlife Management (71): 1158-1162.

Allen, J.H., G.L. Nuechterlein, and D. Buitron. 2008a. Weathering the storm: How wind and waves impact Western Grebe nest placement and success. Waterbirds (31): 402-410.

Allen, J.H., G.L. Nuechterlein, and D. Buitron. 2008b. Bulrush mediation effects on wave action: Implications for over-water nesting birds. Waterbirds (31): 411-416.

Anderson, D.W., T.W. Suchanek, C.A. Eagles-Smith, and T. M. Cahill, Jr. 2008. Mercury residues and productivity in osprey and grebes from a mine-dominated ecosystem. Ecological Applications Supplement 18: A227-A238.

Anderson, S.W., G.L. Rockwell, J.R. Smithson, M.F. Friebel, and M.D. Webster. 2000. Water resources data- California, Water Year 2000, Volume 4. North Central Valley basins and the Great Basin from Honey Lake Basin to Oregon state line. Water Data Report CA 00-4.

Angelstam, P. 1986. Predation on ground-nesting bird’s nests in relation to predator densities and habitat edge. Oikos (47): 365-373.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike’s Information Criterion. Journal of Wildlife Management 74:1175-1178.

Baiser, B., R.L. Boulton, and J.L. Lockwood. 2008. Influence of water depth on nest success of the endangered Cape Sable Seaside Sparrow in the Florida Everglades. Animal Conservation 11:190-197.

Barnes, G.G. and T.D. Nudds. 1990. Temporal variation in microhabitat relationships among grebes and coots. Wilson Bulletin 102:99-108.

Batáry, P., and A. Báldi. 2004. Evidence of an edge effect on avian nest success. Conservation Biology (18): 389-400.

Bent, A.C. 1919. Life Histories of North American Diving Birds. United States National Museum Bulletin 107: 1-9.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, second edition. Springer-Verlag, New York.

Cézilly, F., V. Boy, R.E. Green, G.J.M. Hirons, A.R. Johnson. 1995. Interannual variation in Greater Flamingo breeding success in relation to water levels. Ecology 76:20-26.

Coops, H., M. Beklioglu, and T.L. Crisman. 2003. The role of water-level fluctuations on shallow lake ecosystems- workshop conclusions. Hydrobiologia 506-509:23-27.

Colwell, A.E., N.L. Anderson, D.L. Woodward. 1997. Monitoring of dipteran pests and associate organism in Clear Lake (California), p. 15-32. *In* First Annual Clear Lake Science and Management Symposium , Proceedings Volume, September 13.

Colwell, M.A., and O.W. Taft. 2000. Waterbird communities in managed wetlands of varying depth. Waterbirds 23:45-55.

Davis, D.G. 1961. From field and study: Western Grebe colonies in northern Colorado. Condor 63: 263-266.

Desorbo, C.R., K.M. Taylor, D.E. Kramar, J. Fair, J.H. Cooley, Jr., D.C. Evers, W. Hanson, H.S. Vogel, J.L. Atwood. 2007. Reproductive advantages for common loons using rafts. Journal of Wildlife Management (71): 1206-1213.

Dolcini, A.J. 1972. Eagle Lake: alternative plans for controlling lake levels. California Department of Water Resources, Northern District.

Elbert, R.A. 1996. Reproductive performance and mercury exposure of birds at Clear Lake, CA. M.S. thesis, University of California, Davis, CA.

Elbert, R.A., and D.W. Anderson. 1998. Mercury levels, reproduction, and hematology in Western Grebes from three California lakes, USA. Environmental Toxicology and Chemistry 17:210-213.

Feerer, J.L., and R.L. Garrett. 1977. Potential Western Grebe extinction on California lakes. Cal-Neva Wildlife Transactions 12:80-89.

Fraser, L.H., and P.A. Keddy. 2005. The world's largest wetlands: Ecology and conservation. Cambridge University Press, Cambridge.

Friebel, M.F., M.D. Webster, G.L. Rockwell, and J.R. Smithson. 2004. Water resources data-California, Water Year 2003, Volume 4. North Central Valley basins and the Great Basin from Honey Lake Basin to Oregon state line. Water Data Report CA 03-4.

Gericke, S.M. 2006. Exploring the effects of disturbance events on Western and Clark's Grebes (*Aechmophorus occidentalis* and *A. clarkii*) at Clear Lake, California. M.S. thesis, University of California, Davis, CA.

Gester, G.C. 1962. The geological history of Eagle Lake Lassen County, California. Occasional Papers of the California Academy of Sciences 34: 1-29.

Gould, G.I. 1974. Breeding success of piscivorous birds at Eagle Lake, California. M.S. thesis, Humboldt State University, Arcata, CA.

Hayes, P.D., G.L. Rockwell, S.W. Anderson, J.R. Smithson, and L.A. Freeman. 1999. Water resources data- California, Water Year 1998, Volume 4. North Central Valley basins and the Great Basin from Honey Lake Basin to Oregon state line. Water Data Report CA 98-4.

Hoover, J.P. 2006. Water depth influences nest predation for a wetland-dependent bird in fragmented bottomland forests. Biological Conservation (127): 37-45.

Huntsinger, K.R. and P.E. Maslin. 1976. A limnological comparison of the three basins of Eagle Lake, California. California Fish and Game 64:232-245.

Ivey, G.L. 2004. Conservation assessment and management plan for breeding Western and Clark's Grebes in California. American Trader Trustee Council, c/o California Department of Fish and Game, Office of Spill Prevention and Response, P.O. Box 944209, Sacramento, CA 95814.

Ivey, G.L. and B.D. Dugger. 2008. Factors influencing nest success of Greater Sandhill Cranes at Malheur National Wildlife Refuge, Oregon. Waterbirds 31:52-61.

Koplin, J.R. 1980. Reproductive performance of fish-eating birds at Eagle Lake, California. National Geographic Society Research Reports 12: 427-443.

Kushlan, J.A. 1989. Avian use of fluctuating wetlands, p.593-604. *In* R.R. Sharitz and J.W. Gibbons [eds.], Freshwater wetlands and wildlife, Department of Energy symposium series 61. USDOE Office of Scientific and Technical Information, Oak Ridge, Tennessee.

Laubhan, M.K., and L.H. Fredrickson. 1993. Integrated wetland management: concepts and opportunities, p. 323-334. *In* R.E.McCabe and K.A. Glidden [eds.], Transactions of the fifty-eighth North American wildlife and natural resources conference. Wildlife Management Institute, Washington, DC.

Leira, M. and M. Cantonati. Effects of water-level fluctuations on lakes: an annotated bibliography. Hydrobiologia 613:171-184.

Lindvall, M. L., and J.B. Low. 1982. Nesting ecology and production of Western Grebes at Bear River Migratory Bird Refuge, Utah. Condor 84:66-70.

Lokemoen, J.T. 1966. Breeding ecology of the redhead duck in western Montana. Journal of Wildlife Management (30): 668-681.

Lundquist, E., and T. Smythe. [online]. 2010. Clear Lake Integrated Watershed Management Plan. County of Lake Department of Public Works, Water Resources Division, and West Lake and East Lake Resource Conservation Districts. <ftp://ftp.co.lake.ca.us/Clear%20Lake%20WS%20Management%20Plan/>

Ma, Z., Y. Cai, B. Li, and J. Chen. 2010. Managing wetland habitats for waterbirds: an international perspective. Wetlands 30:15-27.

Miller, R.C., and J.B. Zedler. 2003. Responses of native and invasive wetland plants to hydroperiod and water depth. Plant Ecology (167): 57-69.

Mitsch, W.J. and J.G. Gosselink. 1993. Wetlands, 2nd edition. Van Nostrand Reinhold, New York.

Moreno-Matiella, L.A. and D.W. Anderson. 2005. Water level variation and its effect on nesting habitat configuration and availability for the American White Pelican at Clear Lake Reservoir, California. Waterbirds 28:73-82.

Moseley, E.L. 1930. Fluctuation of bird life with changes in water level. Wilson Bulletin 42:191-193.

Mudge, G.P. and T.R. Talbot. 1993. The breeding biology and causes of nest failure of Scottish Black-throated Divers *Gavia arctica.* Ibis 135:113-120.

Niering, W.A. 1988. Endangered, threatened, and rare wetland plants and animals of the continental United States, Volume 1, p. 133-154. *In* D.D. Hook [ed.], The ecology and management of wetlands. Timber Press, Portland, Oregon.

Nero, R.W., and F.G. Bard. 1958. Dry-land nest site of a Western Grebe Colony. Auk 75:347-349.

Owen, C.R. 1999. Hydrology and history: land use changes and ecological response in an urban wetland. Wetlands Ecology and Management (6): 209-219.

Nuechterlein, G.L. 1975. Nesting ecology of Western Grebes on the Delta Marsh, Manitoba. M.Sc. thesis, Colorado State University, Fort Collins.

Paillisson, J., S. Reeber, A. Carpentier, and L. Marion. 2006. Plant-water regime management in a wetland: consequence for a floating vegetation-nesting bird, Whiskered Tern *Chlidonias hybridus.* Biodiversity and Conservation 15:3469-3480.

Parmelee, D.F., and J.M. Parmelee. 1997. Western Grebe and Clark's Grebe: habitat necessity versus phenology. Colonial Waterbirds 20:95-97.

Paton, P.W.C. 1994. The effect of edge on avian nest success: How strong is the evidence? Conservation Biology(8):17-26.

Picman, J., M. Milks, and M. Leptich. 1993. Patterns of predation on passerine nests in marshes : effects of water depth and distance from edge. Auk (110): 89-94.

Pöysä, H. 1983. Resource utilization pattern and guild structure in a waterfowl community. Oikos 40: 295-307.

Ratti, J.T. 1979. Reproductive separation and isolating mechanisms between sympatric dark- and light-phase Western Grebes. Auk 96:573-586.

Raymond Vail and Associates. 1979. Eagle Lake basin planning study: hydrology. Volume 5. Sacramento, California.

Rich, C.A. 2009. Rich, C. A. [online] 2009. Chief, Complaint Unit, Division of Water Rights, State Water Resources Control Board, 101 I Street, Sacramento, CA 95814. Letter to Dayne Barron, Field Office Manager, Eagle Lake Field Office, Bureau of Land Management, 2950 Riverside Dr., Susanville, CA 96130. <http://eaglelakefishing.net/userfiles/6-1-09%20Bly%20Tunnel%20Ltr(1).pdf> (21 June 2011).

Richerson, P.J., T.H. Suchanek, and S.J. Why. 1994. The causes and control of algal blooms in Clear Lake: clean lakes diagnostic/feasibility study for Clear Lake, California. Lake County and University of California Davis Clean Lakes Project Final Report.

Riensche, D.L., J.D. Mena, and A.B. Shawen. 2009. Western and Clark's Grebe nest platforms designed for fluctuation water levels. Transaction of the Western Section of the Wildlife Society 45:7-16.

Rockwell, G.L., J.R. Smithson, M.F. Friebel, and M.D. Webster. 2002. Water resources data-California, Water Year 2001, Volume 4. North Central Valley basins and the Great Basin from Honey Lake Basin to Oregon state line. Water Data Report CA 01-4.

Rockwell, G.L., M.F. Friebel, M.D. Webster, S.W. Anderson. 1998. Water resources data-California, Water Year 1997, Volume 4. North Central Valley basins and the Great Basin from Honey Lake Basin to Oregon state line. Water Data Report CA 97-4.

Rodgers, J.A., Jr., and H.T. Smith. 1995. Set-back distances to protect nesting bird colonies from human disturbances in Florida. Conservation Biology(9): 89-99.

SAS Institute. 2010. JMP® 9. Cary, North Carolina, USA.

Shaw, D.W.H. 1998. Changes in population size and colony location of breeding waterbirds at Eagle Lake, California between 1970 and 1997. M.S. thesis, California State University, Chico, CA.

Short, H.L. 1984. Habitat suitability index models: Western Grebe. United States Fish and Wildlife Service FWS/OBS-82/10.69.

Skinner, C.J., and D.J. Holmes. 2003. Random effects models for longitudinal survey data, p. 205-218. *In* R.L. Chambers and C.J. Skinner [eds.], Analysis of survey data. Wiley and Sons Ltd, West Sussex, England.

Smithson, J.R., M.F. Friebel, M.D. Webster, and G.L. Rockwell. 2003. Water resources data-California, Water Year 2002, Volume 4. North Central Valley basins and the Great Basin from Honey Lake Basin to Oregon state line. Water Data Report CA 02-4.

State of California, Natural Resources Agency, California Department of Water Resources. [online]. 2010. California's drought of 2007-2009: An overview. <http://www.water.ca.gov/drought/docs/DroughtReport2010.pdf> (14 October 2011).

Storer, R.W., and G.L. Nuechterlein. 1992. Western Grebe/Clark's Grebe. *In* A. Poole, P. Stettenheim, and F. Gill [eds.], The birds of North America.

Suchanek, T.H., P.J. Richerson, D.C. Nelson, C.A. Eagles-Smith, D.W. Anderson, J.J. Cech, Jr., R. Zierenberg, G. Schladow, J.F. Mount, S.C. McHatton, D.G. Slotton, L.B. Webber, B.J. Swisher, A.L. Bern, and M. Sexton. 2003. Evaluating and managing a multiply-stressed ecosystem at Clear Lake, California: A holistic ecosystem approach p. 1233-1265 *In* D.J. Rapport, W.L. Lasley, D.E. Rolston, D.O. Nielsen, C.O. Qualset, and A.B. Damania [eds.], Managing for healthy ecosystems: case studies. CRC Press Boca Raton, FL.

Symonds, M.R.E., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference, and model averaging in behavioral ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65: 13-21.

Taft, O.W., M.A. Colwell, C.R. Isola, R.J. Safran. 2002. Waterbird responses to experimental drawdown: implications for the multispecies management of wetland mosaics. Journal of Applied Ecology 39: 987-1001.

Tori, G.M., S. McLeod, K. McKnight, T. Moorman, and F.A. Reid. 2002. Wetland conservation and Ducks Unlimited: Real world approaches to multispecies management. Waterbirds 25 (Special publication 2): 115-121.

Tozer, D.C., E. Nol, K.F. Abraham. 2010. Effects of local and landscape-scale habitat variables on abundance and reproductive success of wetland birds. Wetlands Ecology and Management 18: 679-693.

United States Department of the Interior. 2010. Eagle Lake water budget report. U.S. DOI Bureau of Land Management 3000 (920) (P).

United States Geological Survey. [online]. 2006. Water resources data- California, Water Year 2005. Water Data Report CA 05. <http://wdr.water.usgs.gov/wy2005/pdfs/ 11450000.2005.pdf> (31 March 2011).

United States Geological Survey. [online]. 2007. Water resources data- California, Water Year 2006. Water Data Report CA 06. < http://wdr.water.usgs.gov/wy2006/pdfs/ 11450000.2006.pdf>. (31 March 2011).

United States Geological Survey. [online]. 2008. Water resources data- California, Water Year 2007. Water Data Report CA 07. < http://wdr.water.usgs.gov/wy2007/pdfs/ 11450000.2007.pdf>. (31 March 2011).

United States Geological Survey. [online]. 2009. Water resources data- California, Water Year 2008. Water Data Report CA 08. <http://wdr.water.usgs.gov/wy2008/pdfs/11450000.2008.pdf>. (31 March 2011).

United States Geological Survey. [online]. 2010. Water resources data- California, Water Year 2009. Water Data Report CA 09. < http://wdr.water.usgs.gov/wy2009/pdfs/ 11450000.2009.pdf>. (31 March 2011).

United States Geological Survey. [online]. 2011. Water resources data- California, Water Year 2010. Water Data Report CA 10. < http://wdr.water.usgs.gov/wy2010/pdfs/ 11450000.2010.pdf>. (31 March 2011).

Vos, D.K., R.A. Ryder, and W.D. Graul. 1985. Response of breeding Great Blue Herons to human disturbance in northcentral Colorado. Colonial Waterbirds (8): 13-22.

Wantzen, K.M., K. Rothhaupt, M. Mörtl, M. Cantonati, L. G.-Tóth, and P. Fischer. 2008. Ecological effects of water-level fluctuations in lakes: an urgent issue. Hydrobiologia 613:1-4.

Ward, M.P., B. Semel, and J.R. Herkert. 2010. Identifying the ecological causes of long-term declines of wetland-dependent birds in an urbanizing landscape. Biodiversity and Conservation 19:3287-3300.

Webster, M.D, G.L. Rockwell, M.F. Friebel, and S.J. Brockner. 2005. Water resources data-California, Water Year 2004, Volume 4. North Central Valley basins and the Great Basin from Honey Lake Basin to Oregon state line. Water Data Report CA04-4.

Webster, M.D., S.W. Anderson, G.L. Rockwell, J.R. Smithson, and M.F. Friebel. 2000. Water resources data- California, Water Year 1999, Volume 4. North Central Valley basins and the Great Basin from Honey Lake Basin to Oregon state line. Water Data Report CA 99-4.

Wharton, C.H., W.M. Kitchens, E.C. Pendleton, and T.W. Sipe. 1982. The ecology of bottomland hardwood swamps of the southeast; a community profile. U.S. Fish and Wildlife Service, Biological Services Program FWS/OBS-81/37, Washington, D.C.

Wright-Myers, S.M., and R. J. Bogiatto. 2007. The ecology of over-water nesting ducks in northeastern California. California Fish and Game 93:23-39.