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Author(s): Lisa M. Baril and Douglas W. Smith Thomas Drummer Todd M. Koel
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IMPLICATIONS OF CUTTHROAT TROUT DECLINES FOR BREEDING OSPREYS AND BALD EAGLES AT YELLOWSTONE LAKE

Lisa M. Baril[1] and Douglas W. Smith
National Park Service, P.O. Box 168, Mammoth, WY 82190 U.S.A.

Thomas Drummer
Department of Mathematical Sciences, Michigan Technological University, Houghton, MI 49931 U.S.A.

Todd M. Koel
National Park Service, P.O. Box 168, Mammoth, WY 82190 U.S.A.

Abstract.—In Yellowstone National Park (YNP), Ospreys (*Pandion haliaetus*) feed primarily on cutthroat trout (*Oncorhynchus clarki bouvieri*) and cutthroat trout represent approximately 23% of prey consumed by Bald Eagles (*Haliaeetus leucocephalus)* during the breeding season (Swenson 1978, *Journal of Wildlife Management* 42:87–90; Swenson et al. 1986, *Wildlife Monographs* 95:3–46). The introduction of exotic lake trout (*Salvelinus namaycush*) to Yellowstone Lake during the late 1980s caused substantial declines in populations of cutthroat trout. Historically, more than half of all breeding pairs of Ospreys and Bald Eagles in YNP have nested near and foraged at Yellowstone Lake and the decline in cutthroat trout numbers may affect rates of reproduction for these two species. We studied the relationship between an index of cutthroat trout abundance and spring weather on Osprey (1987–2009) and Bald Eagle (1987–2007) reproduction. We documented steep declines in an index of cutthroat trout abundance, Osprey productivity and nesting success, and a dramatic decline in the number of Osprey breeding pairs. Bald Eagle productivity and nesting success also declined, but at a slightly slower rate than that of Ospreys, and the number of breeding pairs of Bald Eagles increased over the study period. Osprey reproduction was positively correlated with an index of cutthroat trout abundance and spring temperatures. However, the relationship between Bald Eagle reproduction and the index of cutthroat trout abundance was unclear. Our study suggested that the recovery of cutthroat trout is important to maintaining a breeding population of Ospreys at Yellowstone Lake, but may be less important for the Yellowstone Lake Bald Eagle population.

Key Words: *Bald Eagle*; Haliaeetus leucocephalus; *Osprey*; Pandion haliaetus; *breeding*; *fish*; *productivity*; *reproduction*; *Yellowstone.*

IMPLICANCIAS DE LA DISMINUCIÓN POBLACIONAL DE *ONCORHYNCHUS CLARKI BOUVIERI* EN INDIVIDUOS REPRODUCTIVOS DE *PANDION HALIAETUS Y HALIAEETUS LEUCOCEPHALUS* EN EL LAGO YELLOWSTONE

Resumen.—En el Parque Nacional Yellowstone, *Pandion haliaetus* se alimenta principalmente de truchas de la especie *Oncorhynchus clarki bouvieri* y estas truchas representan aproximadamente el 23% de las presas consumidas por individuos de *Haliaeetus leucocephalus* durante la época reproductiva (Swenson 1978, *Journal of Wildlife Management* 42:87–90; Swenson et al. 1986, *Wildlife Monographs* 95:3–46). La introducción de una especie de trucha exótica (*Salvelinus namaycush*) en el Lago Yellowstone durante la última parte de la década de 1980 causó disminuciones substanciales en las poblaciones de *O. c. bouvieri.* Históricamente, más de la mitad de todas las parejas reproductivas de *P. haliaetus* y *H. leucocephalus* han anidado y forrajeado en el Lago Yellowstone y la disminución en los números de *O. c. bouvieri* podría afectar las tasas reproductivas de estas dos especies. Estudiamos la relación entre el índice de abundancia de *O. c. bouvieri* y el clima de primavera sobre la reproducción de *P. haliaetus* (1987–2009) y *H. leucocephalus* (1987–2007). Documentamos marcadas disminuciones en el índice de abundancia de *O. c. bouvieri*, en la productividad y en el éxito de anidación de *P. haliaetus*, y una dramática disminución en el número de parejas reproductivas de *P. haliaetus.* La productividad y el éxito de anidación de *H. leucocephalus* también disminuyeron,

[1] Email address: Lisa_Baril@partner.nps.gov

pero a una tasa un poco menor que la de *P. haliaetus*, y el número de parejas reproductivas de *H. leucocephalus* aumentó durante el periodo de estudio. La reproducción de *P. haliaetus* estuvo positivamente correlacionada con el índice de abundancia de *O. c. bouvieri* y con las temperaturas primaverales. Sin embargo, la relación entre la reproducción de *H. leucocephalus* y el índice de abundancia de *O. c. bouvieri* no fue clara. Nuestro estudio sugirió que la recuperación de *O. c. bouvieri* es importante para mantener una población reproductiva de *P. haliaetus* en el Lago Yellowstone, pero puede ser menos importante para las poblaciones de *H. leucocephalus* del Lago Yellowstone.

[Traducción del equipo editorial]

Introduced species are considered a leading cause of loss of biodiversity worldwide (Simberloff 2001). Although the vast majority of introduced species fail to become established, those that do may cause considerable changes in ecosystem structure and function. In Yellowstone National Park (YNP), the introduction of exotic lake trout (*Salvelinus namaycush*) to Yellowstone Lake has resulted in dramatic declines in populations of native Yellowstone cutthroat trout (*Oncorhynchus clarkii* bouvieri; Schullery and Varley 1995). Ospreys (*Pandion haliaetus*), Bald Eagles (*Haliaeetus leucocephalus*), and American White Pelicans (*Pelecanus erythrorhynchos*), along with 39 other species of bird and mammal are partially or entirely dependent on cutthroat trout during the breeding season (Schullery and Varley 1995). Furthermore, consumption of cutthroat trout by terrestrial predators (e.g., grizzly bears [*Ursus arctos*] and black bears [*U. americanus*]) serves to maintain potentially important energetic links between the aquatic system and the terrestrial environment (Haroldson et al. 2005). The loss of cutthroat trout could alter, or in some cases eliminate, these important trophic links resulting in diminished ecosystem function for the Yellowstone Lake region.

Lake trout were illegally introduced to Yellowstone Lake during the early 1980s, but were not discovered until 1994 (Munro et al. 2005). Concurrent with the introduction of lake trout, indices of cutthroat trout abundance in Yellowstone Lake have declined by more than 50% since 1990 (Koel et al. 2005). Although several studies have demonstrated that predation by lake trout has caused significant declines in cutthroat trout populations (Ruzycki et al. 2003, Koel et al. 2005), relatively little is known about the potential cascading effects on other species (but see Reinhart et al. 2001, Felicetti et al. 2004, Haroldson et al. 2005, Crait and Ben-David 2006, Tronstad et al. 2010), an important step in understanding ecosystem-wide implications of exotic lake trout in Yellowstone Lake.

More than 50% of all breeding pairs of Bald Eagles and Ospreys park-wide historically nested and foraged along the shores of Yellowstone Lake and connected tributaries (Swenson 1978, Swenson et al. 1986, McEneaney 2002). Ospreys are obligate piscivores (Swenson 1978), whereas Bald Eagles exhibit a wider diet breadth, with fish making up approximately 30% of their diet during the breeding season in the Yellowstone Lake ecosystem (Swenson et al. 1986). Prior to the lake trout introduction, cutthroat trout represented 99% of fish consumed by Ospreys (Swenson 1978) and 23% of the total prey items consumed by Bald Eagles in the Yellowstone Lake ecosystem (Swenson et al. 1986).

Although lake trout are now abundant in Yellowstone Lake they are unavailable as alternative prey because they live in deep water and grow rapidly beyond the mass that Bald Eagles and Ospreys can carry (Ruzycki et al. 2003). Although several other species of fish inhabit Yellowstone Lake, none are as widely distributed or as abundant as cutthroat trout and most are relatively small ($\leq$10 cm) and hence comparatively unimportant as alternative prey species (Swenson 1978, Swenson et al. 1986, Varley and Schullery 1998). The availability of prey is an important factor influencing rates of reproduction in raptors (Van Daele and Van Daele 1982, Hansen 1987, Harmata et al. 2007) and declines in cutthroat trout numbers and the absence of alternative piscine prey may affect rates of reproduction for these species, particularly for Ospreys.

Our objectives were to: (1) assess temporal trends in three measures of raptor reproduction (the number of breeding pairs, nesting success, and reproductive rate) and an index of cutthroat trout abundance; (2) assess the relationship(s) between raptor reproduction, an index of cutthroat trout abundance, and weather; and (3) determine the direction of the trophic flow of the system (top-down, bottom-up, or a feedback system).

Methods

Study Area. Yellowstone Lake is a large, high-elevation, oligotrophic lake located in the southeast corner of YNP with a surface area of 341 km^2, an

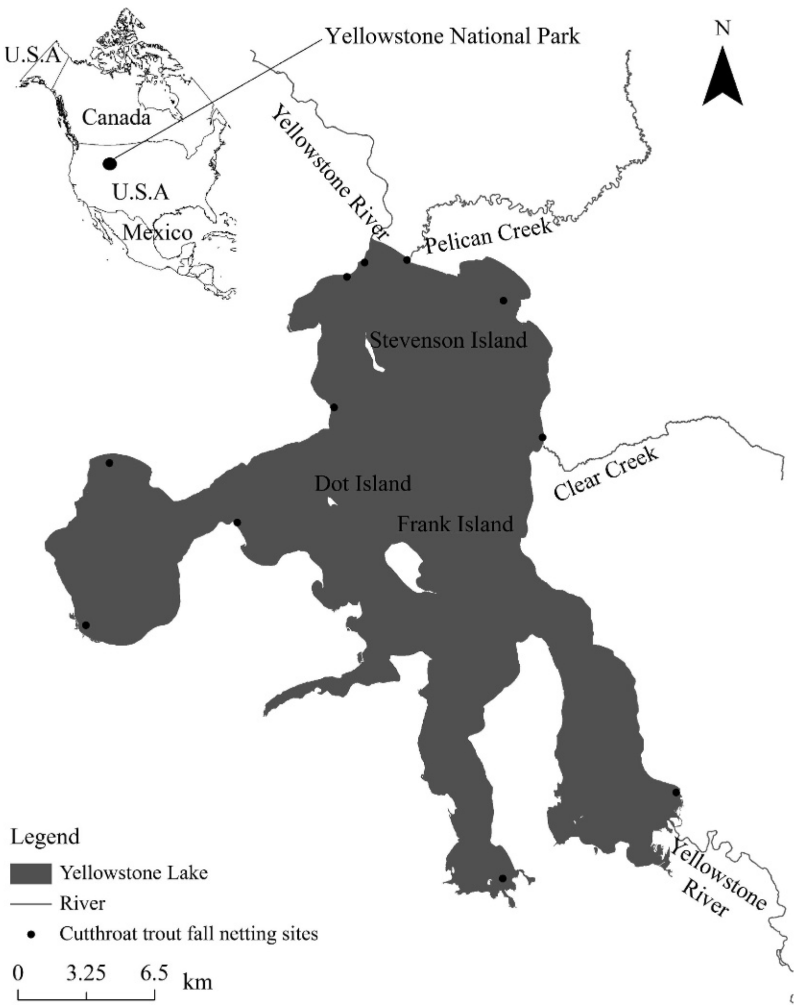

Figure 1. Location of the Yellowstone Lake study area in Yellowstone National Park, Wyoming, U.S.A., where trends in Bald Eagle and Osprey reproduction (breeding pairs, nesting success, and productivity) were examined from 1987–2009. An index of cutthroat trout abundance (CPUE) derived from 11 fall netting assessment sites along with temperature and precipitation data gathered from the Yellowstone Lake weather station from March–July 1987–2009 were examined to determine their relationship(s) with Bald Eagle and Osprey breeding pairs and productivity.

average depth of 48.5 m, and 239 km of shoreline (Gresswell et al. 1994; Fig. 1). Terrestrial vegetation surrounding Yellowstone Lake is dominated by lodgepole pine (*Pinus contorta*; Despain 1990). Willows (*Salix* spp.) occur along tributary streams, whereas subalpine meadows occur in the uplands (Despain 1990). Climate in the region is characterized by short summers with an average temperature of 11.8°C during July and long, cold winters with an average temperature of −10.8°C during December (Crait and Ben-David 2006). The region receives approximately 513 mm of precipitation during the year, most of which falls as snow during the winter months (Crait and Ben-David 2006). Yellowstone Lake remains ice-covered from December through May (Crait and Ben-David 2006).

Bald Eagle and Osprey Surveys. We surveyed all forested areas supporting mature trees up to 1 km from the Yellowstone Lake shoreline, approximately 1 km from the connected tributaries, and all forested islands for evidence of nesting Bald Eagles and Ospreys 2–3 times during the breeding season

(April–June 1987–2007 for Bald Eagles and May–August 1987–2009 for Ospreys) using a fixed-wing Supercub airplane. In addition to aerial surveys, we checked nests occurring along roads from the ground. We monitored all nests in which eggs were laid or an adult was observed in incubation or brooding posture until the nesting attempt failed or nestlings fledged. Nests were checked 2–3 times during each breeding season.

For each breeding season, we determined the number of breeding pairs, nesting success, and productivity for the Yellowstone Lake Bald Eagle and Osprey populations (i.e., birds nesting <1 km from the lakeshore and connected tributaries). We use reproductive terminology following that of Steenhof and Newton (2007) as follows; breeding pairs refers to the number of paired Bald Eagles or Ospreys that laid eggs per breeding season, nesting success refers to the proportion of breeding pairs that raised at least one young to approximately 80% of fledging age per breeding season regardless of the number of breeding attempts made for that pair (Steenhof and Newton 2007), and productivity for Bald Eagles and Ospreys refers to the average number of young that reached approximately 80% of fledging age per breeding pair per breeding season (Steenhof and Newton 2007). We were unable to calculate daily nest survival because we only documented fate of each nest.

Cutthroat Trout Surveys. We used cutthroat trout catch per unit effort (CPUE) derived from fall netting assessments conducted by the National Park Service Fisheries Program as an index of cutthroat trout abundance (Koel et al. 2005). Each September since 1987, except for 1993, the Yellowstone Lake fisheries program placed multi-mesh-size gillnets in sets of five nets at 11 sites throughout Yellowstone Lake for a maximum of 55 nets per year, although actual sites used and nets set ranged from 10–11 sites and 44–55 nets per year (Koel et al. 2005). Fisheries staff placed nets in shallow water (<5 m depth) for one trap-night per year over a 1–2 week period during late September. Surveys were conducted in September to capture the peak annual cutthroat trout abundance prior to thermal turnover of the lake. We calculated CPUE as the mean number of cutthroat trout caught per net per year (Koel et al. 2005). As cutthroat trout widely roam shallow water habitats throughout the summer and fall, the September cutthroat trout surveys provided an annual index of cutthroat trout availability for nesting Bald Eagles and Ospreys.

Weather Data. We used average monthly temperature (°C) and total precipitation (mm) for the months of April–July provided by the Yellowstone Lake weather station located near the northwest portion of the lake (44°32′N, 110°25′W). The National Weather Service manages the station, but data were collected and provided by Snowcap Hydrology, Bozeman, Montana. This period encompasses the nest-building through fledging phases of both Bald Eagles and Ospreys.

Statistical Analyses. We constructed time series plots to assess the temporal trends in reproductive variables (RV) and CPUE. We used scatterplots and Pearson correlation to assess contemporaneous correlations between RV and the CPUE and weather variables. A contemporaneous correlation implies a change in one variable is associated with a change in another variable within the same period. To simplify the temperature data analysis, we combined the four monthly temperature variables into one variable (TEMP) using principal components. The four monthly temperature variables were positively correlated ($r \approx 0.55$ for neighboring months) and the first principal component weights were roughly equal across the four months, so we interpret TEMP as a weighted average of spring temperatures. The four precipitation variables were only weakly correlated with each other so we retained these as independent variables.

For each RV, we fit a multiple regression model with autocorrelated errors. Independent variables were CPUE, the temperature variable, and each of the four precipitation variables. We always included CPUE as an independent variable and added the temperature variable and four precipitation variables one at a time. We compared models with Akaike's Information Criterion corrected for small samples (AIC_c). We regarded $\Delta AIC_c > 2$ as evidence of a meaningful difference between models (Burnham and Anderson 2002). The R^2 values we present measure the contribution of only the independent variables and not the lagged error terms. We conducted all analyses using PROC AUTOREG (SAS Institute, Inc., Cary, NC). Although we present data on the number of breeding pairs, nesting success, and productivity, we present statistical analyses only for the number of breeding pairs and productivity. For both raptor species, nesting success and productivity results were highly correlated over time ($r \approx 0.9$).

A contemporaneous relationship exists between two variables if a change in one variable has an immediate effect on the other variable, but it is possible that changes may be delayed, resulting in a lagged effect. More problematic is that standard regression analysis requires that one variable be the dependent variable and other variables independent variables. In our analyses it is not clear if RV or CPUE are dependent variables, independent variables, or both. CPUE and RV interactions could exist in the form of a change in CPUE leading to a change in RV (bottom-up trophic flow), a change in RV leading to a change in CPUE (top-down trophic flow), or changes in CPUE leading to changes in RV, which in turn leads to changes in CPUE, a condition referred to as feedback.

Mathematically, we regard this as a dynamic system with three endogenous variables; an Osprey reproductive variable (ORV), a Bald Eagle reproductive variable (BERV), and CPUE and the exogenous weather variables. To test for possible lagged variable effects, to accommodate autocorrelation, and to conduct a formal test of trophic flow direction, we used three equations to represent the system: one equation for each of the endogenous variables. Each equation had lagged values of all endogenous variables and exogenous weather variables as independent variables. In time series nomenclature this is called a vector autoregressive (VAR) model (Enders 2004). A VAR(p) model is a set of equations in which each endogenous variable appears as both a dependent and independent variable, with variables lagged up to and including p time intervals. For the three endogenous variables $\mathrm{ORV_t}$, $\mathrm{BERV_t}$, and $\mathrm{CPUE_t}$, and a single exogenous variable $\mathrm{W_t}$ representing exogenous weather variables (either $\mathrm{precipitation_t}$ or $\mathrm{temperature_t}$), the VAR(1) model is:

$$\begin{aligned}\mathrm{ORV_t} &= \alpha_Y + \beta_1 \mathrm{ORV_{t-1}} + \beta_2 \mathrm{BERV_{t-1}} \\ &\quad + \beta_3 \mathrm{CPUE_{t-1}} + \beta_4 \mathrm{W_t} + \varepsilon_t, \end{aligned} \tag{1}$$

$$\begin{aligned}\mathrm{BERV_t} &= \alpha_X + \theta_1 \mathrm{ORV_{t-1}} + \theta_2 \mathrm{ERV_{t-1}} \\ &\quad + \theta_3 \mathrm{CPUE_{t-1}} + \theta_4 \mathrm{W_t} + \upsilon_t, \end{aligned} \tag{2}$$

$$\begin{aligned}\mathrm{CPUE_t} &= \alpha_Z + \lambda_1 \mathrm{ORV_{t-1}} + \lambda_2 \mathrm{ERV_{t-1}} \\ &\quad + \lambda_3 \mathrm{CPUE_{t-1}} + \lambda_3 \mathrm{W_t} + \delta_t, \end{aligned} \tag{3}$$

where ε_t , υ_t , and δ_t are Gaussian error terms that may be correlated. In this model the exogenous weather variable is not lagged, but lagged values can be included. Note that each equation contains a lagged value of the endogenous variable being modeled to account for possible autocorrelation within each time series. The fitting, testing, and interpretation of these models is described in Enders (2004). We restricted our analyses to lags of order ≤ 2 due to the short length of the time series and selected between lag one and lag two models by comparing $\mathrm{AIC_c}$ (Burnham and Anderson 2002). We assessed model adequacy with autocorrelations and cross-correlations of residuals and conducted tests for the presence of cross-correlation in residuals up to lag three using the Hosking Q statistic (Hosking 1980).

To test for the direction of trophic flow between raptors and cutthroat trout we tested

$$\mathrm{H_0} : \beta_3 = \theta_3 = 0,$$

which specifies that CPUE has no effect on BERV and ORV. Rejecting this hypothesis would indicate a bottom-up flow. A test of

$$\mathrm{H_0} : \lambda_1 = \lambda_2 = 0$$

specifies that BERV and ORV do not affect CPUE, and rejecting this hypothesis would indicate a top-down flow. If both null hypotheses were rejected, we would infer a two-way flow. These tests are motivated by the Granger Causality Test, which is a test of the value of variables X and Y in predicting Z given that the effect of past values of Z has been accounted for (Granger 1969). We also tested for Osprey-Bald Eagle interaction by testing

$$\mathrm{H_0} : \beta_2 = \theta_1 = 0.$$

In our initial models we included only the temperature variable which, being a four-month composite, we thought relevant to both Bald Eagle and Osprey. We included monthly precipitation because precipitation patterns could have different effects on these species. If we found no evidence of Osprey-Bald Eagle interaction, we simplified the three-equation system to a two-equation system for Bald Eagle and CPUE and a two-equation system for Osprey and CPUE. This allowed us to use two more years of Osprey data and to incorporate different precipitation variables for the two species. We used t-tests (t = estimate/standard error) to test significance of individual coefficients.

VAR(p) models must be fit to stationary time series that lack trend. Where needed, we detrended series by modeling the first difference

$$\Delta \mathrm{Y_t} = \mathrm{Y_t} - \mathrm{Y_{t-1}},$$

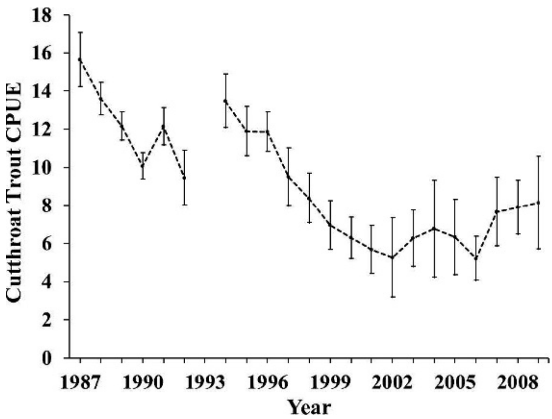

Figure 2. Cutthroat trout catch per unit effort (CPUE) (mean number of cutthroat trout caught per net) ±SE as an index of cutthroat trout abundance from 1987–2009 in Yellowstone Lake, Yellowstone National Park, Wyoming, U.S.A. The CPUE data were collected and provided by the Yellowstone National Park Fisheries Program (Koel et al. 2005).

which represents the change in the series over one time interval. Typically, if one series needs differencing then all series in the VAR(p) model are differenced (Enders 2004). We conducted computations with SAS software PROC ARIMA and PROC VARMAX (SAS Institute, Inc., Cary, North Carolina, U.S.A.).

Results

Cutthroat trout CPUE fluctuated without a clear trend from 1987 to 1998, but declined thereafter for 8 yr with an average decline of 11% per year, followed by 3 yr of increases (Fig. 2). Although highly variable, in the first 15 yr of the study period, the number of Osprey breeding pairs far exceeded the number of Bald Eagle breeding pairs (Fig. 3). In two of those years, the number of Osprey breeding pairs exceeded 60, but after 2001, declined rapidly, reaching a minimum of four breeding pairs in 2009. The number of Bald Eagle breeding pairs was relatively stable, increasing slightly over the study period. Both Osprey productivity and Bald Eagle productivity declined during the study period, with the former reaching zero in 2007 and 2008 (Fig. 3). The linear rate of decline for Osprey productivity (0.05 young per breeding pair/year) was slightly greater than that of Bald Eagle productivity (0.03/year) although we did not test for significant differences between rates of decline between species. For each species, nesting success largely followed the same trajectory as productivity (Fig. 3). Temperature and precipitation data fluctuated over time with no clear trend.

The number of Osprey breeding pairs was strongly positively correlated with cutthroat trout CPUE ($r = 0.70$, Fig. 4) whereas the number of Bald Eagle breeding pairs was negatively correlated with CPUE ($r = -0.52$, Fig. 4). Neither the number of Bald Eagle nor Osprey breeding pairs was significantly correlated with TEMP, or any of the precipitation variables. Both Osprey productivity and Bald Eagle productivity were positively correlated with CPUE ($r = 0.61$, $r = 0.43$, Fig. 4). Osprey productivity was also positively correlated with TEMP (Fig. 5), but the relationship between Bald Eagle productivity and TEMP was comparatively weaker (Fig. 5). Neither Osprey productivity nor Bald Eagle productivity were correlated with any of the precipitation variables.

In our multiple regression analysis the number of Osprey breeding pairs was significantly, positively related to cutthroat trout CPUE ($R^2 = 22.2\%$, $t_{20} = 2.39$, $P = 0.03$) yielding the prediction equation,

$$\text{Osprey breeding pairs} = 10.5 + 19.5 * \text{CPUE}$$

The number of Bald Eagle breeding pairs was negatively related to CPUE ($R^2 = 30.5\%$, $t_{18} = -2.46$, $P = 0.02$) yielding the prediction equation,

$$\text{Bald Eagle breeding pairs} = 19.7 - 3.4 * \text{CPUE}$$

Osprey productivity and Bald Eagle productivity were both related to CPUE and TEMP, but none of the precipitation variables. The regression of Osprey productivity on CPUE and TEMP ($R^2 = 62.2\%$, both t_{19}-tests $P < 0.05$) yielded the prediction equation,

$$\text{Osprey productivity} = -0.11 + 0.54 * \text{CPUE} + 0.14 * \text{TEMP}.$$

Similarly, the regression of Bald Eagle productivity on CPUE and TEMP ($R^2 = 52.4\%$, both t_{17}-tests $P < 0.05$) yielded,

$$\text{Bald Eagle productivity} = 0.09 + 040 * \text{CPUE} + 0.12 * \text{TEMP}.$$

The trends in reproductive variables and CPUE made differencing of all time series necessary. Productivity for both species exhibited a negative lag-one autocorrelation (Bald Eagle: $r_1 = -0.44$;

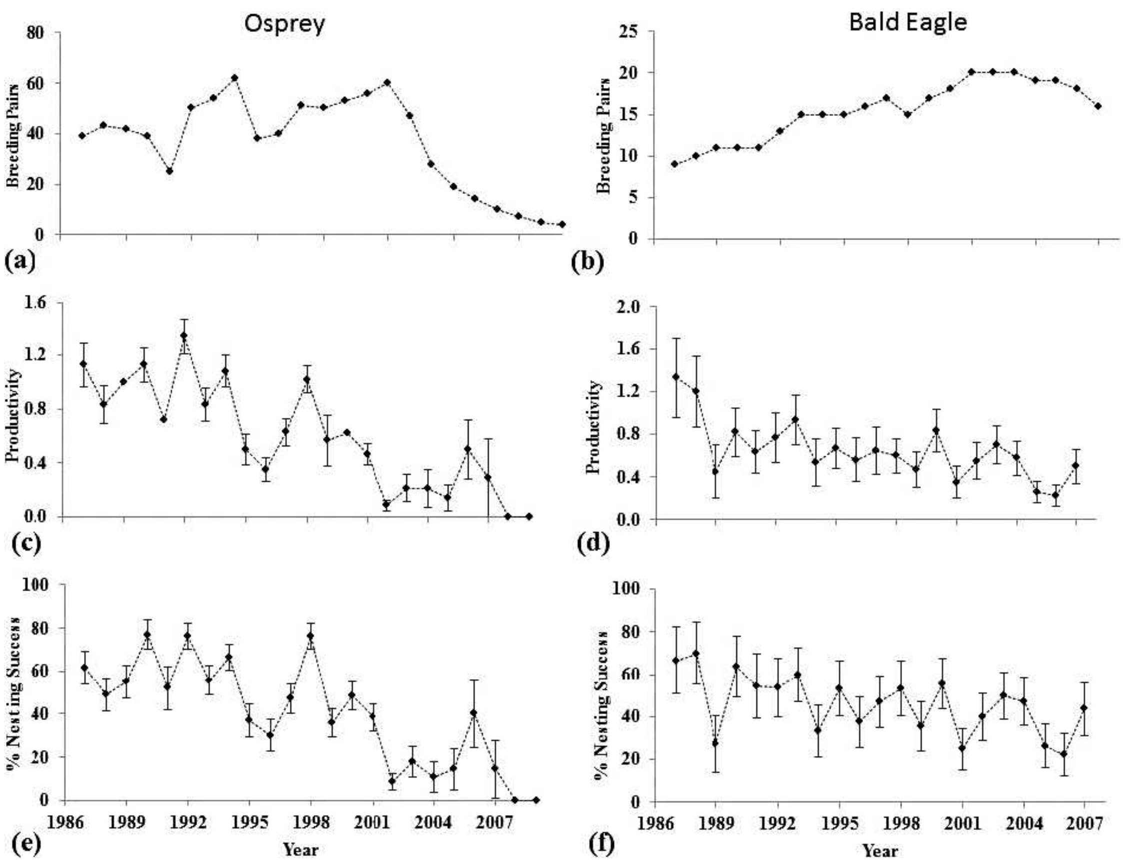

Figure 3. Trends in Bald Eagle and Osprey breeding pairs (a,b), productivity ±SE (c,d), and nesting success ±SE (e,f) for birds nesting within approximately 1 km of the Yellowstone Lake shoreline and connected tributaries, and all forested islands from April–June 1987–2007 for Bald Eagles and May–August 1987–2009 for Ospreys.

Osprey: $r_1 = -0.48$) indicating that a positive change in productivity tended to be followed by a negative change in productivity. We found no evidence of autocorrelation in the number of breeding pairs for either species.

We used a VAR(1) model for inference based on a comparison of AIC_c values with the VAR(2) model although the difference in AIC_c values was small ($\Delta AIC_c = 1.69$). The AIC_c comparisons indicated no model improvement by including lagged values of TEMP. The Bald Eagle model R^2 was very low and none of the predictors were related to breeding pairs (t_{14}-tests, all $P > 0.05$, Table 1). Similarly, none of the predictors were significantly related to CPUE (t_{14}-tests, all $P > 0.05$), and only TEMP was positively related to Osprey breeding pairs ($t_{14} = 2.40$, $P = 0.03$). We failed to reject the null hypothesis that lagged CPUE had no effect on the number of Bald Eagle breeding pairs and Osprey breeding pairs (Granger Causality $\chi^2_2 = 3.49$, $P = 0.17$), failed to reject the null hypothesis that lagged number of Bald Eagle breeding pairs and lagged number of Osprey breeding pairs had no effect on CPUE (Granger Causality $\chi^2_2 = 0.84$, $P = 0.66$), and found no evidence of Bald Eagle-Osprey interaction (Granger Causality $\chi^2_2 = 3.05$, $P = 0.97$). When we fit separate models for Bald Eagles and Ospreys the results did not change, thus we report results for the full model. None of the precipitation variables improved AIC_c values in the Bald Eagle or Osprey models and thus we did not include them in any of our models. We observed some evidence of cross-correlation between residuals (Hosking Q $\chi^2_{18} = 29.68$, $P = 0.05$).

As in the analysis for breeding pairs, we used a VAR(1) model for productivity over the VAR(2)

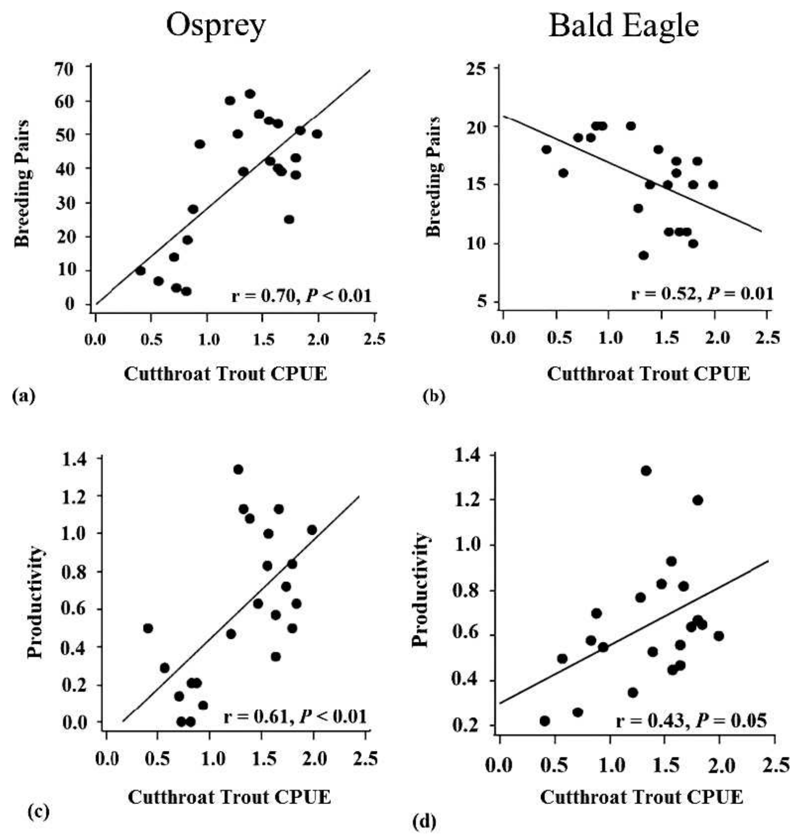

Figure 4. The contemporaneous relationship between Osprey breeding pairs and cutthroat trout catch per unit effort (CPUE, an index of abundance) (a), Bald Eagle breeding pairs and CPUE (b), Osprey productivity and CPUE (c), and Bald Eagle productivity and CPUE (d). Osprey data from 1987–2009 and 1987–2007 for Bald Eagles at Yellowstone Lake, Yellowstone National Park, Wyoming, U.S.A.

model ($\Delta AIC_c = 1.65$). The AIC_c comparisons indicated no model improvement by including lagged values of TEMP. There was no evidence of cross-correlations between residuals at lags zero through three (Hosking Q $\chi^2_{18} = 22.78$, $P = 0.19$). None of the predictor variables were statistically significant in the CPUE model (*t*-tests, all $P > 0.05$, Table 1). Bald Eagle productivity was negatively related to the lagged value of CPUE ($t_{14} = -3.30$, $P < 0.01$), but not related to lagged Osprey productivity ($t_{14} = 0.65$, $P = 0.54$). Osprey productivity was positively related to TEMP ($t_{14} = 3.25$, $P < 0.01$), but not lagged Bald Eagle productivity ($t_{14} = -0.58$, $P = 0.56$) or lagged CPUE ($t_{14} = 1.52$, $P = 0.16$). We rejected the null hypothesis that lagged CPUE had no effect on Bald Eagle productivity and Osprey productivity (Granger Causality $\chi^2_2 = 10.94$. $P < 0.01$) and failed to reject the null hypothesis that lagged Bald Eagle productivity and lagged Osprey productivity had no effect on CPUE (Granger Causality $\chi^2_2 = 1.56$, $P = 0.46$). Jointly these results indicated a bottom-up trophic flow, although this result occurred primarily due to the strong negative correlation between Bald Eagle productivity and lagged CPUE. There was no evidence of a Bald Eagle–Osprey interaction (Granger Causality $\chi^2_2 = 0.74$, $P = 0.69$). When we fit separate models for Bald Eagles and Ospreys the results did not change, thus we report results for the full model. None of the precipitation variables improved the AIC_c value in either the Bald Eagle or Osprey model.

DISCUSSION

We documented steep declines in cutthroat trout CPUE, Osprey productivity and nesting success, and a dramatic decline in the number breeding pairs of

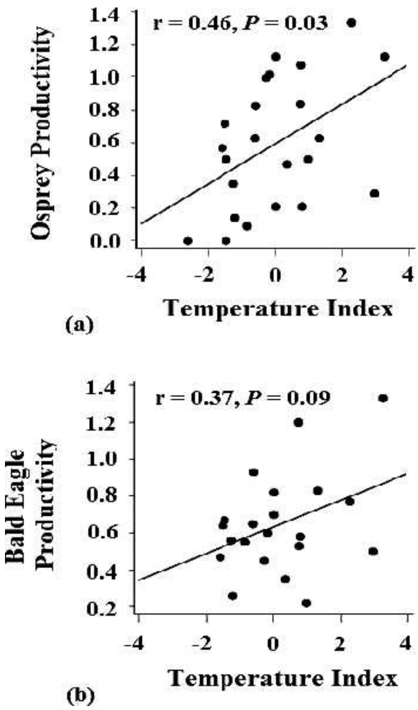

Figure 5. The contemporaneous relationship between Osprey (a) and Bald Eagle (b) productivity and the four-month (April–July) principal components composite temperature index from 1987–2009 for Ospreys and 1987–2007 for Bald Eagles at Yellowstone Lake, Yellowstone National Park, Wyoming, U.S.A.

Ospreys at Yellowstone Lake from 1987–2009. Our results supported a strong relationship between Osprey reproduction and our index to cutthroat trout abundance. Colder temperatures during the breeding season were also associated with declines in Osprey productivity, but not associated with the number of breeding pairs. In our time series models, colder temperatures were associated with declines in the number of breeding pairs. The relationship between Bald Eagle reproduction and CPUE, however, was unclear. In contrast with Ospreys, the number of Bald Eagle breeding pairs increased at Yellowstone Lake, resulting in a negative correlation with CPUE, a result we cannot explain. Bald eagle nesting success and productivity declined, yielding a modest positive contemporaneous correlation between productivity and CPUE, but a strong negative correlation between changes in productivity and the lagged value of change in CPUE. We were surprised by this result, but the negative correlation may have resulted from the lower level of dependence of Bald Eagles on cutthroat trout, which represented approximately 23% of the Bald Eagle diet in the Yellowstone Lake area during 1972–82 (Swenson et al. 1986). Temperature was not correlated with either the number of breeding pairs or productivity for Bald Eagles and precipitation was not correlated with reproduction for either species.

The number of Ospreys that attempted breeding from 1987 through 2001 was highly variable, but relatively stable or increasing slightly. Post-2001, and just one year after CPUE reached its lowest level in 2002, the number of Osprey breeding pairs declined rapidly to just four pairs in 2009. Despite fewer breeding pairs, neither nesting success nor productivity increased after 2001. This suggests that intraspecific competition was not a factor in reduced reproduction. In populations regulated by density-dependent factors reproduction generally

Table 1. Estimated explained variation (R^2) and coefficients (SE) from VAR(1) model of Osprey and Bald Eagle breeding pairs and productivity at Yellowstone Lake from 1987–2007. The CPUE denotes an index of cutthroat trout abundance. Temperature is a weighted average of March through June temperature.

Response Variable	Univariate Model R^2 (%)	Input Variable and Lag			
		Temperature Lag 0	Bald Eagle Lag 1	Osprey Lag 1	CPUE Lag 1
Breeding Pairs					
Bald Eagle	6.8	−0.16 (0.21)	0.19 (0.36)	0.004 (0.04)	0.25 (1.31)
Osprey	35.4	**3.78 (1.57)**[a]	−0.13 (2.68)	0.37 (0.31)	14.1 (9.76)
CPUE	30.5	−0.03 (0.04)	−0.01 (0.06)	0.005 (0.007)	−0.26 (0.21)
Productivity					
Bald Eagle	66.5	0.06 (0.03)	−0.29 (0.17)	0.11 (0.17)	**−0.66 (0.20)**
Osprey	64.5	**0.13 (0.04)**	−0.11 (0.19)	−0.04 (0.20)	0.35 (0.23)
CPUE	33.8	−0.02 (0.03)	0.02 (0.18)	0.24 (0.19)	−0.20 (0.22)

[a] Bold indicates $P(t) < 0.05$.

decreases as the population increases (Bretagnolle et al. 2008, Elliott et al. 2011, Fasce 2011). However, we found that as the number of breeding Osprey pairs declined, nesting success and productivity also declined, supporting our hypothesis that the cutthroat trout population, as indexed by CPUE, had dropped below the threshold able to sustain a breeding population of Ospreys at Yellowstone Lake. Competition could have also occurred between Ospreys and Bald Eagles as has been found in other studies (Ogden 1975, Prevost 1979), but although the number of Osprey breeding pairs began declining as Bald Eagle breeding pairs peaked around 2001, we did not find a significant interaction between the number of breeding pairs of Ospreys and Bald Eagles.

In contrast to our study, Swenson (1978, 1979) found no evidence that food was a limiting factor for Osprey reproduction from 1972–77, but only 15–18 nests were active annually at Yellowstone Lake during Swenson's study. Prior to Swenson's study, Skinner (1917:118) reported that in 1917 ''…30 nests are on the west shore of Yellowstone Lake'' with an estimated 120 breeding pairs park-wide and in 1924, Sawyer (1924) recorded 24 nests along the entire Yellowstone Lake shoreline, whereas Swenson (1979) recorded only 14. These records suggest a decline in the breeding population of Ospreys at Yellowstone Lake from 1917 to 1972; however, there are no population estimates between these dates to assess population trend for the entire period. Declines in the number of breeding pairs of Ospreys at Yellowstone Lake can be most likely attributed to widespread use of DDT resulting in a substantially reduced North American population during the 1950s through the early 1970s (Houghton and Rymon 1997). Although DDT was found in all of four Osprey eggs collected from Yellowstone Lake nests during Swenson's (1979) study, cutthroat trout did not appear to be the source and Swenson (1979) speculated that DDT was introduced from outside the Yellowstone Lake ecosystem. By 1987, the number of breeding Osprey pairs recovered substantially to 39 in 1987 and peaked at 62 in 1994.

Although the number of Osprey breeding pairs from 1987–2001 was relatively stable or increasing slightly, the number of Bald Eagle breeding pairs increased substantially from nine in 1987 to 20 during 2001–04, with subsequent slight declines until 2007. As with the Osprey population, the Bald Eagle population was also recovering from population declines during the DDT era, but their recovery appeared to be slower than that of Ospreys at Yellowstone Lake. Low levels of DDT were found in both Bald Eagle nestlings tested in 1974 and 1981 and eggs tested in 1983 in and around YNP (Swenson et al. 1986). In contrast with Ospreys, Bald Eagles exhibited declining nesting success and productivity associated with an increasing breeding population, which is consistent with density-dependent population growth. In the Yellowstone Lake area, cutthroat trout represented 23% of prey remains found at Bald Eagle nests (Swenson et al. 1986), a large enough proportion to suggest that declines in CPUE may have some influence on reproduction. However, we found only modest evidence of a relationship between the index of cutthroat trout abundance and number of Bald Eagle breeding pairs in our study, which may be a result of the foraging strategy of Bald Eagles, which are able to take advantage of locally abundant resources (Buehler 2000) such as waterfowl that are concentrated in the ice-free portions of Yellowstone Lake during spring (Swenson et al. 1986).

Cutthroat trout represent the only available food resource for Ospreys and nearly a quarter of the prey consumed during the nesting period by Bald Eagles at Yellowstone Lake. Since 2006, Yellowstone Lake cutthroat trout CPUE has increased and there is some evidence of recruitment of cutthroat trout into the adult population as a result of intensive gill-netting operations aimed at suppressing the lake trout population (T. Koel unpubl. data). A recent study indicated the lake trout population is growing, but at a slower rate than it would be in the absence of suppression efforts (Syslo 2010). Given the importance of cutthroat trout to Ospreys, the recovery of cutthroat trout is important to maintaining a breeding population of Ospreys at Yellowstone Lake, but may have a smaller effect on the breeding Bald Eagle population.

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