Landscape-level Habitat Variables Influence Reproductive Output of *Aechmophorus* Grebes

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Abstract.—A quantitative investigation examining the effect of changes in wetland habitat on reproductive output of Western and Clark's grebes (*Aechmophorus occidentalis* and *A. clarkii*, respectively) was conducted. Earlier studies examined local factors influencing nest success. This study supplements earlier work by seeking to determine which landscape-level habitat elements best predict annual landscape-level reproductive output of grebes. Western and Clark's grebes were monitored during the breeding season from 14 September 1998 to 20 September 2010 at Eagle Lake, California, USA. Remotely-sensed images were used to develop habitat indices and quantify changes in wetland availability and quality. The effect of these indices, and lake level, on annual reproductive output was analyzed using an information theoretic approach. Indices of habitat availability (β_i = 0.20, 95% CI = 0.099-0.31) and habitat quality (β_i = 0.28, 95% CI = 0.012-0.45) best predicted and had a positive effect on annual reproductive output. Lake level had little direct predictive power but was highly correlated with the other habitat covariates (Pearson's $r > 0.80$), indicating its importance as an indirect predictor of reproductive output. Thresholds of habitat availability and habitat quality were found, below which steep declines in reproductive output were observed. *Received 5 December 2017, accepted 19 January 2018.*

Key words.—*Aechmophorus clarkii*, *Aechmophorus occidentalis*, Clark's Grebe, habitat availability, habitat quality, lake level, reproductive output, Western Grebe.

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Western and Clark's grebes (*Aechmophorus occidentalis* and *A. clarkii*, respectively; hereafter, grebes) nest colonially on large freshwater lakes that contain extensive areas of open water bordered by wetland vegetation (LaPorte *et al.* 2013). Their nest platforms are low profile, are constructed of and anchored to wetland vegetation, and float on the water surface (Allen *et al.* 2008b; LaPorte *et al.* 2013). Consequently, breeding phenology and nest success and survival are influenced by local habitat characteristics. Structure of wetland vegetation surrounding nest sites has been demonstrated to influence nest survival related to natural and anthropogenic disturbance events (Allen *et al.* 2008a, 2008b; LaPorte *et al.* 2014). In addition, changes in intra-annual water level have been demonstrated to affect grebe nest success and breeding phenology (Nero *et al.* 1958; Parmelee and Parmelee 1997).

Few studies have investigated the effect of habitat changes on grebe reproductive output across time and at broader spatial scales. Landscape-level habitat modeling is an important conservation and management tool that can aid in determining the existence of habitat thresholds and the amount of habitat needed to sustain viable populations (Radford *et al.* 2005). Although maintenance of stable or slowly decreasing water levels during the breeding season has been identified as a critical habitat element for ensuring nest success for grebes (Feerer and Garrett 1977; Riensche *et al.* 2009), little else is known about landscape-level habitat changes and their effect on landscape-level grebe reproductive output.

We monitored grebes during the breeding season at Eagle Lake, California, USA, with the objective of determining which landscape-level habitat characteristics best predict annual grebe reproductive output. We predicted that: 1) population-level reproductive output would be positively correlated with lake level, habitat availability and habitat quality; and 2) a threshold would exist, below which reproductive output would be demonstrably lower.

Methods

Study Area

Eagle Lake, California, USA (40° 38′ 50″ N, 120° 44′ 45″ W) is approximately 12,150 ha in size and is 1,557 m above mean sea level (Huntsinger and Maslin 1976; Fig. 1). Eagle Lake is a naturally closed drainage system consisting of one major inlet, two small tributaries, and no natural surface-water outlet. Because the system is closed, lake level fluctuates annually with run-off, precipitation, evaporation, and groundwater flow (Gester 1962). Eagle Lake has three distinct basins. Its southern basin is deepest (up to 21 m), while its northern basin is shallowest (≤ 5 m). During our study, grebes nested in flooded emergent wetland vegetation within Eagle Lake's central and northern basins. Water depth within these basins ranges between 6-10 m (Wright-Myers and Boggiatto 2007). Hardstem bulrush (*Schoenoplectus acutus* var. *occidentalis*) and Baltic rush (*Juncus balticus*) are the dominant nesting substrates for grebes at Eagle Lake. During our study, the largest stand of wetland vegetation was in Eagle Lake's shallow northern basin.

Data Collection and Processing

Grebe data. We sampled grebe reproductive output annually from 1998 to 2010, except for 2005, when no data were collected due to lack of funding. Nesting phenology varied annually from 17 May to 22 August, with mean nest initiation date of 21 July (Robison *et al.* 2015). Due to this variation in nest initiation date, observations from initial visits were used to time subsequent surveys to gain the most representative sample of reproductive output (Elbert and Anderson 1998; Anderson *et al.* 2008; Robison *et al.* 2015). Because nesting grebes are susceptible to disturbance (LaPorte *et al.* 2013) and do not return to a nest site after their young have hatched (Allen *et al.* 2008b), subsequent surveys were timed for when chicks and adults had moved away from nesting colonies and were dispersed on open water. Grebes have an average incubation period of 23 days (Lindvall and Low 1982) and an approximately 8-week brood rearing period (LaPorte *et al.* 2013). As a result, we timed surveys for approximately 42 days after nest initiation, thus ensuring that chicks could be distinguished from adults (Ratti 1979; Robison *et al.* 2015).

Data were collected via open water strip-transects from an outboard motorboat operating at a constant speed of 8 kmph and constant bearing (Tasker *et al.* 1984). Transects were run annually in each basin of Eagle Lake between June and October. While on transect, two biologists observed from opposite sides of the boat. All chicks and adults within 200 m of each side of the boat were recorded. To ensure greater visibility, surveys were conducted between 09:00 and 16:00 hr during calm conditions (winds < 10 kmph).

Lake level data. Lake level data for our study period were collected and provided by Lassen County Public Works (J. Rathje, pers. commun.). Lake level was measured on a monthly basis, and data used for analyses were those collected in the month grebes initiated nesting. Data were available during the breeding season for all years except 2006, which was also omitted from analysis.

Remote sensing. We obtained remotely sensed imagery, collected by the now retired Landsat 5 earth-observing satellite from 1998 to 2010 (U.S. Geological Survey 2016). Imagery collected by the Thematic Mapper sensor was used because it provided a continuous dataset across our study period. Landsat 5 images have a spatial resolution of 30 m (U.S. Geological Survey 2017). Since Landsat 5 has a 16-day repeat coverage cycle, images collected within 2 weeks of nest initiation were chosen for analysis. Imagery dates were chosen based primarily on the month of nest initiation and secondarily by the amount of atmospheric distortion, in the form of cloud cover, present in the image. Images containing minimal atmospheric distortion were preferred. Imagery from 2005 and 2006 was not analyzed because of a lack of reproductive and lake level data, respectively, in these years.

Pre-processing. ArcGIS (Environmental Systems Research Institute 2013) was used for all image analyses. Eleven composite rasters, one for each year included in the analyses, were generated using Thematic Mapper bands 1-7 and displayed using a natural color band combination. The resulting composite rasters were used to manually digitize annual lake surface area polygons. These rasters were then clipped to the corresponding year's lake surface area polygon so that subsequent analyses were confined to Eagle Lake's surface extent.

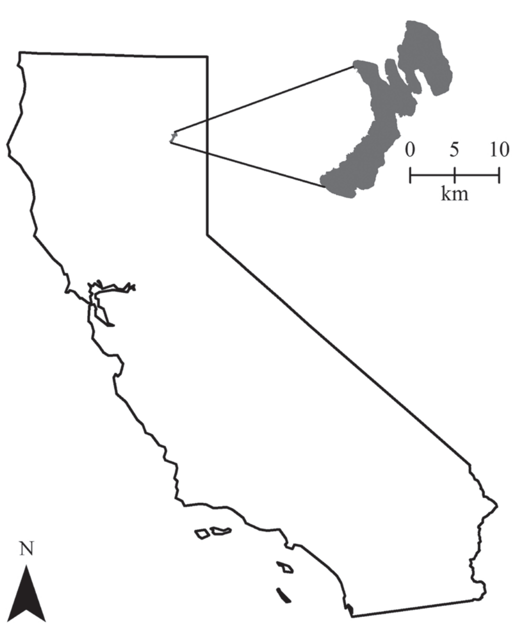

Figure 1. Map of California, USA, showing the location of the Eagle Lake study site.

Change detection. The resulting clipped annual raster composites were classified using the Normalized Difference Vegetation Index (NDVI). This index provides an easily interpreted and reliable estimate of relative biomass, density, and intensity of green vegetation through a ratio of the difference among the natural high reflectivity of plant matter in the near infrared and chlorophyll pigment absorption in the red portions of the spectrum (Environmental Systems Research Institute 2014). ArcMap's algorithm for classifying NDVI produces a range of values from 0-200, with higher numbers representing areas with higher biomass of green vegetation (Environmental Systems Research Institute 2014).

Post-processing. Following NDVI classification, raster pixels were reclassified into two separate categories, wetland and non-wetland. Pixels with NDVI values of ≤ 76 were classified as non-wetland while pixels with values of ≥ 77 were classified as wetland for our study system. Following reclassification, raster pixels were converted to polygons so that areal extent of each category could be quantified.

Statistical Analysis

Habitat conditions were quantified by summarizing remotely sensed data into two separate indices, habitat availability and habitat quality. Habitat availability was indexed as the percentage of wetland area covering Eagle Lake's surface. Habitat quality was indexed as the mean of NDVI pixel values across Eagle Lake's wetland extent.

Grebe survey data were summarized as productivity, indexed as the ratio of young of the year (YY) to adults seen on transect (YY/Adults). This reproductive index was chosen because it allowed us to evaluate habitat quality relative to the overall landscape-level production of grebes, provided an appropriate measure of landscape-level reproductive success within a single season, and allowed for a non-invasive estimate of landscape-level annual reproductive output, thereby eliminating the need to enter nesting colonies (Van Horne 1983; Kushlan 1992).

Model set and selection. We modeled annual lake-wide grebe reproductive output as a function of our three habitat covariates (habitat availability, habitat quality, and lake level). We examined correlations among our habitat covariates and found all three to be highly correlated (Pearson's $r > 0.80$). Consequently, and to avoid model redundancy, we omitted additive models and, aside from our global model including all three habitat covariates, included only multiplicative interaction terms among these covariates (Burnham *et al.* 2011; Freckleton 2011). *A priori,* we developed covariate interactions that we hypothesized would be biologically meaningful, related to synergistic effects among lake level and either habitat availability or habitat quality as well as synergistic effects among habitat availability and habitat quality.

We believed that productivity would be best predicted by an exponential growth model ($(a + b)^{cx}$; where a = asymptote, b = scale, and c = growth rate) of our habitat covariates, representing a saturating functional response of grebe productivity to changes in habitat. Visual examination of these data indicated a non-linear relationship. As a result, we log-transformed our predictor variables to allow for linear comparisons. Following transformation, we tested and confirmed that the assumption of homogeneity of variance was satisfied before proceeding (Zar 2010). In total, a set of eight *a priori* candidate models was evaluated.

Support for each model was evaluated using Akaike's Information Criterion adjusted for small sample size (AIC_c) (Burnham and Anderson 2010). Models ≤ 2 ΔAIC_c of the best model were considered competitive and supported (Arnold 2010; Burnham and Anderson 2010). Cumulative AIC_c weights (w_i), or importance values, were used to further evaluate the strength of evidence for each habitat covariate. Analyses were conducted in JMP Pro 11 (SAS Institute, Inc. 2013). Means are reported ± 1 standard error (SE).

RESULTS

Habitat Covariates

Eagle Lake's level dropped a total of 3.73 m from a high of 1,556.93 m observed in 1998 to a low of 1,553.20 m in 2010 ($\bar{x}$ ± SE = 1,555.17 m ± 0.38 m, Range = 1,553.20-1,556.93 m, $n = 11$; Fig. 2A). Habitat availability peaked in 1998 and underwent a steady decline across our study period ($\bar{x}$ ± SE = 0.023% ± 0.004%, Range = 0.003-0.040%, $n = 11$; Fig. 2B). The lowest habitat availability estimate (0.003%) was recorded in 2010 and represented a 93% decline in wetland habitat cover when compared to our highest habitat availability estimate (0.040% in 1998; Fig. 3). Habitat quality was more variable ($\bar{x}$ ± SE = 55.27 ± 8.08, Range = 13.96-99.03, $n = 11$; Fig. 2C), though it still followed an overall downward trend across our study period. The lowest habitat quality estimate was recorded in 2010 and represented an 86% decline when compared to our highest estimate of 99.03 in 2002.

Productivity

Throughout our study period, productivity was variable ($\bar{x}$ ± SE = 0.44 ± 0.061 YY/Adults, Range = 0.054-0.670 YY/Adults, $n = 11$; Fig. 2D). Two of the lowest estimates occurred in 2007 (0.087) and 2010 (0.054). These estimates represent an 87% and 92% decline in productivity for 2007 and 2010, respectively,

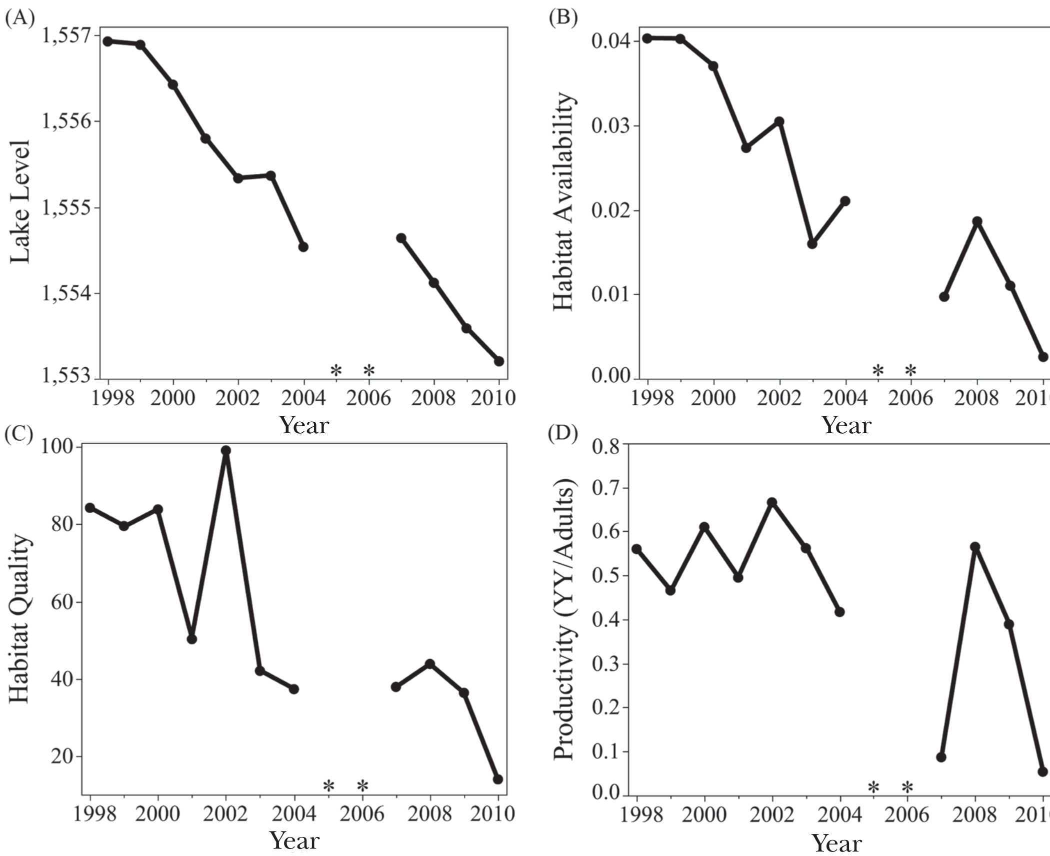

Figure 2. Time series of the three habitat covariates (A) lake level, (B) habitat availability, and (C) habitat quality, and the response variable (D) productivity. An asterisk (*) indicates a year excluded from analysis.

when compared to our highest productivity estimate of 0.670 YY/Adults in 2002.

Model Selection

Examination of ΔAIC_c, AIC_c weights (w_i), importance values, and the maximized log-likelihood function of our initial candidate set of eight models indicated redundancy among models when lake level was included as a multiplicative interaction term with our other two habitat covariates. Consequently, we removed the two models containing lake level as an interaction term from consideration and conducted a post-hoc analysis of a reduced set of six candidate models. Results of the post-hoc analysis indicated that the model containing habitat availability as the only predictor received the most support (w_i = 0.63, ΔAIC_c = 1.80 for next best model), given our data and candidate set of models (Table 1). The estimate from the top model suggested a positive relationship between grebe reproductive output and habitat availability (β_i = 0.20, 95% CI = 0.099-0.310; Fig. 4A). In addition, habitat availability had the highest importance value ($\sum w_i$ = 0.70) across all models considered. The model containing habitat quality as the only predictor was competitive with our top model (ΔAIC_c = 1.80; Table 1) and also suggested a positive relationship between grebe reproductive output and habitat quality (β_i = 0.28, 95% CI = 0.012-0.450; Fig 4B); however, its importance value ($\sum w_i$ = 0.33) was lower than that of habitat availability. These findings demonstrate model selection uncertainty, given our data and set of candidate models.

Lake level did not receive support as a direct predictor of grebe reproductive

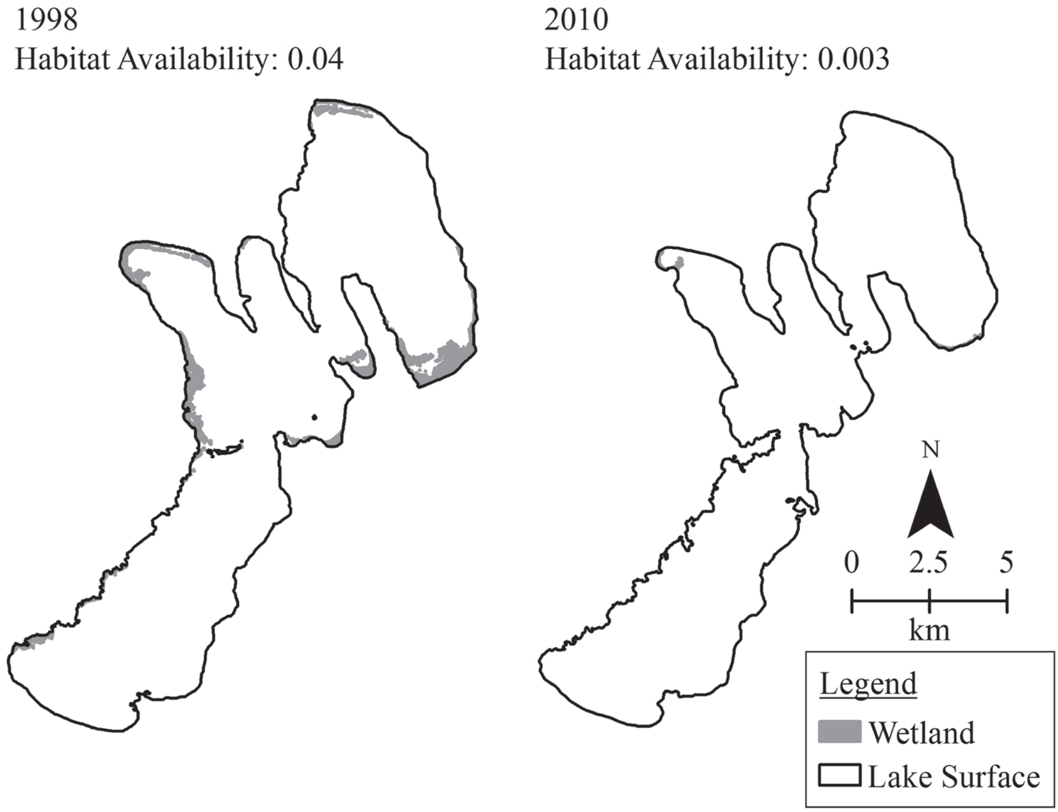

Figure 3. Comparison of the highest (1998) and lowest (2010) wetland habitat availability during the study period.

output. The model containing lake level alone ranked higher than only the null model (ΔAIC_c = 8.18 and 8.67, respectively; Table 1). Lake level also had a low importance value ($\sum w_i$ = 0.08), further indicating its lack of predictive power. However, habitat availability and habitat quality were highly correlated with lake level (Pearson's r = 0.92 and 0.80, respectively; Fig. 4C, 4D, respectively).

Through examination of the raw, untransformed data, we found that habitat availability values ≥ 0.015 reliably resulted in productivity estimates of ≥ 0.40 YY/Adults, representing a threshold in this habitat covariate. Below this amount of habitat, grebe productivity was reduced and in 2 years it fell below 0.10 YY/Adults (Fig. 5A). Further analysis revealed that lake levels of ≥ 1,554.6 m reliably resulted in higher habitat avail-

Table 1. Post-hoc model selection results of log-transformed habitat functions used to assess the influence of landscape-level habitat characteristics on annual grebe reproductive output at Eagle Lake, Lassen County, California, USA, 1998-2010. For each model, K is the number of estimated parameters; ΔAIC_c represents the AIC_c distance from the minimum AIC_c model; w_i is the AIC_c weight; and $LogL(\theta|y)$ represents the maximized log-likelihood function. The lowest AIC_c for this candidate set of models was -8.26.

Model	K	ΔAIC_c	w_i	$LogL(\theta\|y)$
Habitat Availability	3	0	0.63	23.35
Habitat Quality	3	1.80	0.26	22.45
Lake Level + Habitat Availability + Habitat Quality	5	4.40	0.07	21.15
Habitat Availability x Habitat Quality	3	6.63	0.02	20.03
Lake Level	3	8.18	0.01	19.26
Null Model	2	8.67	0.01	17.63

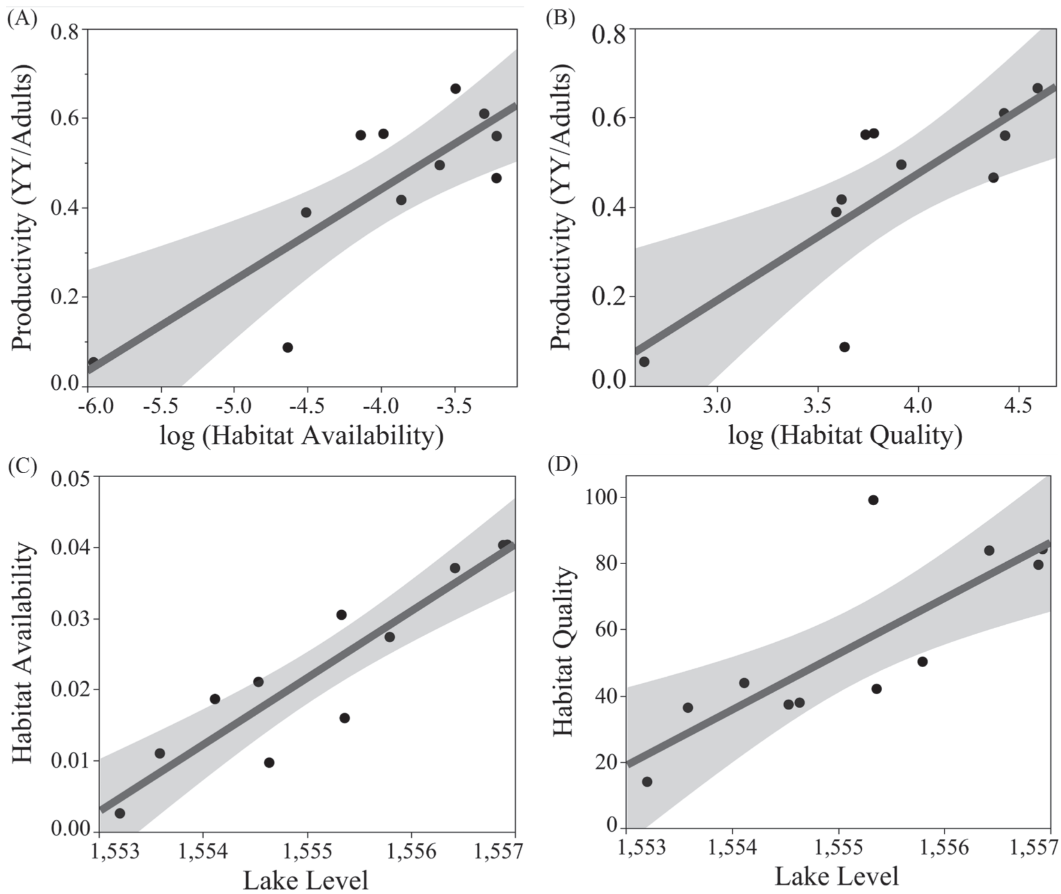

Figure 4. Regression among (A) habitat availability and productivity; (B) habitat quality and productivity; and Pearson's correlations among (C) lake level and habitat availability; and (D) lake level and habitat quality. Gray shading represents the 95% confidence interval.

ability values and, hence, higher grebe reproductive output. A similar analysis of habitat quality revealed that average NDVI values of ≥ 40 reliably resulted in productivity estimates of ≥ 0.4 YY/Adults, again, representing a threshold in this habitat covariate (Fig. 5B). These values were also most reliably produced when lake levels were ≥ 1,554.6 m.

DISCUSSION

As predicted, grebe reproductive output increased with increasing wetland habitat availability and quality. For our study system, the relationship between grebe reproductive output and both habitat availability and habitat quality were non-linear and asymptotic, indicative of a threshold. These findings demonstrate that areal extent of wetland cover and robustness of wetland vegetation are positively correlated with grebe reproductive output at Eagle Lake.

Lake level did not receive support as a direct predictor of grebe reproductive output. Despite this, lake level was highly correlated with our indices of both habitat availability and habitat quality, indicating its importance as an indirect effect. Our findings also demonstrate an approximately 2-m range of lake levels that result in habitat availability and habitat quality measures associated with higher levels of grebe reproductive output. Relative to the depth of Eagle Lake's northern and central basins, where grebes nested during the study, and the overall variation of lake level observed, this finding indicates that inter-annual lake

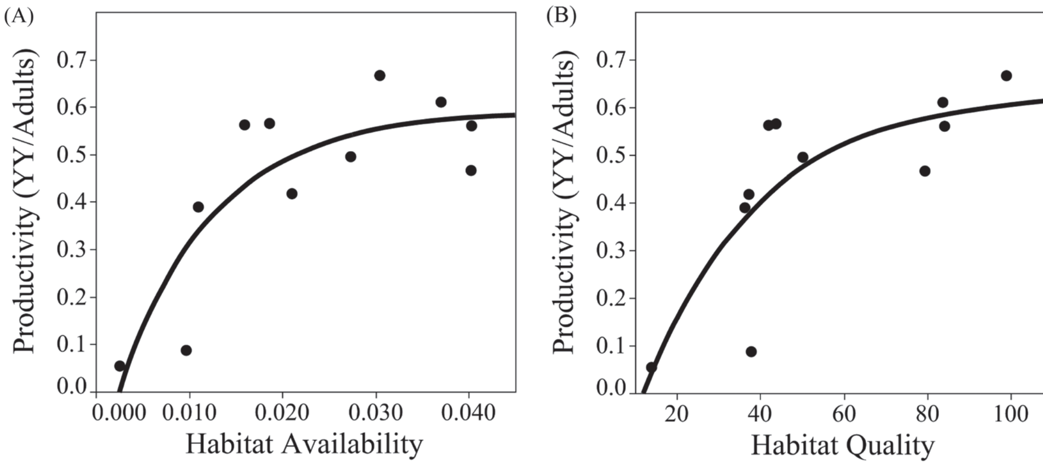

Figure 5. Thresholds among productivity and (A) habitat availability and (B) habitat quality.

levels do not need to be strictly stabilized to benefit nesting grebes. In fact, LaPorte *et al.* (2014) found that long-term artificial stabilization of lake level is detrimental to grebe nesting habitat, affecting species composition, structure, and growth of native emergent wetland vegetation. However, it is important to note that for the purposes of our study, inter-annual lake levels were compared, and that rapid changes in intra-annual lake levels have been demonstrated to be detrimental to grebe nesting (Parmelee and Parmelee 1997).

Although our results indicated model selection uncertainty among habitat availability and habitat quality, this finding is not surprising given that waterbird reproductive output is influenced by more than landscape-level habitat factors. For instance, anthropogenic disturbance (Rodgers and Smith 1995; Desorbo *et al.* 2007), food abundance (Allen *et al.* 2007), and physiological condition (Crossin *et al.* 2013) have all been demonstrated to affect waterbird reproductive success.

Grebes nest over water in littoral zone wetlands (LaPorte *et al.* 2013). At Eagle Lake, this habitat is in the shallowest portions of the lake and, as our study demonstrates, is susceptible to changes in lake level. Existing stands of suitable nesting habitat become inaccessible to nesting grebes when lake level declines are extreme or occur over short time periods (Wantzen *et al.* 2008). In addition, hydrologic conditions can affect entire wetland plant communities, resulting in changes in total biomass, presence and absence of species, seedling establishment, and degree of openness (open-, hemi-, or closed-marsh) (Owen 1999; Miller and Zedler 2003; Ward *et al.* 2010). For these reasons, grebe colony locations within lacustrine wetland systems like Eagle Lake are dynamic and can change inter-annually (LaPorte *et al.* 2013). Prior studies of overwater nesting birds at Eagle Lake found that breeding population, colony locations, and overall annual reproductive output are variable (Lederer 1976; Wright-Myers and Bogiatto 2007), which was also true for grebes during our study period.

Our findings indicate that there is a range of habitat availability, habitat quality, and lake levels at which grebe reproductive output is reliably maintained at Eagle Lake. However, a threshold of habitat characteristics exists, under which reproductive output is greatly diminished. Although not likely applicable to every waterbody that supports nesting grebes, these findings do underscore the need for careful consideration of overwater nesting birds and wetland habitat for wildlife, particularly at reservoirs where water fluctuations are routine and occur over shorter time periods.

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