J. Great Lakes Res. 24(1):32–44
Internat. Assoc. Great Lakes Res., 1998

Low Reproductive Rates of Lake Superior Bald Eagles: Low Food Delivery Rates or Environmental Contaminants?

Cheryl R. Dykstra[1†], Michael W. Meyer[2], D. Keith Warnke[3‡], William H. Karasov[1], David E. Andersen[4], William W. Bowerman, IV[5*], and John P. Giesy[6]

[1]*Department of Wildlife Ecology*
University of Wisconsin-Madison, Madison, Wisconsin 53706

[2]*Bureau of Integrated Science Services*
Wisconsin Department of Natural Resources, Rhinelander, Wisconsin 54501

[3]*Department of Fisheries and Wildlife, Cooperative Research Unit*
University of Minnesota, St. Paul, Minnesota 55108

[4]*U.S. National Biological Service*
Minnesota Cooperative Fish and Wildlife Research Unit, St. Paul, Minnesota 55108

[5]*Eagle Environmental Inc., Haslett, Michigan 48840*

[6]*Department of Fisheries and Wildlife*
Pesticide Research Center and Institute for Environmental Toxicology
Michigan State University, East Lansing, Michigan 48824

ABSTRACT. *Reproductive rate (productivity) of bald eagles (*Haliaeetus leucocephalus*) nesting on the shores of Lake Superior was significantly less than that of neighboring eagles nesting in inland Wisconsin (1.0 vs. 1.3 young per breeding attempt, 1989–1993), and at other inland lake/riverine habitats in the Great Lakes Basin. It is possible that the current causes of low productivity on Lake Superior might include exposure to organochlorine contaminants and/or low food availability. Levels of dichloro-diphenyl-dichloroethylene (DDE) and total polychlorinated biphenyls (PCBs) in addled eggs and eaglet blood from Lake Superior and inland Wisconsin reference sites were measured. Food delivery rates by parent eagles to nestlings, a possible index to food availability, were quantified at both locations. Concentrations of both DDE and total PCBs in addled eggs declined significantly from 1969 to 1993 ($p < 0.001$, $p = 0.006$ respectively), and current concentrations of DDE are at or below the no observable adverse effect level (NOAEL) for reproductive impairment. Concentrations of DDE and total PCBs in plasma were greater in individual nestlings from the shores of Lake Superior than in nestlings at inland locations (18.9 µg/kg vs. 3.0 µg/kg DDE, $p < 0.001$, and 109.1 µg/kg vs. 42.6 µg/kg, $p = 0.002$), but were not correlated to the 5-year average history of productivity for the territory ($p > 0.05$). Food delivery rates by parent eagles to nestlings at Lake Superior were 56% lower than those to inland nestlings (2.16 vs. 4.87 prey items per day, $p = 0.002$). Food delivery rates were significantly correlated to average 5-year productivity for inland Wisconsin reference sites ($p < 0.001$, $r^2 = 0.90$), although not for Lake Superior sites ($p = 0.593$). It is concluded that it is likely that the current low productivity of Lake Superior eagles is at least partly attributable to low food availability, but some other factor, possibly PCBs, may also contribute to low productivity.*

INDEX WORDS: *Bald eagle, DDE, PCBs, Lake Superior, food, reproductive rates.*

†Corresponding author: Present address: Oak Ridge Institute of Science and Education, USEPA, NERL, Mail Stop 642, 26 W. Martin Luther King Dr., Cincinnati, OH 45268. Phone: (513) 569-7120, Fax: (513) 569-7609.

‡Present address: Wisconsin Department of Natural Resources, Madison, WI 53707.

*Present address: Lake Superior State University, Sault Ste. Marie, MI 49783.

INTRODUCTION

Between 1940 and 1970, populations of bald eagles nesting in the continental United States declined due to reproductive failure caused mainly by DDE, a metabolite of the organochlorine insecticide DDT (Wiemeyer *et al.* 1972, Grier 1982, Colborn 1991). After the use of DDT and other organochlorines was banned, the North American eagle population rebounded quickly throughout most of its range. However, bald eagle populations in a few regions, including the Great Lakes shorelines (Colborn 1991, Best *et al.* 1994), have not increased as rapidly. The mean productivity of eagles near the shores of the Great Lakes (excluding Lake Ontario) from 1989-1993 was 0.79 young/occupied territory, compared to 1.0 young per occupied territory in inland Michigan and Minnesota (data in Bowerman 1993).

On Lake Superior, the proportion of reproductive efforts that failed had reached 100% by 1970 (Postupalsky 1971). The reproductive rate did not improve until 1977, when six young were fledged (Postupalsky 1978). Three addled eggs collected in 1970 contained 34, 65, and 71 μg/g wet weight DDE (Postupalsky 1971), averaging more than three times the amount associated with near-total reproductive failure of eagles (Wiemeyer *et al.* 1984, 1993), suggesting that organochlorine contaminants, particularly DDE, caused the historic reproductive failure on Lake Superior. Since the 1970s, the concentrations of DDE and total PCBs in the biota of Lake Superior have decreased significantly (DeVault *et al.* 1986, Weseloh *et al.* 1994). Despite this decrease, bald eagle reproduction on Lake Superior was still significantly less than that of neighboring eagles nesting in inland Wisconsin (1.0 vs. 1.3 young per breeding attempt, 1989–1993). Thus, in the mid-1980s, some researchers still considered that organochlorine contaminants were depressing productivity of eagles in the Apostle Islands National Lakeshore, in southern Lake Superior (Kozie 1986, Kozie and Anderson 1991).

However, contaminants may no longer be the primary cause of low productivity in bald eagles nesting in some regions of the Great Lakes, including Lake Superior. It is possible that the reproductive rate of Lake Superior eagles has now stabilized at a naturally-low level, perhaps because Lake Superior is simply marginal habitat for nesting bald eagles.

In the absence of direct anthropogenic effects, the most important determinants of raptor reproductive rates are food availability and weather (Newton 1979). On the shores of Lake Superior, bald eagles may suffer from low food abundance and availability. Lake Superior is a deep, cold, oligotrophic lake with few shoals where fish can spawn and where eagles can effectively forage. In 1984–1985, there was evidence that nestlings found dead in Lake Superior nests may have been food-stressed, as muscle fat content was very low compared to that of inland nestlings found dead (Kozie and Anderson 1991). Foraging and productivity of other avian species are also impaired by the oligotrophic nature of Lake Superior; it has recently been concluded that the low productivity of herring gulls (*Larus argentatus*) on Lake Superior is likely caused by low food availability (Weseloh *et al.* 1994).

The bald eagles of the Great Lakes shores (and specifically their reproductive rate) have been recommended as a biosentinel species for ecosystem health and water quality of the Great Lakes (International Joint Commission 1990). However, it would be incorrect to use the bald eagle as a biosentinel without a complete understanding of how reproductive rates are influenced by both ecological and anthropogenic factors in the Great Lakes ecosystem.

To this end, contaminant loads and ecological variables were studied that might affect eagle reproduction. Described here is bald eagle productivity for the Wisconsin shore of Lake Superior, and reference sites in inland northern Wisconsin. DDE and total PCB concentrations are reported in addled eggs and eaglet blood, and food delivery rates by adult eagles to nestlings, which may represent an index to food availability in the environment. Because of the bald eagle's classification as a threatened species, the study was limited to observational, rather than experimental, data. Hence, a behavioral protocol was designed which allowed correlative comparisons between reproduction and potential limiting factors.

METHODS

Reproductive Rate

Bald eagle reproductive rates at a portion of the nests in Wisconsin were assessed by the Wisconsin Department of Natural Resources by inspecting nests using fixed-wing aircraft twice during the breeding season, once during incubation and again when chicks were 4 to 7 weeks old. In the first aerial survey, the eagle pairs that were attempting reproduction (i.e., incubating eggs) were counted, and in the second flight, the number of nestlings was counted. A regional estimate of productivity, the "number of young per breeding attempt," was determined by dividing the total number of young produced by the total number of territories where birds attempted breeding. As in Steenhof (1987), a breeding attempt was defined as occurring only if eggs have been laid; this classification is also termed "active territory" by the State of Wisconsin.

Contaminant Concentrations in Nestling Blood

Between 1989 and 1994, blood samples were collected from 89 bald eagle nestlings at 53 nesting territories in Wisconsin (Fig. 1). Fifteen nests were located within 8 km of the Wisconsin Lake Superior shore. Thirty-eight nests ("inland Wisconsin" nests) were located more than 8 km from any Great Lakes shore, on the industrialized portions of the Wisconsin River (n = 7), the Menominee River (n = 2), the Peshtigo River (n = 1), the lower Fox River (n = 1), and in the rest of interior northern Wisconsin, but

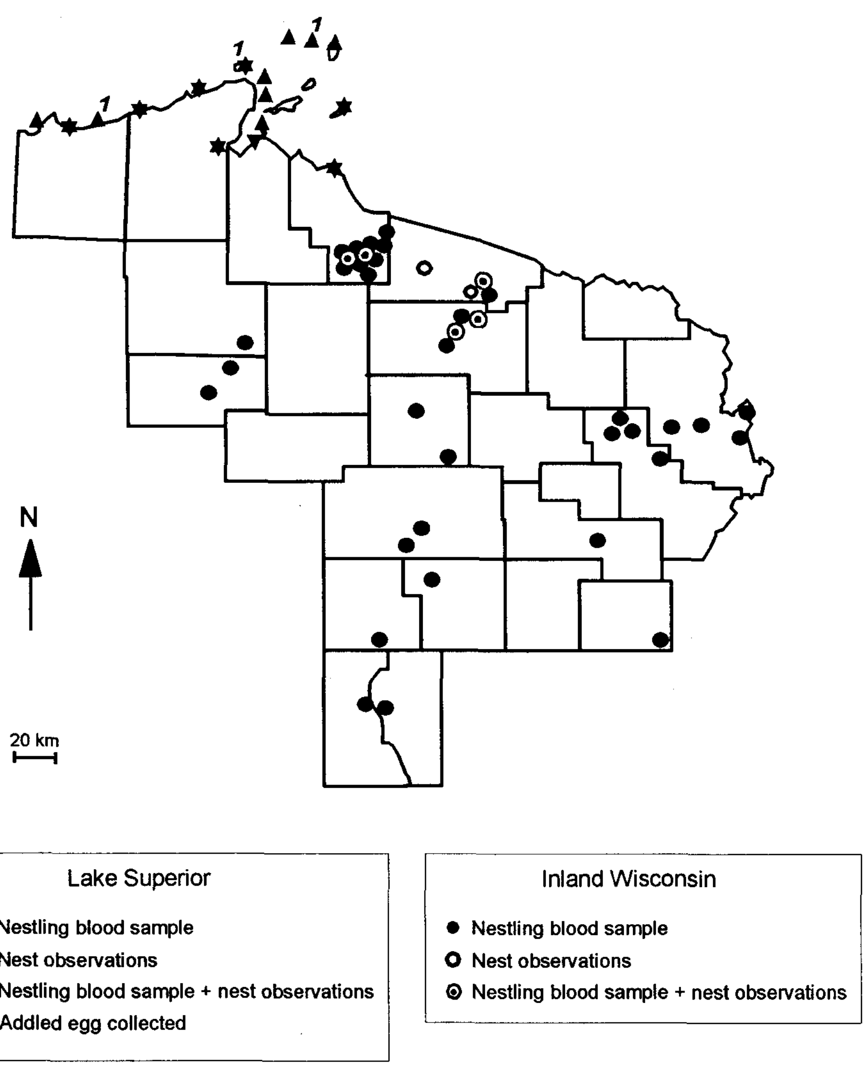

FIG. 1. Locations of Wisconsin eagle nests at which observations were conducted and nestling blood samples were collected. Nests where addled eggs were collected are shown for Lake Superior sites only. One inland nest which was observed but lacked sufficient productivity data for inclusion in analyses is not shown.

not associated with one of the above rivers (n = 27). Most of the last category were located on lakes in the northeast and north-central parts of the state.

Nestlings were sexed by footpad length, and aged by the length of the eighth primary (Bortolotti 1984). Nestlings were aged 5 to 10 weeks at the time of the blood collection. Syringes used were sterile plastic or glass previously washed with hexanes and acetone. Approximately 10 mL of blood was drawn from the brachial vein. Blood was transferred to heparinized vacutainers, stored on wet ice until the end of the day, and separated by centrifuging in the evening, or stored in a refrigerator for 1 day and then centrifuged less than 48 hours after collection. Plasma was drawn off, transferred to another vacutainer, and frozen upright at approximately –20°C. At the end of the field season, all frozen plasma samples were shipped on dry ice to Michigan State University.

Organochlorine pesticides and total PCB concentrations in the nestling plasma were determined by gas chromatography, with electron capture detection, and were confirmed by mass spectrometry by the Michigan State University Aquatic Toxicology Laboratory. Methods have already been described (Bowerman 1993, Mora *et al.* 1993). Detection limits were 2.5 µg/kg for DDE and 5.0 µg/kg for total PCBs. Contaminant values falling below the detection limits were assigned a value of one-half the detection limit for statistical analyses. Residue levels measured in the plasma of sibling nestlings in the same year were averaged (geometric mean) to produce one value, and residue levels measured at the same nesting territory in different years were averaged (geometric mean) to produce one value.

Contaminant Concentrations in Addled Eggs

Between 1986 and 1993, addled bald eagle eggs were collected from 20 inland Wisconsin and three Lake Superior nests at the time of banding. Inland Wisconsin samples were mostly from northern lakes and did not include eggs from any of the major rivers. These eggs were wrapped in aluminum foil, and refrigerated until processing in late summer. Prior to opening, the eggs were weighed, and their lengths and widths were measured with calipers. After opening, the egg contents were frozen in chemically-clean jars until analysis. The Wisconsin State Lab of Hygiene analyzed the eggs for organochlorine pesticides and total PCBs using gas chromatography, with confirmation by mass spectrometry (Wisconsin State Laboratory of Hygiene 1996). Residue concentrations were corrected for moisture loss as in Stickel *et al.* (1973). For seven eggs which were too damaged to permit measurement of length and width, the average correction factor (0.69, determined from 18 eggs) was used to estimate the corrected residue concentration. Values were measured as µg/g wet weight, but reported as µg/kg wet weight for comparability with plasma residues. Data from two pairs of sibling eggs were averaged. Complete methodology has been described (Wisconsin State Laboratory of Hygiene 1996).

Food Delivery Rates

Food delivery rates at eight Lake Superior nests and eight reference inland nests were measured in 1992 and 1993 (Fig. 1). Seven reference nests were located near inland lakes in Iron, Vilas, and Oneida counties in north-central Wisconsin; one reference nest was located along the northern portion of the Wisconsin River in Oneida county. Food delivery rates were measured by two techniques. Remote time-lapse video cameras were mounted at nests at ten locations, and at nine nests, dawn-to-dusk observations were made using 20–60X spotting scopes. (Three nests had combinations of cameras and observations.) Observation blinds were placed 110 to 300 m from the nests. Observers recorded prey deliveries and documented other behaviors such as brooding, feeding, and resting. Observer fatigue was prevented by switching observers every 4 hours without disturbing the nesting eagles. Simultaneous observations (validations) with video cameras indicated that the two techniques were not significantly different for number of prey deliveries (n = 18 validation sessions, paired t-test, t = 0.81, df = 17, p = 0.43, Warnke, unpub. data). For more details of both techniques, see Warnke (1996).

Sixteen individual nests were observed from dawn-to-dusk for ≥ 6 full days throughout the nesting season. Fourteen nests were observed from hatching to fledging and two nests were observed only from week 5 or 6 to fledging; however, prey delivery rates in this population do not vary as nestlings age (D.K. Warnke, pers. comm.), so the different observation schedules likely did not bias prey delivery data.

Statistical Analyses

All analyses were performed with SYSTAT (Wilkinson 1988). Productivities of Lake Superior and inland Wisconsin were compared with a t-test.

Concentrations of DDE and total PCBs were log-transformed before calculation of any statistics. Log-transformed values were used to calculate the geometric mean and 95% C.I. for residue concentrations in Lake Superior and inland Wisconsin nestling plasma (Frenzel 1985, Frenzel and Anthony 1989) and eggs. Plasma and egg concentrations from the two regions were compared by t-test. Egg residue concentrations from three Lake Superior nests in Michigan were included to increase sample size (data in Bowerman *et al.* 1994). Log-transformed residue concentrations in eggs were analyzed by linear regression to determine trends in concentrations.

To assess possible relationships between contaminants, food delivery rates, and productivity, contaminant concentrations and food delivery rates were correlated to 5-year average productivities for Lake Superior and inland Wisconsin eagle territories. Blood residue data were log-transformed for use in linear regressions with productivity data.

Because most successful pairs produce one or two chicks per year, a single year's productivity values do not provide enough variance for statistical analyses. Thus, for correlations with productivity, average territory productivity over 5 years was used, because it is a better measure of the productivity at the territory than a single year (as in Wiemeyer *et al.* 1984; Table 1). Since breeding adult eagles return to the same territory each year, it is likely that the territorial productivity over 5 years represents the productivity record for one pair of adults; however, there is no way of assuring that adults were not replaced or that the adult-replacement rates for inland and Lake Superior were similar. For each territory, the mean 5-year productivity value ($Pr_{5\text{-yr}}$) was calculated as:

$$Pr_{5\text{-}yr} = \frac{\text{(number of young produced in 5 yr)}}{\text{(number of years breeding attempts occurred in those 5 yr)}} \quad (1)$$

The 5 years included in the calculation were the year in which the blood sample was taken, the 3 previous years, and the year after the sample was taken (as in Wiemeyer *et al.* 1984, 1993). Nests at which a breeding attempt occurred (i.e., eggs were laid) in fewer than 2 years of the 5 were excluded from the data set (n = 2 for contaminant analyses, n = 1 for food delivery analyses; after Wiemeyer *et al.* 1984). For nests with more than one blood sample, a different $Pr_{5\text{-yr}}$ was associated with each blood sample; each $Pr_{5\text{-yr}}$ included productivity data from different years, centered around the year the blood sample was collected. Because samples from successive years at a nesting territory were not independent, each nesting territory was represented by only one pair of values in the correlation analyses between contaminants and productivity. The $Pr_{5\text{-yr}}$ used in the analyses was that associated with the most recent blood sample (and hence included productivity data from the year of the blood sample, the previous 3 years, and the following year). The residue concentration used in the analyses was the geometric mean of residue levels measured at the same nesting territory in different years. [For nesting territories where the earliest sample and the most recent sample were collected 5 or more years apart, the earliest sample was excluded from the mean (n = 4 samples).]

RESULTS

Productivity of Lake Superior and Inland Wisconsin Eagles

Productivity of Lake Superior bald eagles from 1983 to 1994 was significantly less than that of inland Wisconsin eagles (young per breeding attempt, paired t-test, $t = 5.14$, $df = 11$, $p < 0.001$). In recent years (1989–1993), overall productivity on the Lake Superior shoreline was 0.99 young per breeding attempt (72 young in 73 breeding-attempts), compared to 1.26 young per breeding attempt in the reference region in inland Wisconsin (660 young in 523 breeding-attempts). During 1989–1993, the Wisconsin population on Lake Superior was fairly stable, varying from 15 to 17 occupied territories per year; the statewide population, however, increased from approximately 320 active pairs in 1989 to 460 active pairs in 1993 (Wisconsin Department of Natural Resources, unpub. data). Variability in productivity at the two sites did not differ [Levene's test of variability (Snedecor and Cochran 1980), $\chi^2 = 19.01$, $0.75 > p > 0.50$, $df = 22$, 1983–1993].

Total PCBs and p,p′-DDE Concentrations in Eggs and Plasma

Published and unpublished data for residue concentrations in eggs from the Lake Superior shore were combined in an analysis of historical trends. Log-transformed DDE concentrations in addled eggs decreased between 1969 to 1993 (linear regression, $r^2 = 0.85$, $p < 0.001$, $n = 16$; Fig. 2). Simi-

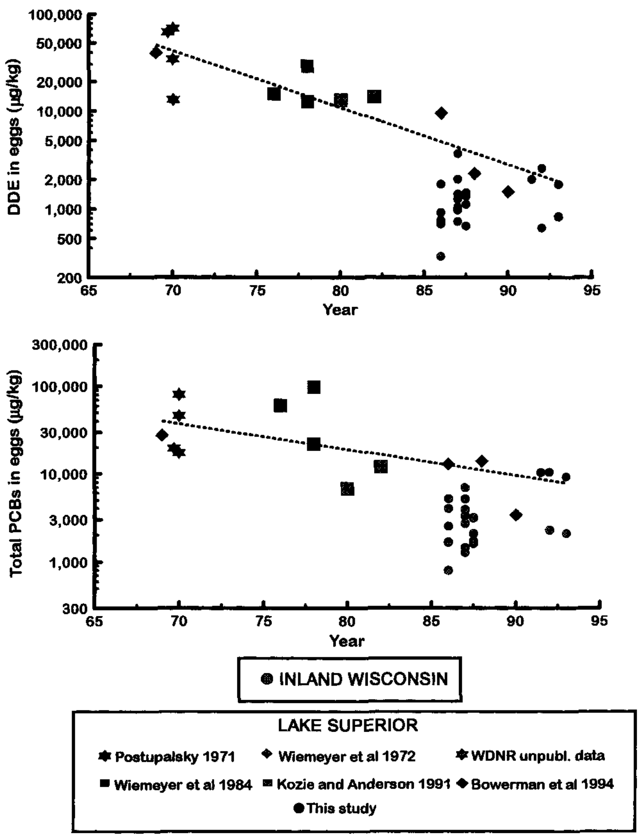

FIG. 2. Total PCB and p,p'-DDE concentrations in addled bald eagle eggs collected on Lake Superior, 1969–1993, and in inland Wisconsin 1986–1993. Circles indicate eggs collected in the state of Wisconsin in this study; dark circles are Lake Superior data, light circles are inland data. Sibling eggs were averaged. Some 1987 inland Wisconsin data points were slightly displaced for clarity. Line for p,p'-DDE is the regression $y = -0.058\,x + 8.68$ where y = log(DDE in µg/kg) and x = year. Line for PCBs is the regression $y = -0.030\,x + 6.64$ where y = log(PCBs in µg/kg) and x = year. All residue concentrations were corrected for moisture loss by the method of Stickel et al ***(1973) except those reported in Postupalsky (1971), where a correction factor derived from water volume measurements was used. Analytical techniques (especially for total PCBs) may vary. Unpublished data used with the investigators' permissions. Complete literature citations in References.***

larly, the concentration of total PCBs in eggs from the Lake Superior shoreline has declined significantly since 1969 ($r^2 = 0.43$, $p = 0.006$, $n = 16$; Fig. 2).

For p,p'-DDE, log-transformed residues in Lake Superior eggs were significantly greater than those from inland Wisconsin eggs ($n = 6$ and $n = 20$, $t = 3.37$, $df = 24$, $p = 0.003$, Fig. 2). Concentrations of p,p'-DDE in Lake Superior eggs averaged 2,540 µg/kg (95% C.I: 1,265–5,100), compared to 1,066 µg/kg (95% C.I.: 835–1,361) in eggs from inland Wisconsin. Total PCB concentrations in Lake Superior eggs were also significantly greater than those in inland eggs ($n = 6$ and $n = 20$, $t = 5.32$, $df = 24$, $p < 0.001$). Lake Superior eggs averaged 9,111 µg/kg (95% C.I.: 5,322–15,597), compared to 2,420 µg/kg (95% C.I.: 1,881–3,114) in inland eggs.

For p,p'-DDE, log-transformed residues in plasma samples from Lake Superior nestlings were significantly greater than those from inland Wisconsin ($n = 15$ and $n = 38$, $t = 5.52$, $df = 51$, $p < 0.001$, Table 1). Concentrations of p,p'-DDE in Lake Superior nestlings averaged 18.9 µg/kg, compared to 3.0 µg/kg in plasma of inland Wisconsin nestlings. Total PCB concentrations in Lake Superior nestlings were also greater than those in inland nestlings ($n = 15$ and $n = 38$, $t = 3.21$, $df = 51$, $p = 0.002$, Table 1). Lake Superior nestlings averaged 109.1 µg/kg, compared to 42.6 µg/kg in inland nestlings.

Prey Delivery Rates at Lake Superior and Inland Nests

Lake Superior adults delivered fewer prey items per day than did inland Wisconsin adults ($n = 8$ and $n = 7$, $t = 3.91$, $df = 13$, $p = 0.002$). Lake Superior parents averaged only 2.16 ± 0.22 (s.e.m.) prey items delivered to the nest per day, compared to 4.87 ± 0.70 prey items per day at inland nests. Even when prey delivery rates were adjusted to account for brood size, Lake Superior parents brought significantly fewer prey items per chick per day ($n = 8$ and $n = 7$, $t = 2.63$, $df = 13$, $p = 0.021$; means 1.67 ± 0.33 vs. 3.21 ± 0.50).

Correlations of Plasma Residues and Food Delivery Rates with Productivity

The log-transformed concentrations of p,p'-DDE in nestling plasma were not correlated to average 5-year productivity when adjusted for region (ANCOVA with region as the categorical covariate,

TABLE 1. Concentrations of p,p'-DDE and total PCBs in plasma of nestling bald eagles in Wisconsin, 1989–1994. Contaminants reported as µg/kg in plasma, wet weight. Productivity is the (number of young produced in 5 years)/(number of times a breeding attempt occurred in 5 years). Samples with contaminant concentrations below the detection limits were assigned a value of one- half the detection limit for calculation of means (n = 16 individual DDE samples, n = 0 PCB samples). SEM and 95% C.I. not calculated for n ≤ 2.

Location	Years	# territories (# samples)	Geo. mean p-p ′ DDE (95% C.I.) (µg/kg)	Geo. mean Total PCBs (95% C.I.) (µg/kg)	5-year mean productivy (mean ± sem)
LAKE SUPERIOR	1989–93	15 (36)	18.9 (12.1–29.1)	109.1 (69.7–170.1)	0.99 ± 0.13
INLAND WISCONSIN					
Northern lakes & rivers	1990–93	27 (31)	3.3 (2.2–4.9)	28.3 (20.1– 38.3)	1.22 ± 0.11
Wisconsin River	1990–91	7 (9)	2.6 (1.2–5.5)	122.0 (64.6–231.1)	1.76 ± 0.15
Menominee River	1990–91	2 (3)	5.0	86.6	1.42
Fox River	1991–94	1 (4)	3.2	262.8	2.60
Peshtigo River	1991	1 (1)	n.d.	24.0	1.25

n.d. = not detected

$F_{1,48}$ = 1.21, p = 0.276 for p,p′-DDE concentrations, and $F_{1,48}$ = 1.41, p = 0.241 for regions, r^2 = 0.12, n = 51, Fig. 3). There was no significant interaction between contaminant concentration and region (p = 0.350). When tested separately by region, plasma p,p'-DDE concentrations were not correlated to productivity for inland Wisconsin (linear regression, n = 36, r^2 = 0.02, p = 0.369), or Lake Superior (n = 15, r^2 = 0.03, p = 0.558).

Similarly, the log-transformed concentrations of total PCBs in nestling plasma were not correlated to average 5-year productivity when adjusted for region, although the two regions did vary significantly (ANCOVA with region as the categorical covariate, $F_{1,48}$ = 2.59, p = 0.114 for PCB concentrations, and $F_{1,48}$ = 7.43, p = 0.009 for regions, r^2 = 0.14, n = 51, Fig. 3). There was no significant interaction between contaminant concentration and region (p = 0.418). When tested separately by region, plasma concentrations of total PCBs were not correlated to productivity for inland Wisconsin (n = 36, r^2 = 0.08, p = 0.086), or Lake Superior (n = 15, r^2 = 0.00, p = 0.95).

For the correlation of prey delivery rates and productivity, 5-year mean productivity was calculated as above, except that for two nests at which prey delivery rate was measured in both 1992 and 1993, the productivity was averaged for 6 years (1989 to 1994), and prey delivery rates from the 2 years were averaged. Prey delivery rates at inland nests alone were highly correlated with productivity (r^2 = 0.90, p = 0.001, n = 7, Fig. 4). Lake Superior nests had both low productivity and low prey delivery rates, but these were not significantly correlated (r^2 = 0.05, p = 0.593, n = 8, Fig. 4).

DISCUSSION

Determinants of Reproductive Rate in Inland Wisconsin

Reproductive rates of inland eagles were highly correlated to food delivery rate of adult eagles, but not to either DDE or total PCB concentrations in nestling plasma. In addition, both DDE and total PCB concentrations in addled eggs were uniformly low, below the no-effect concentrations associated with normal reproduction (Wiemeyer *et al.* 1984, 1993; Giesy *et al.* 1995). Thus, it appears that food delivery rates by parents is a more likely determinant of reproductive rate in inland Wisconsin eagles than contaminant levels.

Determinants of Reproductive Rate at Lake Superior

These results for Lake Superior eagles were more ambiguous than those for inland Wisconsin birds. Lake Superior reproductive rates were not correlated to concentrations of either contaminant, or to food delivery rates, although Lake Superior eagles had significantly higher concentrations of both DDE and total PCBs as well as significantly lower

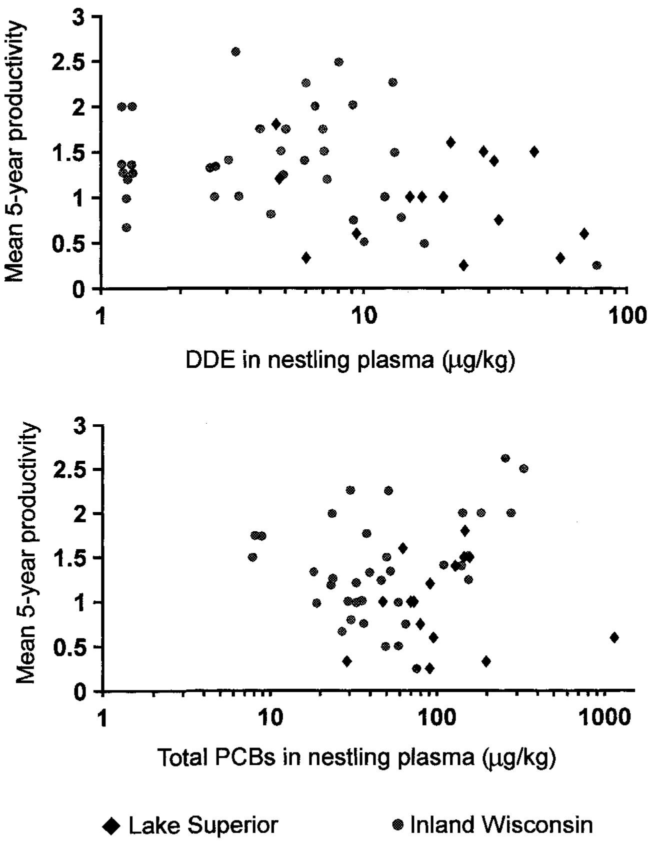

FIG. 3. Mean 5-year productivity (young per breeding attempt) at individual nest sites as a function of log-transformed p,p'-DDE and total PCB concentration in nestling plasma, 1989–1994. Sibling samples from the same year were averaged. Samples from the same territory in different years were averaged. Samples in which a contaminant was not detected were assigned a value of one-half the detection limit. Some DDE data points were slightly displaced for clarity. Lake Superior subpopulation includes nests < 8 km from the shore. Inland Wisconsin includes nests > 8 km from any Great Lakes shore.

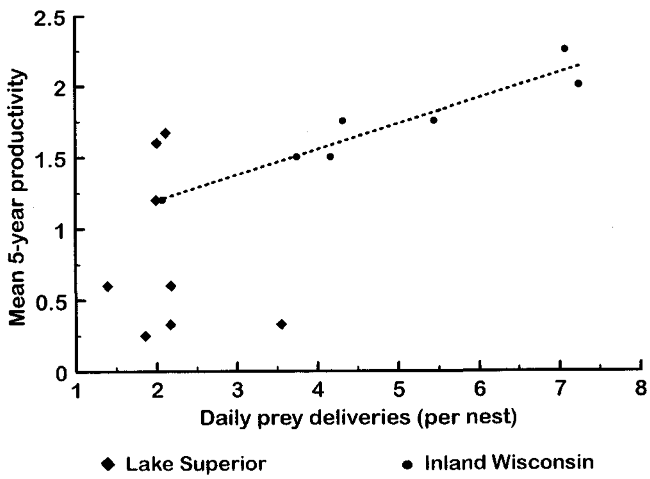

FIG. 4. Mean 5-year productivity of individual pairs (young per breeding attempt) as a function of daily prey delivery rate. All nests with ≥ 6 dawn-to-dusk observation days and adequate productivity data are shown. Prey delivery rates shown are the season-long averages for each nest. Circles represent inland nests; diamonds represent Lake Superior nests. Line is the regression for all inland nests ($y = 0.18 x + 0.84$, $r^2 = 0.90$, $p < 0.001$, $n = 7$).

prey delivery rates than inland eagles. Nevertheless, as described below, the Lake Superior data, in conjunction with the inland Wisconsin data, suggested that low productivity on Lake Superior was at least partly attributable to low food delivery rates by adult eagles. Additional contribution to low productivity by some other factor could not be ruled out.

Food Delivery Rates

The strong correlation between food delivery rates and productivity in inland Wisconsin eagles permits assessment of the adequacy of the food delivery rates of the Lake Superior eagles. From the correlation between productivity and prey delivery rates, inland eagles with prey delivery rates of 2.2 prey items per day (the mean Lake Superior prey delivery rate) might be expected to have average productivity ($Pr_{5\text{-yr}}$) of only 1.2 (compared to the inland Wisconsin mean of 1.7). If it is assumed that the correlation is truly indicative of an ecological cause-and-effect relationship, and that Lake Superior and inland Wisconsin eagles are subject to similar ecological constraints, then it would be expected that Lake Superior eagles would have similarly low productivity, based solely on their food delivery rates (average 2.2 ± 0.2 prey items per day). Indeed, it was found that the Lake Superior eagles studied did have low productivity ($Pr_{5\text{-yr}}$ averaged 0.8). Having no ecological information to invalidate the above assumptions, it can be concluded from this evaluation that low prey delivery rates by Lake Superior eagles determined a cap or upper limit on productivity. Thus, low productivity of Lake Superior eagles is likely attributable, at least in part, to low prey delivery rates. As a caveat, it can be emphasized that this evaluation is subject to the limitations inherent in correlations; a more robust conclusion would require a food-provisioning experiment to conclusively demonstrate the effects of food abundance on productivity of Lake Superior eagles.

The relationship between Lake Superior prey delivery rates and productivity was more variable that than for inland bald eagles. Two Lake Superior nests had productivities higher than expected, based on predictions from the inland Wisconsin regression, while five nests had lower than expected productivity. Thus, the mean productivity of Lake Superior eagles ($Pr_{5\text{-}yr}$ = 0.8) was substantially lower than that predicted from the inland Wisconsin regression (i.e., $Pr_{5\text{-}y}$ = 1.2). There are several possible interpretations for this increased variation on Lake Superior, as compared to inland Wisconsin. One possibility is that food availability on Lake Superior is more variable than at inland sites, which may result in differences in prey delivery rates between years. Similarly, the prey availability on Lake Superior may vary between seasons; low prey availability during the courtship or incubation but not the nestling stage could decrease eagle productivity, but would not be recorded using observations of prey delivery rate during the nestling stage. We have no information on food availability during courtship or incubation. Another interpretation of the lack of correlation between Lake Superior productivity and prey delivery rates is that some other factor may also be depressing Lake Superior productivity, in conjunction with low prey delivery rates.

Other observations at Lake Superior nests also suggest that low food delivery rate may be partly responsible for lower productivity. Much of the depression in reproduction for Lake Superior eagles is due to (1) lower nestling survival than at inland sites, and (2) a lower percentage of occupying pairs that actually lay eggs, relative to inland-nesting eagles (Dykstra 1995), although the latter does not influence productivity values as presented in this study (i.e., the number of young per active pair). More than half of the depression in Lake Superior productivity is attributable to lower nestling survival at Lake Superior than in inland Wisconsin, based on a subset of nests observed throughout the breeding season (Dykstra 1995). Nestling mortality was greater in nests on Lake Superior than in inland Wisconsin in 1991–1994 (27.3% vs. 8.6%, Dykstra 1995), and greater than that usually found in the continental U.S. (11% or 15%; Fraser 1981, Stalmaster 1987). Most (≥ 78%) of the Lake Superior nestling mortality occurred in broods of two nestlings. Nestlings in Lake Superior broods of two received significantly fewer prey deliveries per nestling than Lake Superior nestlings in broods of one (Warnke 1996); in contrast, inland nestlings in broods of one and two did not differ in number of items received per nestling (Warnke 1996). Such a difference would not be significant had lakeshore parents of broods of two compensated by delivering larger prey items or items with higher energy density. However, the biomass and energy content of prey items delivered were calculated based on estimated prey sizes and published energy contents of various prey species, and no evidence was found of such compensation (Dykstra 1995). In fact, the amount of energy received by Lake Superior nestlings in broods of two was less than that typically expended for normal growth and development (energy received 1,393 kJ/d per nestling on Lake Superior vs. 2,556 kJ/d for normal growth and development, age 5 to 9 weeks, $p < 0.001$; Dykstra 1995).

In 1992 and 1993, lesser food delivery rates themselves may not have caused increased mortality, as few nestling deaths were directly attributable to starvation. However, in 1992-1993, parents of Lake Superior broods of two were absent from the nest significantly more of the time (36.3%) than Lake Superior parents of broods of one (14.3%) or inland parents of any size brood (8.3%, inland not significantly different from Lake Superior parents of one, ages 2 to 4 weeks; Warnke 1996). Possibly Lake Superior parents needed to make a larger effort to find food than did inland parents or Lake Superior parents of one chick. This behavior left the nestlings more exposed to predation by fishers (*Martes pennanti*), raccoons (*Procyon lotor*), or bears (*Ursus americanus*). Increased nestling mortality was observed mainly in broods of two on Lake Superior compared to inland nests, and Lake Superior mortality in 1991-1994 was mostly due to predation or unknown causes (unpubl. data). Thus, increased parental absence from the nest may have indirectly resulted in increased nestling mortality.

Currently, there is only anecdotal evidence linking food availability to the lowered percentage of occupying birds laying eggs for Lake Superior. In early spring on Lake Superior, food availability may be influenced by ice conditions, which vary between years and between locations along the lakeshore. Late ice-out or local ice might make it difficult for eagles to forage along Lake Superior until mid-April. Productivity might be expected to fluctuate yearly with ice conditions, if the probability of laying or clutch size is correlated with female condition or available food. In 1994, when Lake Superior was completely frozen over, eagle productivity on the shoreline declined to 0.5 young per occupied territory, then rebounded to 1.0 young per occupied territory in 1995 (pers. obs.). Ice-out date was thought to be related to bald eagle productivity in Voyageurs National Park, in northern Minnesota (Grimm and Kallemeyn 1995).

In the above analysis, it was asserted that low food delivery rates to nestlings cause the depressed Lake Superior productivity, at least in part. It was assumed that low food delivery rate reflects low food availability in the environment, as suggested by Bortolotti (1986). However, there are two other potential causes for lesser prey delivery rates. Lake Superior eagles may be younger, and hence less experienced breeders, than inland eagles. Younger breeders may be inexperienced at foraging, and tend to have lesser reproductive rates than older birds, even with abundant food available (Newton 1979). If Lake Superior parents are younger than breeding adults inland, the low productivity may be explained by this alone. It has been suggested that Great Lakes shoreline subpopulations may experience greater adult mortality than inland subpopulations, which allows young birds to enter the breeding population (Bowerman 1991, Bowerman *et al.* 1995). Unfortunately, there are currently no data to support or refute this hypothesis, as causes and rates of adult mortality remain unknown. Anecdotal information suggests young birds bred at Lake Superior in 1983 (Sindelar 1983) and 1985, when two visibly-young breeding females (brown-streaked heads) were observed in the Apostle Islands (n = 3 nests; Kozie and Anderson 1991). Conversely, no visibly-young birds were observed in the Lake Superior breeding population in 1992 to 1994 (n = 14 nests).

Another potential reason for lesser prey delivery rates is that adult birds may be impaired by contaminants that affect their ability to forage and/or to parent effectively. Contaminated birds sometimes demonstrate reduced nest attentiveness during incubation (Fox *et al.* 1978, Kubiak *et al.* 1989), or spend less time feeding their young (McArthur *et al.* 1983). At the site observed in this study, Lake Superior parents of broods of two chicks were absent from their nests significantly more time than both lakeshore parents of single chicks and inland parents of any size brood (see above; Warnke 1996). In contrast, Lake Superior parents of one chick were not absent from the nest more than inland parents of any size brood ($p > 0.05$, Warnke 1996). If organochlorine contaminants caused reduced nest attentiveness in Lake Superior eagles, it is unlikely that they would affect only parents of two chicks, and not parents of one chick. Hence, the inattentiveness almost certainly resulted from increased nestling energy requirements, and the accompanying increase in the amount of time needed for foraging.

Contaminants

The concentrations of p,p′-DDE and total PCBs in eaglet blood were not correlated with adult productivity at either site, and the lack of a strong correlation for inland Wisconsin sites made it impossible to assess Lake Superior levels based on inland Wisconsin regressions, as was done for prey delivery rates. The lack of correlation may indicate that all the eaglets contained concentrations of p,p′-DDE and total PCBs that were less than the threshold level associated with impaired adult productivity. It is also possible that nestling blood concentrations are not as meaningful a predictor of adult productivity as are egg contaminant concentrations. However, the data suggest that bald eagle eggs and nestling blood samples both reflect a similar contaminant source, that is, the environmental contamination in the nesting territory. Both nestling blood concentrations and egg concentrations are uniformly low at inland Wisconsin sites (Figs. 2, 3), mid-range at Lake Superior sites (Figs. 2, 3), and highest at Lake Michigan sites (Bowerman 1993, Dykstra and Meyer unpubl. data). A robust individualistic test of the relationship between egg and nestling blood contaminant concentrations requires sibling egg and nestling blood samples.

The available evidence indicates that DDE is no longer responsible for depressed bald eagle productivity observed on the Lake Superior shoreline, despite significantly greater concentrations of p,p′-DDE in eaglet plasma and egg samples from Lake Superior than in those from inland Wisconsin. First, concentrations of DDE in addled eggs have declined significantly since 1969, and concentrations of DDE in the three contemporary eggs (mean 2,100 μg/kg) were at or below the no-effect concentration associated with normal reproduction (œ 3,000 to 3,600 µg/kg DDE; Wiemeyer *et al.* 1984, 1993), and well below the concentration associated with near-total reproductive failure (>15,000 µg/kg DDE; Wiemeyer *et al.* 1984). Unfortunately, there are no similar comparators for the relationship between nestling blood contaminant concentrations and productivity.

Second, the timing of reproductive failure indicates a mainly non-contaminant cause. More than half of the depression in Lake Superior productivity is attributable to loss of nestlings. Neither p,p′-DDE nor PCBs are likely to cause an increase in nestling mortality at the middle stage of the nestling period, when most mortality occurred; rather, the presence of these compounds would most likely cause a decrease in hatchability of eggs, due to embryotoxicity or shell-thinning (Colborn 1991). Conversely, nutritional stress due to reduced food abundance during the nestling period is likely to cause nestling mortality, especially during the mid-nestling period when energy demands are greatest due to rapid growth.

The available evidence does not support the hypothesis that total PCBs may contribute to the depressed bald eagle productivity observed at Lake Superior; however, neither does it allow us to reject that hypothesis. As indicated above for DDE, the plasma concentrations of total PCBs were not correlated to adult productivity, the concentrations of total PCBs in addled eggs declined significantly since 1969, and the general timing of reproductive failure seemed to indicate a non-contaminant causative agent.

However, the current concentrations of total PCBs in addled eggs were more difficult to interpret than those of DDE, primarily because of a lack of information on the critical concentrations associated with reproductive depression and failure. The critical concentrations for total PCBs are less evident than those for DDE, because of the ubiquitous co-occurrence of PCBs and DDE (Nisbet 1989, Wiemeyer *et al.* 1993), but near-total reproductive failure was associated with concentrations of > 33,000 µg/kg in addled eggs (Wiemeyer *et al.* 1984), which greatly exceeds contemporary concentrations in eggs from the Lake Superior shore (mean 10,000 µg/kg). A no observable adverse effect concentration (NOAEC) of 4,000 µg/kg has been suggested (Giesy *et al.* 1995), but the underlying data set was confounded by the presence of DDE in eggs, as in Wiemeyer *et al.* (1984, 1993). However, the suggested NOAEC was also partially supported by controlled laboratory data. Data from other regions of Wisconsin may also be used to address the question of critical PCB concentrations. Bald eagles nesting on the Wisconsin River have total PCB exposures nearly identical to those nesting on Lake Superior, as indexed by nestling blood PCB levels (Table 1) and also egg concentrations (unpubl. data), yet have high productivity (Table 1). This observation suggests that the total PCB concentrations measured in Lake Superior eagles do not depress reproduction.

A second factor confounding the interpretation of egg concentrations of PCBs is that the specific PCB congeners in Lake Superior eggs are unknown. The Lake Superior mixtures may be more or less toxic than those in inland Wisconsin or in Wiemeyer's data set, and thus are not necessarily comparable to either.

CONCLUSIONS

The current low productivity of Lake Superior eagles is at least partly attributable to low food availability, but some other factor, possibly PCBs, may also contribute to low productivity. The results suggest a need to perform a food-provisioning experiment to conclusively demonstrate the effects of food abundance on productivity of Lake Superior eagles, and also a need to identify specific PCB congeners in Lake Superior eagles. Finally, the study also indicated that ecological information is critical for appropriate utilization of bald eagles (and other species) as biomonitors of environmental pollution.

ACKNOWLEDGMENTS

We thank Sergej Postupalsky for helpful insight and valuable unpublished data. We are grateful to Dave Evans and Ron Eckstein, Wisconsin Department of Natural Resources, for climbing to nests to retrieve nestlings. The Wisconsin Department of Natural Resources has monitored bald eagle productivity for 20+ years, and many individuals have contributed to this effort. Additional field assistance was provided by Julie Van Stappen and Tom Doolittle, U.S. National Park Service, Apostle Islands National Lakeshore, and Jeff Wilson, Wisconsin Department of Natural Resources. Field assistants who monitored prey delivery rates include Ann Bellman, Darrel Covell, Dan Dopkins, Miles Falck, Maria Fernandez, Helene Hanson, Jerry Hartigan, Mark Jaunzems, Dan Kelner, Kathy Mooney, John Neuce, Robin Schweickert, Gretchen Seebolde, Matt Solensky, and Jim Woodford. For their generous permission to use their unpublished data we thank Julie Van Stappen and Sergej Postupalsky. Funding for this study was provided by the Great Lakes Protection Fund, Wisconsin Department of Natural Resources, National Park Service, U.S. Fish and Wildlife Service, Wisconsin Society for Ornithology, Lois Almon Fund, and Sigma Xi.

REFERENCES

Best, D.A., Bowerman, W.W., IV, Kubiak, T.J., Winterstein, S.R., Postupalsky, S., Shieldcastle, M.C., and Giesy, J.P., Jr. 1994. Reproductive impairment of bald eagles *Haliaeetus leucocephalus* along the Great Lakes shorelines of Michigan and Ohio. In *Raptor Conservation Today*, eds. B.-U. Meyburg and R.D. Chancellor, pp. 697–702. World Working Group on Birds of Prey. East Sussex, Great Britain: Pica Press.

Bortolotti, G.R. 1984. Criteria for determining age and sex of nestling bald eagles. *Journal of Field Ornithology* 55:467–481.

______. 1986. Evolution of growth rates in eagles: sibling competition vs. energy considerations. *Ecology* 67:182–194.

Bowerman, W.W., IV. 1991. Factors influencing breeding success of bald eagles in upper Michigan. M.S. thesis, Northern Michigan University, Marquette, MI.

______. 1993. Regulation of bald eagle (*Haliaeetus leucocephalus*) productivity in the Great Lakes basin: an ecological and toxicological approach. Ph.D. dissertation, Michigan State University. East Lansing, MI.

______, Best, D.A., Giesy, J.P., Jr., Kubiak, T.J., and Sikarskie, J.G. 1994. The influence of environmental contaminants on bald eagle *Haliaeetus leucocephalus* populations in the Laurentian Great Lakes, North America. In *Raptor Conservation Today*, eds. B.-U. Meyburg and R.D. Chancellor, pp. 703–707. World Working Group on Birds of Prey. East Sussex, Great Britain: Pica Press.

______, Giesy, J.P., Best, D.A., and Kramer, V.J. 1995. A review of factors affecting productivity of bald eagles in the Great Lakes region: implications for recovery. *Environmental Health Perspectives* 103:51–59.

Colborn, T. 1991. Epidemiology of Great Lakes bald eagles. *Journal of Toxicology and Environmental Health* 33:395–453.

DeVault, D.S., Wilford, W.A., Hesselberg, R.J., Nortrupt, D.A., Rundberg, E.G.S., Alwan, A.K., and Bautista, C. 1986. Contaminant trends in lake trout (*Salvelinus namaycush*) from the upper Great Lakes. *Archives of Environmental Contamination and Toxicology* 15:349–356.

Dykstra, C.J.R. 1995. Effects of contaminants, food availability and weather on the reproductive rate of Lake Superior bald eagles (*Haliaeetus leucocephalus*). Ph.D. dissertation. University of Wisconsin-Madison, Madison, WI.

Fox, G.A., Gilman, A.P., Peakall, D.R., and Anderka, F.W. 1978. Behavioral abnormalities of nesting Lake Ontario herring gulls. *Journal of Wildlife Management* 42:477–483.

Fraser, J.D. 1981. The breeding biology and status of the bald eagle on the Chippewa National Forest. Ph.D. dissertation. University of Minnesota, St. Paul, MN.

Frenzel, R.W. 1985. Environmental contaminants and ecology of bald eagles in southcentral Oregon. Ph.D. dissertation. Oregon State University, Corvallis, OR.

______, and Anthony, R.G. 1989. Relationships of diets and environmental contaminants in wintering bald eagles. *Journal of Wildlife Management* 53:792–802.

Giesy, J.P., Bowerman, W.W., Mora, M.A., Verbrugge, D.A., Othoudt, R.A., Newsted, J.L., Summer, C.L., Aulerich, R.J., Bursian, S.J., Ludwig, J.P., Dawson, G.A., Kubiak, T.J., Best, D.A., and Tillitt, D.E. 1995. Contaminants in fishes from Great Lakes-influenced sections and above dams of three Michigan rivers: III. Implications for health of bald eagles. *Archives of Environmental Contamination and Toxicology* 29:309–321.

Grier, J.W. 1982. Ban on DDT and subsequent recovery of reproduction in bald eagles. *Science* 218: 1232–1235.

Grimm, L.H., and Kallemeyn, L.W., 1995. *Reproduction and distribution of bald eagles in Voyageurs National Park, Minnesota, 1973–1993*. Biological Science Report 1, National Biological Service, U.S. Department of the Interior.

International Joint Commission. 1990. *Draft: Final report of the ecosystems objectives committee*. Unpubl. report.

Kozie, K.D. 1986. Breeding and feeding ecology of bald eagles in the Apostle Islands National Lakeshore. M.S. thesis. University of Wisconsin-Stevens Point, Stevens Point, WI.

______, and Anderson, R.K. 1991. Productivity, diet, and environmental contaminants in bald eagles nesting near the Wisconsin shoreline of Lake Superior. *Archives of Environmental Contamination and Toxicology* 20:41–48.

Kubiak, T.J., Harris, H.J., Smith, L.M., Schwartz, T.R., Stalling, D.L., Trick, J.A., Sileo, L., Docherty, D.E., and Erdman, T.C. 1989. Microcontaminants and reproductive impairment of the Forster's tern on Green Bay, Lake Michigan-1983. *Archives of Environmental Contamination and Toxicology* 18:706–727.

McArthur, M.L.B., Fox, G.A., Peakall, D.B., and Philogene, B.J.R. 1983. Ecological significance of behavioral and hormonal abnormalities in breeding ring doves fed an organochlorine chemical mixture. *Archives of Environmental Contamination and Toxicology* 12:343–353.

Mora, M.A., Auman, H.J., Ludwig, J.P., Giesy, J.P., Verbrugge, D.A., and Ludwig, M.E. 1993. Polychlorinated biphenyls and chlorinated insecticides in plasma of Caspian terns: relationships with age, productivity and colony site tenacity in the Great Lakes. *Archives of Environmental Contamination and Toxicology* 24:320–331.

Newton, I. 1979. *Population Ecology of Raptors.* Vermillion, South Dakota: Buteo Books.

Nisbet, I.C.T. 1989. Organochlorines, reproductive impairment and declines in bald eagles *Haliaeetus leucocephalus* populations: mechanisms and dose-response relationships. In *Raptors in the Modern World*, eds. B.-U. Meyburg and R.D. Chancellor, pp. 483–489. World Working Group on Birds of Prey. Berlin.

Postupalsky, S. 1971. *Toxic chemicals and declining bald eagles and cormorants in Ontario.* Unpublished report to the Canadian Wildlife Service, No. 20.

———. 1978. The bald eagles return. *Natural History* 87(7):62–63.

Sindelar, C.R. 1983. *Historical breeding of eagles amongst the Apostle Islands and the adjacent mainland shore. Historical records, current status, and brief recommendations.* Report to National Park Service.

Snedecor, G.W., and Cochran, W.G. 1980. *Statistical Methods*, seventh edition, Ames, Iowa: Iowa State University Press.

Stalmaster, M.V. 1987. *The Bald Eagle.* New York, New York: Universe Books.

Steenhof, K. 1987. Assessing raptor reproductive success and productivity. In *Raptor management techniques manual,* eds. B.A. Giron Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird, pp. 157–170. Washington, D.C.: National Wildlife Federation.

Stickel, L.F., Wiemeyer, S.N., and Blus, L.J. 1973. Pesticide residues in eggs of wild birds: adjustment for loss of moisture and lipid. *Bulletin of Environmental Contamination and Toxicology* 9:193–196.

Warnke, D.K. 1996. A comparison of nesting behavior of bald eagles breeding along Western Lake Superior and adjacent inland Wisconsin. M.S. thesis. University of Minnesota, St. Paul, MN

Weseloh, D.V. Chip, Ewing, P.J., Struger, J., Mineau, P., and Norstrom, R.J. 1994. Geographical distribution of organochlorine contaminants and reproductive parameters in herring gulls on Lake Superior in 1983. *Environ. Monitor. Assess.* 29:229–251.

Wiemeyer, S.N., Mulhern, B.M., Ligas, F.J., Hensel, R.J., Mathisen, J.E., Robards, F.C., and Postupalsky, S. 1972. Residues of organochlorine pesticides, polychlorinated biphenyls, and mercury in bald eagle eggs and changes in shell thickness, 1969 and 1970. *Pesticide Monitoring Journal* 6:50–55.

———, Lamont, T.G., Bunck, C.M., Sindelar, C.R., Gramlich, F.J., Fraser, J.D., and Byrd, M.A. 1984. Organochlorine pesticide, polychlorinated biphenyls, and mercury residues in bald eagle eggs—1969–1979—and their relationship to shell thinning and reproduction. *Archives of Environmental Contamination and Toxicology* 13:529–549.

———, Bunck, C.M., and Stafford, C.J. 1993. Environmental contaminants in bald eagle eggs—1980–84—and further interpretations of relationships to productivity and shell thickness. *Archives of Environmental Contamination and Toxicology* 24:213–227.

Wilkinson, L. 1988. *Systat: the system for statistics.* Evanston, IL: Systat, Inc.

Wisconsin State Laboratory of Hygiene, 1996. *Methods of Organic Analysis Manual—January 1, 1996.* Wisconsin State Laboratory of Hygiene, Madison, WI.

Submitted: 2 January 1997
Accepted: 7 January 1998
Editorial handling: Thomas J. Murphy