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THE INFLUENCE OF TIDE AND WEATHER ON PROVISIONING RATES OF CHICK-REARING BALD EAGLES IN VANCOUVER ISLAND, BRITISH COLUMBIA

KYLE HAMISH ELLIOTT
Canadian Wildlife Service, 5421 Robertson Road, Delta, British Columbia V4K 3N2 Canada

CHRISTOPHER E. GILL
Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6 Canada

JOHN E. ELLIOTT[1]
Canadian Wildlife Service, 5421 Robertson Road, Delta, British Columbia V4K 3N2 Canada

ABSTRACT.—We investigated how tide and weather (temperature and rainfall) influenced Bald Eagle (*Haliaeetus leucocephalus*) provisioning rates on the east and west coasts of Vancouver Island, British Columbia during the 1996 breeding season. Eagles nesting on the west coast had less frequent prey-delivery rates (3.2 ± 1.0 deliveries/d, $N = 6$ nests) than those nesting on the east coast (7.2 ± 2.8 deliveries/d, $N = 7$ nests). Prey-delivery rates were negatively correlated with precipitation on the west coast, but not on the east coast. On both coasts, prey-delivery rates were negatively related with temperature ($r = -0.45$), as nestlings have lower energetic needs during warm weather, and positively related with adult attendance ($r = 0.35$). Prey-delivery rates were highest at intermediate tide height and early in the day, reflecting food availability. Intertidal fish were a major component of eagle diet on the east coast (plainfin midshipman [*Porichthys notatus*] = 46% by frequency) while pelagic fish were the major component on the west coast (Pacific mackerel [*Scomber japonicus*] = 92%). We concluded that landscape features (e.g., tidal flats) and weather (e.g., rain and temperature) interact to influence provisioning rates of Bald Eagles on Vancouver Island, and that these factors may drive spatial variation in eagle productivity.

KEY WORDS: *Bald Eagle;* Haliaeetus leucocephalus; *British Columbia; productivity; weather; tides.*

LA INFLUENCIA DE LA MAREA Y EL CLIMA EN LAS TASAS DE APROVISIONAMIENTO DE *HALIAEETUS LEUCOCEPHALUS* QUE SE ENCONTRABAN CRIANDO EN VANCOUVER ISLAND, BRITISH COLUMBIA

RESUMEN.—Investigamos cómo la marea y el clima (temperatura y precipitaciones) influenciaron las tasas de aprovisionamiento por parte de individuos de *Haliaeetus leucocephalus* en las costas este y oeste de Vancouver Island, British Columbia, durante la estación reproductiva de 1996. Las águilas que estaban nidificando en la costa oeste presentaron tasas de entrega de presas menos frecuentes (3.2 ± 1.0 entregas/d, $N = 6$ nidos) que aquellas que estaban nidificando en la costa este (7.2 ± 2.8 entregas/d, $N = 7$ nidos). Las tasas de entrega de presas estuvieron negativamente correlacionadas con la precipitación en la costa oeste, pero no en la costa este. En ambas costas, las tasas de entrega de presas estuvieron relacionadas negativamente con la temperatura ($r = -0.45$), debido a que los pichones

[1] Email address: john.elliott@ec.gc.ca

tienen necesidades energéticas menores durante períodos cálidos, y relacionadas positivamente con la presencia de los adultos ($r = 0.35$). Las tasas de entrega de las presas fueron más altas a niveles intermedios de altura de la marea y al comienzo del día, reflejando la disponibilidad de alimentos. Los peces de la zona intermareal constituyeron un componente importante de la dieta de las águilas en la costa este (*Porychthys notatus* = 46% por frecuencia), mientras que los peces pelágicos constituyeron el componente más importante en la costa oeste (*Scomber japonicus* = 92%). Concluimos que las características del paisaje (e.g., planos mareales) y el clima (e.g., lluvia y temperatura) interactúan para influenciar las tasas de aprovisionamiento en *H. leucocephalus* en Vancouver Island, y que estos factores podrían conducir a variaciones espaciales en la productividad de las águilas.

[Traducción del equipo editorial]

Food availability is a key factor regulating raptor productivity in natural ecosystems (Newton 1979, 1998), including Bald Eagles (*Haliaeetus leucocephalus*; Hansen 1987, Dykstra et al. 1998), White-tailed Sea Eagles (*Haliaeetus albicilla*; Helander 1985), African Fish-Eagles (*Haliaeetus vocifer*; Harper et al. 2002), Wedge-tailed Eagles (*Aquila audax*; Ridpath and Brooker 1986), Golden Eagles (*Aquila chrysaetos*; Watson et al. 1992), and Ospreys (*Pandion haliaetus*; van Daele and van Daele 1982), among others (Platt 1976, Dykstra et al. 2003, Hakkarainen et al. 2003). Although some Bald Eagle populations are still at least partly influenced by toxic contamination (Anthony et al. 1993, 1994, 1999, Kumar et al. 2002, Bowerman et al. 2003, Dominguez et al. 2003), several populations now appear to be regulated by natural agents, primarily food abundance (e.g., Dzus and Gerrard 1993, Donaldson et al. 1999, Anthony 2001, Stout and Trust 2002, Gill and Elliott 2003).

Landscape features, especially tidal flats, influence eagle-prey availability, and therefore, productivity (Hansen 1987, Watson et al. 1991, Dzus and Gerrard 1993, Gende et al. 1997, Wilson and Armstrong 1998, Watson 2002). Weather also influences raptor reproductive success, either by affecting adult or chick energetic needs (Newton 1978, 1998, Stalmaster and Gessaman 1984), prey availability (Seavy et al. 1998, Panasci and Whitacre 2000, Harper et al. 2002, Jaksic et al. 1997), or adult foraging effectiveness (Grubb 1977, Newton 1978, Stinson 1980, Gilchrist and Gaston 1997, Gilchrist et al. 1998, Fritz 1998). Whereas rainfall usually increases foraging success for tropical raptors, due to increased productivity at lower trophic levels during the rainy season and decreased heat stress in canopy nesters (Seavy et al. 1998, Panasci and Whitacre 2000, Harper et al. 2002, Jaksic et al. 1997, Touchton et al. 2002), rainfall usually reduces prey availability, increases chick energetic needs, and adult-nest attendance in temperate regions (Newton 1978, 1998, Kruger and Lindstrom 2001, McDonald et al. 2004). For example, rain reduced the ability of Ospreys to locate prey by increasing the number of ripples on the water surface (Grubb 1977). In addition, the number of rainy days during early spring was negatively correlated with Bald Eagle productivity in southeastern Alaska (Gende et al. 1997), but not in the drier interior regions of Alaska (Steidl et al. 1997).

In this study, we investigated the factors influencing provisioning rates at Bald Eagle nests along the Vancouver Island shoreline in coastal British Columbia. Elliott et al. (1998) and Gill and Elliott (2003) showed that eagles nesting on the west coast had lower productivity than those nesting on the east coast, and conjectured that this was due to wetter springs and fewer tidal flats limiting the amount of food brought to nests. We therefore hypothesized that (1) provisioning rates would be negatively correlated with tide height and (2) provisioning rates would be lower during periods of rain.

Previous investigators (Gerrard et al. 1979, Bortolotti 1984a, Jenkins 1989, Kennedy and McTaggart-Cowan 1998, Warnke et al. 2002) have described Bald Eagle nesting behavior using direct observation and time-lapse photography. Warnke et al. (2002) established several benchmarks for the nest provisioning and chick behavior of an inland population that did not seem to be limited by food. In this paper, we used both methods to compare the behavior of eagles from coastal Vancouver Island with those presented by Warnke et al. (2002) for Wisconsin.

STUDY AREA AND METHODS

Study Area. During May–July 1996, we monitored Bald Eagle nests on the east (Crofton, 48.9°N, 123.7°W) and west (Barkley Sound, 48.9°N, 125.3°W) coast of southern Vancouver Island, British Columbia. On the west coast, the marine environment drops off steeply from shore while the sheltered waters on the east coast include large tidal flats where many eagles forage. In addition, the exposed west coast tends to be cooler and windier, with more storm events, than the protected east coast, and nesting begins ca. 1 mo later (Elliott et al. 1998). Within each study area, we selected nests where placement of video recording equipment afforded a good vantage for nesting observations.

Observations. We positioned six (three on each coast) miniature CCD cameras (V-1205, Sony, Vancouver, BC, Canada) 2 m above the nests when nestlings were ca. 4 wk old. Our observations corresponded ca. to the "middle nesting stage" identified by Warnke et al. (2002). Cameras were housed in waterproof compartments, camouflaged using paint and vegetation and connected via power and RG-8UM video lines (RG-8UM, CB World, Lansing, MI U.S.A.) to a DC VCR (Panasonic AG-1070 one frame·s^{-1}, Secaucus, NJ U.S.A.) on the ground. We replaced the videotapes every 3 d. VCRs were housed in waterproof compartments 20 m from the nest tree and programmed to record from 0500–1100 H and 1430–2030 H (812 hr total footage). Two 12-volt deep-cycle-marine batteries in protective housing supplied power. We analyzed video recordings by viewing on a television monitor.

We conducted direct observations using 20–60× spotting scopes from a blind at four nests on the east coast and three on the west coast (≥6 d/nest, each 16 continuous hours dawn to dusk) for 1344 hr total. Nestlings were 2–10 wk old. Observers worked in pairs 100–300 m from the nest, with individual observers switching every 2 hr (Warnke et al. 2002).

To corroborate the compatibility of observation methods, we collected direct observation and video data simultaneously for 20 hr. As was found by Dykstra et al. (1998) and Warnke et al. (2002), both methods had good compatibility (>98% agreement) for determining the number of prey deliveries, prey species delivered, and chick and adult behavior. We consequently pooled both data sets.

We recorded adult nest attendance, number and type (class and species when possible) of prey delivered, and eaglet behavior (standing, feeding, preening, fighting with siblings, exercising wings, playing with nest material, and walking around the nest; Warnke et al. 2002). All behaviors except "standing" were considered "active." We classified prey items into four length categories (7–15 cm, 15–23 cm, 23–30 cm, 30–40 cm) using the prey item's size relative to adult bill or toe-pad length. Prey length and species was then used to estimate biomass using equations and experimental values from the literature as described by Dykstra et al. (1998) and Gill and Elliott (2003). Our analyses focused on the relationships between variables and prey deliveries (rather than energy delivered) as prey-delivery rates were estimated with greater certainty. Environment Canada weather stations at Ucluelet (west coast) and Crofton (east coast) provided weather data.

Statistical Analyses. Statistical analyses were performed using STATISTICA. Data for individual nests were pooled on each coast if an analysis of covariance (ANCOVA) gave no significant difference among nests. We pooled the data for both coasts if the interaction term (coast × variable) was not significant. We used a multiple linear regression to examine the effects of adult nest attendance (percent of each day when at least one adult was present, averaged over each week), mean daily temperature, and chick age (independent variables) on mean daily prey and energy deliveries, averaged over each week (dependent variables). Within this multiple linear regression, we used ANCOVAs to compare prey deliveries on days with and without rain on each coast and to compare prey deliveries relative to temperature on each coast. In addition, we employed multiple linear regression, using a quadratic model, to examine the effect of tide height, time of day, and prey deliveries (hourly mean) between coasts. Prior to using parametric statistics, we tested for homogeneity of variance (Levene's test) and normality (Kolmogorov-Smirnov). Bonferroni adjustments were completed on multiple comparisons We considered results to be significant if $P < 0.05$. The values reported are means ± SD.

RESULTS

All nestlings present at the beginning of the study period survived to the end of the study period, with more young produced at the sampled nests on the east coast (2 young per occupied nest) than on the west coast ($\bar{x}$ = 1.2) of Vancouver Island (Table 1).

Factors Influencing Provisioning Rates. Prey-delivery rates varied significantly between coasts. The west coast had fewer prey deliveries (t = 2.3, df = 8, P = 0.008) per day and lower mean prey biomass (t = 1.9, df = 8, P = 0.04) than the east coast (Table 1). However, there was no difference (t = 2.2, df = 10, P = 0.43) in the mean daily energy delivered (Table 1). There was also no difference in the prey-size distributions (t = 0.73, df = 3, P = 0.25) for Pacific herring (*Clupea harengus*), the only species for which there was significant overlap between the two coasts (Table 2). A multiple linear regression (R^2 = 0.22, F = 2.61, df = 2103, P = 0.07) indicated no correlation between nestling age and the number of prey deliveries (t = 1.34, df = 202, P = 0.66). However, there was a peak in prey deliveries at about 4 wk, corresponding to the period of maximum growth (Warnke et al. 2002). Using this regression we found a negative relationship between mean daily temperature and number of prey deliveries (t = −2.35, df = 202, P = 0.02), and the mean number of prey deliveries and the presence of rain on the west coast (t = −3.6, df = 103, P < 0.001), but not on the east coast (t = 0.65, df = 98, P = 0.54). In addition, prey-delivery rates at both coasts were strongly influenced by the time of day (Fig. 1). On both coasts, there was a significant quadratic relationship between tide height and prey-delivery rates (Fig. 2), with the

Table 1. Provisioning rates to Vancouver Island Bald Eagle nests during 1996. Values indicated are daily means (SD) averaged over the entire nestling period.

NEST ID	NO. NESTLINGS	OBSERVATIONS	PREY-DELIVERY RATE	ENERGY DELIVERED PER NESTLING (kJ)	PREY BIOMASS (g)
CN-Br[a]	2	6	7.7 (3.5)	1517 (345)	630 (87)
CN-Ch[a]	2	6	10.8 (3.4)	3681 (780)	955 (199)
CN-Mo[a]	2	6	9.0 (4.1)	3210 (2008)	821 (523)
CN-WN[b]	2	14	9.6 (6.6)	872 (692)	209 (136)
CN-WS[b]	3	12	4.5 (2.2)	1490 (990)	380 (367)
CS-MB[b]	2	11	5.0 (3.5)	1539 (794)	417 (212)
CS-PM[b]	1	11	3.6 (2.3)	1448 (539)	373 (135)
Mean, east	2.0		7.2 (2.8)	1965 (1046)	541 (270)
BS-AI[b]	1	12	2.3 (1.1)	2314 (777)	345 (101)
BS-Ch[a]	1	6	4.8 (3.2)	3547 (1060)	510 (151)
BS-Nu[a]	2	6	4.0 (1.9)	1691 (1124)	236 (158)
BS-Ri[a]	1	5	2.6 (1.1)	2584 (834)	365 (111)
BS-SB[b]	1	13	2.9 (1.4)	1811 (548)	295 (81)
BS-Sp[b]	1	11	2.8 (1.5)	2201 (674)	330 (94)
Mean, west	1.2		3.2 (1.0)	2358 (669)	347 (92)
Mean, pooled	1.6		5.4 (2.9)	2147 (880)	451 (224)

[a] Video cameras.
[b] Direct observations.

greatest prey-delivery rates at intermediate tide heights. Therefore, we reject the hypothesis that provisioning rates were negatively related to tide height, at either coasts, and accept the hypothesis that provisioning rates were negatively correlated with rain only on the west coast.

Adult and Nestling Behavior. On both coasts, adult nest attendance was positively correlated with brood size ($r = 0.33$, $P < 0.01$) and mean number of prey deliveries per hour per eaglet ($r = 0.34$, $P < 0.002$; Fig. 3), and negatively correlated with eaglet age ($r = 0.27$, $P < 0.01$). Mean daily eaglet activity levels were higher on the west coast (42 ± 5% of the day) than east coast (27 ± 3%) of Vancouver Island. Eaglets on the west coast spent more time standing, feeding, preening, fighting with siblings, exercising wings, playing with nest material, and walking around the nest than their counterparts on the east coast. On both coasts, eaglet mean daily activity was independent of hatching order ($P > 0.6$), negatively correlated with adult nest attendance ($r = 0.46$, $P < 0.001$) and positively correlated with eaglet age ($r = 0.34$, $P < 0.005$; Fig. 4).

Prey Type. There was considerable variation in prey type between the east and west coasts. Fish made up the majority of the diet at both locations (Table 2). However, on the east coast the most common prey item was plainfin midshipman (*Porychthys notatus*) while on the west coast it was Pacific mackerel (*Scomber japonicus*). At both locations, Pacific herring (*Clupea harengus*) was the second most common prey item. Direct observations tend to overrepresent easily identified, common species so that actual percentages for major prey items may be exaggerated (Mersmann et al. 1992, Dykstra et al. 1998).

DISCUSSION

Bald Eagle provisioning rates were clearly influenced by time of day, tide, and weather. High provisioning rates tended to be at intermediate tide heights, at low temperatures, during rainless periods, and early during the day. The decline in provisioning rate with time of day likely reflects both nestling satiation and declining prey activity, as Watson et al. (1991) reported in the Columbia River estuary.

The mean prey-delivery rate for Vancouver Island eagles (5.4 prey/d) was remarkably similar to the benchmark of 5.2 prey/d reported by Warnke et al. (2002), which they considered to indicate adequate prey availability to support high Bald Eagle reproductive success. Our data support this benchmark, as territories on the east coast had consistently high productivity, while those on the west

Table 2. Prey delivered to Vancouver Island Bald Eagle nests in 1996.

PREY TYPE	PERCENT OF DIET[a]	NO. OF DELIVERIES	ENERGETIC VALUE (kJ)[b]
East Coast			
Fish	85.1	215	438
Plainfin midshipman (*Porichthys notatus*)	43.0	65	403
Pacific Herring (*Clupea harengus*)	10.0	23	265
Coho Salmon (*Oncorhynchus kisutch*)	10.9	2	3304
Pollock (*Theragra chalcogramma*)	5.0	1	3075
Flounder (Bothidae/Pleuronectidae spp.)	1.7	2	526
Ling cod (*Ophiodon elongates*)	1.7	3	349
Surf Perch (*Hyperprosopon ellipticum*)	0.6	1	352
Bird	4.0	2	2220
Mallard duckling (*Anas platyrhynchos*)	1.7	1	1046
Pigeon Guillemot (*Cepphus columba*)	5.6	1	3394
Mammal	10.9	4	3029
European rabbit (*Sylvilagus* spp.)	19.6	2	5967
Rodent (Rodentia spp.)	0.1	1	90
West Coast			
Fish	94.7	85	963
Pacific Mackerel (*Scomber japonicus*)	90.8	37	1713
Pacific Herring (*Clupea harengus*)	6.2	14	307
Coho Salmon (*Oncorhynchus kisutch*)	1.9	1	1343
Flounder (Bothidae/Pleuronectidae spp.)	1.0	2	334
Sculpin (Cottidae spp.)	0.1	1	88
Shiner Perch (*Cymatogaster aggregate*)	0.1	1	37
Surf Perch (*Hyperprosopon ellipticum*)	0.0	1	15
Bird	6.5	1	4555
Mallard duckling (*Anas platyrhynchos*)	1.2	1	1046

[a] By energy.
[b] Averaged over all deliveries.

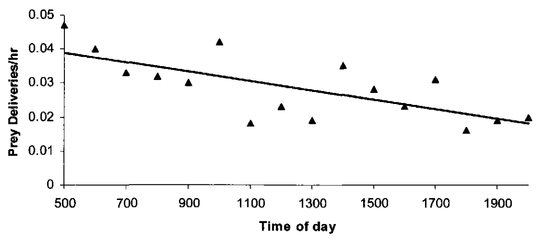

Figure 1. Linear regression of mean number of prey deliveries per hour relative to time of day at Vancouver Island Bald Eagle nests in 1996 (prey deliveries = −0.033 [time of day] + 0.0458; $r^2 = 0.50$). Data were pooled for east and west coasts.

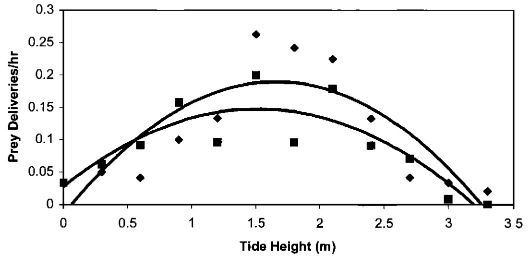

Figure 2. Quadratic regression of provisioning rates for Bald Eagles on the east (◆) and west (■) coasts of Vancouver Island during 1996 relative to tide height (east: prey deliveries = $-0.75 \times [\text{tide height}]^2 + 0.25 \times [\text{tide height}] - 0.016$, $r^2 = 0.69$; west: prey deliveries = $-0.052 \times [\text{tide height}]^2 + 0.16 \times [\text{tide height}] + 0.027$; $r^2 = 0.68$).

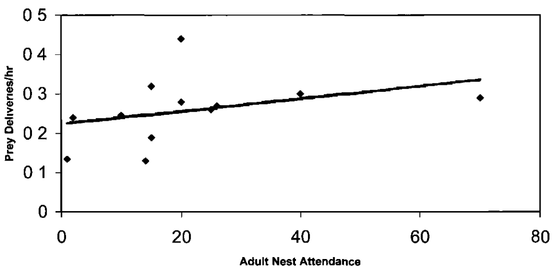

Figure 3. Vancouver Island Bald Eagle adult nest attendance (percent of total observation time when adult was at nest) relative to prey-delivery rate (prey deliveries per chick per hr). Each data point represents one nest, averaged over the 1996 season (prey deliveries = 0.0016 [adult nest attendance] + 0.22; r^2 = 0.12).

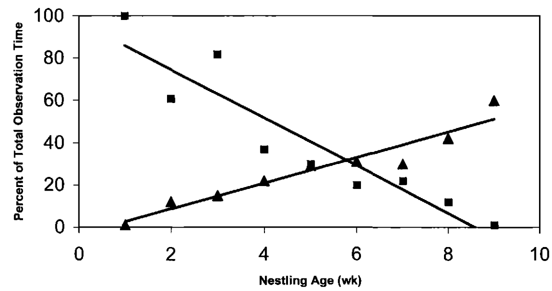

Figure 4. Mean Bald Eagle nestling activity (▲—percent of total observation time when nestling was active) and adult attendance (■—percent of total observation time when adult was present) relative to nestling age (nestling activity = 6.1 × age − 3.5; r^2 = 0.92; adult attendance = −11.3 × age + 97; r^2 = 0.87). Nests (N = 13) were studied on Vancouver Island in 1996.

coast, a region with consistently low productivity, were below this benchmark. Despite the difference in number of prey items and biomass delivered, the total energy delivered per chick was higher on the west coast than the east coast, although the mean total energy delivered to the nest was similar, as east coast nests averaged more chicks. Nestlings on the west coast met the field energetic requirements of 2427 ± 100 kJ/d for nestlings in northern Wisconsin (Dykstra et al. 2001a), while those on the east coast did not. Nestlings may have experienced higher energetic demands on the west coast due to substantially cooler conditions more similar to Wisconsin. Eagles on the west coast foraged primarily on Pacific mackerel, a high-energy species (1713 kJ; Ann 1973) that was unusually abundant due to surface water warming in the late 1990s (Gill and Elliott 2003). Thus, eagles on the west coast seem to make up for the low quantity of prey delivered by increasing prey quality (Wright et al. 1998, Hilton et al. 1998), as has been known to occur in other raptors (Barton and Houston 1993).

Many studies have shown a strong relationship between food abundance and reproductive success in raptors. For example, reproductive success in many temperate and arctic raptors closely follows changes in small mammal populations (e.g., McInvaille and Keith 1974, Smith et al. 1981, Korpimaki 1992, Wiehn and Korpimäki 1997), while fish abundance influences productivity in piscivores such as Ospreys (van Daele and van Daele 1982), White-tailed Sea Eagles (Helander 1985), African Fish-Eagles (Harper et al. 2002), and Bald Eagles (Hansen 1987, Dzus and Gerrard 1993). Our results demonstrate one mechanism by which prey availability can affect spatial variation in productivity. The east-coast population, which consistently produced more young than needed to replace individuals lost to mortality (Elliott et al. 1998), had higher prey-delivery rates than the west-coast population, which did not produce enough young to compensate for mortality (Elliott et al. 1998).

The relationship between tide height and provisioning rates highlights the importance of tidal flats for nesting eagles. The influence of tide on Bald Eagle foraging habits has been documented in Alaska (Ofelt 1975, Wilson and Armstrong 1998), British Columbia (Hancock 1964, Elliott et al. 2003), and Washington (Watson et al. 1991, Garrett et al. 1993), and appears to be characteristic of coastal populations in the Pacific Northwest. The peak in prey deliveries at intermediate tide heights is likely because the plainfin-midshipman-breeding zone is exposed at this tide level (Elliott et al. 2003); in the Columbia River estuary, where eagles forage primarily on fish that are most easily captured in shallow water, foraging success peaks at low tide (Watson et al. 1991).

Weather also influenced provisioning rates. The decline in provisioning rates with temperature likely reflects lower chick-energy demands during warm weather, while the lower provisioning rates on rainy days may reflect reduced adult foraging efficiency due to altered visibility (Grubb 1977) or prey behavior (Newton 1978). Furthermore, rain increases eagle energetic requirements by up to 21% (Stalmaster and Gessaman 1984), and adults may need to eat more during rainy days, leaving less prey for them to deliver to their nestlings. The larger impact of rainfall on the outer coast on prey-delivery rates supports the conjecture that low productivity on the outer coast is partially attributable to harsh and unpredictable weather (Gende et al. 1997, Elliott et al. 1998). Storms impact the reproductive success of other raptors. For example, winter severity delays reproduction and reduces productivity in Bald Eagles from northern Saskatchewan (Gerrard et al. 1992), as well as Golden Eagles (Tjernberg 1983, Steenhof et al. 1997) and Gyrfalcons (Poole and Bromley 1988), while hail storms caused >30% of the reproductive failure in Swainson's Hawks in North Dakota (Gilmore and Stewart 1984).

Food availability may also impact nestling survival indirectly. Adults with high prey-delivery rates have higher nest attendance, because eagles that are more successful hunting can spend less time foraging (Watson et al. 1991), reducing eaglet mortality through predation or exposure. This is particularly critical during the first 4 wk when increased nest attendance aids in nestling thermoregulation (Warnke et al. 2002).

Brown (1993), Knight and Knight (1983), Hansen (1986), Knight and Skagen (1988), Watson et al. (1991), and Bennetts and McLelland (1997) showed that the ability of eagles to obtain food increases with age. As with many other bird species, reproductive success in raptors usually increases with age (Newton 1998); fecundity peaks at age 5 yr among Eurasian Sparrowhawks (*Accipiter nisus*; Newton and Rothery 2002) and at age 7 yr among Northern Goshawks (*Accipiter gentilis*; Nielsen and Drachmann 2003), declining thereafter in both species. In addition adult-adult Spanish Imperial Eagle (*Aquila adalberti*) pairs monopolize high quality territories, hence have higher average fecundity than juvenile-juvenile pairs (Ferrer and Bisson 2003). Therefore, older individuals presumably provision at higher rates than younger ones. We did not know the age of adults in our study, and this factor may explain some of the variability between individual nests.

Examination of prey remains at nests from both study areas suggested that birds were the primary food source, as have most prey remains studies in the Pacific Northwest (e.g., Norman et al. 1989, Vermeer et al. 1989, Vermeer and Morgan 1989, Knight et al. 1990, Watson 2002). However, birds made up less than 7% of prey at either location during our study, as revealed by direct observation. The major prey source at both locations in our study was fish (Table 2), outlining the importance of using direct observations, as analysis of prey remains at nests often leads to the underestimation of fish prey (Todd et al. 1982, Mersmann et al. 1992). For comparison, the proportion of fish in diets of eagles nesting in coastal regions varied from 42% in Louisiana (Dugoni et al. 1986) to 71% in the Columbia estuary (Watson et al. 1991), and 76–85% in southeastern Alaska (Ofelt 1975). While Watson et al. (1991) noted that several eagle pairs in the Columbia River estuary were "specialists," preferentially taking certain food species, such as waterfowl, relative to other eagle pairs, we found no such specialization. Any variation in diet breadth could be traced to differences in local food availability, such as the presence of large tidal flats near nests that consumed large numbers of plainfin midshipman.

We conclude that time of day, temperature, rainfall, and tide height all impact eagle provisioning rates, and therefore, adult nest attendance and chick activity. Our results support the hypotheses advanced by Elliott et al. (1998) and Gill and Elliott (2003) that nesting success is greater on the east coast because there are more tidal flats and fewer storms. Steenhof et al. (1997) documented similar results for Golden Eagles in Idaho, in which reproductive success was determined by prey (black-tailed jackrabbit [*Lepus californicus*]) abundance and weather (frequency of hot days).

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