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Research Article

Density-Dependence in the Survival and Reproduction of Bald Eagles: Linkages to Chum Salmon

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ABSTRACT During the late 20th Century, due to decreases in both contamination and persecution, bald eagle (*Haliaeetus leucocephalus*) populations increased dramatically. Currently, mechanisms regulating eagle populations are not well understood. To examine potential regulating processes in the Pacific Northwest, where eagles are no longer primarily regulated by contaminants or direct persecution, we examined bald eagle reproductive success, breeding populations, winter populations, mortality, and salmon stream use. Wintering and breeding eagle populations in south-coastal British Columbia (BC) quadrupled between the early 1980s and the late 1990s, and have since stabilized. Density-dependent declines in reproduction occurred during 1986–2009, but not through changes in site quality. Mid-winter survival was crucial as most mortality occurred then, and models showed that density-dependent reductions in population growth rates were partially due to reduced survival. Wintering eagles in British Columbia fed heavily on chum salmon (*Oncorhynchus keta*) runs, and then switched to birds in late winter, when mortality was highest. Eagles tended to arrive after the peak in salmon availability at streams in BC as part of a migration associated with salmon streams from Alaska to northern Washington. Eagles were most abundant in southern BC during cold Alaskan winters and in years of high chum salmon availability. We suggest that eagle populations in the Pacific Northwest are currently partially limited by density on the breeding grounds and partially by adult mortality in late winter, likely due to reduced late winter salmon stocks forcing eagles to exploit more marginal prey supplies. Larger eagle populations have affected some local prey populations. © 2011 The Wildlife Society.

KEY WORDS bald eagle, British Columbia, *Haliaeetus leucocephalus*, population trends, salmon stocks, top-down population regulation.

Pacific Northwest bald eagle (hereafter eagle) populations have largely recovered following restrictions on hunting, lead shot, and organochlorine contaminants, such as DDT (dichlorodiphenyltrichloroethane), PCBs (polychlorinated biphenyls), and dieldrin (Grier 1982, Elliott et al. 1996, Wayland et al. 2003), and several are now at or near carrying-capacity (Jacobsen and Hodges 1999, Buehler 2000, Dunwiddie and Kuntz 2001, Watson et al. 2002). Thus, although some eagle populations may still be partly regulated by toxic contamination (Kumar et al. 2002, Bowerman et al. 2003, Best et al. 2010), those in the Pacific Northwest (Elliott et al. 1996b, 1998; Gende and Wilson 1997; Gill and Elliott 2003) and other remote regions of North America (Dzus and Gerrard 1993, Donaldson et al.

1999), now appear to be largely regulated by natural agents, primarily food abundance (Dzus and Gerrard 1993; Dykstra et al. 1998, 2001). Nonetheless, there is still persistent endocrine disruption in nestlings associated with legacy PCB exposure in the Pacific Northwest (Cesh et al., 2010).

British Columbia supports a substantial proportion of the total North American wintering population (Buehler 2000); however, little is known about populations in the province and trend information is vague and sometimes contradictory (Table 1). Despite the paucity of information on bald eagle wintering numbers in this Pacific Canadian province and suggestions that populations are stable (Table 1), many studies attribute declines in prey populations in south-coastal British Columbia and nearby regions partially to increased disturbance and predation by eagles (Table 2; see also Zaun 2009). Population increases of generalist predators are known to sometimes severely affect rare prey items (Conry 1988, Elliott 2004) and top-down effects are increasingly reported in waterbird studies (Tella et al. 1995, Smith et al. 2010). First Nations groups and media have raised the

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Table 1. Bald eagle population size and trend for south coastal British Columbia, Canada, and for Washington, USA.

Location	Population size	Population trend	Source
British Columbia		Generally stable prior to 1990	Campbell et al. (1990)
British Columbia	30,000 on coast	Either stable or increasing prior to 1994	Blood and Anweiler (1994)
British Columbia	30,000 with 24,000 in the southwest quarter		Gerrard (1983) using Christmas Bird Count data
British Columbia	20,000–30,000		Farr and Dunbar (1988) using Mid-Winter Surveys
British Columbia	28,507	No change between 1982 and 1997	Buehler (2000)
Gulf Islands, British Columbia		30% increase from 1960s to 1980s for both wintering and breeding	Hancock (1964), Trenholme and Campbell (1975), Vermeer et al. (1989)
Skagit River, Washington		Doubled 1987–1992; stable at 1.5 times 1987 levels during late 1990s	Dunwiddie and Kuntz (2001)
Coastal British Columbia ^a	9,000		Hodges et al. (1984)
Washington ^a	4,900 (estimate at equilibrium)	Increased at 10.1% per year 1980–1998	Watson et al. (2002)
San Juan Islands, Washington ^a	Approx. 80 territories	Increased 1962–1994; stable 1995–1998	Watson et al. (2002)

^a Breeding populations; all other rows refer to wintering populations except where described otherwise.

possibility of culling eagles for ceremonial use, citing the threat of increased eagle populations to the conservation of provincially threatened great blue heron (*Ardea herodias*) and double-crested cormorant (*Phalacrocorax auritus*) populations; news outlets have stated that provincial attorneys will no longer prosecute individuals from First Nations that kill eagles to circumvent the possibility that the courts will rule that it is a traditional right. At the same time Elliott et al. (1996a, 2008) attributed an increase in the number of eagle poisonings in south-coastal British Columbia to an increase in the number of eagles.

Models are useful tools in the search for robust mechanistic explanations for population trends in small, closed populations (e.g., Reid et al. 2003), but are less often applied to large, open populations that represent most animal species (McDonald and Amstrup 2001, Chamaillé-Jammes et al. 2008). Eagles are an example of such a

population where it is unclear what demographic mechanisms underlie population changes. To accurately understand the relationship between eagle abundance and the rate of poisonings or the population trends in other species, it is essential to identify the status of eagle populations. We therefore investigated whether eagle populations increased in south coastal British Columbia, whether they are now stable and what mechanisms may underlie eagle population trends.

STUDY AREA

We defined south-coastal British Columbia as the eastern coast of Vancouver Island north to Campbell River and the western coast of the Mainland south of Desolation Sound (Fig. 1). The region forms the Canadian portion of the Salish Sea ecoregion (Fig. 1). Historically, the region was dominated by western hemlock (*Tsuga heterophylla*), Douglas fir

Table 2. Declines in waterbird populations or reproductive success in the Pacific Northwest attributed to increases in bald eagle abundance. We indicate birds listed as threatened or endangered at the provincial, state or federal level with a (+). We indicate sites where the primary effect of eagles is through flushing many adults off their eggs, which allows gulls and crows to access the eggs, with a (*).

Species	Region	Notes
Great blue heron ⁺	British Columbia (Salish Sea)	Vennesland and Butler (2005); increase in eagle numbers may affect heron reproductive success
Double-crested cormorant ⁺	British Columbia (Salish Sea)*	Moul and Gebauer (2002); lower reproductive success attributed to indirect effect of increased eagle numbers
Common murre	Oregon (Oregon Coast National Wildlife Refuge)*	US Fish and Wildlife Service, unpubl. data; population decline at Three Arch Rocks, Cape Meares, and other colonies; partial redistribution to colonies elsewhere in Oregon
Common murre	Washington (Tatoosh Island)*	Parrish et al. (2001); 3% annual decline in murre population attributed to direct and indirect effects of eagles
Common murre ⁺	British Columbia (Triangle Island)*	Hipfner et al. (2011); near complete failure once eagles accessed colony (following departure of falcons)
Black-legged kittiwake, pelagic cormorant, common and thick-billed murre	Alaska (Middleton Island)*	T. van Nus, S. Hatch, US Geological Survey, pers. comm.; late 1980s–2006: eagles increased from 0 to 6 pairs plus subadults; seabirds declined to <20% of their former size; remaining productive seabirds mostly at sites inaccessible to predators, which include rapidly increasing gull populations that access seabird nests when eagles flush adults; eagles may have contributed to declines, along with changes in nest site quality and food abundance
Glaucous-winged gull	British Columbia (Salish Sea)	Sullivan et al. (2002); rapid increase in eagles coincided with a decline in gulls
Glaucous-winged gull	Washington (Salish Sea)	Hayward et al. (2010); rapid increase in eagles coincided with 44% decline in gulls 1993–2008; many direct observations of predation
Canada goose ⁺	Alaska (Copper River)	Anthony et al. (2004); 72% of destroyed nests consumed by eagles for a goose subspecies with declining reproductive success

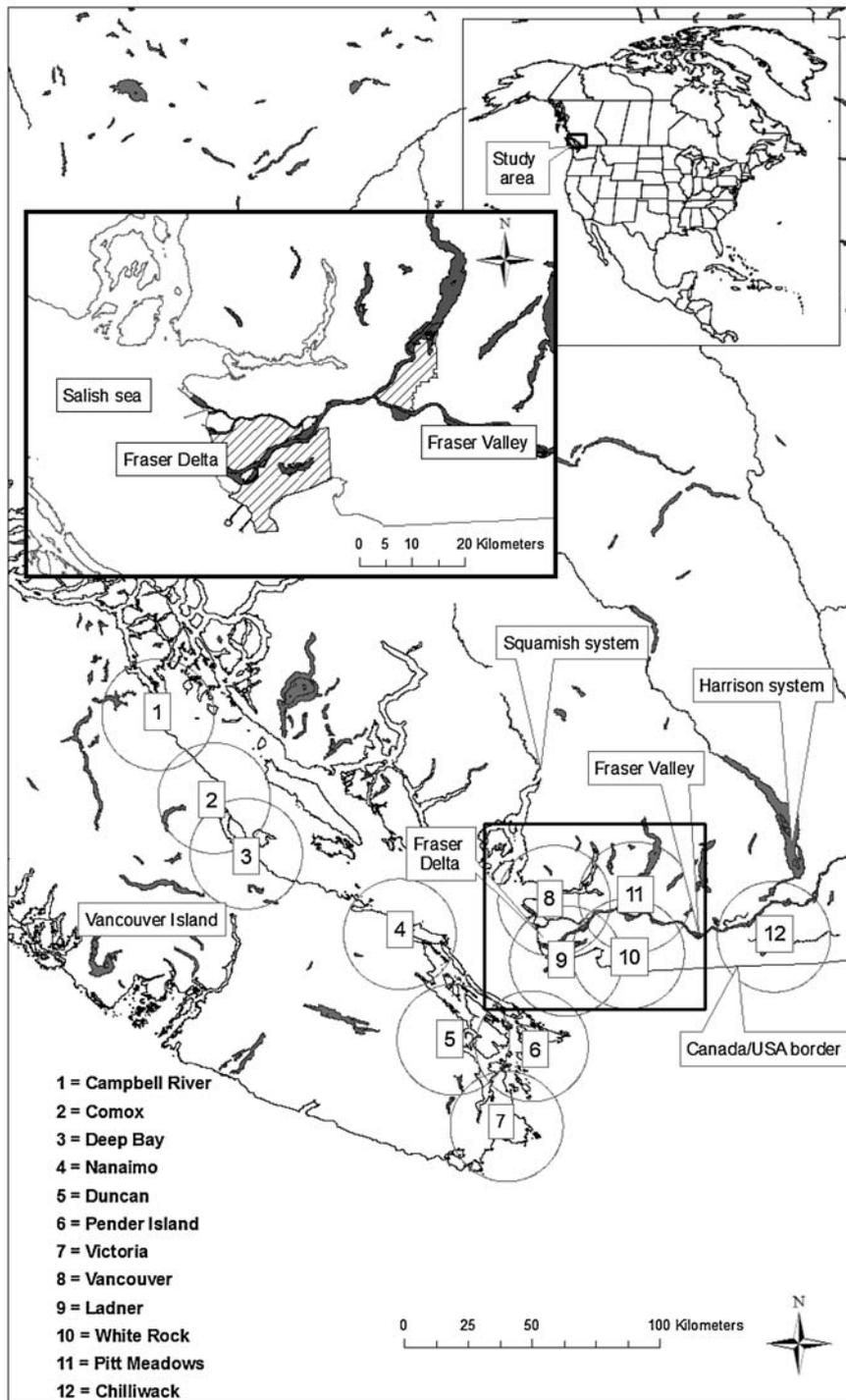


Figure 1. Sampling locations for bald eagles within south-coastal British Columbia, Canada (1973–2010) showing the outline of the Salish Sea ecoprovince, the location of each Christmas Bird Count (1–12), the location of the Fraser delta and valley for breeding counts, and the location of salmon spawning streams (Harrison and Squamish systems). Hatched lines show Vancouver Raptor Census area, which also includes Sea, Iona and Westham Islands.

(*Pseudotsuga menziesii*), and western red cedar (*Thuja plicata*) although now the landscape includes 3 major urban centers: Nanaimo, Victoria, and Vancouver, as well as extensive agricultural zones in the Fraser delta and eastern Vancouver Island. Managed forests still occur along the coast north of Vancouver, in the Gulf Islands, and over some portions of southern Vancouver Island. The Harrison/

Lower Fraser and Squamish Rivers and their tributaries are the 2 main chum salmon (*Oncorhynchus keta*) rivers that attract large concentrations of eagles, although there are also smaller eagle numbers along many other river systems. We monitored breeding populations at the Fraser delta (Delta to Coquitlam) and the Lower Fraser Valley (Abbotsford to Hope).

METHODS

Population Trends

Capture–mark–recapture data do not exist for our population, and the large size, and open nature of winter eagle populations means that resighting probabilities would be low and survival estimates uncertain. Thus, we matched outputs of a Leslie matrix model with population counts to determine what types of model inputs could best explain changes in population size. We monitored breeding populations by attempting to locate all nests in 2 study areas of the Fraser Valley and surveying them once in late March and early April for occupancy and once in June for productivity (see Elliott et al. 1998, Elliott and Norstrom 1998 for details). We considered territories occupied if there was a bird in incubating posture on the nest or an adult in the immediate vicinity of the nest. We calculated productivity as the number of young produced per occupied breeding territory (Elliott and Norstrom 1998).

We based our estimates of winter population trends for south coastal British Columbia on 4 volunteer-based surveys: 1) Christmas Bird Counts (CBC) from 12 count circles in south-coastal British Columbia that have been regularly conducted since the winter of 1972–1973 (Campbell River, Chilliwack, Comox, Deep Bay, Duncan, Ladner, Nanaimo, Pender Island, Pitt Meadows, Vancouver, Victoria, and White Rock), 2) Vancouver Natural History Society raptor census (VRC) conducted monthly October to April during 1970–1980 and 1997–2003 and covering all of Delta, Richmond, and Pitt Meadows, 3) bald eagle mid-winter surveys (MWS) that covered all of south-coastal British Columbia during 1985–1995, and 4) coastal waterbird surveys (CWS) which are monthly surveys covering much of coastal British Columbia 1999–2004 and whose results are presented by Badzinski et al. (2006). The methods were similar for each census type; areas were subdivided and teams of observers were requested on a single day to record all birds (CBC), all waterbirds (CWS), all raptors (VRC), and all eagles (MWS) with coverage areas being larger for MWS than for VRC, CBC, or CWS. For CBC, VRC, and MWS, observers also identified the number of adults, subadults, and unknown. Unknown were generally <5%. We calculated the proportion of subadults as the number of subadults divided by the number of adults and subadults. On 3 dates in 2001, we used a double survey method (Anthony et al. 1999a) to estimate the precision of volunteer-based counts by organizing 3 teams to count the same VRC region at the same time, with starting points and routes designed so that the 3 teams did not encounter one another. Each team counted the number of eagles they encountered while covering the defined area such that the entire area was surveyed.

Based on these double surveys (see Results Section), we used raw counts (rather than observer number or party-hour corrected counts) as our sampling unit for wintering eagle populations, and only included CBCs with at least 10 participants. We used 10 as our cutoff because 1) a general linear model showed no significant effect of number of CBC participants on eagle counts, after accounting for year and

January temperature, when there were more than 10 participants and 2) a CBC team of 10 would be about the same number of people per km² covered as a VRC team of 2 used in the above validation for the VRC. We excluded 24 (6% of the total) CBCs because they did not meet that criterion. To account for the effect of missed counts, we multiplied the average of the counts (for each particular CBC circle, VRC area, or MWS area) occurring 2 yr previous and 2 yr subsequent to the missed year by the average proportional ratio across all counts of that year compared to the previous and subsequent 2 yr. We used identical methods to also quantify changes in population size for 6 prey items (double-crested cormorant, pelagic cormorant [*Phalacrocorax pelagicus*], great blue heron, glaucous-winged gull [*Larus glaucescens*], common murre [*Uria aalge*], and pigeon guillemot [*Cepphus columba*]), 4 of which have been identified as affected by eagle population increases (Table 2).

To estimate population parameters of eagles, we used a density-dependent Leslie matrix model (Caswell 2001, Miller et al. 2002):

$$N_{t+1} = N_t + (1 - \beta)(M - I)N_t$$

where N_t is the vector of age classes at year t , M is the projection matrix, I is the identity matrix, and β is the strength of the density-dependent term. We assumed a maximum age of 25 and a minimum age of reproduction of 5 (Dzus and Gerrard 1993, Jacobsen and Hodges 1999—variation in those assumptions did not change the model substantially, see Results Section) giving

$$M = \begin{matrix} & 0 & 0 & 0 & 0 & F & \dots & \dots & F & F & F \\ S_1 & 0 & 0 & 0 & 0 & 0 & \dots & \dots & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 & 0 & \dots & \dots & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 & 0 & \dots & \dots & 0 & 0 & 0 \\ 0 & 0 & 0 & S_4 & 0 & 0 & \dots & \dots & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_a & \dots & \dots & 0 & 0 & 0 & 0 \\ \dots & \dots \\ \dots & \dots \\ 0 & 0 & 0 & 0 & 0 & \dots & \dots & S_a & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \dots & \dots & 0 & S_a & 0 & 0 \end{matrix}$$

where F is the average fecundity (including non-breeders) and S_n is the mortality at year n . We based S_n on the age distribution of dead eagles brought in to the Canadian Wildlife Service in south coastal British Columbia (see next section). We assumed that S_n was proportional to the age-specific number of dead eagles retrieved. Only subadult eagles were aged to the year, and we therefore assumed that adult mortality was age-independent: $S_5 = S_6 = \dots = S_{24} = S_a$. As a χ^2 Test showed no variation in mortality among age classes for subadults, and an ANOVA showed no variation among years, we assumed that $S_1 = S_2 = S_3 = S_4$. Based on our observed distribution of adult:subadult mortality among years, we assumed that $S_a = 0.45 + 0.55S_1$. To estimate β , F , and N_0 , we used Newton's method to minimize the least squares distances for the total number of eagles and the proportion of subadults. We used the term β_R to represent

density-dependence in reproduction and β_S to represent density-dependence in survival. Three models were calculated: $\beta_R = \beta_S = 0$ (density-independent growth), $\beta_S = 0$ (density-dependence through reproduction alone) and 1 that allowed separate values for both β_R and β_S (density-dependence through survival and fecundity). As we directly demonstrated density-dependence in fecundity (see Results Section), we did not consider a model that only allowed density-dependence in survival.

Leslie matrices have been criticized for being sensitive to initial conditions and for including a large number of parameters (e.g., Yearsley 2004). We overcame some of these difficulties by using Akaike's information criterion (AIC) to select models with the most parsimonious number of parameters and by using a long-term data set with several different inputs (reproductive success, population count, and percentage in each age class) rather than just total population count.

To further test the influence of observer bias on counts, as well as the influence of weather, we created a general linear model with model outputs from above (the most parsimonious Leslie matrix model given the data), number of observers per count, number of party hours per count, and average December temperatures in southeast Alaska (average monthly values for Juneau, Ketchikan, and Sitka from www.wunderground.com and for Prince Rupert from www.weatheroffice.gc.ca) and southeast British Columbia (average value at all 12 CBC communities from www.weatheroffice.gc.ca) as independent variables. We used Akaike's information criterion to select the most parsimonious models.

Mortality, Winter Diet, and Population Dynamics

To determine what potential mechanisms were involved in population regulation we determined causes of death for eagles in south coastal British Columbia. Eagle carcasses were obtained from a network of wildlife rehabilitation centers; British Columbia Ministry of Environment, Lands and Parks (BC MELP) offices; veterinarians; taxidermists; and the general public. Carcasses were stored frozen at -20°C . Post-mortem examinations to determine probable cause of death were conducted semi-annually by a veterinarian at the end of each field season.

To examine the potential role of food supply in winter population dynamics, we monitored diet and counted eagle populations from 1 October to 30 April in south coastal British Columbia. We monitored both of the major salmon spawning systems in south coastal British Columbia: the Squamish and Harrison/Lower Fraser systems. At Squamish, Christmas we used data from Christmas Bird Counts 1980–2010 and annual January counts 1986–2011. We counted eagles and salmon carcasses from 1000 hours to 1200 hours weekly on the Harrison system (1 Oct to 31 Mar) during 1995–1996, 1996–1997, 2001–2002, 2002–2003, and 2004–2005, and at least twice a year during peak eagle concentrations every other year 1995–2009. We counted eagles at 1000 hours to 1200 hours weekly on the Squamish system during 2001–2002 and 2002–2003, and

combined our data with earlier data presented by Booth and Merckens (2000). We also visited 4 eagle concentrations in the Fraser delta twice per week (1 Nov to 30 Apr) during the winters of 1993–1994, 1994–1995, 1995–1996, and 2001–2002 (the South Arm, Deas and Alaksen roosts, and the Vancouver landfill). We counted the number of adults and subadults, and aged subadults to the year. We calculated eagle-use days following Stalmaster and Kaiser (1997).

To determine eagle diet in south-coastal British Columbia, we collected anecdotal sightings from naturalists following the methods devised by Stocck (2000). Requests for sightings of eagles consuming prey were posted to naturalists via meetings, newsletters and email during 1989–2005. We only used observations from experienced naturalists. Although such observations are biased towards readily identifiable prey items, all other methods, such as analyses of pellets and prey remains are also biased, usually towards large prey items (Todd et al. 1982, Mersmann et al. 1992, Elliott et al. 2003). Presumably, any bias would be equivalent across dates.

To examine salmon availability, we obtained chum salmon escapement (total salmon not caught by fishing vessels and therefore available to eagles) and water level from Fisheries and Oceans Canada.

RESULTS

Breeding and Winter Populations

The breeding population roughly tripled between the late 1980s and the early 2000s, before reaching a zone of apparent stability (Fig. 2d). Over the same time period, reproductive success (productivity) and the proportion of subadults observed in winter and found dead decreased, and the slopes were statistically indistinguishable once all 3 metrics were normalized to the same starting value (Fig. 2c). Number of nestlings per occupied territory declined with population size ($t_{24} = -3.56$, $P < 0.001$) whereas number of nestlings per successful territory did not ($t_{24} = -1.11$, $P = 0.30$). Assuming that eagle populations at the start of our study period (1986) were similar to those found in 1980 (Hodges et al. 1984), and that populations increased in a similar fashion across south coastal BC, we estimate $12,000 \pm 4,000$ breeding adults in south coastal BC and $17,000 \pm 5,000$ breeding adults in all of coastal BC, assuming no increase in north coastal BC.

Winter double surveys averaged 0.92 ± 0.04 repeatability, and there was a strong correlation in eagle numbers for each year between different survey methods (CBC and VRC: $r^2 = 0.93$, $t_{12} = 12.20$, $P < 0.001$; CBC and MWS: $r^2 = 0.85$, $t_9 = 7.31$, $P < 0.001$; CBC and CWS: $r^2 = 0.71$, $t_4 = 3.12$, $P = 0.04$). All survey methods showed an increase in bald eagle numbers, except for CWS during 1999–2004. The other counts also showed a decline during 1999–2004, which was a period of increasingly warmer winters (Fig. 2a). Assuming similar population increase throughout the province (our study area comprises about 75% of the province's eagle population), and that the estimate of 28,400 eagles for winter 1987–1988 was correct

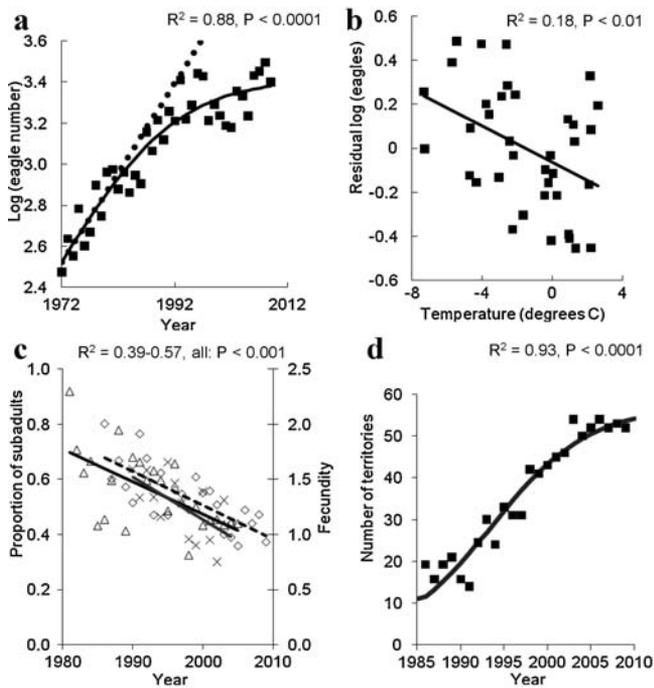


Figure 2. (a) Bald eagle counts in south coastal British Columbia, Canada, 1973–2010 (squares), after correcting for temperature using the residual from (b). We also show predicted eagle numbers from the model described in the text (solid line) and number assuming no stabilization (exponential growth, dashed line). Year refers to the year preceding each winter (e.g., 1972 is the winter of 1972–1973). (b) Residual of eagle counts in British Columbia on the number predicted by the model described in the text (squares minus line in [a]) calculated for each square, but on the natural logarithm values) compared to average December temperature in southeast Alaska. (c) Fecundity (number of offspring per occupied territory; diamonds, dashed line) for eagles in the Fraser Valley, proportion of subadults counted (triangles, black line), and proportion of subadults found dead (crosses, gray line) for south coastal British Columbia. (d) Number of breeding territories (squares) and predicted eagle numbers from the model described in the text (solid line) for the survey area along the Fraser delta and valley.

(Farr and Dunbar 1988; assuming observer precision of 92%), an average of $56,000 \pm 8,000$ eagles wintered in BC during 2000–2009.

Model Output and Causes of Mortality

The wintering population in south-coastal British Columbia increased approximately 4.5-fold between the mid-1970s and late 1990s, and has since stabilized (Fig. 2a). The most parsimonious models for describing population increases showed density-dependent growth with the number of eagles present each year correlated to winter temperatures in southeast Alaska (Table 3; Fig. 2b). Varying maximum age by ± 5 yr, age of first breeding by ± 2 yr and allowing adult mortality to vary quadratically, to account for senescence, changed model outputs by $<10\%$ and had no effect on the ranking of any of the models.

The primary causes of mortality for eagles found dead were anthropogenic (Table 4). The proportion of subadults was similar for most causes of mortality, but was significantly lower for eagle attacks and gunshot wounds (Table 4). Most mortalities occurred during January to April (Fig. 5).

Table 3. Akaike's information criterion (AIC) ranking for models for bald eagle populations in southwestern British Columbia 1973–2010 including terms that are density-independent ($\beta = 0$), density-dependent in fecundity alone ($\beta_S = 0$), density-dependent in both survival and fecundity ($\beta_S \neq 0$), and terms for average temperature in southeast Alaska (Alaska), average temperature in southwest British Columbia (BC) and observer coverage (Observer).

Model	k	ΔAIC	AIC weight
$\beta_S \neq 0$ + Alaska	5	0.0	0.72
$\beta_S = 0$ + Alaska	4	1.1	0.24
$\beta_S \neq 0$ + BC	5	3.1	0.03
$\beta_S \neq 0$ + Observer	5	4.5	0.01
$\beta_S \neq 0$	4	6.6	0.00
$\beta_S = 0$	3	7.5	0.00
$\beta_R = \beta_S = 0$ + Alaska	3	17.8	0.00
$\beta_R = \beta_S = 0$	2	20.2	0.00

Relationship to Salmon Stocks

Eagle numbers at salmon streams peaked in December and early January, after the peak in Chilkat, Alaska and before the peak in Washington (Fig. 3). Numbers in the Fraser delta were highest in February and early March (Fig. 3). The number of chum salmon carcasses at Harrison peaked in late October, well before the peak in eagle numbers (Fig. 3). Total eagle-use days per year at Squamish correlated with chum salmon escapement but not water levels in the week prior to surveys (general linear model: $r^2 = 0.23$; salmon escapement: $t_{29} = 3.29$, $P = 0.003$; water level: $t_{29} = 0.20$, $P = 0.85$; Fig. 4). Total eagle-use days per year at Harrison correlated with water levels in the week prior to surveys but not chum salmon escapement (general linear model: $r^2 = 0.24$; salmon escapement: $t_{11} = 0.23$, $P = 0.82$; water level: $t_{11} = 3.05$, $P = 0.01$). After accounting for date, the residual of the above models were inversely correlated with one another for each week that counts were simultaneously conducted at both salmon streams ($r^2 = 0.26$, $t_{44} = 3.29$, $P = 0.02$). The proportion of subadults increased with date at Harrison ($r^2 = 0.35$; $t_{14} = 3.45$, $P = 0.002$) and the Fraser delta ($r^2 = 0.28$; $t_{14} = 3.23$, $P = 0.008$).

Diet

In late winter, eagles fed primarily on waterfowl (Fig. 5). Specifically, waterfowl made up 70.7% of observed eagle prey (captured alive = 107 observations; scavenged = 88 observations) and gulls made up 12.3% of observed eagle prey

Table 4. Age at death for seven causes of death for bald eagles collected in British Columbia, Canada, 1990–2004 ($n = 749$). We indicate groups that are significantly different using a sequential Bonferroni correction with a (+).

Cause of death	Subadults	Adults	χ^2_1	P -value
Vehicle collision	27	22	0.84	0.36
Electrocution	79	67	1.80	0.18
Gun shot ⁺	7	22	6.92	0.008
Disease	41	46	0.07	0.79
Trauma	93	93	0.15	0.70
Poison	55	49	0.77	0.38
Eagle attack ⁺	3	24	15.2	<0.001
Total	305	323		

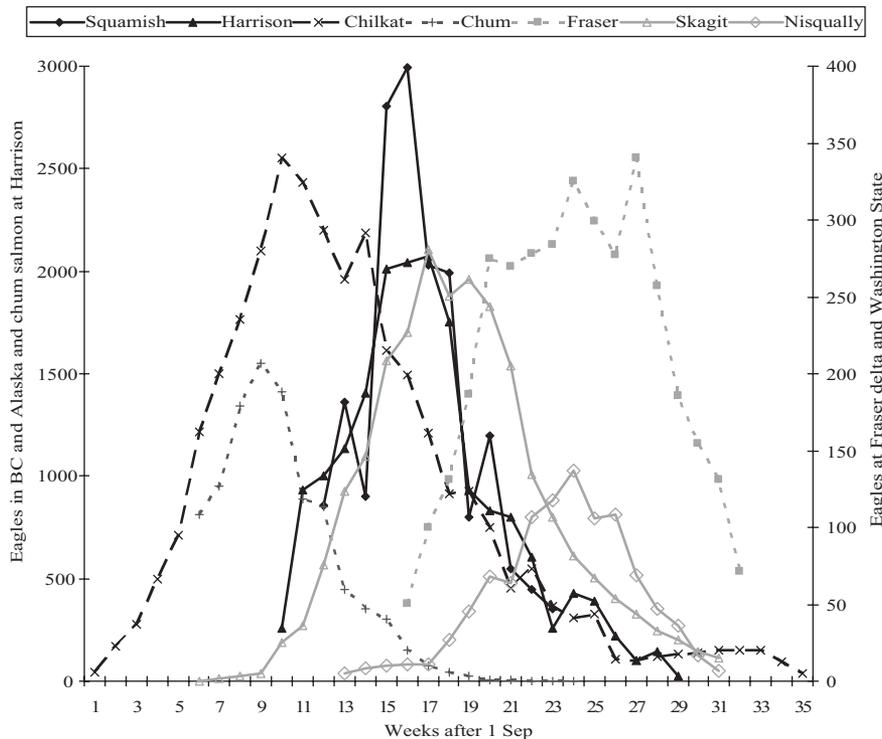


Figure 3. Average number of bald eagles counted in British Columbia, Canada at the Chilkat (1980–1983), Squamish (1995–1997 and 2000–2001), Harrison (1996–1998 and 2001–2005), Skagit (1982–1999)–Nooksack (1975–1977), Nisqually–Muck (1991–1994), and Crooked (1986–1987)–Upper John Day (1991–1993) Rivers and at 4 roosts in the Fraser delta (1993–1996 and 2001–2002). We also show average number of chum salmon carcasses (chum) counted at Harrison (2001–2005). Chilkat data were from Hansen et al. (1984). Skagit–Nooksack data were from Dunwiddie and Kuntz (2001) and Stalmaster et al. (1979). Nisqually data were from Stalmaster and Kaiser (1997) and Oregon data were from Isaacs et al. (1993, 1996).

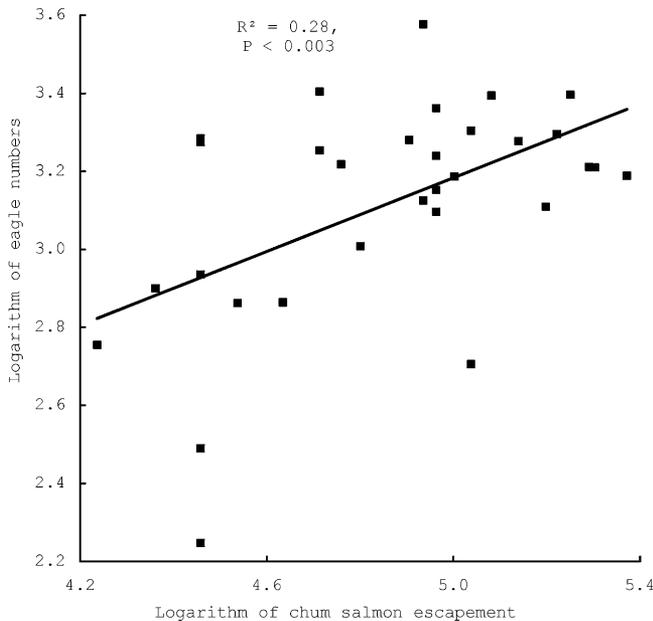


Figure 4. Annual eagle–use days increased with chum salmon availability at Squamish, British Columbia, Canada, 1980–2010. Availability (escapement) data was obtained from Fisheries and Oceans Canada. For those years without escapement data for the Squamish River system, we estimated escapement from the regression between Squamish escapement and Fraser River escapement.

(captured alive = 21 observations; scavenged = 13 observations; other non-gull, non-waterfowl birds were all scavenged = 10 observations) whereas mammals made up 3.3% (all scavenged = 9 observations) and fish made up 10.1% (captured alive = 23 observations; scavenged = 5 observations). We counted prey items pirated from other species (2% of total) and other eagles (1% of total) as scavenged and counted only once even if pirated by multiple individuals. The rest of the year, eagles fed primarily on fish (Fig. 5). None of the 6 winter prey species examined showed a decreasing trend in CBC total counts for south coastal BC over 1973–2010 ($r^2 < 0.01$, $P > 0.5$).

DISCUSSION

The number of eagles wintering in south coastal British Columbia increased dramatically during the 1970s through early 1990s, before reaching an approximate asymptote in the late 1990s and 2000s (Fig. 2). Our results contradict other reports over the same time period suggesting no or a small increase in eagle numbers in BC, and are similar to reports of larger increases in Washington (Table 1). During cold years, BC, especially south-coastal BC, is now home to the largest concentration of wintering eagles (roughly $56,000 \pm 8,000$) in the world during December and January, a point highlighted by record highs at the Squamish River salmon run (e.g., 3,769 in 1996–1997). Frequent reports during the early 2000s of large concentrations of immature and adult

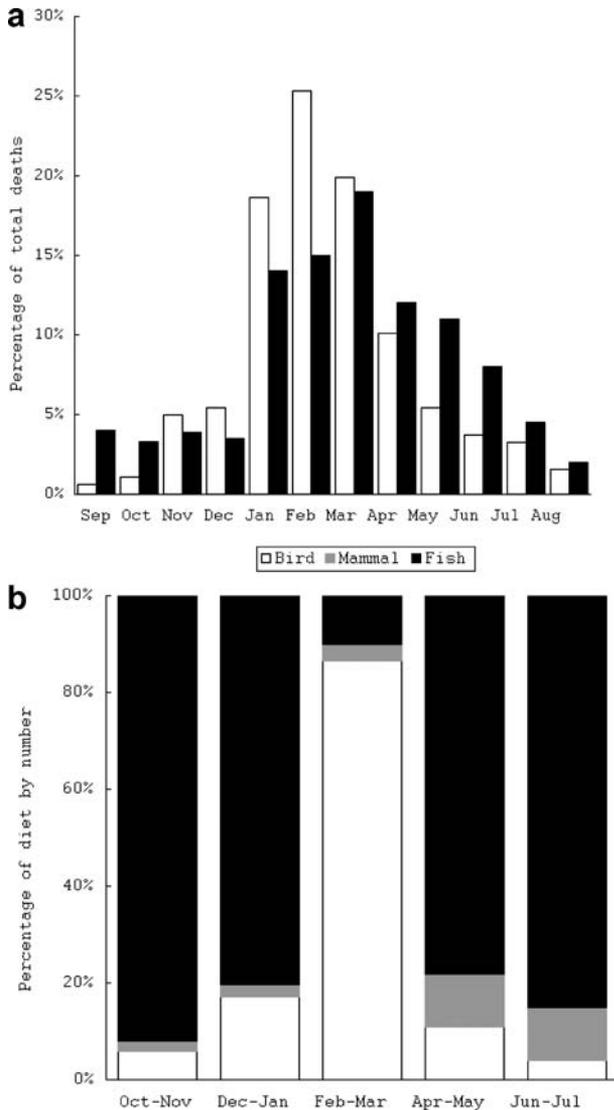


Figure 5. (a) Proportion of eagles (white) and proportion corrected for the number of eagles present (black) for each month reported dead in south coastal British Columbia, Canada, 1990–2004 ($n = 749$). (b) Percentage of diet by number of observations for eagles in south coastal British Columbia, Canada, 1989–2005 ($n = 782$). We excluded August to September because there were only 22 observations; all other bimonthly periods had at least 100 observations.

non-breeders support the idea of a population increase limited by breeding density (i.e., Elliott et al. 2003).

There are several reasons for the increase in the observed number of eagles. Many eagles were once taken by Alaska salmon fishermen wintering in Washington and BC, who then presented the talons for bounty in Alaska (Hancock 2003). In addition, during the 1950s to 1970s, many areas in south coastal BC had sufficient levels of DDT and possibly PCBs to impair eagle reproduction (Elliott et al. 1996b; Anthony et al. 1993, 1994, 1999b; Elliott and Harris 2001). High rates of clear cutting and urban development may have selected for more tolerant eagles in south coastal BC (Hancock 2003). Although pesticide poisoning was a significant cause of death over the past 2 decades (Table 4), and likely affected populations local to the Fraser delta over

several years in the 1990s (Elliott et al. 2008), the main carbamate and organophosphorus pesticides involved in those dieoffs have now been eliminated from most of south-coastal BC (Elliott et al. 2008). Similarly, although polybrominated diphenyl ethers (PBDEs), which have increased dramatically in the Pacific Northwest, may be limiting reproduction of raptorial birds (including eagles) at a few sites, PBDEs are relatively low at most locations and are now regulated (Elliott et al. 2005a, 2009; Cesh et al. 2008; Henny et al. 2009). Electrocutation continues to be a significant cause of mortality (Table 4) despite efforts by electrical transmission utilities to attenuate bird losses, but its importance has not been assessed in British Columbia. We suggest that factors such as winter food supply and territoriality now play a more important role in regulating eagle populations than contamination or other proximate human factors. In particular, the decline in reproductive success over time is unlikely to be due to increased contamination because DDE and PCBs, the contaminants most often associated with reduced reproductive success and nestling health in eagles, generally declined over the sampled period (Elliott and Harris 2001; Harris et al. 2002; Cesh et al. 2008, 2010; Best et al. 2010).

We based our winter estimates on volunteer counts, which can lead to severe bias for some bird populations. However, double surveys showed that counts were highly repeatable, with an estimated 92% of eagles seen by each observing group, and number of observers had no significant effect on the number of eagles counted once group size was above a threshold of 10 observers (no best model included observers or party-hours in Table 3). Eagles are likely ideal birds for volunteer counts as they are conspicuous and easily identified. Furthermore, population indices were similar for 4 different count types, including 2 that covered the entire winter (CWS, VRC) and 2 that covered larger geographical areas (CWS, MWS), so we are confident that our population indices were robust.

Similar population recoveries occurred in Alaska (Jacobsen and Hodges 1999) and northwestern Washington (Dunwiddie and Kuntz 2001, Watson et al. 2002). Eagles wintering in BC are part of this larger metapopulation, as radio and satellite telemetry confirmed that eagles from throughout much of the Pacific Northwest, Alaska, and northwestern Canada migrate to salmon streams in Alaska during the late summer and early fall, and subsequently follow the progression of increasingly late salmon spawnings south to northwestern Washington (Servheen and English 1979, Hodges et al. 1987, Hunt et al. 1992a, Garrett et al. 1993). Wintering eagles regularly move among salmon streams and waterfowl concentrations throughout northwestern Washington and south coastal BC (Hunt et al. 1992a, Elliott et al. 2006). Our data confirmed that trend, with eagles peaking at BC salmon streams after eagle numbers diminish in Alaska and before they peak at Washington salmon streams (Fig. 3) and with an inverse relationship between eagle numbers at Squamish and Harrison (when conditions are good at a particular site, many birds move to that site).

Winter severity was the main predictor of eagle abundance, apart from intrinsic population changes, as more eagles visited BC during cold Alaskan winters (Table 3). Furthermore, whereas eagle numbers closely reflect salmon carcass abundance in Alaska (Hansen et al. 1984), eagle numbers peaked a month after the peak in salmon carcass abundance in BC (Fig. 3). Annual eagle numbers at Squamish were related to salmon escapement (Fig. 4), partially because there have been fewer eagles at Squamish since the collapse of the Squamish salmon run in the mid-2000s (the low values in our Fig. 4). In contrast, eagle numbers at Harrison were related ($r^2 = 0.24$) to water levels rather than salmon escapement. When water levels are high at Harrison, few carcasses are left by the time the eagles arrive. As the relationship between the number of eagles and fish carcass availability is usually very high (i.e., $r^2 > 0.80$: Hansen et al. 1984; 4 out of 5 yr: Restani et al. 2000; with tide, which determined carcass availability: Elliott et al. 2003), we suggest that eagle numbers in south-coastal BC are primarily determined by events elsewhere. Birds linger north of BC until they are forced to move by weather conditions or salmon scarcity in Alaska, and then move among many different salmon streams and food sources such that food availability at other streams may be more important than food availability at a particular stream. For example, there is an inverse relationship between eagle numbers at Squamish and Harrison.

Eagles wintering in the Salish Sea switch their diet from salmon to waterfowl as they migrate from salmon streams to waterfowl concentrations (Fig. 5). Watson et al. (1991) and Hunt et al. (1992a, b) documented similar switches for the Columbia River estuary and Puget Sound, respectively. Waterfowl appear to be a major prey source for wintering eagles throughout their range (Maine, Todd et al. 1982; Missouri, Griffin and Baskett 1985; coastal New Brunswick, Stocck 2000; contra southern Ontario and southern British Columbia, Hancock 1964, Ewins and Andress 1995), and major concentrations of eagles on Christmas Bird Counts coincide with major waterfowl concentrations (Root 1988). Most of our observations were of either scavenged, weak, or crippled small waterfowl, particularly American wigeon (*Anas americana*) and mallard (*Anas platyrhynchos*) such as those exposed by frozen ponds or caught in shallow water by the receding tide (Peterson et al. 2001). However, we also recorded eagles capturing live, healthy waterfowl in shallow water by forcing them under; Watson et al. (1991) and Hunt et al. (1992b) also noted the importance of shallow water for eagles. Early reports suggested that eagles nesting in British Columbia feed primarily on birds, but more recently direct observations and stable isotopes showed that >90% of prey deliveries to eaglets are fish, so reliance on avian prey is confined primarily to late winter except for a few seabird colonies where eagles primarily prey on seabirds (Table 2; Fig. 5; Gill and Elliott 2003; Elliott et al. 2003, 2005b, 2009).

As populations are now at or near a carrying capacity, the question arises: what now regulates growth? Part of the answer is related to reproductive success; productivity

declined linearly with population size. Density-dependence in reproduction does not occur because sites that are more marginal are now occupied. Rather, breeding declined across all sites, possibly because females arrive in poorer condition due to food shortages in winter, because of increased incursions by other eagles, or because intraspecific competition reduces territory size and food availability uniformly (Hansen 1987, Bretagnolle et al. 2008). Productivity was also inversely related to population size at Kodiak Island (Zwiefelhofer 2007) and nearest-neighbor distance in Oregon (Anthony et al. 1994). Our data contradict other studies on growing or already-stable populations that suggest density-dependence occurs mainly through the abundance of floaters, with more floaters occurring at large population size because all territories are filled (Hunt et al. 1992b, Watson et al. 2002, Bretagnolle et al. 2008). Density-dependence through reduced productivity may not be detected in samples only including growth or stable (not both) components of the growth curve. In any case, mechanisms likely vary among regions and population size varies among different subpopulations even for stable populations due to temporal variation in habitat quality (Anthony et al. 2008). As is usual in raptors, there was no change in the number of young per successful nest in our data set or at Kodiak Island (Zwiefelhofer 2007) showing that there are few losses at the nestling stage or that partial failure is rare (Elliott et al. 1998, 2005b).

As is expected for long-lived organisms, another major factor limiting population growth is density-dependence in survival. Most observed mortality is anthropogenic (Table 4), as was the case for 1,428 dead eagles (1963–1984) in the United States, where 23% died from trauma (wires or vehicles), 22% gunshot, 11% poisoning, 9% electrocution, 5% trapping, 8% emaciation, and 2% disease (Wood et al. 1990). Earlier reports included much higher rates of birds shot, such as 59% of 76 eagles found in the United States 1960–1965, and lower rates of birds electrocuted (<2%, Coon et al. 1969). No doubt, animals dying from anthropogenic causes are more likely to be detected than animals dying naturally, but detection rates are presumably highest in summer (when people are more active) whereas we observed the opposite trend, so we feel our monthly trends are robust. Furthermore, the age-related trends are as expected; adults are more likely to be fighting for territories and killed by poachers whereas subadults are more likely to be inexperienced and die of other causes. Perhaps the density-dependence in survival occurs through increased searching for food which leads to increased encounters with anthropogenic sources of mortality, or perhaps emaciated corpses are less likely to die near human thoroughfares, and consequently we overestimate anthropogenic causes of mortality. Most mortality occurs in late winter (Jan to Apr), even though eagle numbers peak in early winter (Nov to Dec). Thus, we suggest that eagle populations are currently limited by food shortages post-salmon availability in late winter, possibly exacerbated by the decimation of the late winter Columbia River salmon stocks or due to poor initial condition in years of low salmon stocks (but see McCollough et al. 1994).

The drastic decline of salmon populations at streams in the Columbia basin and elsewhere may be forcing eagles to feed on alternative prey and affecting threatened waterbirds (Table 2). Increases in gull and cormorant populations in south coastal British Columbia during the 20th Century (Moul and Gebauer 2002, Sullivan et al. 2002) may have been a response to eagle population declines, and the return of this apex predator may lead to a return of cormorant and gull populations to pre-1900 levels. A similar change occurred in Alaska following the decline in sea otter abundance, with eagles switching from kelp-associated fish to non-kelp-associated fish and from sea otters to alternative prey (Anthony et al. 2008). We found no declines in seabird winter population size over the period of rapid eagle increase (1973–2010) for those prey species where declines have been previously attributed to eagles (winter prey populations also either significantly increased or remained stable during Coastal Waterbird Surveys; Badzinski et al. 2008). As our winter counts include longer time and larger spatial scales than any of the studies presented in Table 2, we suggest that declines in breeding numbers at single or a small number of seabird colonies (Table 2) may be offset by emigration to colonies or subcolonies where seabirds are less vulnerable to eagle predation. In any case, eagle populations appear to be now within a zone of apparent stability and we anticipate that prey populations will eventually become balanced, provided recent fluctuations or actual declines in salmon stocks do not cause further perturbations.

MANAGEMENT IMPLICATIONS

Whereas management of the impact of the decline of salmon fisheries in Columbia River Basin and elsewhere in the Pacific Northwest has historically focused primarily on human social and economic concerns, our results emphasize the importance of salmon for other components of the ecological community, namely eagles. The dramatic decline in BC salmon stocks in the last 4 yr, especially coastal chum stocks, will have impacted the panmictic eagle populations throughout the Pacific Northwest, implying that management of those stocks could play an important role in maintaining eagle populations throughout the region. Historically, eagles would have continued their southward trend by migrating in January and February from British Columbia to salmon streams in the Columbia drainage and further south. Whereas 86% of Fraser Basin salmon stocks are considered stable and unthreatened, 73% of Columbia River salmon stocks are extinct and a further 17% at risk (Nehlsen et al. 1991, Slaney et al. 1996). Because eagles can no longer continue their southward movement towards Columbia River salmon streams in January and February, eagles currently migrate to other areas, including regions of the Salish Sea adjacent to the last (Dec to Jan) healthy salmon streams, choosing to feed on alternative prey sources, including threatened seabirds. Management of late-winter coastal salmon stocks, and restoration of salmon stocks in the Columbia River, would increase eagle populations throughout the Pacific Northwest while minimizing late-winter predation by eagles on other wildlife. As eagle numbers

are now relatively stable, we suggest there is no need to cull eagles to prevent negative impacts on prey populations associated with continued eagle population growth.

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