J. Raptor Res. 47(2):96–107
© 2013 The Raptor Research Foundation, Inc.

POPULATION TRENDS AND REPRODUCTION OF BALD EAGLES AT BESNARD LAKE, SASKATCHEWAN, CANADA 1968–2012

FRANÇOIS MOUGEOT[1]
Estación Experimental de Zonas Áridas (EEZA-CSIC), Carretera de Sacramento s/n, 04120 La Cañada de San Urbano, Almería, Spain

JON GERRARD
119 Brock Street, Winnipeg, MB, R3N 0Y5 Canada

ELSTON DZUS
Box 686, Plamondon, AB, T0A 2T0 Canada

BEATRIZ ARROYO
Instituto de Investigación en Recursos Cinegéticos (IREC-CSIC-UCLM-JCCM), Ronda de Toledo s/n, 13005 Ciudad Real, Spain

P. NAOMI GERRARD
119 Brock Street, Winnipeg, MB, R3N 0Y5 Canada

CONNIE DZUS
Box 686, Plamondon, AB, T0A 2T0 Canada

GARY BORTOLOTTI
Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK, S7N 5E2 Canada

ABSTRACT.—The study of population regulation is crucial for understanding population dynamics and for conservation. We report on trends in population size and reproduction of Bald Eagles (*Haliaeetus leucocephalus*) at Besnard Lake, Saskatchewan, Canada, during 1968–2012. We investigated the relative importance of density-dependent (population size) and density-independent (climate) factors in explaining variation in population growth rate and productivity. The number of occupied Bald Eagle territories increased until ca. 1988, but remained stable afterwards, fluctuating around ca. 26 pairs. The number of successful pairs increased until only ca. 1977 and remained relatively stable or slightly declined afterwards (ca. 16 successful breeding pairs per year). We found a strong negative density-dependence in all reproduction parameters (mean productivity, nesting success, mean brood size at fledging). Annual production initially increased in the 1970s, but decreased afterwards, while nesting success decreased throughout the whole study period. We also found a strong density-dependence in population growth rate, indicating that the stabilized population was regulated. It probably reached its carrying capacity in the late 1970s, although population size continued to increase until the late 1980s. Mean brood size at fledging was negatively related to the number of failed nesting pairs. Density alone explained most of the variation in breeding performance, although milder springs were weakly associated with a higher nesting success. Finally, we found evidence for regular fluctuations in mean productivity, and particularly in nesting success, with a 5-yr period. We discuss possible mechanisms behind the observed patterns of density-dependent reproduction and implications for our knowledge of how this eagle population is regulated.

KEY WORDS: *Bald Eagle*; Haliaeetus leucocephalus; *climate*; *density-dependence*; *population regulation*; *reproduction*.

[1] Email address: francois.mougeot@eeza.csic.es

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-08-23 via free access

TENDENCIAS POBLACIONALES Y REPRODUCCIÓN DE *HALIAEETUS LEUCOCEPHALUS* EN EL LAGO BESNARD, SASKATCHEWAN, CANADÁ 1968–2012

RESUMEN.—El estudio de la regulación poblacional es crucial para entender la dinámica poblacional y para la conservación. Informamos sobre las tendencias del tamaño poblacional y la reproducción de *Haliaeetus leucocephalus* en el Lago Besnard, Saskatchewan, Canadá, durante el periodo 1968–2012. Investigamos la importancia relativa de los factores dependientes de la densidad (tamaño poblacional) e independientes de la densidad (clima) para explicar la variación de la tasa de crecimiento poblacional y la productividad. El número de territorios ocupados por *H. leucocephalus* aumentó hasta ca. 1988, pero se mantuvo estable después, fluctuando alrededor de ca. 26 parejas. El número de parejas exitosas aumentó sólo hasta ca. 1977 y permaneció relativamente estable o declinó ligeramente después (ca. 16 parejas reproductivas exitosas por año). Encontramos una fuerte dependencia de la densidad negativa en todos los parámetros reproductivos (productividad media, éxito de nidificación, tamaño medio de la nidada en el periodo de volantón). La producción anual aumentó inicialmente en la década de 1970, pero decreció luego, mientras que el éxito de nidificación disminuyó a lo largo de todo el periodo de estudio. También encontramos una fuerte dependencia de la densidad en la tasa de crecimiento poblacional, lo que indica que la población estable estuvo regulada. Esta población probablemente alcanzó su capacidad de carga a fines de la década de 1970, aunque el tamaño poblacional continuó aumentando hasta fines de la década de 1980. El tamaño medio de la nidada en el periodo de volantones estuvo negativamente relacionado con el número de fracasos de parejas reproductivas. La densidad sola explicó la mayor parte de la variación del desempeño reproductivo, aunque las primaveras más suaves estuvieron débilmente asociadas con un éxito de nidificación mayor. Finalmente, encontramos evidencia de fluctuaciones regulares en la productividad media, en particular en el éxito de nidificación, en un periodo de cinco años. Discutimos los posibles mecanismos que subyacen detrás de los patrones observados de reproducción dependiente de la densidad y las implicancias para nuestro conocimiento de cómo se regula esta población de águilas.

[Traducción del equipo editorial]

A fundamental issue in population ecology lies in understanding the processes that limit or regulate animal populations (Newton 1979, 1998). Our understanding of these processes has been illuminated by several long-term studies on raptors, particularly on those populations that recovered after strong human-induced declines associated with persecution or DDT poisoning (e.g., Newton and Wyllie 1992, Ferrer and Donazar 1996, Nicoll et al. 2003, Bretagnolle et al. 2008, Watts et al. 2008, Elliott et al. 2011).

Population growth and dynamics may be constrained or affected by many different factors, both biotic and abiotic, which may affect available resources in the environment and competition levels for these resources (Newton 1979). Density-independent factors, such as climate, can influence demographic rates, and thus population growth and distribution patterns (Caughley 1988, Garcia and Arroyo 2001, Redpath et al. 2002). Additionally, if competition for limiting resources such as food, breeding territories, nesting sites, or mates occurs, the degree of competition typically increases with population size or density (e.g., Carrete et al. 2006a, 2006b, Bretagnolle et al. 2008). Density therefore often affects demographic parameters such as reproduction, emigration probability and survival rates, and thereby rates of population growth or decline.

Long-term studies of large raptors are relatively rare, because of the logistic constraints of monitoring large areas over many years. Despite potential methodological limitations (Balbontín and Ferrer 2008, Carrete et al. 2008), long-term monitoring projects remain extremely valuable for understanding the processes limiting or regulating populations. Understanding whether density-dependence occurs, with which demographic parameters and by which mechanisms, is crucial not only for understanding population dynamics but also for conservation (e.g., Carrete et al. 2006a).

In raptors there is broad evidence that population density influences breeding performance (Houston and Schmutz 1995, Ferrer and Donazar 1996, Nicoll et al. 2003, Bretagnolle et al. 2008, Elliott et al. 2011), and also some evidence that density influences survival (e.g., Nicoll et al. 2003, Serrano et al. 2005), thereby potentially contributing to the regulation of stable populations around a certain carrying capacity. However, the density-dependence relationships are complex and variable (Penteriani et al. 2006) and the mechanisms underlying the density-dependence relationships are still debated (Balbontín and Ferrer 2008, Carrete et al. 2008). The first steps consist of looking for evidence of population regulation, and determining the

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-08-23 via free access

relative importance of density-dependent and density-independent factors (such as climate) in explaining variation in population growth rate and key demographic parameters such as reproduction and survival.

The Bald Eagle (*Haliaeetus leucocephalus*) is a large diurnal fish-eating raptor that occurs throughout the U.S.A., Canada, and northern Mexico (Gerrard and Bortolotti 1988, Buehler 2000). It is found near large bodies of open water with an abundant food supply and mature trees for nesting. Its diet consists mainly of fish, but it is also an opportunistic feeder (Gerrard and Bortolotti 1988, Dzus and Gerrard 1993, Buehler 2000). In Canada, except for British Columbia and Nova Scotia, it is mainly a breeding summer visitor, leaving after breeding to winter in the U.S.A.

In the mid- to late 1960s, the Bald Eagle became rare in the contiguous United States, mainly due to persecution by humans and negative effects of pesticides (DDT) on reproduction (Buehler 2000). The species was listed for protection under the Bald Eagle Protection Act in 1940, and the entire Bald Eagle population in the United States was listed for protection in 1978 under the Endangered Species Act of 1973. From the 1970s and 1980s, many Bald Eagle populations recovered following reductions in human persecution and DDT use (Kirk and Hyslop 1998, Buehler 2000, Watts et al. 2008). The species was removed from the U.S. federal government's list of endangered species (transferred to the list of threatened species) in 1995, and was completely delisted in 2007. In Canada, the Bald Eagle is currently considered ''Not-At-Risk,'' and as ''secure'' in the province of Saskatchewan (G Rank: G5; S Rank S5B, S4M, S4N; Saskatchewan Conservation Data Center 2012). There have been many studies on aspects of its breeding biology and population studies in the areas where the species had been decimated but recovered (Steidl et al. 1997, Buehler 2000, Elliott et al. 2005, Watts et al. 2008, Elliott et al. 2011). However, fewer studies have evaluated longer term population changes in the species' core populations (Gerrard et al. 1992, Dzus and Gerrard 1993), or the density-dependent and density-independent factors affecting those populations (Watts et al. 2008, Elliott et al. 2011).

In this study, our aim was to evaluate long-term changes in population size and breeding performance of Bald Eagles, using 45 yr of data from a nesting population located in the center of its breeding distribution in Canada (Besnard Lake, Saskatchewan). We also assess the relative importance of density-dependent (local population size) and of density-independent (local climate) factors in explaining variation in breeding performance and population change.

METHODS

Study Area. The study was carried out on Besnard Lake, Saskatchewan, situated along the southern boundary of the Canadian Shield (55°22′58.79″N, 106°2′9.03″W). Besnard Lake encompasses 160 km² of water area and has a very convoluted shoreline with approximately 250 islands. Its average depth is 7.9 m, with a maximum depth of approximately 30 m (Chen 1974). It is surrounded by low forested hills (not exceeding 100 m in height). White spruce (*Picea glauca*), black spruce (*P. mariana*), jack pine (*Pinus banksiana*) and trembling aspen (*Populus tremuloides*) predominate near the lake shore. Besnard Lake freezes in the winter, with ice breaking up usually by mid-May. Bald Eagles return to Besnard Lake from their wintering quarters located in midwestern U.S.A. in late March–early April and usually lay eggs in April and May (Gerrard et al. 1978, Gerrard and Bortolotti 1988). Trees used for nesting are mostly trembling aspen (54%), spruce (30%) and jack pine (15%; Gerrard et al. 1975). Females lay up to three eggs, but most commonly only one or two young fledge in successful nests. During breeding, Bald Eagles on Besnard Lake feed mostly on fish, in particular on cisco (*Coregonus artedii*) and white sucker (*Catostomus commersonii*; Gerrard and Bortolotti 1988). Nest failures have been associated with poor position of nest sites, human disturbances, inexperience of adults, or occasionally illness (Whitfield et al. 1974, Gerrard et al. 1983, Gerrard and Bortolotti 1988, Gerrard et al. 1992).

Population Monitoring. The Bald Eagle nesting population at Besnard Lake has been monitored yearly since 1968. The status of nests was evaluated during incubation in April or May, and then at intervals during June, July, and August (Gerrard et al. 1983, Gerrard et al. 1992). In order to estimate total population size (number of occupied breeding areas), aerial censuses were performed in July 1968, May 1969, July 1969, April 1973 and May 1974, April 1986, May 1987, May 1997, May 2003, and May 2012. All other censuses were conducted by boat (Gerrard et al. 1990, Gerrard et al. 1992). Coverage between 1968 and 1971 may be incomplete, but subsequently it is assumed that all nests were found annually

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-08-23 via free access

(Gerrard et al. 1992). From this monitoring, we obtained the population and breeding parameters used in this study.

An occupied breeding area was defined as an area with one or more nests within the range of one mated pair, and with a mated pair consistently using the area in a given year. Nests with no incubating adult, eggs, or young were also considered as occupied breeding areas if the average number of adults seen within 0.8 km of the nest on multiple visits to the nest was one or more (Gerrard et al. 1983, 1992). The number of occupied breeding areas was used as an estimate of total population size (N), and as an index of the total number of territorial pairs in a given year. Population growth rate from year t to t+1 was calculated as the Log_e ($N_{\text{year t+1}}/N_{\text{year t}}$). The number of successful pairs was defined as the number of occupied breeding areas where at least one young that reached the minimum acceptable age for assessing success (here 6–9 wk old, i.e., when the young eaglets were banded). Data on population size (N) were available for 45 yr (1968–2012).

Data on the reproduction of Bald Eagles were summarized and defined as follows, following Steenhof and Newton (2007): annual production, as the total number of young that reached the minimum acceptable age for assessing success (here 6–9 wk old) in the population in a given year; nesting success, as the percent of occupied breeding areas where at least one young was raised to a minimum acceptable fledging age (6–9 wk old) in a given year; mean productivity, as the mean number of young that reached the minimum acceptable age for assessing success per occupied breeding area in a particular year; mean brood size at fledging, as the mean number of young that reached the minimum acceptable age for assessing success per successful pair in a particular year. Data on reproduction (annual production, nesting success, mean productivity and mean brood size at fledging) were available for 44 yr (1968–2011).

Climate Data. We obtained climate data from the National Climate Data and Information Archive (www.climate.weatheroffice.gc.ca) for the locality of La Ronge, Saskatchewan (Climate ID: 4064150; Latitude: 55°09′00.000″N, 105°16′00.000″W; elevation: 378.6 m). We selected this weather station because it was nearest to the study area (50–60 km away) and had the longest time series of data available over the study period. We obtained for the period 1968–2007 data that consisted of monthly average temperature (in °C) and precipitation (mm of rainfall and water equivalent of snowfall per day). In order to simplify the climate data for a given year, we calculated average spring temperature (spring T) and precipitation (spring P) as averages for the months of March, April, and May (corresponding to the arrival to breeding grounds and incubation period of Bald Eagles) and average summer temperature (summer T) and precipitation (summer P) as averages for the months of June, July, and August (corresponding to the rearing period of Bald Eagles).

Statistical Analyses. We used SAS 9.2 for all the analyses. We used GLMs and piecewise regression (NLIN procedure) to analyze temporal trends in population and reproduction parameters. Piecewise regression allowed us to determine potential changes in linear trends before and after a certain year or cut-off point, by estimating simultaneously four parameters (intercept, year when the relationship changed, slope before that year and slope after that year). We used GLMs to analyze density-dependence in study parameters. We used stepwise regression with a backward selection (proc REG) to investigate climate effects on population parameters. Initial models included population size (N), year, as well as climate variables (spring T, spring P, summer T, and summer P). Finally, we tested for autocorrelation in reproduction parameters using the Durbin-Watson test (AUTOREG procedure in SAS). All tests are two-tailed and all data and parameter estimates are given as means ± SE.

RESULTS

Trends in Population Size and Reproduction. Throughout the study period (1968–2012), the number of occupied breeding areas at Besnard Lake initially increased during the 1970s and then stabilized (Fig. 1a). Using piecewise regressions, we identified two separate linear trends with a cut-off point in 1988 (±2.5 yr; NLIN procedure; $F_{3,41} = 22.46$; $P < 0.001$). The eagle population increased until 1988 (slope ± SE: 0.581 ± 0.103) and remained relatively stable afterwards (slope: −0.077 ± 0.084; Fig. 1a). Changes in the number of successful pairs also followed this pattern. Piecewise regression identified an earlier cut-off point in 1977 (±1.9 yr; NLIN; $F_{3,40} = 9.02$; $P < 0.001$). The number of successful pairs increased until 1977 (slope: 0.855 ± 0.261), but stabilized or slightly declined between 1977 and 2011 (slope: −0.057 ± 0.041; Fig. 1a). Annual production showed a sim-

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-08-23 via free access

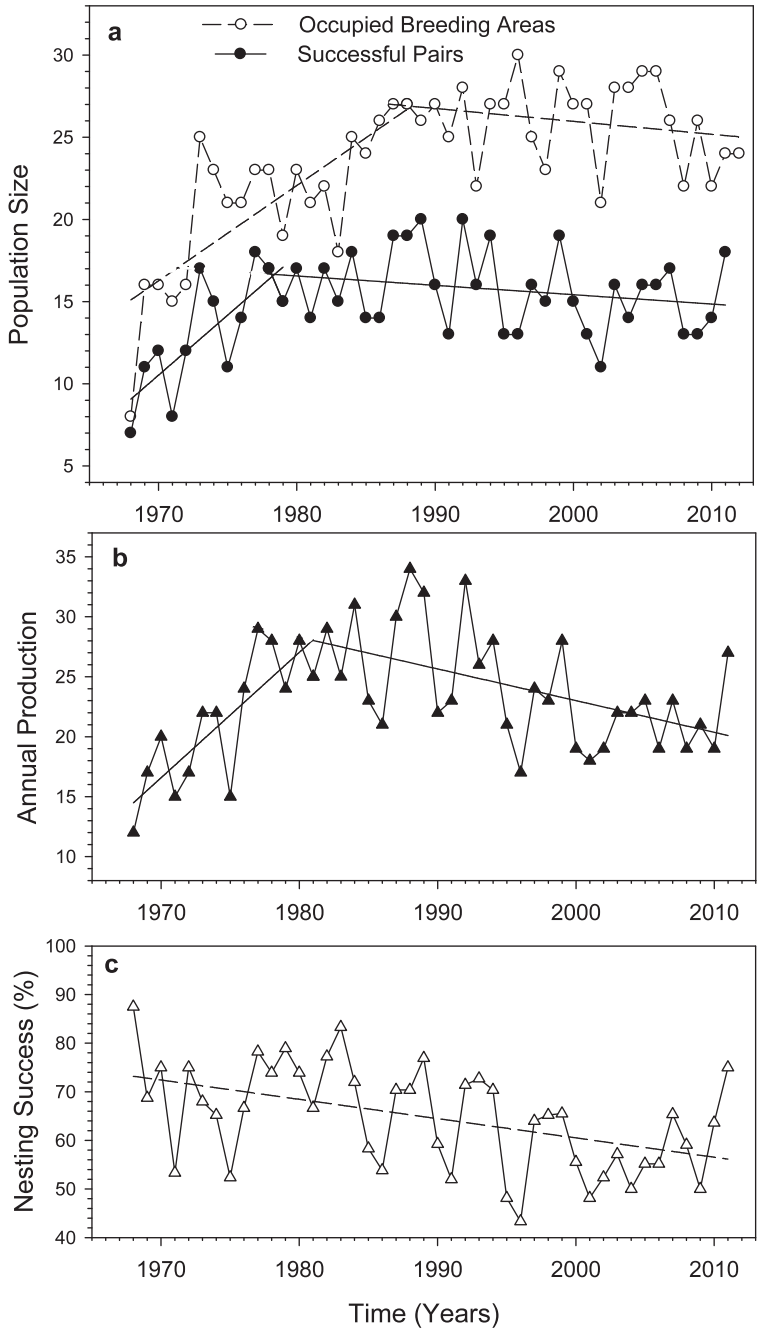

Figure 1. Changes over time (1968–2012) in the (a) population size (number of occupied breeding areas [open circles] and number of successful breeding pairs [filled circles]), (b) annual production (black triangles) and (c) nesting success of Bald Eagles at Besnard Lake 1968–2012.

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-08-23 via free access

ilar initial increase until 1981 (±1.9 years; NLIN procedure; $F_{3,40} = 11.07$; $P < 0.001$; slope: 1.046 ± 0.258), followed by a slow decrease between 1981 until 2011 (slope: −0.285 ± 0.082; Fig. 1b). Throughout the study period (1968–2011), nesting success declined linearly (Genmod: $F_{1,33} = 12.10$; $P < 0.01$; slope: −0.023 ± 0.007; Fig. 1c).

Density-dependence. Population growth rate (Log N_{t+1}/N_t) was negatively related to population size (N_t; $F_{1,42} = 31.47$; $P < 0.001$; slope: −0.026 ± 0.005; $R^2 = 0.428$; Fig. 2a). Similarly, mean productivity was significantly negatively related to population size ($F_{1,42} = 20.09$; $P < 0.001$; slope: −0.028 ± 0.006; $R^2 = 0.323$; Fig. 2b): the more eagles occupying territories, the fewer young they produced per pair. Both the nesting success (Genmod: $F_{1,42} = 11.67$; $P = 0.006$; slope: −0.056 ± 0.017) and mean brood size at fledging were negatively correlated with population size (GLM: $F_{1,42} = 9.44$; $P = 0.004$; slope: −0.015 ± 0.005; $R^2 = 0.183$; Fig. 2b). If we excluded one outlier (for the year with a population size of 8; Fig. 2b), similar relationships were found between population and productivity ($F_{1,41} = 12.61$; $P < 0.0001$; slope: −0.0262 ± 0.007), nesting success ($F_{1,41} = 9.15$; $P < 0.001$; slope: −0.053 ± 0.018) and mean brood size at fledging ($F_{1,41} = 8.29$; $P < 0.001$; slope: −0.0168 ± 0.006).

Considering the number of failed nesting pairs in a given year (the number of occupied breeding areas without success), there was an even stronger negative relationship between mean brood size at fledging and numbers of failed nesting pairs (GLM: $F_{1,42} = 10.44$; $P = 0.002$; slope: −0.021 ± 0.006; $R^2 = 0.200$). Thus, when there were more unsuccessful nesting eagles within the population, the successful pairs produced fewer young.

Climate Effects. Throughout the study period for which we obtained climate data (1968–2007), we did not detect significant temporal trends in mean spring temperature ($F_{1,38} = 0.30$; $P = 0.588$), spring precipitation ($F_{1,38} = 1.47$; $P = 0.232$) or summer precipitation ($F_{1,38} = 0.94$; $P = 0.340$). However, there was a tendency for increasing mean summer temperatures ($F_{1,38} = 3.31$; $P = 0.077$; slope: 0.025 ± 0.014).

We investigated whether climate, in addition to population size (N_t), explained the Bald Eagle population growth rate or reproduction, using stepwise regressions and a backward selection process. Variation in population growth rate was explained by population size (N_t), but not by any of the climate variables (all $P > 0.150$). Variation in mean productivity was explained by population size (N_t; $F_{1,36} = 18.27$; $P < 0.001$; slope: −0.029 ± 0.006; partial $R^2 = 0.331$) and marginally explained by spring temperature ($F_{1,36} = 2.55$; $P = 0.119$; slope: 0.027 ± 0.016; partial $R^2 = 0.044$), but not by any other climate variable (all $P > 0.15$). There was a tendency for a relatively greater productivity in years with warmer springs. Nesting success varied with population size ($F_{1,36} = 12.19$; $P = 0.001$; slope: −1.229 ± 0.317; partial $R^2 = 0.248$) and with spring temperature ($F_{1,36} = 3.49$; $P = 0.069$; slope: 1.558 ± 0.834; partial $R^2 = 0.067$), but not with other climate variables (all $P > 0.15$). Again, nesting success was relatively higher in years with warmer springs. Variation in mean brood size at fledging was only explained by population size ($F_{1,37} = 9.93$; $P = 0.003$; $R^2 = 0.217$), but not by any of the climate variables (all $P > 0.15$).

Fluctuations in Breeding Performance. After controlling for the effect of density on reproduction parameters (using the residuals from GLMs of mean productivity, nesting success or mean brood size at fledging on population size, N), we found evidence for autocorrelation with a 5-yr time-lag for the relative productivity (Durbin-Watson test; DW = 1.142; $P = 0.006$ for an order of 5). For the relative nesting success, the autocorrelation was significant for time-lags of 5 yr (DW = 0.989; $P < 0.001$ for an order of 5) and 10 yr (DW = 1.091, $P = 0.037$ for an order of 10; Fig. 3). No significant autocorrelation was detected for the relative mean brood size at fledging.

DISCUSSION

Analyses of Bald Eagle population trends on Besnard Lake, Saskatchewan, showed a period of increase during the 1970s and 1980s, followed by a relatively stable phase (Fig. 1a). In trying to understand these changes in population dynamics, we considered factors influencing eagles on their wintering grounds in the midwestern U.S.A. and on their breeding grounds of northern Saskatchewan. In 1940, the United States passed legislation to protect Bald Eagles, after which there was a gradual increase in the number of Bald Eagles wintering in the midwestern U.S.A. until at least the early 1970s (Buehler 2000, Steenhof et al. 2002). In the 1970s and 1980s, Bald Eagle populations in the western Great Lakes were recovering from DDT (Buehler 2000). Unlike most other North American populations (Bowerman et al. 1998, Watson et al. 2002, Watts et al. 2007), the Bald Eagle population of Besnard Lake was unlikely to have been affected by DDT, as DDT was not used in Saskatchewan's

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-08-23 via free access

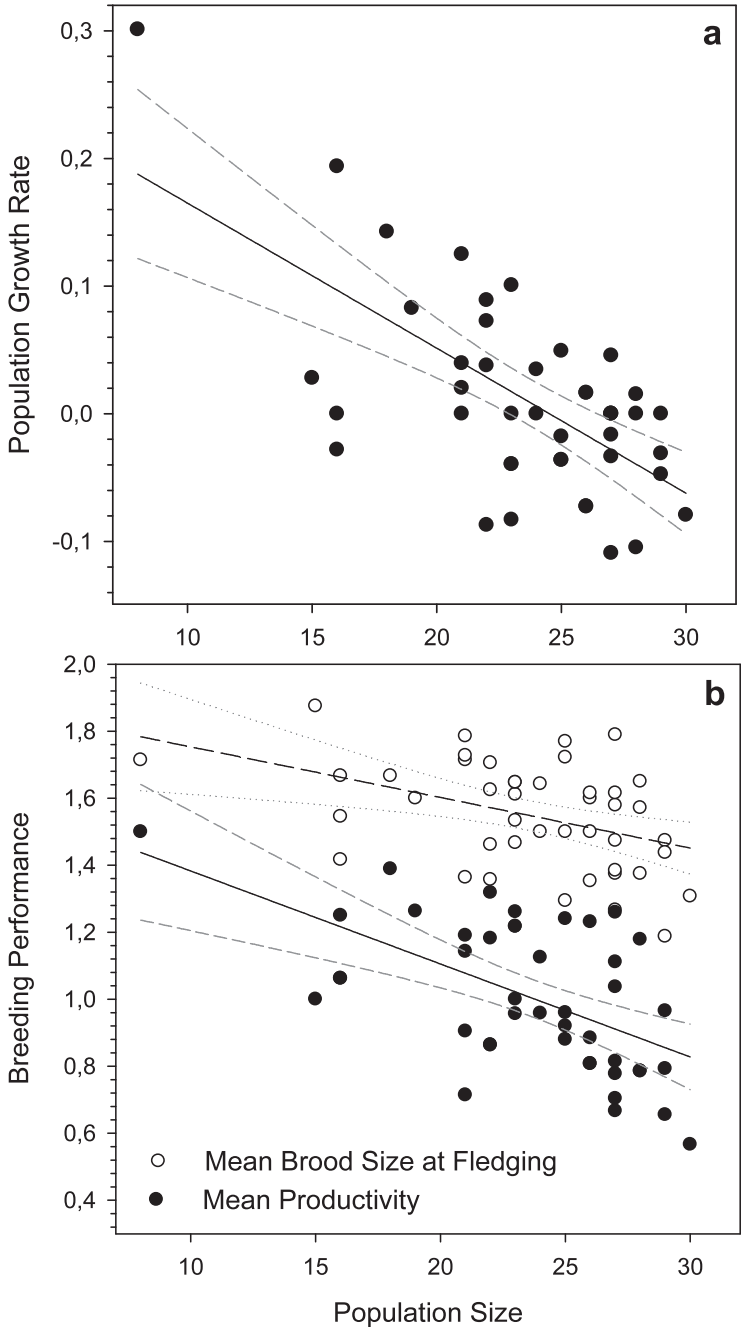

Figure 2. Density-dependence of the (a) population growth rate from year t to t+1 and (b) reproduction in year t (mean productivity [open circles] or mean brood size at fledging [filled circles]) of Bald Eagles at Besnard Lake. On the X-axis, population size refers to the number of occupied breeding areas in year t.

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-08-23 via free access

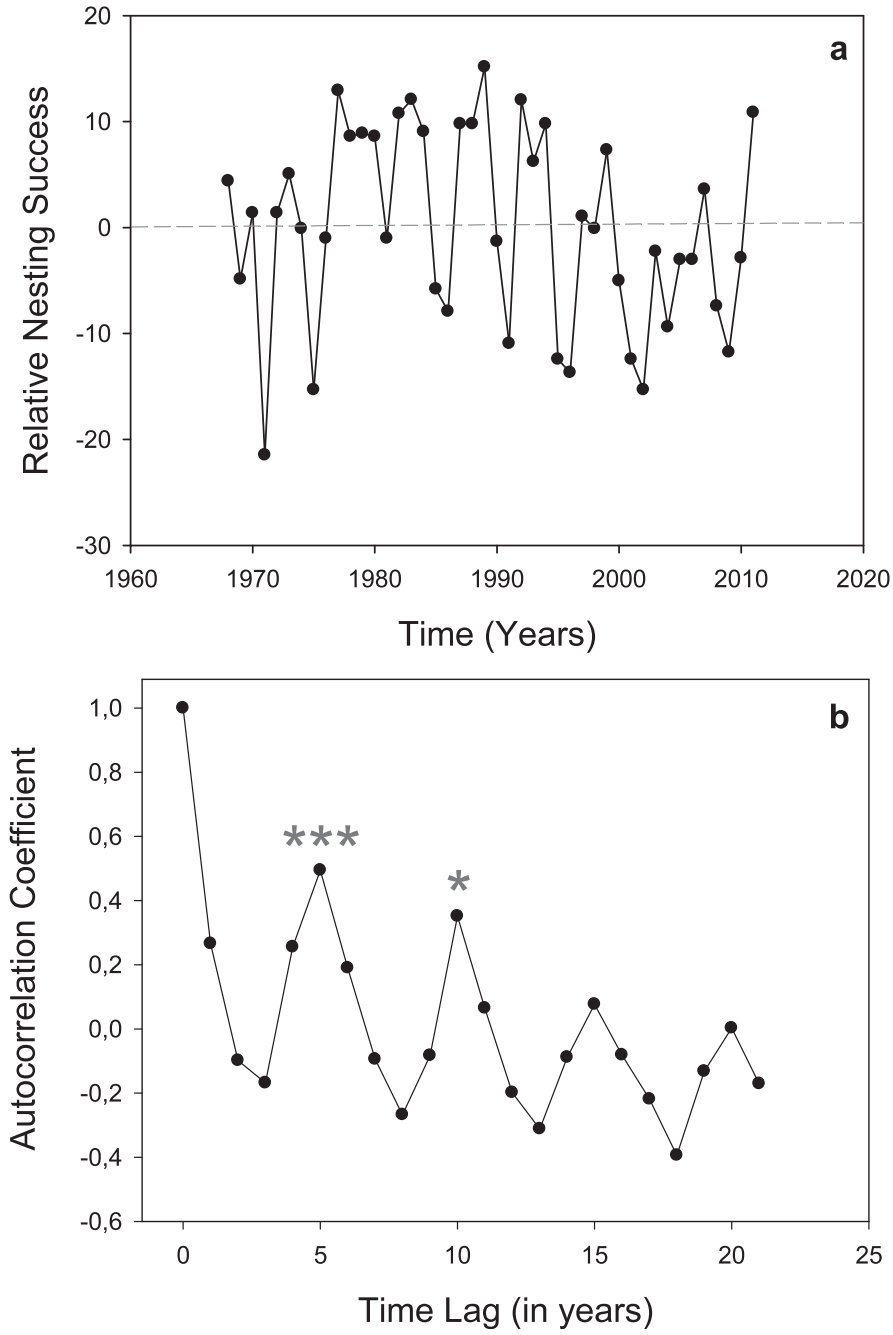

Figure 3. (a) Changes over time (1968–2011) in the relative nesting success of Bald Eagles (nesting success corrected for population size; see text) and (b) auto-correlogram for this variable, showing a 5-yr period (***: indicates a significant correlation at the $P < 0.001$ level; *: indicates a significant correlation at the $P < 0.05$ level).

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-08-23 via free access

boreal forests and Saskatchewan Bald Eagles tended to winter in areas which were less contaminated by DDT (Gerrard and Bortolotti 1988). So, potentially, the population increase at Besnard Lake in the 1970s and 1980s had to do with a reduced persecution and higher winter survival, and may have been the tail end of an earlier increase. Interestingly, the total nesting population size increased until ca. 1988, but the number of successful breeding pairs increased only until 1977, i.e., 10 yr earlier, suggesting two carrying capacities for this population of ca. 26 territorial pairs and of ca. 15 successful breeding pairs, respectively. In parallel with the initial population increase, annual production increased until ca. 1981, potentially contributing to local recruitment and the increase in the number of occupied eagle territories until the late 1980s. However, annual production decreased afterwards, from an average of 30–35 young fledged per year in the 1980s to 20–25 young fledged per year in the 2000s (Fig. 1b). Throughout the whole study period (1968–2011), the proportion of territorial eagles successfully fledging young declined linearly (Fig. 1c). To better understand these changes over time, we looked at density-dependent and climate effects on breeding performance.

We found strong evidence of density-dependence in the Besnard Lake Bald Eagle population. Population growth rate from year to year was strongly negatively related to population density (Fig. 2a), indicating that the population had reached its carrying capacity and was regulated. Bald Eagle breeding performance parameters (annual production, nesting success, mean productivity, and mean brood size at fledging) also negatively correlated with population density (Fig. 2b), indicating that reproduction may be one of the demographic targets of density-dependent regulation.

In raptors, density-dependent reproduction has been found in many species and populations that have been studied. It has been explained in terms of either reduced prey availability (Houston and Schmutz 1995), an increased use of territories of lower quality (Ferrer and Donazar 1996) or a negative impact of floaters (i.e., subadults or adults that are not associated with specific nesting territories and do not reproduce) on the performance of breeding birds (Carrete et al. 2006a, Bretagnolle et al. 2008). Floaters often account for a large proportion of the population at high density (Kenward et al. 2000), and, when abundant, they may strongly affect breeding population properties such as density-dependence (Penteriani et al. 2005, 2006, Bretagnolle et al. 2008). A negative relationship between reproduction and density may also result from habitat heterogeneity, as at low density only the best habitats are occupied (Ferrer and Donazar 1996), or from a buffer effect, with younger or lower-quality individuals occupying lower-quality sites thus reducing average reproductive rates (Ferrer et al. 2006). Sequential habitat occupancy (whereby the best habitats for breeding are occupied first and the poorer habitats occupied subsequently) may therefore be an alternative explanation for a decline in productivity with higher breeding density, as the increase in the number of pairs may have led birds to use poorer habitats. In that case, however, the birds in good habitats should show a constant breeding performance (Mearns and Newton 1988, Ferrer and Donazar 1996). In another study, density-dependent declines in Bald Eagle reproduction were found to be independent of nesting site quality or territory (Elliott et al. 2011). Unfortunately, we had no precise information to control for territory quality, or marked birds of known age to control for difference in breeding experience. Previous works suggest that food supply rather than nest-site availability explains variation in Bald Eagle densities in Saskatchewan (Dzus and Gerrard 1993). Moreover, at Besnard Lake the variance in productivity did not appear to have increased, but rather decreased during the study period (J. Gerard, E. Dzus, and G. Bortolotti, unpubl. data), suggesting that density-dependence similarly affected all pairs. An alternative explanation may be regulation by competition, which may occur through two main processes: direct behavioral interference and resource depletion (Carrete et al. 2006a, Bretagnolle et al. 2008). Although interference refers to food intake rate, it can also apply to territory establishment or mating and mate choice (e.g., Mougeot et al. 2002, Bretagnolle et al. 2008). The higher competition for food resources when the population is at carrying capacity, or a higher interference competition when there are more breeding birds and floaters around, may drive the density-dependent effects on reproduction. Boat surveys of Bald Eagle numbers on Besnard Lake were carried out between 1976 and 2011 (J. Gerrard unpubl. data). The numbers of adults in the first two weeks of July on half the lake slightly increased throughout that time (being 32 in 1976, 32 in 1979, 35 in 1984, 35 in 1990, and 35 in 2003–2005), whereas the number of immature eagles (1 to 3 yr of age) strongly decreased (21 in 1976, 21 in 1979, 10 in 1984, 14 in 1990 and 6 in 2003–2005). The observed decline in

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-08-23 via free access

mean productivity was not strong enough to explain this decline in the abundance of immature eagles, so these data support the contention that the adult population of Bald Eagles became saturated by the early 1980s and that immature eagles may have been crowded out and forced to forage off Besnard Lake. A crowded population may be more exposed to interference competition, with more intrusions by nonbreeding eagles at nest sites and more competition at foraging sites, which may ultimately result in a poorer breeding performance (Carrete et al. 2006a, Bretagnolle et al. 2008). The observation that the breeding performance of successful pairs was negatively related to the number of failed nesting birds in the population is consistent with this idea, but further work is needed to determine the mechanism of density-dependent depression of reproduction. Data on differences in breeding performance at the territory level, and on the distribution of productivity each year should be used in the future in order to determine the exact mechanisms of density dependent reproduction (Ferrer et al. 2006) but are unfortunately unavailable at this stage for the Besnard Lake population.

Variation in annual breeding performance was mostly explained by density-dependence, much more so than by local climate. We found only a weak positive effect of average spring temperatures on breeding performance, which explained <5% of the variation, whereas density-dependence alone explained 32% of the variation in mean productivity. A positive association between spring temperature and nesting success and mean productivity is consistent with previous studies on Bald Eagles (Gerrard et al. 1992), and adverse weather conditions are known to cause egg failure or the death of young nestlings, thereby causing nest abandonment, as well as reducing food provisioning rates to young (Stalmaster and Plettner 1992, Steidl et al. 1997, Elliott et al. 2005). A weak influence of local climate is not surprising, as the negative effects of climate on demographic rates, and therefore on population growth rates are likely to be greatest at range boundaries (Caughley 1988, Garcia and Arroyo 2001) and Besnard Lake is within the core of the Bald Eagle range. In 1968–2007, local climate change was apparent, in terms of increasing summer temperatures, but this was unlikely to explain the changes in mean productivity or the observed population trends. We had no evidence that local climate influenced population growth rate. However, future studies should look for impacts of climate and density-dependence on wintering areas, which may affect overwinter survival, the condition of Bald Eagles upon their return to their breeding grounds, or the timing of their return, and thereby have indirect effects on their reproduction.

The long-term data on reproduction also showed evidence of regular cyclic fluctuations in Bald Eagle breeding performance (mean productivity, and more specifically, nesting success; Fig. 1c; Fig. 3). After taking into account the effect of density on reproduction, we found that nesting success fluctuated with a regular 5-yr period (Fig. 3). This may be related to fluctuations in food abundance, a primary factor affecting the reproduction of eagles (Whitfield et al. 1974, Whitfield and Gerrard 1985, Gerrard et al. 1992, Anthony et al. 1999; Dykstra et al. 1998, Hoff et al. 2004). Fish are an important part of the diet of Bald Eagles both in breeding and wintering areas (Gerrard and Bortolotti 1988) and fish populations are often characterized by predictable cyclic fluctuations in abundance, with a cycle period equal to the time taken to reach maturity (Kendall et al. 2002, Townsend 2006). Future studies should further investigate which factors drive these fluctuations in Bald Eagle breeding performance, and in particular if some of the main prey species of Bald Eagles at Besnard Lake (i.e., cisco or white sucker) fluctuate in abundance. Factors influencing cyclic variation in eagle productivity may also relate to fluctuating conditions or resources on the wintering areas or areas used during the return migration, with potential carry-over effects on the condition of birds prior to breeding.

ACKNOWLEDGMENTS

We dedicate this work to Gary Bortolotti, who had the original idea of looking at density-dependence patterns in the long-term data on Bald Eagles of Besnard Lake. The individual author's contributions were as follows: JG, ED, PNG, CD and GB collected the long-term data on Bald Eagles; FM did the statistical analyses, following preliminary ones made by GB; FM and BA led the writing with help from JG and ED. Over the 45 years of the study, many people have assisted in the collection of data, and we greatly appreciate their contributions. We particularly thank Zachary Waldner, Pauline, Charles and Thomas Gerrard who helped in collecting the data. We also thank S. Postupalsky and an anonymous referee for their help in improving the manuscript.

LITERATURE CITED

ANTHONY, R.G., A.K. MILES, J.A. ESTES, AND F.B. ISAACS. 1999. Productivity, diets, and environmental contaminants in nesting Bald Eagles from the Aleutian archipelago. *Environmental Toxicology and Chemistry* 18: 2054–2062.

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-08-23 via free access

BALBONTÍN, J. AND M. FERRER. 2008. Density-dependence by habitat heterogeneity: individual quality versus territory quality. *Oikos* 117:1111–1114.

BOWERMAN, W.W., D.A. BEST, T.G. GRUBB, G.M. ZIMMERMAN, AND J.P. GIESY. 1998. Trends of contaminants and effects in Bald Eagles of the Great Lakes basin. *Environmental Monitoring and Assessment* 53:197–212.

BRETAGNOLLE, V., F. MOUGEOT, AND J.C. THIBAULT. 2008. Density dependence in a recovering Osprey population: demographic and behavioural processes. *Journal of Animal Ecology* 77:998–1007.

BUEHLER, D.A. 2000. Bald Eagle (*Haliaeetus leucocephalus*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 506. The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union, Washington, DC U.S.A.

CARRETE, M., J.A. DONAZAR, AND A. MARGALIDA. 2006a. Density-dependent productivity depression in Pyrenean Bearded Vultures: implications for conservation. *Ecological Applications* 16:1674–1682.

———, J.A. SANCHEZ-ZAPATA, J.L. TELLA, J.M. GIL-SANCHEZ, AND M. MOLEON. 2006b. Components of breeding performance in two competing species: habitat heterogeneity, individual quality and density-dependence. *Oikos* 112:680–690.

———, J.L. TELLA, J.A. SANCHEZ-ZAPATA, M. MOLEON, AND J.M. GIL-SANCHEZ. 2008. Current caveats and further directions in the analysis of density-dependent population regulation. *Oikos* 117:1115–1119.

CAUGHLEY, A. 1988. The edge of the range. *Journal of Animal Ecology* 57:771–785.

CHEN, M.Y. 1974. The fisheries biology of Besnard Lake, 1973. Sask. Dept. Tourism Renewable Res., Fisheries Tech. Rep. 74-7. Saskatoon, Saskatchewan, Canada.

DYKSTRA, C.R., M.W. MEYER, D.K. WARNKE, W.H. KARASOV, D.E. ANDERSEN, W.W. BOWERMAN, IV, AND J.P. GIESY. 1998. Low reproductive rates of Lake Superior Bald Eagles: low food delivery rates or environmental contaminants? *Journal of Great Lakes Research* 24:32–44.

DZUS, E.H. AND J.M. GERRARD. 1993. Factors influencing Bald Eagle densities in northcentral Saskatchewan. *Journal of Wildlife Management* 57:771–778.

ELLIOTT, K.H., J.E. ELLIOTT, L.K. WILSON, I. JONES, AND K. STENERSON. 2011. Density-dependence in the survival and reproduction of Bald Eagles: linkages to chum salmon. *Journal of Wildlife Management* 75:1688–1699.

———, C.E. GILL, AND J.E. ELLIOTT. 2005. The influence of tide and weather on provisioning rates of chick-rearing Bald Eagles in Vancouver Island, British Columbia. *Journal of Raptor Research* 39:1–10.

FERRER, M. AND J.A. DONAZAR. 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. *Ecology* 77:69–74.

———, I. NEWTON, AND E. CASADO. 2006. How to test different density-dependent fecundity hypotheses in an increasing or stable population. *Journal of Animal Ecology* 75:111–117.

GARCIA, J.T. AND B.E. ARROYO. 2001. Effect of abiotic factors on reproduction in the centre and periphery of breeding ranges: a comparative analysis in sympatric harriers. *Ecography* 24:393–402.

GERRARD, J. AND G.R. BORTOLOTTI. 1988. The Bald Eagle: haunts and habits of a wilderness monarch. Smithsonian Institution Press, Washington, DC U.S.A.

———, ———, E.H. DZUS, P.N. GERRARD, AND D.W.A. WHITFIELD. 1990. Boat census of Bald Eagles during the breeding season. *Wilson Bulletin* 102:720–726.

———, P.N. GERRARD, G.R. BORTOLOTTI, AND E.H. DZUS. 1992. A 24-year study of Bald Eagles on Besnard Lake, Saskatchewan. *Journal of Raptor Research* 26:159–166.

———, ———, ———, AND D.W.A. WHITFIELD. 1983. A 14 year study of Bald Eagle reproduction on Besnard Lake, Saskatchewan. Pages 47–57 *in* D.M. Bird [ED.], Biology and management of Bald Eagles and Ospreys. Harpell Press, Ste. Anne de Bellevue, Quebec, Canada.

———, P. GERRARD, W.J. MAHER, AND W.D.A. WHITFIELD. 1975. Factors influencing nest site selection of Bald Eagles in northern Saskatchewan and Manitoba. *Blue Jay* 33:169–176.

———, D.W.A. WHITFIELD, P. GERRARD, P.N. GERRARD, AND W.J. MAHER. 1978. Migratory movements and plumage of Saskatchewan Bald Eagles. *Canadian Field Naturalist* 92:375–382.

HOFF, M.H., M.W. MEYER, J. VAN STAPPEN, AND T.W. FRATT. 2004. Relationships between Bald Eagle productivity and dynamics of fish populations and fisheries in the Wisconsin waters of Lake Superior, 1983–1999. *Journal of Great Lakes Research* 30:434–442.

HOUSTON, C.S. AND J.K. SCHMUTZ. 1995. Declining reproduction among Swainson's Hawks in prairie Canada. *Journal of Raptor Research* 29:198–201.

KENDALL, B.E., J. PRENDERGAST, AND O. BJØRNSTAD. 2002. The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles. *Ecology Letters* 1:160–164.

KENWARD, R.E., S.S. WALLS, K.H. HODDER, M. PAHKALA, S.N. FREEMAN, AND V.R. SIMPSON. 2000. The prevalence of non-breeders in raptor populations: evidence from rings, radio-tags and transect surveys. *Oikos* 91:271–279.

KIRK, D.A. AND C. HYSLOP. 1998. Population status and recent trends in Canadian raptors: a review. *Biological Conservation* 83:91–118.

MEARNS, R. AND I. NEWTON. 1988. Factors affecting breeding success of peregrines in south Scotland. *Journal of Animal Ecology* 57:903–916.

MOUGEOT, F., J.C. THIBAULT, AND V. BRETAGNOLLE. 2002. Effects of territorial intrusions, courtship feedings and mate fidelity on the copulation behaviour of the Osprey. *Animal Behaviour* 64:759–769.

NEWTON, I. 1979. Population ecology of raptors. T. and A.D. Poyser, Berkhamsted, U.K.

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-08-23 via free access

———. 1998. Population limitation in birds. Academic Press, London, U.K.

——— AND I. WYLLIE. 1992. Recovery of a sparrowhawk population in relation to declining pesticide contamination. *Journal of Applied Ecology* 29:476–484.

NICOLL, M.A.C., C.G. JONES, AND K. NORRIS. 2003. Declining survival rates in a reintroduced population of the Mauritius Kestrel: evidence for non-linear density dependence and environmental stochasticity. *Journal of Animal Ecology* 72:917–926.

PENTERIANI, V., F. OTALORA, AND M. FERRER. 2005. Floater survival affects population persistence: the role of prey availability and environmental stochasticity. *Oikos* 108:523–534.

———, ———, AND ———. 2006. Floater dynamics can explain positive patterns of density-dependent fecundity in animal populations. *American Naturalist* 168:697–703.

REDPATH, S.M., B.E. ARROYO, B. ETHERIDGE, F. LECKIE, K. BOUWMAN, AND S.J. THIRGOOD. 2002. Temperature and Hen Harrier productivity: from local mechanisms to geographical patterns. *Ecography* 25:533–540.

SASKATCHEWAN CONSERVATION DATA CENTER. 2012. Vertebrate species list. Saskatchewan Conservation Data Center, Regina, Saskatchewan, Canada.

SERRANO, D., D. ORO, U. ESPERANZA, AND J.L. TELLA. 2005. Colony size selection determines adult survival and dispersal preferences: allee effects in a colonial bird. *American Naturalist* 166:E22–E31.

STALMASTER, M.V. AND R.G. PLETTNER. 1992. Diets and foraging effectiveness of Bald Eagles during extreme winter weather in Nebraska. *Journal of Wildlife Management* 56:355–367.

STEENHOF, K., L. BOND, K.K. BATES, AND L.L. LEPPERT. 2002. Trends in midwinter counts of Bald Eagles in the contiguous United States, 1986–2000. *Bird Populations* 6:21–32.

——— AND I. NEWTON. 2007. Assessing nesting success and productivity. Pages 181–192 *in* D.M. Bird and K.L. Bildstein [EDS.], Raptor research and management techniques. Hancock House, Blaine, WA U.S.A.

STEIDL, R.J., K.D. KOZIE, AND R.G. ANTHONY. 1997. Reproductive success of Bald Eagles in interior Alaska. *Journal of Wildlife Management* 61:1313–1321.

TOWNSEND, C.R. 2006. Population cycles in freshwater fish. *Journal of Fish Biology* 35:125–131.

WATSON, J.W., D. STINSON, K.R. MCALLISTER, AND T.E. OWENS. 2002. Population status of Bald Eagles breeding in Washington at the end of the 20th century. *Journal of Raptor Research* 36:161–169.

WATTS, B.D., G.D. THERRES, AND M.A. BYRD. 2007. Status, distribution, and the future of Bald Eagles in the Chesapeake Bay area. *Waterbirds* 30:25–38.

———, ———, AND ———. 2008. Recovery of the Chesapeake Bay Bald Eagle nesting population. *Journal of Wildlife Management* 72:152–158.

WHITFIELD, D.W.A. AND J.M. GERRARD. 1985. Correlation of Bald Eagle density with commercial fish catch. Pages 191–193 *in* J.M. Gerrard and T.N. Ingram [EDS.], The Bald Eagle in Canada. White Horse Plains Publishers, Headingley, Manitoba, Canada.

———, ———, W.J. MAHER, AND D.W. DAVIS. 1974. Bald Eagle nesting habitat, density, and reproduction in central Saskatchewan and Manitoba. *Canadian Field Naturalist* 88:399–407.

Received 25 August 2012; accepted 6 January 2013

Downloaded from https://prime-pdf-watermark.prime-prod.pubfactory.com/ at 2025-08-23 via free access