Brood Size and Nesting Phenology in Western Grebe (*Aechmophorus occidentalis*) and Clark's Grebe (*Aechmophorus clarkii*) in Northern California

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Abstract.—Western (*Aechmophorus occidentalis*) and Clark's (*A. clarkii*) grebes are long-lived, migratory waterbirds that are sensitive to human-caused disturbance while nesting. Sampling the age distribution of post-hatch chicks provides a method for estimating the timing of nest initiation without causing disturbance to breeding colonies. The goals of this work were to describe trends in breeding productivity at two of the largest nesting colonies in northern California and illustrate how brood size can be used to evaluate nesting phenology in *Aechmophorus* grebes. No differences were found in brood size between species. Brood size decreased linearly as nest initiation date increased, showing no differences in the rate of decline among age classes of young. Within seasons, older broods were found to be significantly smaller than younger broods, suggesting that mortality was occurring after hatching thereby reducing the potential number of chicks recruited into the adult population. *Received 28 May 2014, accepted 25 October 2014.*

Key words.—*Aechmophorus clarkii*, *Aechmophorus occidentalis*, brood size, Clark's Grebe, disturbance, nest initiation, nesting phenology, productivity, Western Grebe.

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Western (*Aechmophorus occidentalis*) and Clark's (*A. clarkii*) grebes (hereafter "grebes") are ideal species for studying brood size and nesting phenology fluctuations. They are conspicuous, surface-dwelling waterbirds with nidifugous young whose ages are readily approximated. Adults brood their chicks for approximately 8 weeks, leaving ample time to evaluate the age structure of chicks without entering nesting colonies and creating disturbance.

Studies that require observers to inspect nest contents can provide valuable data on nest survival, nest success, clutch size, and nest initiation (Johnson 2007), but can be time intensive and disturbing to sensitive species (Anderson and Keith 1980). Further, systematic nest studies are not always feasible in the context of long-term population monitoring with limited, ever-shrinking conservation budgets (Waldron *et al.* 2013). Brood evaluation measures breeding output after hatching and provides relevant reproductive data without causing nesting colony disturbance (Elbert and Anderson 1998; Murray 2000; Thompson *et al.* 2001). While aspects of brood ecology have been investigated in grebes (Ratti 1979; Nuechterlein 1981), the use of brood age evaluation as a tool for analyzing nesting phenology has not been formally assessed, thus the nesting phenology of grebes remains largely unknown.

Here, we examine multi-year samples of brood size and brood age structure to investigate how brood size changes among and between seasons at two California lakes. Our objectives were to determine: 1) if Western and Clark's grebes differ in brood size (the number of young produced per successful pair); and 2) how brood size varies as a function of chick age and nesting phenology.

Methods

Study Area

We studied grebes at Clear and Eagle lakes in northern California. Clear Lake (39° 03' 29.5" N, 122° 49' 51.7" W) is located at an elevation of 404 m in the north coast mountain range (Fig. 1). Eagle Lake (40° 38' 47.1" N, 120° 44' 26.7" W) is located at an elevation of ~1,554 m on the ecotone of northern Sierra Nevada and southern Cascade conifer forest (southern basin) and Great Basin desert (northern basin) (Huntsinger and Maslin 1976) (Fig. 1).

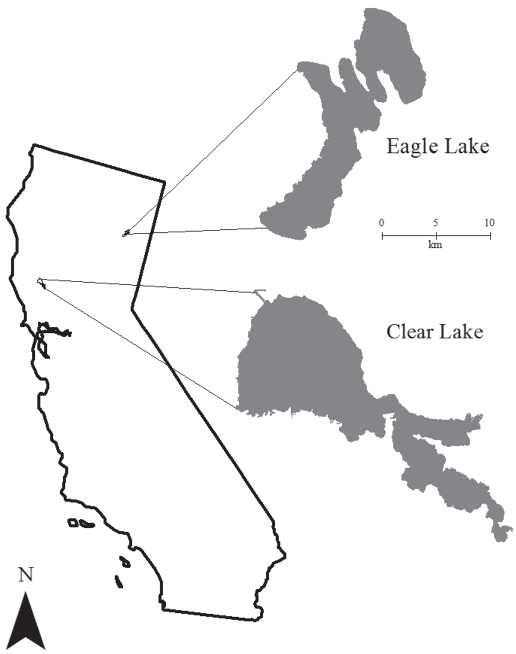

Figure 1. Map of California depicting the study sites.

Brood Surveys

We sampled grebe chicks annually at each lake. Surveys were timed to attain the most representative sample of nesting productivity (Elbert 1996; Elbert and Anderson 1998; Anderson *et al.* 2008). In most years, a single sampling effort was sufficient to capture the major pulse of breeding activity. In years when the nesting period was especially protracted or asynchronous, additional visits were made to capture each pulse of breeding activity while retaining independent samples.

Brood surveys were conducted by strip transect via motor boat at constant speed and bearing (Tasker *et al.* 1984) when winds were ≤ 10 kmph. Observations were made from both sides of the boat extending out to 200 m, enabling positive identification of species, chick age, and brood size. All birds encountered were organized into the following categories: species (Western, Clark's, or *Aechmophorus*), reproductive status (single, paired, courting, with young, without young), and brood size sorted by chick age. Western x Clark's pairs with young were excluded from these analyses, but accounted for 1.75% (n = 1,545) and 0.33% (n = 2,417) of all sampled pairs with young at Clear Lake and Eagle Lake, respectively. Chicks were grouped into seven age classes based on their proportional size and plumage color relative to an adult (Robison 2012).

Nesting Phenology

The approximate date of nest initiation was determined by subtracting (in number of days) age of young, incubation period, and nest building period from the survey date. Each age class encompassed a span of approximately 7 days. This is based on a size/plumage maturation period of about 6-8 weeks (Ratti 1979). The midpoint of each age-range was used to calculate age of young.

Data were analyzed by lake and year with lake-year as the general sampling unit. Single adults with young were excluded from brood size analyses to avoid sampling bias, unless otherwise stated. Only half-grown and older broods were analyzed to avoid observational bias associated with the youngest three age classes, especially back-brooded chicks (La Porte *et al.* 2014), unless otherwise stated.

Some years were excluded from analyses due to: 1) observed severe and direct human disturbance to nesting colonies (Clear Lake: 1999, 2002); 2) lack of nesting effort (Clear Lake: 2007, 2008; Eagle Lake: 2007); or 3) lack of data (Eagle Lake: 2005). Data from both lakes were combined to increase sample size and testing power.

Statistical Analysis

Inter-specific differences. We tested inter-specific differences in brood size in two ways. The first test compared samples of each species on a lake-year basis without consideration of chick age due to small sample sizes in some age classes. Due to a non-normal distribution of data from Clear Lake, we tested data from both lakes using a non-parametric Wilcoxon Ranks-Sum test. The second test assessed differences in the frequency of each brood size category on a year-by-year basis. We analyzed these frequencies for each lake and year separately using Chi-square Likelihood-ratio tests with Bonferroni corrections to avoid Type I errors (Tables 1 and 2) (Zar 2010).

Age-specific differences. We tested for age-specific differences in brood size with respect to nest initiation date. We first compared the relationship, as measured by the slope of the model, among age-specific brood size and nest initiation date with an ANCOVA model using standard least squares regression. The dependent variable, brood size or young per successful pair, was regressed on chick age, nest initiation date, and the interaction of age*nest initiation date across all lake-year samples (Fig. 2). We used the slope of the model without an interaction term to describe the rate of decline in brood size over the range of nest initiation dates. Data were then evaluated with Tukey-Kramer Honest Significant Difference All Pairs tests to assess age-related differences in average brood size (Table 3). All tests and analyses were conducted using JMP (SAS Institute, Inc. 2010).

Inter-lake differences. We summarized the variability in nesting phenology for each respective lake (Fig. 3). These summaries considered all age classes of grebe chicks observed and multiple survey visits performed to capture as much reproductive information as possible. Nesting phenology was examined on an inter- and intra-annual basis.

RESULTS

Inter-specific Differences

We found no inter-specific differences in brood size at Clear Lake (χ^2_1 = 0.78, P =

Table 1. Yearly Western vs. Clark's grebe brood size frequency tests for Clear Lake, Lake County, California. Chi-square Likelihood Ratio tests used to compare differences in brood size distribution between species. "—" = sample-size too small for Chi-square test.

	Western Grebe Brood Size as % of *n*						Clark's Grebe Brood Size as % of *n*						
Year	1	2	3	4	5	*n*	1	2	3	4	*n*	χ^2_{df}	*P*
1998	65.9	34.1	0	0	0	91	62.5	37.5	0	0	8	—	—
2000	62.8	32.4	4.8	0	0	188	55.2	37.9	6.9	0	29	0.7_2	0.72
2001	75.0	24.3	0.7	0	0	152	69.6	30.4	0	0	23	0.6_2	0.73
2003	44.3	49.2	6.5	0	0	61	41.7	41.7	8.3	8.3	12	3.8_3	0.28
2004	74.6	21.8	3.6	0	0	138	78.8	18.2	3.0	0	33	0.3_2	0.88
2005	35.4	46.3	14.6	3.7	0	82	35.4	39.0	21.9	3.7	82	1.7_3	0.63
2006	26.0	50.0	14.0	8.0	2.0	50	43.3	33.3	13.3	10.1	30	3.9_4	0.41
2009	75.9	24.1	0	0	0	29	100.0	0	0	0	1	—	—
2010	79.7	18.9	1.4	0	0	74	100.0	0	0	0	4	—	—

0.38) or Eagle Lake ($\chi^2_1 = 0.83$, $P = 0.36$). Additionally, we found no differences between species in the distribution of brood sizes at either lake (Tables 1 and 2). As a result of these findings showing no differences, data for both species were combined for further analyses.

Age-specific Differences

The relationship between brood size and nest initiation date was similar across age classes of young with no significant model interaction ($F_3 = 0.65$, $P = 0.59$). Model residuals were tested for normality using a Shapiro-Wilk *W*-test and were normal ($W = 0.97$, $P = 0.21$). Thus, the interaction term was not included in the final model. Across years and age classes, brood size decreased as nest initiation date increased (Fig. 2; slope = -0.005 ± 0.001, adj. $r^2 = 0.32$, $P = < 0.001$). Since the range of nest initiation dates used in this analysis spanned May to late-August, a projected decrease of approximately 0.5 chicks per brood would be possible if nest initiation commenced in late-August vs. May. Tukey-Kramer Honest Significant Difference All Pairs tests showed that half-grown broods were significantly larger than seven-eighths-grown and full-grown broods, and two-thirds-grown broods were significantly larger than full-grown broods (Table 3). In other words, broods originating from nests hatched later in the breeding season (i.e.,

Table 2. Yearly Western vs. Clark's grebe brood size frequency tests for Eagle Lake, Lassen County, California. Chi-square Likelihood Ratio tests used to compare differences in brood size distribution between species. "—" = sample-size too small for Chi-square test.

	Western Grebe Brood Size as % of *n*					Clark's Grebe Brood Size as % of *n*					
Year	1	2	3	4	*n*	1	2	3	*n*	χ^2_{df}	*P*
1998	48.2	40.0	11.8	0	135	36.4	45.4	18.2	11	0.7_2	0.71
1999	83.9	14.9	1.2	0	87	50.0	50.0	0	2	—	—
2000	46.3	46.4	7.4	0	164	27.8	66.7	5.5	18	2.8_2	0.25
2001	67.5	30.9	1.6	0	126	75.0	25.0	0	40	1.7_2	0.42
2002	46.4	45.2	8.0	0.4	250	38.9	55.6	5.5	18	0.9_3	0.83
2003	52.2	41.8	6.0	0	201	55.7	37.7	6.6	61	0.3_2	0.85
2004	64.5	31.8	3.7	0	107	75.0	25.0	0	4	—	—
2006	56.7	42.2	1.1	0	90	57.1	42.9	0	21	0.4_2	0.81
2008	32.7	53.4	13.5	0.4	281	48.0	52.0	0	25	8.1_3	0.05
2009	59.0	37.9	3.1	0	190	47.1	50.0	2.9	68	3.0_2	0.22
2010	69.4	27.8	2.8	0	36	100.0	0	0	1	—	—

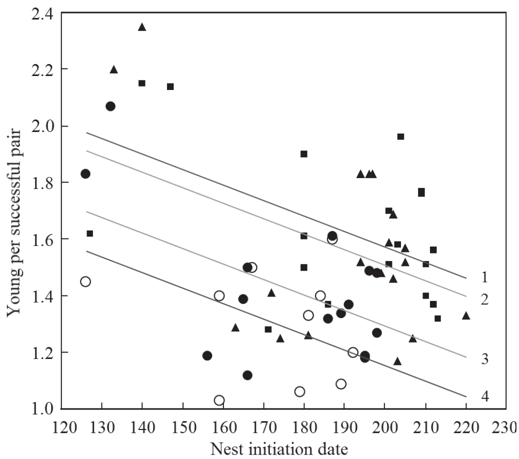

Figure 2. Graphical representation of an ANCOVA model of *Aechmophorus* grebe nesting phenology by age class for Clear and Eagle lakes, California; interaction term among age classes removed. Half-grown broods are shown with filled squares (line 1); two-thirds-grown with filled triangles (line 2); seven-eighths-grown with filled circles (line 3); and full-grown with open circles (line 4).

half-grown at time of survey) were significantly larger than broods originating from nests hatched earlier in the breeding season (i.e., two-thirds-grown and full-grown).

Inter-lake Differences

Clear Lake. In 9 years of data collection at Clear Lake, the earliest estimated date of nest initiation was 28 April 2004 and the latest was 26 August 2009, resulting in a total range of 121 days. The intra-annual nest initiation period ranged from approximately 23 days in 2003 to 91 days in 2004, with an average period of approximately 51 days. Mean nest initiation date for the study period was 3 July.

Eagle Lake. In 11 years of data collection at Eagle Lake, the earliest estimated date of nest initiation was 17 May 2000 and the latest was 22 August 2010, resulting in a total range of 98 days. The intra-annual nest initiation period ranged from 7 days in 2010 to 83 days in 2008, with an average period of approximately 44 days. Mean nest initiation date for the study period was 21 July.

DISCUSSION

Our evaluation of nesting phenology and age-specific brood size in *Aechmophorus* grebes provided reasonable, approximate

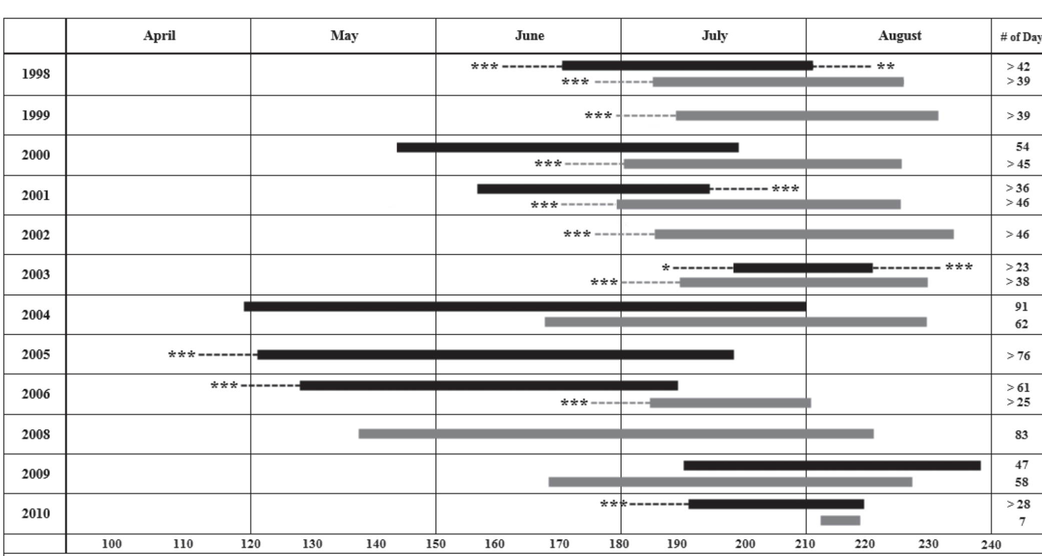

Figure 3. Yearly nesting period for *Aechmophorus* grebes at Clear and Eagle lakes, California. Clear Lake is represented in black and Eagle Lake in gray. Number of days in the nest initiation period are approximate when accompanied by signs ("- - - -" and ">"). These estimates are conservative; the actual nest initiation period is longer when (*) nesting was observed during the initial survey of the season with no broods present, (**) nesting was observed on the last survey of the season, or (***) full-grown chicks were present.

Table 3. Brood size comparison of *Aechmophorus* grebes at Clear and Eagle lakes combined using Tukey-Kramer Honest Significant Difference All Pairs tests. Comparisons of age-specific average brood size were conducted to assess differences in average brood size between age classes of young. Half = half-grown brood; Two-thirds = two-thirds-grown brood; Seven-eighths = seven-eighths-grown brood; and Full = full-grown brood. "*" denotes statistically significant $P = 0.05$.

Brood Age Class Comparison	Mean Difference $\bar{X}_B$-$\bar{X}_A$	Confidence Interval	*P*-value
Half vs. two-thirds	1.66-1.60 = 0.06	-0.14-0.27	0.840
Half vs. seven-eighths	1.66-1.39 = 0.27	0.050-0.50	0.009*
Half vs. full	1.66-1.25 = 0.41	0.16-0.67	0.003*
Two-thirds vs. seven-eighths	1.60-1.39 = 0.21	-0.009-0.44	0.070
Two-thirds vs. full	1.60-1.25 = 0.35	0.10-0.61	0.003*
Seven-eighths vs. full	1.39-1.25 = 0.14	-0.12-0.40	0.490

measurements of nest initiation while limiting colony disturbance. While our methods precluded specific causal explanations of the variation observed, our results are consistent with previous studies on seasonal decline in breeding productivity. For example, clutch size is well known to decrease as the nesting season progresses in many avian species (Lack 1947; Cooke *et al.* 1984; Burger *et al.* 1996). This has also been previously demonstrated for Western Grebes (La Porte *et al.* 2013), and thus it is plausible that decreases in brood size resulted from seasonal decreases in clutch size.

Brood size is known to be influenced by ecological constraints such as prey availability (Herring *et al.* 2010) and weather-induced egg loss (Allen *et al.* 2008). These constraints mostly impart their influence before chicks leave the nest, although reduced prey can continue to limit brood size throughout the rearing period (Herring *et al.* 2010). However, our age-specific brood size analysis suggested post-nesting limitations on breeding productivity. Broods originating from nests hatched later in the season were larger than broods originating from nests hatched earlier in the season. Although seemingly contradictory, this can be explained by several potential mechanisms, including post-nesting chick mortality.

Ecological constraints imparted after the nesting period can contribute to brood size decline. For example, sibling competition resulting from asynchronous hatching is a condition exhibited by Western and Clark's grebes and can lead to siblicide and fratricide (Nuechterlein 1981). Chick mortality resulting from sibling competition is most pronounced when chicks are very young, diminishing after a few weeks (Nuechterlein 1981; Ulenaers and Dhondt 1994; Kloskowski 2003). Although this phenomenon is known to fluctuate depending on food availability, it could help to describe our results if consistent in magnitude across years. However, our data were collected after the period of early chick development.

Post-hatch chick mortality may also limit potential recruitment into the breeding population. Full-grown chicks are at least 42 days old and represent the final age class in which differentiation from adults can occur. Brood size samples from this age class can effectively indicate the recruitment potential for the breeding population. Based on our results, and if recruitment were calculated based on hatching success or even younger-age-based brood size, estimates could be biased high. As chronic mortality during the non-breeding season is known to be a significant and unmitigated contributor to population viability in grebes (Humple *et al.* 2011), active grebe management should strive to maximize reproductive success and population recruitment. Further study into the specific reasons for brood size limitations should be evaluated. Other potential contributions to brood reduction that also deserve further investigation include effects from predation (Bogiatto *et al.* 2003), recreation-induced chick mortality (Gericke 2006), and prey-related effects such as prey-induced selective starvation (Herring *et al.* 2010). Marking studies would help facilitate these (and other) avenues of grebe research.

Finally, our findings have important management implications where water level fluctuation is a concern for nesting grebes. Abrupt changes in water level can leave nests stranded, making them prone to terrestrial mammalian predators in particular (Nero *et al.* 1958). If water levels can be successfully managed within a time window that allows early season nesting, productivity might be optimized.

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