

*Aquila
chrysaetos*FRENCH:
Aigle royal
SPANISH:
Aguila real

Golden Eagle

The Golden Eagle inhabits a wide range of latitudes throughout the Northern Hemisphere and uses a variety of habitats ranging from arctic to desert. Rare in the eastern half of North America, it is most common in the West near open spaces that provide hunting habitat and often near cliffs that supply nesting sites. Northern breeders migrate thousands of kilometers to wintering grounds; southern pairs tend to be resident year-round. As one of North America's largest predatory birds, this eagle has been prominent in human lore and culture, inspiring awe, reverence, and sometimes fear and hatred. Humans kill Golden Eagles both intentionally and accidentally by trapping, shooting, poisoning, and electrocution; at the same time, urbanization, agricultural development, and wildfires encroach on this eagle's traditional shrub-steppe foraging

The Birds of North America

Life Histories for
the 21st Century

hunting techniques to capture prey, including soaring, still-hunting from a perch, and low contouring flight. Although capable of killing large prey such as cranes, wild ungulates, and domestic livestock, this species subsists primarily on rabbits, hares, ground squirrels, and

habitat. The species persists, but some U.S. nesting populations may be declining. In the twenty-first century, humans will determine the fate of this species and its habitat.

The Golden Eagle has astonishing speed and maneuverability for its size and uses a wide variety of



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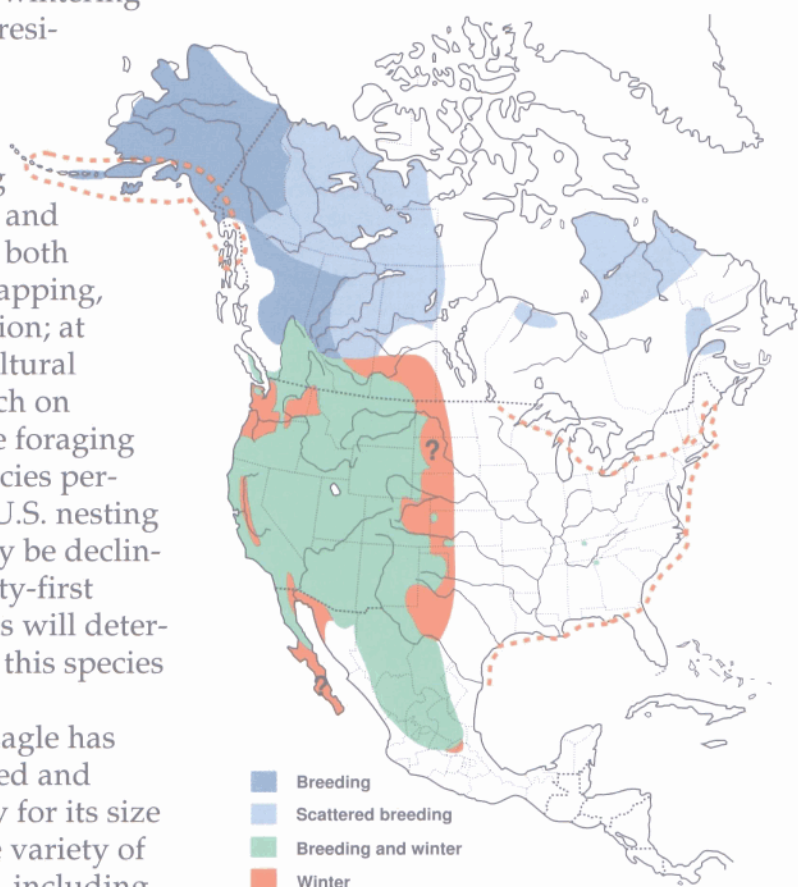


Figure 1.

Distribution of the Golden Eagle in North America. This species winters locally within the areas enclosed by the dashed lines. Blue dots in n.-central Tennessee and nw. Georgia depict isolated recent breeding locations. Question marks denote areas of suspected nesting. This species also breeds in Europe and Asia. See text for details.

prairie dogs. Most do not acquire a nesting territory until they are at least 4 years old, after they have molted into Definitive plumage. Once an individual establishes a territory, it tends to stay there, defending an area of approximately 20–30 square kilometers from conspecifics. A territory may contain up to 14 nests, which a pair maintains and repairs as part of their courtship. The nesting season is prolonged, extending more than 6 months from the time eggs are laid until young reach independence. A typical Golden Eagle raises an average of only 1 young per year and up to 15 young over its lifetime. Pairs commonly refrain from laying eggs in some years, particularly when prey is scarce. The number of young that Golden Eagles produce each year depends on a combination of weather and prey conditions. The black-tailed jackrabbit (*Lepus californicus*) is a key prey species throughout much of the range, and eagle reproductive rates fluctuate with jackrabbit population cycles.

Although much information on Golden Eagle life history comes from studies in Europe (Watson 1997), important North American research has provided insights about developmental behavior (Ellis 1979), survival rates (Hunt 2001, Harmata 2002), and migration (Brodeur et al. 1996, Craig and Craig 1998, CLM). Much information about Golden Eagle ecology comes from southwestern Idaho, where research on this species has been conducted in and near the Snake River Birds of Prey National Conservation Area (NCA) for more than 35 consecutive years, beginning with Hickman (1968). NCA studies have focused on diet (Beecham 1970, Kochert 1972, Steenhof and Kochert 1988), food consumption/energetics (Collopy 1980, 1983a, 1983b), parental care and feeding ecology (Collopy 1984), long-term reproduction (Steenhof et al. 1983, 1997), dispersal (Steenhof et al. 1984), home-range characteristics (Dunstan et al. 1978, Marzluff et al. 1997), and effects of habitat alterations on nesting populations (Steenhof et al. 1997, Kochert et al. 1999). Despite the wealth of information from this one study area, much remains unknown about populations in other parts of this eagle's range, particularly Alaska and western Canada. New work in these areas is shedding light on Golden Eagle ecology and may suggest differences between northern migratory populations and southern resident ones.

DISTINGUISHING CHARACTERISTICS

From Clark and Wheeler 1987, Watson 1997, and others as noted. Large, dark-brown raptor with long, broad wings. Length ranges from 70 to 84 cm; wingspan 185–220 cm. Mass of males 3,000–4,475 g; females 3,940–6,125 g (see Measurements, below). Adults (Definitive Basic plumage) entirely dark brown except for golden rear crown, nape, and sides of neck;

gray bars on tail; and rear underparts and upper wing-coverts often paler than rest of feathers, the latter forming a tawny diagonal bar on upper wing; visible both on flying and perched birds. Some individuals also have small white "epaulet" at upper end of scapulars (Spofford 1961). Additionally, feathered tarsi vary from almost white to dark brown (Jollie 1947). Bill and talons black-tipped, fading to slate gray near the base. Cere, orbital ring, and feet yellow. Sexes similar in appearance, although females average larger than males. Suspected sexual differences in pattern and number of bands on tails of adults (Wheeler and Clark 1995) not verified in subsequent studies; not a reliable method for distinguishing sexes (W. Clark pers. comm.). Plumages the same throughout the year, but feathers dark, shiny, and smooth on edges when plumage fresh, while old feathers appear faded, more brownish, and frayed on edges.

Adult plumage differs from Juvenal and subsequent subadult plumages. Juvenal plumage (0–1 yr) distinguished from adults by much darker (unfaded) color, and by white at base of secondaries and inner primaries (Brown and Amadon 1968). These white areas form a white "window" at carpal joint of wing, visible in flight from above and below. Occasionally some upper wing-coverts also white (Johnsgard 1990). Amount of white varies individually, and a few juveniles lack white on wing entirely (Jollie 1947). Rectrices have wide, black band at tip with narrow, white terminal band. White terminal band wears away quickly as feathers age. Basal two-thirds of tail is usually white, although some dark flecks, particularly near the dark band, may occur (Jollie 1947). Amount of white in tail and wing gradually diminishes with each progressive molt. Adult plumage usually acquired in fifth summer, but older individuals may retain white in tail. Physiological condition of individual can influence rate of molt (Jollie 1947, T. and E. Craig unpubl.). See Appearance, below, for more detail.

Golden Eagles most often seen soaring or gliding with wings held in slight dihedral. Flapping flight consists of 6–8 deep wing-beats interspersed by short glides lasting several seconds.

Distinguished from most other North American raptors by combination of large size and all or mostly dark-brown coloration. However, confusion possible with immature Bald Eagle (*Haliaeetus leucocephalus*), which has similar size and coloration. Most striking differences involve distribution of white in plumage. Immature Bald Eagle has irregular white/tawny areas on much of body (especially underparts) as well as on under wing (coverts, flight feathers, axillaries) and undertail surfaces, while Golden Eagle lacks extensive white on body and has white on undersurface of wing restricted to base of flight feathers and white on

undersurface of tail cleaner and more sharply divided from wide, dark, terminal band. Immature Bald Eagle also has darker (blackish) bill and cere. With experience, structural and behavioral differences also useful in distinguishing these species. In flight, Golden Eagle's head does not project more than half the length of the tail (head projects more than half the length of tail in Bald), and Golden Eagle has longish outer secondaries, which produce a noticeable round bulge on the trailing edge of the wing (trailing edge straighter in Bald Eagle). At close range, Bald Eagle has naked tarsi (feathered in Golden Eagle; Clark and Wheeler 1987). Golden Eagle wing-beats also somewhat shallower than those of Bald Eagle, and wings held flatter on soaring Bald Eagle than on soaring Golden Eagle (Dunne et al. 1988).

Soaring Golden Eagle could be confused with the California Condor (*Gymnogyps californianus*) or Turkey Vulture (*Cathartes aura*). Condor larger with white or mottled under wing-coverts. Vulture smaller, with small head, underwing black in front and silver on trailing edge; holds wings in a dihedral and soars with rocking motion. For more information on Golden Eagle identification, see Wheeler and Clark 1995, Clark and Wheeler 1987, and Dunne et al. 1988.

DISTRIBUTION

THE AMERICAS

Breeding range. Mainly w. North America (west of 100th meridian) from Alaska south to central Mexico (Fig. 1) with small numbers in e. Canada and a few isolated pairs in e. U.S.

ALASKA. From north slopes of Brooks Range (north to 69°30'N in the east and to the Lisborne Peninsula in the west) south throughout most of Alaska (including e. Aleutians west to Unalaska), except rare on Kodiak I. and in s.-coastal and se. Alaska (Armstrong 1995, Young et al. 1995, Am. Ornithol. Union 1998, B. Ritchie unpubl.).

CANADA. From southern coast of Beaufort Sea (east to Coronation Gulf; Poole and Bromley 1988) south throughout w. Canada to U.S. border. Absent from coastal portions of British Columbia (except se. Vancouver I. and Fraser Lowlands; Campbell et al. 1990), and much of Saskatchewan (except Lake Athabasca, Foster Lakes, Lower Churchill River, and S. Saskatchewan River regions; Smith 1996). Breeding records scattered for Northwest Territories, Nunavut, se. Yukon, ne. British Columbia, n. and all but southern portions of e. Alberta, and much of Saskatchewan. Also discontinuous nesting in e. Canada in nw. Ontario south of Hudson Bay (De Smet and James 1987), n. Quebec, n. Labrador, and se. Quebec especially on Gaspé Peninsula (Kirk 1996, Robert 1996, Brodeur and Morneau 1999). May breed in Manitoba, s. Ontario,

s. Quebec (Godfrey 1986), New Brunswick, and Nova Scotia (Erskine 1992), but breeding records unknown or very few in these areas (De Smet 1987, K. D. De Smet pers. comm.).

UNITED STATES. In West, from Canadian border south through Washington, Idaho, and Montana to Mexican border and east to sw. North Dakota (Stewart 1975, Ward et al. 1983), w. South Dakota (Peterson 1995), panhandle of w. Nebraska (Wingfield 1991, Sharpe et al. 2001), n.-central and se. Colorado (Barrett 1998), western panhandle of Oklahoma (Baumgartner and Baumgartner 1992), panhandle of Texas (Swepton et al. 1984, Texas Breeding Bird Atlas [BBA] 1987–1992 unpubl.), e. New Mexico (Hubbard 1978), and the Trans-pecos of Texas. Within this area, rare or absent west of Cascades in Washington (except Olympic Mtns.) and Oregon (except some southern valleys and some higher portions of Cascades), the immediate coast and flat portions of Central Valley of California, the Salton Sea, the lower Colorado River, desert regions of se. California and sw. Arizona, agricultural portions of e. Washington, and mountains of the panhandle of Idaho (Bruce et al. 1982, Gilligan et al. 1994, Small 1994, Smith et al. 1997, Stephens and Sturts 1997, Arizona BBA 1993–2000 unpubl.). Patchy nesting in w. Kansas (Weigel 1993), and suspected nesting in central S. Dakota west of the Missouri River (Peterson 1995). Breeds irregularly in w. Nebraska (Sharpe et al. 2001).

In East, 2 nesting pairs in Maine (Todd 1989, Maine Dept. Inland Fisheries and Wildlife [DIFW] unpubl.) and 1 each in Tennessee and nw. Georgia (B. Anderson and T. Touchstone pers. comm.); both the result of reintroductions (see Conservation and management: management, below).

MEXICO. N. Baja California and highlands of central Mexico, including ne. Sonora (Russell and Monson 1998), and from Chihuahua and Coahuila south to San Luis Potosí, Guanajuato, and Queretaro (Howell and Webb 1995, Instituto Nacional de Ecología 1999). Suspected nesting in s. Baja California (Rodríguez-Estrella et al. 2002). May be extirpated as breeding in Guanajuato and Queretaro (E. Inigo-Elias pers. comm.).

Winter range. Winters in sw., s.-coastal, and se. Alaska (rare; Armstrong 1995), and from southernmost British Columbia, s. Alberta, and s. Saskatchewan, south throughout breeding range in w. U.S. and Mexico, and in areas of lower elevations not occupied during breeding season west to Pacific Coast (rarely), south to s. Baja California and nw. Sonora and Hidalgo, Mexico (Howell and Webb 1995, Am. Ornithol. Union 1998, Russell and Monson 1998), and (regularly) east to central Dakotas, central Kansas, w. Oklahoma, and w. Texas (Sauer et al. 1996). Also winters very locally east throughout e. U.S. north to Great Lakes and mid-Atlantic states (e.g., n. Wisconsin, n. Pennsylvania, se.

New York, central Massachusetts, and se. Maine) and south to Gulf Coast and Florida Panhandle (Millsap and Vana 1984, Mitchell and Millsap 1990, Robbins 1991, Robertson and Woolfenden 1992, Veit and Petersen 1993, Am. Ornithol. Union 1998, Levine 1998, McWilliams and Brauning 2000, Turcotte and Watts 1999, Maine DIFW unpubl.), with rare reports south to Florida Keys (Robertson and Woolfenden 1992, Am. Ornithol. Union 1998). Emigrates from northern latitudes and higher elevations in winter, but can winter at $>66^{\circ}\text{N}$ latitude whenever sufficient prey is available (Kessel 1989). Rare in Kuskokwim River drainage and Alaska and Brooks Ranges, AK, and Mackenzie Mtns., Northwest Territories (Fleck et al. 1987, Petersen et al. 1991, T. and E. Craig unpubl., CLM).

OUTSIDE THE AMERICAS

Holarctic distribution spanning latitudes from approximately 20° to 70°N , with scattered populations farther south (Orta 1994, Watson 1997, Snow and Perrins 1998). Occurs throughout Europe, Asia, and n. Africa. Northern extent of range stretches from n. Europe (n. British Isles and Scandinavia) to Kola Peninsula and on to e. Siberia and Kamchatka Peninsula. Breeds in s. Europe from Iberian Peninsula to Turkey and much of Asia south to Israel, Saudi Arabia, Yemen, Oman, Afghanistan, the Himalayas, s. China, Korea, and Japan. Nests in n. Africa and large Mediterranean islands from Mauritania and Niger to Egypt; isolated sub-Saharan population in Bale Mtns. in s. Ethiopia. Accidental in Belgium, Netherlands, Cyprus, Kuwait, Canary Is., and Hawaiian Is.; 1 individual seen in Hawaiian Is. for 17 yr (Pyle 1984).

HISTORICAL CHANGES

Historically nested throughout most of North America (Bent 1937), but breeding records lacking for Iowa, Minnesota, and Indiana (Wingfield 1991). Formerly nested in e. Nebraska, se. South Dakota, Wisconsin, and Central Valley of California (Harlow and Bloom 1989, Wingfield 1991). Historical nesting confirmed in Maine, New Hampshire, New York, and Vermont (Todd 1989). Last reported nesting in New Hampshire in 1961 and New York in 1972 (Todd 1989). In Maine, 2 pairs nested in 1983, only 1 pair between 1984 and 1998, and 2 in 1999 (Todd 1989, C. Todd pers. comm.). Historical nesting suspected in Pennsylvania, Massachusetts, N. Carolina, Tennessee, Kentucky, W. Virginia, Virginia, S. Carolina, and Georgia (Smith 1982, Palmer 1988, Todd 1989, C. Todd pers. comm.). Nesting not confirmed in s. Appalachians (Lee and Spofford 1990) until late 1990s after successful reintroduction efforts (see Conservation and management: management, below). Nested historically in s.-central Mexico (Guanajuato and Querétaro de Arteaga; Instituto Nacional de Ecología 1999).

Most breeding records for Maritime Provinces of Canada unsubstantiated (De Smet 1987). Believed to have nested in Nova Scotia in late 1800s, and evidence exists for nesting in New Brunswick. Casual visitor to Maritime Provinces in late 1980s, with a large increase in sightings between late 1960s and 1980s. More common historically in Ontario and Quebec; currently rare, particularly in southern portions (De Smet 1987).

FOSSIL HISTORY

Pleistocene records of Golden Eagle in North America for Oregon, California, Nevada, New Mexico, Texas, Utah, and Mexico (Emslie and Heaton 1987, Palmer 1988). Remains also found at archaeological sites inhabited by prehistoric Native Americans in Utah (Parmalee 1980) and New Mexico (Emslie 1981). *Aquila* remains reported in fossils from the Upper Miocene in Nebraska (Wetmore 1923), and *Aquila*-like remains reported in fossils from the Upper Eocene or Lower Oligocene in Europe (Brodkorb 1964). Considerable overlap and gradation between contemporary Golden Eagle and Pleistocene specimens (Howard 1947).

SYSTEMATICS

GEOGRAPHIC VARIATION; SUBSPECIES

Of 5 or 6 subspecies worldwide, only one occurs in North America: *A. c. canadensis*. No information on geographic or genetic variation within the North American subspecies. Individuals from ne. Asia may be the same subspecies (Brown and Amadon 1968), but are larger (female wing 690 vs. 650 mm for North America) and may represent a distinct subspecies, *A. c. kamtschatica* (Watson 1997). Range of *A. c. kamtschatica* extends across ne. Asia from w. Siberia and the Altai, where it intergrades with *A. c. chrysaetos*, to Kamchatka Peninsula and the Anadyr District of ne. Russia. Four other subspecies recognized; descriptions and female wing lengths from Watson 1997. The palest, *A. c. chrysaetos* (medium size; wing 670 mm), occurs in n. Europe and w. Asia. *A. c. homeyeri* (small; wing 640 mm) found in Spain and n. Africa east to Iran, and the largest race, *A. c. daphanea* (wing 700 mm), is in e. Asia (Iran to central China). The smallest and darkest race, *A. c. japonica* (wing 630 mm), breeds in Korea and Japan.

RELATED SPECIES

Member of the genus *Aquila*, one of several allied genera known as "booted" eagles that are medium to large eagles with feathering down to toes (Amadon 1982); regarded as the most highly evolved group within family Accipitridae, even perhaps within order Falconiformes (Brown and Amadon 1968). Closely related to Lesser Spotted (*A. pomarina*), Greater Spotted

(*A. clanga*), Steppe (*A. nipalensis*), Tawny (*A. rapax*), Imperial (*A. heliaca*), Verreaux's (*A. verreauxii*), Gurney's (*A. gurneyi*), and Wedge-tailed (*A. audax*) eagles (Watson 1997). These species have feathered tarsi, no crests, moderately long wings, medium to long tails, and large bills, legs, and talons (Brown and Amadon 1968, Brown 1976).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Short- to medium-distance partial migrant. Individuals from northern breeding areas ($>55^{\circ}\text{N}$) usually migratory (Brown and Amadon 1968, Kerlinger 1989); migrate longer distances than individuals nesting farther south (McGahan 1966, Mead 1973). Former can migrate $>5,000$ km from breeding to wintering areas (Kuyt 1967, CLM). Migratory adults and juveniles usually fly directly to wintering areas (Brodeur et al. 1996, CLM). Overwintering in interior and n. Alaska coincides with high abundance of snowshoe hare (*Lepus americanus*; Kessel 1989). Many individuals breeding south of 55°N are not migratory; winter ranges of individuals from Canada and U.S. probably overlap extensively. Juveniles from sw. Idaho moved in almost all directions from natal areas after breeding season (Steenhof et al. 1984).

TIMING AND ROUTES OF MIGRATION

Autumn. Individuals leave northern areas from Sep to early Oct; main exodus from Alaska occurs before end of Sep (Kessel 1989). Juveniles from Denali National Park, AK, tracked by satellite telemetry, initiated migration between mid-Sep and early Oct (mean $24 \text{ Sep} \pm 5 \text{ d SD}$ [$n = 43$]; CLM). A radio-tagged adult remained in its northern ($>55^{\circ}\text{N}$) breeding area in ne. Quebec until 30 Oct (Brodeur et al. 1996) before migrating south. Autumn flights occur from early Sep through Dec at raptor migration count sites in n. U.S. and s. Canada, with most peak flights in Oct. Long-term median passage dates with 95% C.I. at sites with ≥ 8 yr of observations between 1983 and 1999: $1 \text{ Oct} \pm 1.7 \text{ d}$ at Wellsville Mtns., UT (Tidhar and Peacock 1999); $7 \text{ Oct} \pm 2 \text{ d}$ at Goshutes Mtns., NV (Lanzzone 1999); $10 \text{ Oct} \pm 3.3 \text{ d}$ at Bridger Mtn., MT (Neal 1999); $13 \text{ Oct} \pm 2 \text{ d}$ for Manzano Mtns., NM (Rossman 1999); 14 Oct for w. Alberta (Sherrington 2000). Maximum passage rates early Oct in Glacier National Park, MT (Yates et al. 2001). Peak flights usually later at eastern raptor migration sites; median passage date 4 Nov for Hawk Mtn., PA (Hawk Mountain Sanctuary unpubl.).

Immatures migrate earlier in autumn than adults at most locations. Median passage dates $\pm 95\%$ C.I. follow. Bridger Mtn., MT: immatures, $7 \text{ Oct} \pm 4 \text{ d}$; adults, $11 \text{ Oct} \pm 2.5 \text{ d}$ (Neal 1999). Manzano Mtns.,

NM: immatures, $13 \text{ Oct} \pm 2.8 \text{ d}$; adults, $16 \text{ Oct} \pm 2.8 \text{ d}$ (Rossman 1999). Hawk Mtn., PA: immatures, 31 Oct ; adults, 6 Nov (Hawk Mountain Sanctuary unpubl.). However, median passage dates for adults ($29 \text{ Sep} \pm 3.1 \text{ d}$) slightly earlier than for immatures ($1 \text{ Oct} \pm 2.2 \text{ d}$) at Wellsville Mtns., UT (Tidhar and Peacock 1999).

Juveniles from Denali National Park, AK, reached their wintering areas in $28\text{--}58 \text{ d}$ (mean $44 \text{ d} \pm 9 \text{ SD}$ [$n = 26$]), arriving on winter ranges throughout w. North America from s. Alberta to se. New Mexico from 26 Oct to 19 Nov (mean $7 \text{ Nov} \pm 7 \text{ d SD}$ [$n = 16$] CLM). Second-year eagles from Denali National Park arrived on winter ranges from 1 to 8 Oct in 2000 (mean $5 \text{ Oct} \pm 3.9 \text{ d SD}$ [$n = 3$]; CLM). Radio-tagged adults from e. Hudson Bay took $26\text{--}40 \text{ d}$ to reach their wintering areas in central Michigan, e. West Virginia, s. Pennsylvania, and ne. Alabama, arriving early Nov–early Dec (Brodeur et al. 1996). Individuals arrive on wintering areas in New Mexico and w. Texas in Oct, reaching peak numbers from Dec to Feb (Boeker and Ray 1971).

Spring. Adults from e. Hudson Bay departed winter ranges early to late Mar and arrive on breeding areas from late Mar to mid-May (Brodeur et al. 1996). Juveniles from Denali National Park, AK, departed wintering areas in s. Canada and w. U.S. $6 \text{ Apr}\text{--}8 \text{ May}$ (mean $21 \text{ Apr} \pm 12 \text{ d SD}$ [$n = 12$]; CLM). Travel time between wintering areas and summering areas in Alaska and nw. Canada, determined from satellite telemetry, ranged from 22 to 47 d (mean $35 \text{ d} \pm 6 \text{ SD}$ [$n = 12$] CLM). Adults departed wintering areas in sw. Idaho $20 \text{ Mar}\text{--}13 \text{ Apr}$ in 1993 (mean $29 \text{ Mar} \pm 12 \text{ d SD}$ [$n = 3$]) and $9\text{--}20 \text{ Mar}$ in 1994 (mean $14 \text{ Mar} \pm 6 \text{ d SD}$ [$n = 3$]; L. Schueck, J. Marzluff, M. Vekasy, M. Fuller, and T. Zarriello unpubl.); both age groups leave wintering areas in sw. U.S. in Mar (Boeker and Ray 1971). Travel time between sw. Idaho wintering areas and breeding areas in Alaska and nw. Canada, determined from satellite telemetry, ranged from 7 to 15 d ($n = 3$; L. Schueck et al. unpubl.). Median passage date $\pm 95\%$ C.I. at Sandia Mtns., NM, is $20 \text{ Mar} \pm 4 \text{ d}$ (Smith 1999). Maximum passage rates during second and third weeks of Mar at Glacier National Park, MT (Yates et al. 2001). Peak flights from 8 to 27 Mar at Rogers Pass, MT (Tilly and Tilly 1998), and 19 to 25 Mar in w. Alberta (Sherrington 1998). Spring migration in w. Alberta spans $\geq 92 \text{ d}$ (Sherrington 1997): first migrants seen in mid-Feb, with large movements of immatures from mid-Apr to May (Sherrington 1997). Adults arrive on breeding areas in Alaska from late Feb to late Mar (Kessel 1989, Young et al. 1995, CLM).

Adults usually migrate earlier in spring than immatures. Median passage date for adults at Sandia Mtns., NM ($9 \text{ Mar} \pm 1.7 \text{ d}$), significantly earlier than for immatures ($3 \text{ Apr} \pm 3.4 \text{ d}$; Smith 1999). Proportion of immatures migrating at Glacier National Park

increased from mid-Mar to mid-Apr (Yates et al. 2001). Adults move through s. Alberta earlier than immatures; adults common in Mar, immatures in Apr (Sherrington 1998).

Routes. Poorly known except for small numbers tagged with satellite-received radio transmitters. Large concentrations at raptor-migration count sites in U.S. and s. Canada suggest migration corridors exist along Rocky Mtns. and Appalachian Mtns. Largest autumn and spring passages in w. Alberta (Dekker 1970; Sherrington 1993, 1997) and w. Montana (Tilly and Tilly 1998, Neal 1999). In n. continental U.S. and w. Canada, most concentrated flights detected along north-south-oriented mountain ranges, (e.g., Rocky and Appalachian Mtns.); concentrated flights also noted in Great Lakes region. Smaller passages along Cascade Mtns. in Oregon and Washington (van der Geld 1998). Concentrations also observed in spring at Anaktuvuk Pass, AK (Irving 1960). Spring migration corridor near Marsh Lake and Whitehorse, Yukon, Canada; upper Tanana River Valley, AK; e. and central Alaska Range, AK (CLM); and the Matanuska Valley, AK (T. Swem and B. Dittick pers. comm.). Migration corridors in sw. U.S. include Sandia Mtns. and Manzano Mtns., NM (Grindrod 1998, Rossman 1999). Spring migration corridors in e. U.S. include ridges on or near Appalachian and Allegheny Mtns. in New York, Pennsylvania, w. Maryland, Virginia, W. Virginia, N. Carolina, and Tennessee (Brodeur et al. 1996, Brandes 1998). Spring migration evident in Great Lakes region; increasing numbers observed at Whitefish Point, MI, since 1986 (Nicoletti 1998). Very rare at coastal raptor-migration sites (i.e., Sandy Hook, NJ; Cape Henlopen, DE; Plum I., MA); and at raptor-migration count sites in Massachusetts, Vermont, and Maine (Brandes 1998, Kellog 2000).

Satellite-telemetry studies provide detailed information on migration routes of adults and juveniles (Brodeur et al. 1996, CLM). Four adults radio-tagged at nesting areas in n. Quebec used different migration routes to reach their winter ranges. Three flew south through central Quebec, around Lake Ontario and south along Appalachian Mtns. to their winter ranges in Pennsylvania, W. Virginia, and Alabama, while another migrated along Hudson Bay, south through Ontario, crossing Great Lakes by Straits of Mackinac to its winter range in Michigan (Brodeur et al. 1996). In spring, 2 of the 4 adults generally retraced their southbound route to return to their breeding areas, and 1 wandered westward, remained west of Hudson Bay for a month, before heading back to e. Hudson Bay (Brodeur et al. 1996). Juveniles from Denali National Park, AK, used different migration routes in autumn and spring. In autumn, most flew eastward along Alaska Range, southeast through Yukon, and south along Rocky Mtns. through Alberta into the U.S. Others flew eastward along Alaska Range, southeast through

Yukon, and south through Rocky Mtn. trench in British Columbia to winter range. Followed similar routes in spring until reaching central Alberta, where they veered east of Rocky Mtns., flying north through Alberta, across central Yukon, and to summer ranges throughout Alaska and n. Yukon (CLM).

Migration patterns of adults and immatures may differ; immatures move through New Mexico and w. Texas at beginning and end of wintering period (Nov and Mar), but winter in unknown areas (Boeker and Ray 1971). Immature:adult ratios recorded at autumn raptor-migration count sites vary geographically. Mean immature:adult ratio 0.27 in Alberta (P. Sherrington unpubl.) and 1.2 at Bridger Mtn., MT (Neal 1999). Ratios \pm 95% C.I. are 1.74 ± 0.401 at Goshute Mtns., NV (Lanzzone 1999); 1.8 ± 1.15 at Wellsville Mtns., UT (Tidhar and Peacock 1999); 2.5 ± 0.86 in Manzano Mtns., NM (Rossman 1999); and 1.03 at Hawk Mtn., PA (Hawk Mountain Sanctuary unpubl.). Most individuals observed at coastal raptor-migration counts in e. U.S. are immatures (Greenstone 1996).

Little information continent-wide on age ratios in spring. Mean immature:adult ratios 0.12 in Alberta (P. Sherrington unpubl.); 0.08 at Rodgers Pass, MT (Tilly and Tilly 1998); and 5.51 ± 1.85 C.I. in Sandia Mtns., NM (Smith 1999). Differences between immature:adult ratio in fall and spring at raptor-migration count sites might reflect age class differences in survival rates or migration routes.

MIGRATORY BEHAVIOR

From Kerlinger 1989, Brodeur et al. 1996, and others as noted. Diurnal migrant; nonflocking (Omeland and Hoffman 1996), but observed in small "kettles" near thermals (Sherrington 1993). Up to 137/h counted in nw. Montana in autumn (Yates et al. 2001). Mean number seen/h (\pm 95% C.I.) in autumn: 0.06 at Hawk Mtn., PA; 0.26 ± 0.05 in Manzano Mtns., NM; 0.44 ± 0.37 at Goshute Mtns., NV; 5.4 near Mt. Lorrette, Alberta; 5.6 ± 0.67 at Bridger Mtn., MT; and 0.66 ± 0.17 at Wellsville Mtns., UT (Lanzzone 1999, Neal 1999, Rossman 1999, Tidhar and Peacock 1999, Hawk Mountain unpubl., P. Sherrington pers. comm.).

Uses orographic lift (uplifts of thermal convection: Kerlinger 1989: 79, 86) along ridges, but also migrates over large flat or featureless terrain. Might compensate for potential flight-path displacement caused by winds; radio-tagged eagles deviated little from a direct line during migration. Water crossings >50 km not recorded; large water bodies may divert migrating eagles.

Individuals from northern breeding areas migrate to wintering areas with little or no wandering, but some wander after reaching winter destinations (Applegate et al. 1987, Brodeur et al. 1996, CLM). Migrants commonly use continuous gliding flight (Yates et al. 2001). Speed during migratory flights up

to 51 km/h (Broun and Goodwin 1943). Radio-tagged eagles from e. Hudson Bay migrated mean of 65 km/d (range 49–81) during fall migration and 68 km/d (range 32–91) during spring migration. No evidence that adults and juveniles in northern areas start migration together, as reported by Palmer (1988). Significant shifts in magnitude of hourly passage rates at Hawk Mtn., PA, related to cold fronts; passage rates peaked 1 d after a cold front and declined steadily for next 3 d (Allen et al. 1996). Four radio-tagged eagles from e. Hudson Bay usually stayed <2 d in any local area during migration (Brodeur et al. 1996). Immatures may abandon summer ranges earlier than adults because they have less experience in foraging (Omland and Hoffman 1996). Compared to adults, immatures in sw. Montana spent more time migrating each day and were less selective about time of day for migrating; at autumn migration lookouts in sw. Montana, immatures observed more frequently than adults from 08:00 to 12:00 and >17:00 (Omland and Hoffman 1996). Individuals often hunt during migration (Dekker 1985).

CONTROL AND PHYSIOLOGY

Few data on proximate cues for migration. Tendency to migrate is strongest at northern latitudes (Kerlinger 1989). Departure from northern breeding areas coincides with first lasting snowfall, freeze-up, or decreasing prey abundance; also north winds (Brodeur et al. 1996). Poor winter foraging conditions due to low jackrabbit abundance in w. U.S.'s Great Basin may stimulate migratory movements among otherwise sedentary eagles (Rossman 1999), but individuals from sw. Idaho did not exhibit "irruptive" movement patterns during prey shortages (Steenhof et al. 1984). Eagles respond opportunistically to varying weather factors in complex landscapes with high topographic relief. Numbers of migrating individuals increased with increasing air temperature, rising barometric pressure, and decreasing relative humidity at Glacier National Park, MT in autumn; numbers increased with increasing wind speed and rising barometric pressure in spring (Yates et al. 2001).

HABITAT

BREEDING RANGE

Breeds in open and semiopen habitats from near sea level to 3,630 m (Poole and Bromley 1988, G. R. Craig pers. comm.)—tundra, shrublands, grasslands, woodland-brushlands, and coniferous forests (Kochert 1986). Also in farmland and riparian habitats (Kochert 1972, Menkens and Anderson 1987). Avoids heavily forested areas.

Occurs primarily in mountainous canyon land, rimrock terrain of open desert and grassland areas of

w. U.S. Also nests extensively in riparian habitats in e. Great Plains (Menkens and Anderson 1987) and occasionally in forested areas. Nesting territories in sw. Montana are at lower elevations and contain more sagebrush (*Artemisia* spp.)-grassland habitat than unused areas (Baglien 1975). Nesting density in s.-central Idaho was higher in areas bordered by sagebrush/grass seedings than in areas bordered by agriculture (Craig and Craig 1984b). In ne. Colorado, nests primarily in grasslands near cliffs and avoids cultivated areas (Olendorff 1973). In n. Utah, nests mainly in grass, shrub, and juniper (*Juniperus* spp.) habitats (Peterson 1988). In e. Utah, used valley, aspen (*Populus* spp.)-conifer, and piñon (*Pinus* spp.)-juniper habitats as expected based on availability and talus habitat less than expected (Bates and Moretti 1994). In Wyoming, nests primarily in grassland, shrubland, or riparian habitats; absent or rare in flat desert terrain, farmlands, and dense forests (Phillips et al. 1984). In central California, nests primarily in open grasslands and oak (*Quercus* spp.) savanna and to a lesser degree in oak woodland and open shrublands (Hunt et al. 1995, 1999). In Arizona, prefers desert grasslands and chaparral habitats (Millsap 1981).

Typically forages in open habitats: grasslands or steppelike vegetation. In sw. Idaho, prefers to forage in shrub habitat; avoids agriculture, grassland, and burned habitats (Marzluff et al. 1997, USGS unpubl.). In central California, forages in open grassland habitats (Hunt et al. 1999). In forests west of Cascade Mtns., associated with open habitats (Anderson and Bruce 1980, Bruce et al. 1982). In e. North America, nests near burns, open marshes, meadows, bogs, and lakes and forages in open and semiopen mountainous or hilly terrain (Spofford 1971, Singer 1974, Brodeur and Morneau 1999).

Farther north in interior and n. Alaska and interior w. Canada, breeds in habitat dominated by rugged topography or mountainous terrain, near or above timberline, and along riparian areas (Ritchie and Curatolo 1982, Petersen et al. 1991, Young et al. 1995). Also breeds on bluffs and cliffs along rivers below timberline in Alaska (Ritchie and Curatolo 1982) and on sea cliffs in nw. Alaska (K. Titus pers. comm.). Common in mountainous areas dominated by subalpine and alpine vegetation between 300 and 1,525 m in Denali National Park, AK (CLM). Associated with tundra areas, river outwash plains, and alpine-subalpine ecotypes in e.-central Yukon (Hayes and Mossop 1981). Occurs in areas with high topographic relief dominated by low-arctic tundra plant species in coastal central Canadian Arctic (Poole and Bromley 1988); in areas with cuesta relief (asymmetric hills or ridges with gentle slopes and steep escarpments) and rugged topography in e. Hudson Bay region (Morneau et al. 1994). Forages on alpine tundra slopes at edges of subalpine scrub in sw. Alaska; rarely in open areas

below timberline (Petersen et al. 1991). Forages in wet marsh tundra, heath tundra, tussock-heath tundra, and hillside heath tundra valleys in Alaska along the Kolomak River and Yukon-Kuskokwim Delta and in the Atigun and Sagavanirktok River valleys (Holmes and Black 1973, Sage 1974).

SPRING AND FALL MIGRATION

In w. U.S. and Canada, may hunt over wetlands, agricultural areas, and grassy foothills during migration (Dekker 1985). In w. Canada, may select areas with strong thermal activity and uplifts for energy-efficient migration (Sherrington 1993). Radio-tagged eagles followed topographical features in e. U.S., but where these features were lacking in central Quebec and Ontario, they migrated over largely flat or featureless terrain (Brodeur et al. 1996).

WINTER RANGE

From Root 1988 and others as noted. Primarily Humid Temperate and Dry ecoregion domains (Bailey 1989) from s. Alaska and Canada to central Mexico. Frequents areas in w. North America >457 m in elevation and winters up to 2,500 m (e.g., San Luis Valley, CO). Generally absent from harsh, dry areas (<20 cm annual precipitation) of Sonoran Desert and central Nevada; does not winter in western temperate forests in and west of Rocky Mtns. Winter habitat east of Canadian Rockies skirts northern edge of grasslands and excludes mixed mesophytic and deciduous forest. Forages at edges of woodland-scrub habitat in valley floors, riparian areas, and over areas dominated by dwarf shrub mat at northern limit of wintering distribution in Alaska (Petersen et al. 1991). In s. Yukon, may frequent local dumps and roadways searching for road kills (Burles and Frey 1981).

Across w. U.S., prefers open habitats with native vegetation and avoids urban, agricultural, and forested areas (Millsap 1981, Fischer et al. 1984, Craig et al. 1986, Marzluff et al. 1997). Uses sagebrush communities, riparian areas, grasslands, and rolling oak savanna (Knight et al. 1979, Fischer et al. 1984, Hayden 1984, Estep and Sculley 1989). In sw. Idaho, forages primarily in shrubland and avoids grassland and agriculture, with foraging points concentrated in sagebrush/rabbitbrush (*Chrysothamnus* spp.) habitat and cliff areas (Marzluff et al. 1997). Common in grazed areas; much remaining habitat in central and s. California in patches of relatively inaccessible mountainous country, primarily livestock ranches (Thelander 1974).

Common near reservoirs and wildlife refuges that provide foraging opportunities at winter waterfowl concentrations in midwestern U.S. (Wingfield 1991). Associated with riverine or wetland systems east of Mississippi River (Millsap and Vana 1984). Most sightings in e. U.S. concentrated within or along

southwestern border of the Appalachian Plateau (30% of records) and within the Coastal Plain physiographic region (33% of records). Associated with steep river valleys, reservoirs, and marshes in inland areas; estuarine marshlands, barrier islands, managed wetlands, sounds, and mouths of major river systems in coastal areas. These wetlands are attractive due to a dominance of open vegetation, large concentrations of prey, and absence of human disturbance. Winters on montane grass and heath balds in the Appalachian Plateau region (Millsap and Vana 1984). Immatures more common along coastal plain on lower river estuaries, adjacent marshlands, and barrier islands of e. U.S.; adults more common than immatures near inland waterways on Appalachian and New England plateau (Millsap and Vana 1984, Todd 1989).

FOOD HABITS

FEEDING

Main foods taken. Small to medium-sized mammals: hares (*Lepus* spp.) and rabbits (*Sylvilagus* spp.); also ground squirrels (*Spermophilus* spp.), prairie dogs (*Cynomys* spp.), marmots (*Marmota* spp.).

Microhabitat for foraging. See Habitat, above. Takes most prey on or near ground.

Food capture and consumption. Three main strategies to search for prey: soaring, still-hunting from a perch, and low contouring flight (Edwards 1969, Dunstan et al. 1978, Dekker 1985, Palmer 1988). Strategy determined by weather conditions, topography, and prey's escape response (Dekker 1985, Watson 1997). Soars more often on sunny and windy days; hunts from perches on overcast, calm, or rainy days; uses contour flight in broken topography and high soar in open habitats. Uses contour hunting to surprise prey that might escape to burrows. Contour hunting is most common overall (Watson 1997), but perch hunting was most common in sw. Idaho where habitat was open and perches (power lines, canyon rims, and rock outcrops) were abundant (Dunstan et al. 1978).

Usually attacks prey from upwind (Palmer 1988). Uses 7 techniques to attack prey (Watson 1997: 48): (1) "high soar with glide attack" to attack solitary or widely dispersed prey (hare, grouse [Phasianidae]) from a thermal (>50 m) with a long (≥ 1 km), low angle glide; (2) "high soar with a vertical stoop" to attack slow-flying or flocking prey (geese [*Branta* spp.], cranes [*Grus* spp.], sage grouse [*Centrocercus urophasianus*]; EHC) from a high (>50 m) soar; (3) "contour flight with a short glide attack" to surprise colonial prey (ground squirrels and prairie dogs) from low-level flight quartering over the ground; (4) "glide attack with tail chase" to flush, chase, and capture agile mammals and birds in flight from a low angle

stoop; (5) "low flight with slow descent attack" to capture slow-moving prey (tortoise [Testudinidae], snakes [Serpentes]) from a low-level quartering flight and slow "parachute" stoop; (6) "low flight with sustained grip attack" to kill ungulates by landing on victim's back or neck, and riding it until the animal dies (Deblinger and Alldredge 1996); and (7) "walk and grab attack" to capture quarry protected by an obstruction (Dixon 1937, M. Collopy pers. comm.).

Frequently feeds on carrion, especially during winter and even when live prey is available (Kalmbach et al. 1964, Watson 1997); consumes fresh carrion during nesting season (Bogg 1977). Locates carrion from high-soaring flight; often cues in on activity of crows (*Corvus* spp.) and other scavengers (Watson 1997).

Also hunts cooperatively with conspecifics; most cooperative hunting involves large prey (e.g., ungulates, red fox [*Vulpes fulva*], Wild Turkeys [*Meleagris gallopavo*] in winter; Thomas et al. 1964, Hatch 1968, Deblinger and Alldredge 1996). Mated pairs also hunt jackrabbits cooperatively during breeding season; pairs pursue prey with one individual following the other at different elevations above the ground. Initial pursuer diverts prey's attention by stooping while the second makes the kill (Willard 1916, Hunsicker 1972, Collopy 1983b).

Tandem hunting less successful than solo hunting in sw. Idaho (Collopy 1983b). Overall prey-capture success 20% ($n = 115$ capture attempts); capture success 4.6% for tandem hunting ($n = 42$), 29% for solo hunting ($n = 73$). Males initiated significantly more prey-capture attempts when solo hunting; females used both foraging methods equally.

Less common feeding behaviors include kleptoparasitism, piracy, nest-robbing, cannibalism, and fishing. Takes prey from corvids (Ladygin 1994, Marzluff et al. 1994), foxes (Meinertzhagen 1959), Bald Eagles (T. and E. Craig unpubl.), Great Horned Owls (*Bubo virginianus*; Henderson 1920), Northern Harriers (*Circus cyaneus*; MNK), Red-tailed Hawks (*Buteo jamaicensis*; Dekker 1985), Prairie Falcons (*Falco mexicanus*; J. McKinley pers. comm.), and other Golden Eagles (Dekker 1985). Takes eggs and young from nests. Preys on Canada Goose (*Branta canadensis*) eggs (Valutis and Marzluff 1997) and nestling Gyrfalcons (*Falco rusticolus*; Dittrick and Moorehead 1983). Remains of Prairie Falcon, Ferruginous Hawk (*Buteo regalis*), Great Horned Owl, Barn Owl (*Tyto alba*), Common Raven (*Corvus corax*), Yellow-billed (*Pica nuttalli*) and Black-billed (*P. hudsonia*) magpie, and Rock Dove (*Columba livia*) nestlings in Golden Eagle nests suggest nest-robbing (Carnie 1954, Houston 1985, Hunt et al. 1995, USGS unpubl.). Cannibalism occurs rarely. Collopy (1983a) reported apparent cannibalism of a nestling by its sibling in a nest in sw. Idaho, and partially eaten remains of a Golden Eagle

nestling in a Montana nest suggest cannibalism by a sibling or parent (Palmar 1954). Fishing rare, but ≥ 5 individuals frequently captured live trout from shallow streams and pools in Arizona during winter (Brown 1992).

Hunts from 1 h before sunrise to 1 h after sunset during the breeding season in sw. Idaho (Dunstan et al. 1978). Hunting pattern bimodal in n.-central Utah: 08:30–12:00 and 14:45–18:30 (Smith and Murphy 1973). In central Idaho in winter, hunting activity usually greatest from midmorning until late afternoon (T. and E. Craig unpubl.).

DIET

Major food items. Feeds mainly on mammals (80–90% of prey items), secondarily on birds, and less often on reptiles and fish during nesting season (Olen-dorff 1976). Preys principally on leporids (hares and rabbits) and sciurids (ground squirrels, prairie dogs, marmots); the 2 groups combined constituted 49–94% of individual prey items reported in 24 studies throughout w. North America during nesting season (Appendix 1). Relative importance of taxa varies by region. Arctic ground squirrels (*Spermophilus parryi*), snowshoe hares, and arctic hares (*Lepus arcticus*) are principal prey in Alaska and n. Canada (Poole and Bromley 1988, Appendix 1). White-tailed (*Lepus townsendii*) and black-tailed jackrabbits, cottontails (*Sylvilagus* spp.), and white-tailed (*Cynomys leucurus*) and black-tailed (*C. ludovicianus*) prairie dogs are primary prey species in the n. Great Plains, with yellow-bellied marmots (*Marmota flaviventris*) and Richardson's (*Spermophilus richardsonii*) or Wyoming ground squirrels (*S. elegans*) important secondary prey (McGahan 1968, Reynolds 1969, Lockhart et al. 1977, MacLaren et al. 1988). Black-tailed jackrabbits and cottontails are main prey in Great Basin, with yellow-bellied marmots and Piute ground squirrels (*S. mollis*) or rock squirrels (*S. variegatus*) chief secondary prey (Arnell 1971, Bloom and Hawks 1982, USGS unpubl.). Yellow-bellied marmots are primary prey in e. Washington (Marr and Knight 1983). California ground squirrels (*S. beecheyi*) and black-tailed jackrabbits constitute most remains in central California (Carnie 1954, Hunt et al. 1995). In sw. U.S., black-tailed jackrabbits and cottontails are main prey, and rock squirrels and prairie dogs are chief secondary prey (Mollhagen et al. 1972, Lockhart 1976, Eakle and Grubb 1986).

Gallinaceous birds (pheasants, grouse, and partridge) are main birds taken (Olen-dorff 1976). Ptarmigan (*Lagopus* spp.) are important secondary prey in central Alaska (McIntyre and Adams 1999), and waterfowl are secondary prey in arctic Canada (Poole and Bromley 1988). Ring-necked Pheasants (*Phasianus colchicus*) and Chukars (*Alectoris chukar*) are secondary prey in the Great Basin (Hickman 1968, Arnell 1971, Marr and Knight 1983, USGS unpubl.).

Occasionally kills large prey, including seals (Phocoidea), ungulates (mountain goat [*Oreamnos americanus*], bighorn sheep [*Ovis canadensis*], Dall sheep [*O. dalli*], caribou [*Rangifer* spp.], deer [*Odocoileus* spp.], and pronghorn [*Antilocapra americana*]), coyotes (*Canis latrans*), badger (*Taxidea taxus*), bobcat (*Lynx rufus*), turkeys, geese, Trumpeter (*Olor buccinator*) and Tundra (*O. columbianus*) swans, Sandhill (*Grus canadensis*) and Whooping (*G. americana*) cranes, Ospreys (*Pandion haliaetus*), and Great Blue Herons (*Ardea herodias*; Bent 1937, Brandborg 1955, LaFontaine and Fowler 1976, Olendorff 1976, Ellis et al. 1999, Mason 2000, R. Ritchie unpubl.). Mainly takes young ungulates, but also kills adults (Deblinger and All-dredge 1996). Also preys on domestic animals, including sheep (*Ovis aries*), goats (*Capra hircus*), calves (*Bos taurus*), pigs (*Sus scrofa*), poultry (*Gallus gallus*), dogs (*Canis familiaris*), and cats (*Felis catus*; Bent 1937, Olendorff 1976). May kill livestock even when preferred prey is available (Phillips et al. 1996). In studies where sheep and goat remains were found at nests, these species constituted 0.2 to 7% of remains and accounted for only 1.4% of 7,094 prey items identified in studies throughout the w. U.S. (Reynolds 1969, Mollhagen et al. 1972, Olendorff 1976, Bloom and Hawks 1982). Livestock remains include both carrion and eagle kills (Olendorff 1976).

Diet data lacking for e. North America. Although snowshoe hare, cottontails, and marmots are common prey, e. North American nests have a high proportion of American Bitterns (*Botaurus lentiginosus*), Canada Geese, and Great Blue Herons (Spofford 1971, Weik 1987, Todd 1989, Brodeur and Morneau 1999).

Winter diet does not appear to differ appreciably from nesting-season diets in temperate areas, but few data exist. Of 65 individuals identified in stomachs of 50 eagles killed Mar 1948 in Colorado, 52% were hares and rabbits (Woodgerd 1952). Of items identified in 63 eagle stomachs collected between Nov and Mar from 15 states throughout the U.S., 59% were hares/rabbits and 27% were suspected ungulate and jack-rabbit carrion (Kalmbach et al. 1964). Sheep and goats constituted 11% of items, but proportion taken as carrion was unknown. Winter diet in central Utah consisted almost entirely of black-tailed jackrabbits (Edwards 1969). Also preys on waterfowl during winter (Kalmbach et al. 1964, McWilliams et al. 1994); waterfowl important in winter diets on Chesapeake Bay and eastern coastal areas (D. Buehler pers. comm.).

Quantitative analysis. Appendix 1. Data available primarily for the nesting season. Usually based on analyses of pellets and prey remains collected at nests; some data derived from direct observation of prey deliveries. Intensity variable, ranging from systematic collections every 4 d during the nesting season for >10 yr to 1 collection/nest for only 1 season. Results may not be reliable for quantitative estimates

of food intake, particularly with longer intervals between collections (McGahan 1967), but are reliable for interpreting relative importance of prey species. Earlier dietary estimates derived from analysis of stomach samples (Kalmbach et al. 1964), but quality of data collected from stomach samples from individual raptors is minimal compared to other available methods (Marti 1987).

Most extensive information about diet composition comes from Snake River Birds of Prey National Conservation Area in sw. Idaho where >2,200 individual prey items were identified from 1971 to 1981 (Steenhof and Kochert 1988). Proportion of main prey in diet varied annually, and proportion of jackrabbits in diet correlated with jackrabbit density in the environment. Diet breadth was smaller than that of Red-tailed Hawks but larger than that of Prairie Falcons from the same area. Golden Eagles had smallest variation in sizes of prey taken; sizes of prey varied from 10 to 5,800 g (geometric mean 609 g, $n = 2,203$). Diets vary within nesting season, reflecting opportunistic hunting. In sw. Idaho, proportions of Ring-necked Pheasants in nests highest in Apr, coinciding with the peak of pheasant breeding activity; subsequently decreased when pheasant incubation began (Kochert 1972).

FOOD SELECTION AND STORAGE

Opportunistic predator; wide variety of prey species and sizes, but in North America focuses on leporids and sciurids 500–2,000 g (Watson 1997; see Diet, above). Generally eats large prey at kill site; fresh limbs of young ungulates in nests suggest eagles may disarticulate animals before bringing to nests (Kalmbach et al. 1964; MNK). Parents may bring more food to nests than young can eat. Sometimes excess food is carried away from the nest, but in most cases, it is left there (see Breeding: parental care, below). Caching of prey rare, but a pair in Scotland deposited prey on a cliff near the nest before feeding it to the young (Macpherson 1910).

NUTRITION AND ENERGETICS

Pairs delivered 885 g of prey biomass/d to nests in w. Texas (Lockhart 1976) and 1,417 g/d during the 10-wk brood-rearing period in sw. Idaho (Collopy 1984). Pairs in Montana brought an estimated 1,470 g of prey/d to a nest during a 39-d portion of the brood-rearing period (McGahan 1967). See Breeding: parental care, below, for additional information on prey-delivery rates.

Between 23.9 and 33.2 kg of food needed to raise a chick from hatching to fledging (10 wk), based on estimates from feeding trials (Collopy 1980). Prey biomass consumed by nestlings increased during brood-rearing with peak at 7–9 wk of age (Collopy 1984). Amount of food consumed/d by 2 male and 2

female captive nestlings increased steadily from 11 to 15 d of age, peaked at 28–44 d, and declined slightly until experiments ended at 53–57 d (Collopy 1986). Food consumption did not differ between male and female nestlings. During late brood-rearing (47–57 d old), captive eaglets consumed 12–15% of their body mass/d; much greater than consumption rates of adults and juveniles (5.7–6.6%/d; Fevold and Craighead 1958). Greater food consumption by nestlings reflects cost of producing body tissue and feathers. Captive nestlings were 74.4% efficient at assimilating food energy consumed; no difference between males and females. Assimilation efficiency is related to fat content of prey (Collopy 1986). Ground squirrels contain 4–17 times more fat and provide 1.7 times more energy than rabbits (U.S. Dept. of Interior 1979, M. Collopy unpubl.).

METABOLISM AND TEMPERATURE REGULATION

Overall mean gross and net energy efficiency (proportion of total ingested and metabolized energy, respectively, converted to feathers, fat, and other body parts) of 4 captive nestlings was 31% and 42%, respectively, and did not differ between sexes (Collopy 1980). Growth efficiency (ratio of biomass produced to biomass consumed) of nestlings decreased linearly with age and did not differ between males and females (Collopy 1986). Growth efficiency averaged 27% at 2 wk of age and steadily decreased to <5% at fledging. As chicks aged, more of their energy budget was allocated to maintenance. Trends in metabolized energy (ME) paralleled food consumption and peaked at about 2,500 kJ/d, with no difference between sexes. ME of wild males peaked 7–8 wk of age at about 2,000 kJ/d, and females peaked at about 3,100 kJ/d during week 8 (Collopy 1986). Energy metabolism ranged from 4.33 to 4.01 W/kg for 2 captive Golden Eagles (Gessaman et al. 1991). Body temperature of a telemetered nestling ranged from 37.9 to 39.1°C over 18 d (Rudeen and Powers 1978).

DRINKING, PELLET-CASTING, AND DEFECATION

Drinks occasionally, but most or all liquid requirements, particularly for nestlings, are met by ingesting prey (Brown and Amadon 1968). Adults and immatures in Nevada drank in mountain bogs and springs and ingested snow near or above timberline (Charlet and Rust 1991, Johnson 1994). Drinking was a frequent daily activity of a captive adult female (Kish 1970). Casts pellets, usually once early in the day (M. Collopy pers. comm.). To cast, eagle arches neck with face down and forward and gapes widely while rapidly shaking head laterally. Behavior repeated several times with brief pauses between head-shakes; soft squeaks or whistles often accompany casting. Often bobs head in a Neck Pump prior to casting, and conspicuous swallowing often follows

casting attempt. Adults do not cast at nest; chicks cast 1–3 pellets/d from age 20 d to fledging, but some chicks did not cast every day (Ellis 1979). Two captive male and 2 captive female chicks produced an average of 7.7 g/d (dry mass) and 6.9 g/d (dry mass) of pellets (Collopy 1980). The same captive eaglets defecated an average of 57.0 g/d (dry mass) and 59.6 g/d (dry mass), respectively (Collopy 1980). Number of defecations/d increases linearly to about 20 d in wild nestlings and then levels off to 10–16/d until fledging ($n = 4$; Ellis 1979).

SOUNDS

VOCALIZATIONS

Mostly silent except during breeding season, but vocalizations not well studied or documented outside breeding season. Most known calls associated with food deliveries by adults and food-begging by nestlings. Food-begging call probably most commonly heard vocalization; calls from larger nestlings can be heard ≥ 1.6 km away from the nest (CLM).

Development. Newly hatched eaglet emits a clear chirp; developing voice proceeds through a series of chirps, cheeps, and high-pitched chitters (Jollie 1943). Per Ellis 1979, unless specified: Nestlings begin chirping 2 d before hatching and continue throughout nestling period. By 10 d of age, chirp largely replaced by rattle-chirp in stressful situations, and feeding chirp replaced by a disyllabic *tsik*. At 15 d, *tsik* evolved into a 2-syllable *seeir* call. At 25 d, *seeir* merges into louder and harsher *pssa* or *tsycuk tsycuk* (Brown and Amadon 1968) when eaglet is very hungry or highly stimulated to solicit feeding. Food-begging calls may become more frequent and harsher with age (Watson 1997). By 40 d old, many of nestling calls indistinguishable from those of adult.

Vocalizations of nestling and fledgling usually associated with food solicitation (chirp, *seeir*, *pssa*), temperature stress (chirp), aggression, stimulation of parental care, or appearance of a parent (Brown and Amadon 1968, Hickman 1968, Ellis 1979, Watson 1997, O'Toole et al. 1999). *Seeir* and *pssa* intergrade; *pssa* is louder (Ellis 1979). In w. Montana, *chirps* usually used only at feeding time or when tiny eaglets are exposed to hot or cold weather (Ellis 1979). Nestlings may hiss when an intruder enters the nest (Sumner 1929a, Ellis 1979) or may emit harsh high-pitched chattering when angry (Brown and Amadon 1968). Fledglings use *pssa* and *yarp/yelp* to solicit food (Watson 1997) or may call to facilitate location by parents (O'Toole et al. 1999). Other vocalizations of nestling and fledgling include *weeo-hyo-hyo-hyo* and *weeo* (Brown and Amadon 1968).

Array of sounds. Vocalizations used in communication not as song or territorial markers. Vocal array

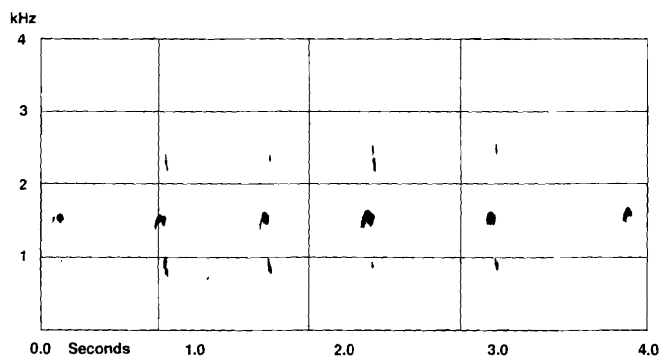


Figure 2. Flight calls of the adult male Golden Eagle. Prepared by the staff of the Borror Laboratory of Bioacoustics (BLB), The Ohio State University, from BLB recording no. 25828, Yukon, Northwest Territories, Canada, 10 Jun 1997, using a Kay Elemetrics DSP 5500 Sona-Graph (with an effective frequency resolution of 75 Hz and a 200-point FFT transform size).

is limited. No information on geographic variation. Nine distinct calls (chirp, *seeir*, *pssa*, *skonk*, rattle-chirp or cluck, *wonk*, *wip*, honk, and hiss) described in w. Montana (Ellis 1979). Vocal array and calls of immature not described; assumed to be similar to those of adults. Common adult vocalizations are yelping and mewling-type calls (Snow and Perrins 1998), doglike barks (Watson 1997), *skonk* or *wonk* (Ellis 1979), or *yaps* (Jollie 1943). Adult vocalizations associated with copulation (*pssa*), nest-building, entering nest, threatening or alarming situations (*skonk*), food deliveries (*wip*), meeting or approaching each other (*wonk*), coming into an evening roost, or intruders approaching a nest (*cherop*; Sumner 1929a, Jollie 1943, Camenzind 1969, Ellis 1979, Bergo 1987). Incubating female may call from nest when she sees male approaching with prey (Bergo 1987); may emit *pssa* during copulation and when approached by adult male on nest (Ellis 1979), and may call or cluck in anticipation of a nest visit by the male (Dixon 1937). Adult male may emit a long series of brief calls, *wip*, interspersed with an occasional *wonk*, during food deliveries at nest (Ellis 1979); *wip* is distinctly shorter and of higher frequency than *wonk* (Ellis 1979). The *wonk* is a greeting call used in various contexts including deliveries of prey and nesting material and incubation changes (Ellis 1979). Adult male also may call before entering a nest during incubation (Dixon 1937). During courtship, both members of pair *yarp* rapidly (Snow 1973). Pitches of individual males and females may differ enough in tone to be distinguishable (Dixon 1937, Jollie 1943); male has a more high-pitched *yarp*, female a more "barking" voice (Jollie 1943). Figure 2 shows flight calls of an adult male near a nest.

Phenology. In w. North Dakota, calling rate of juveniles did not change with time since fledging and did not differ between sexes (O'Toole et al. 1999). Call

rate/h nearly doubled with a parent present (mean 21.8 calls/h \pm 3.526 SE) versus a parent absent (mean 11.5 calls/h \pm 1.739 SE; O'Toole et al. 1999).

Daily pattern. No information.

Places of vocalizing. Nestlings and adults vocalize near nest during breeding season (biased to nests, as this is where most studies are conducted).

Social context and presumed functions. See above.

NONVOCAL SOUNDS

None known with a communicative function.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing, etc. Walks with awkward gait. May land and walk when approaching carrion during winter; also walks uphill when crop is full to gain elevation for flight (T. and E. Craig unpubl.). Often runs along ground, flapping wings, prior to flight; flapping always accompanies running. Unsuccessful aerial attempts to capture prey often followed by flapping and running wildly in an attempt to catch prey on ground (Ellis 1979). Recently fledged young often walk uphill to gain elevation to become airborne again. See Breeding: young birds, below.

Flight. Soars with outstretched wings and tail held in one plane, although wings sometimes held in a slight dihedral; primary tips spread fingerlike (Ellis 1979, Watson 1997). Two types of soaring flight: slow gliding flight, which includes parachuting, and fast gliding flight (Bergo 1987). May glide in high winds on partially folded wings (Ellis 1979). Glides can be 190 km/h (Darling 1934). Parachutes with wings and tail elevated and spread; legs dangling. Suggested functions of soaring include gaining height for gliding to other areas, hunting, territorial advertisement, courtship, migration, and exploration (Bergo 1987, Collopy and Edwards 1989). Flapping flight appears labored and consists of 6–8 deep wing-beats, interspersed with 2- to 3-s glides; less common than soaring or gliding flights (Watson 1997). Stoops with wings tightly closed, legs raised against tail. Speeds of 240–320 km/h attained in these vertical dives (Brown and Amadon 1968); can exceed speed of diving Peregrine Falcons (*Falco peregrinus*; Darling 1934). Also uses Delta-Wing Stoop, with wing-tips nearly touching, wrist areas extended laterally, alulae flared; legs sometimes dangling (Ellis 1979). Often makes conspicuous, long dives to eyries; dives occasionally preceded by undulating flight (Bergo 1987). Undulating display flight (sky-dancing) involves series of steep dives and upward swoops with 3 or 4 strong wing-beats near each apex; repeated in rapid succession with up to 20 undulations in a single display (Ellis 1979, Bergo 1987, Collopy and Edwards 1989). Special

form of undulating display is Pendulum flight; eagle dives, regains height, turns over, and repeatedly re-traces same course (Bergo 1987). Undulating flights function most often as a territorial display (Harmata 1982, Bergo 1987, Collopy and Edwards 1989; see Spacing, below), but also may be associated with courtship behavior (Harmata 1982, Bergo 1987).

Swimming and wading. Swims only when necessary; one waded in water toward duck decoy (Sperry 1957). Two nestlings forced into river by human intruders swam to shore by paddling with wings (Hickman 1971). Captive immatures paddled with both wings and feet when swimming (Ellis 1979).

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, etc. Variety of preening methods to oil feathers, rearrange barbs, etc.; scratches head, neck, upper throat with claw of middle toe; may shake, ruffle feathers during preening; see Ellis 1979 for details.

Bathing often associated with drinking; observed in wild eagles in Nevada (Charlet and Rust 1991, Johnson 1994) and a frequent activity of captive birds (Sumner 1934, Kish 1972). In Arizona, a pair bathed and drank in a pool every morning (Bailey 1917). Communal bathing of up to 12 individuals reported in Arizona and Texas (Brandt 1951, Spofford 1964).

Sleeping, roosting, sunbathing. Nestling often sleeps on belly, with head resting on nest. Adult sometimes sleeps with head drooped; may tuck head under back- and scapular-feathers. Eyes sometimes covered by feathers during sleep; lower lids may cover cornea. Adults and large nestlings often stand on one leg when perched (Ellis 1979). During nesting season, both males and females have preferred perches near nest (Bergo 1987); female often roosts at nest during nesting season (Collopy 1984). Uses several preferred perches and spends long periods of time during the day roosting on prominent perches with good views of the landscape; usually perches above nest site but below ridge during nesting season (Watson 1997). During nonnesting season, both members of resident pair may spend many hours together on prominent perches; prefer sunny aspect in winter and avoid windy, exposed locations (Watson 1997). Rarely perches communally, but see Social and interspecific behavior, below.

From Ellis 1979: spreads wings wide to shade young, dry plumage, or absorb radiant energy. Responds to overheating by moving into shade or next to cool object, panting, and/or wing-drooping. Maximum recorded panting: 50 cycles in 25 s. Maximum rate accompanied by salt secretion running from nostrils. Wing-droop often accompanies panting and probably facilitates heat loss from under-wing surface; performed with back to sun, and sometimes with scapulars erected.

Daily time budget. In Idaho, males perched average of 78% of daylight hours, females 85% (Collopy and Edwards 1989). Males in Idaho spent 1.9, 19.1, 0.4, and 1.4% of daylight hours during chick-rearing in direct flight, soaring, undulating flight, and self-maintenance, respectively. Females spent 0.9, 13.9, 0.1, and 0.8% of daylight hours performing same functions. Agonistic encounters constituted <1% of male's or female's time (Collopy and Edwards 1989). Average time spent flying or soaring during breeding season: 20% for males and 28% for females in 1 Idaho study (Dunstan et al. 1978), 22% for males and 15% for females in another (Collopy and Edwards 1989); time spent in flight fluctuated with chick-rearing. Aerial activity may be reduced in some areas during cold winter weather, which is less conducive to soaring (Bergo 1987). Average time spent flying during winter in Idaho: males, 21%; females, 16% (Dunstan et al. 1978). Time not flying is spent perched, often in shaded area during hot summer afternoons. Males incubated 13.8% and females 82.5% of day (Collopy 1980). Females brooded/shaded 10.9% of time; males 0.08%. Males attended the nest 0.6%, females 24.0%. Females fed young 3.1% and males fed 0.04% of daylight hours during 1,194.6 h of observation during brood-rearing from 1978 to 1979 (Collopy 1980).

AGONISTIC BEHAVIOR

Physical interactions. Territorial defense usually accomplished adequately by undulating flight and occasionally chase behaviors (Collopy and Edwards 1989, Marzluff et al. 1997). In Europe, physical contact during territory defense uncommon; individuals sometimes killed or wounded by other Golden Eagles in a saturated population in the Alps (Haller 1996). Three resident adults and a floater apparently killed by other eagles in California and Scotland (Grant and McGrady 1999, Hunt et al. 1999). Aggressive behavior toward nonbreeders by territorial adults may involve a steep dive followed by a chase after the intruder (Haller 1982, Bergo 1987). Flights sometimes preceded or followed by intense bouts of undulating displays (Bergo 1987). Invader often responds by rolling over and presenting talons to the aggressor. Rarely, lock talons and tumble through the air; sometimes fall several revolutions and other times tumble to the ground before releasing grip (Ellis 1979). Talon-grappling probably most often an aggressive encounter, rather than courtship; 2 adult females in Montana locked talons in the air, fell to the ground, and fought for >2 h in what appeared to be a territorial conflict. An observer broke up fight before either eagle was killed (Harmata 1982). Conflicts with conspecifics at carcass feeding sites during winter/migration period often involve both display threats and physical contact (Halley and Gjershaug 1998, T. and E. Craig unpubl.). Five of 7 aggressive encounters at carcasses during

winter in Norway were won by females; in 15 of 21 conflicts, the younger bird dominated an older conspecific, but the difference was not significant (Halley and Gjershaug 1998).

Reactions of territorial adults to immatures varies. Adults usually reacted passively to immatures near nests during the breeding season in Scotland and sw. Idaho (Brown and Watson 1964, Kochert 1972, M. Collopy pers. comm.). Parents were not aggressive toward their own offspring during the postfledging period in N. Dakota (O'Toole et al. 1999). However, 2 instances of talon-grappling in Montana both occurred near an eyrie after a "rushing attack" by an adult at an immature (Ellis 1979), and talon wounds on a fledgling and 2 nestlings close to fledging in central California suggest they were killed by another eagle (Hunt et al. 1997, G. Hunt pers. comm.). Residents chased 4 of 8 intruding subadults from territories in Norway and performed undulating displays in response to ≥ 2 of the other 4 intruders (Bergo 1987).

Communicative interactions. From Ellis 1979, Bergo 1987, and others as noted. Threat displays include Undulating Flight and aggressive direct Flapping Flight with exaggerated downstroke; function as threats to intruders in territory and do not usually end in physical contact (Marzluff et al. 1997). Aggressive encounters occur most often before egg-laying, less often during nesting (Watson 1997). Fledged young sometimes make mock attacks on their parents; adults sometimes engage in mock attacks and displacement behavior against recently fledged offspring (Bahat 1992). Sometimes utter a shrill *cherop* call when disturbed at nest site by human or other intruder (Camenzind 1969). Aggressive perch posture: head and body upright, feathers on head and neck erect; wings may be slightly spread and beak open; often accompanied by intense gaze. Similar posture with wings spread wide and oriented toward the threat; may rock back on tail and even flop over on back with talons extended upward as defense. Behavior may be accompanied by wing slap against threatening intruder. When approached by an intruder, turns away, partially spreads tail, lowers head, and remains still; adult on nest may lower head and "freeze" when approached by a person or a helicopter. To protect prey from other eagles, mantles by spreading wings, head, and tail over prey, while perched (Ellis 1979).

SPACING

Territoriality. In Idaho, breeding home ranges overlapped slightly (mean $3.7\% \pm 1.7$ SE), and pairs defended boundaries of the entire home range (Collopy and Edwards 1989, Marzluff et al. 1997). Undulating flight displays and high soaring flight usually sufficient to maintain territory boundaries (Marzluff et al. 1997, Watson 1997); aggressive attacks and

chases among neighbors uncommon. Undulating display was main territorial behavior in Israel (Bahat 1989); mostly performed by adults, but sometimes by immatures or juveniles (Harmata 1982, Bahat 1989). Adults establishing themselves in nesting territories may display more often than established breeders (Bergo 1987). Females in Israel displayed more than males and mostly against interspecific intruders; males displayed primarily as part of courtship (Bahat 1989). Most (67% for males and 76% for females) Undulating Flights in Idaho occurred near the territory boundary or within view of a neighboring territorial eagle rather than near the nest site ($n = 388$; Collopy and Edwards 1989). Eagles from adjacent territories sometimes perform flights simultaneously (Collopy and Edwards 1989), usually directed toward intruders (Bergo 1987, Bahat 1989). Frequent territorial encounters may stress resident pairs and decrease the number of copulations (Haller 1996). Undulating flight by adults observed year-round (Ellis 1979, T. and E. Craig unpubl., M. Vekasy pers. comm.); 46% of undulating displays in Montana occurred during winter (Harmata 1982), suggesting that some residents defend and maintain territories year-round (Marzluff et al. 1997). Aggressive encounters in Israel and Scotland occurred more often in autumn/winter and before egg-laying than during breeding season (Bergo 1987, Watson 1997), but vagrant nonbreeders or winter residents often in territories of residents wintering in Idaho with no defensive behavior observed (Marzluff et al. 1997). Wintering migrants do not defend a wintering territory; no aggression observed among eagles wintering in sw. Idaho (L. Schueck et al. unpubl.).

Individual distance. Up to 7 observed roosting on a single power pole in se. Idaho (Craig and Craig 1984a); individuals perched within 0.25 m of each other (T. and E. Craig unpubl.). Gather communally at carcasses; dominant individual tends to feed while subordinates wait their turn (Halley and Gjershaug 1998, T. and E. Craig unpubl.). Are aggressive and generally do not tolerate another bird within 2 m (Halley and Gjershaug 1998).

Mean distances between adjacent occupied nests ranged from 3.1 to 8.2 km (mean 5.3) in 12 areas of Wyoming (Phillips et al. 1984) and 9.8 to 44.7 km (mean 26.5) in Quebec (Morneau et al. 1994). Nearest-neighbor distances between pairs are rarely < 1 km, even in optimal habitat. Nearest-neighbor distances range from 1.5 to 8 km ($n = 72$ pairs; mean 6) in Denali National Park, AK (CLM), and 0.8 to 16 km ($n = 56$ pairs; mean 4.3) in sw. Idaho (Kochert 1972). Distances between nearest nests along Salmon Falls Creek, ID, averaged $4.39 \text{ km} \pm 2.3 \text{ SD}$ (Craig and Craig 1984b). Pairs on Kisaralik and Tuluksak Rivers of Alaska are regularly spaced, with 4.8 km between nearest adjacent territory centers (Weir 1982).

SEXUAL BEHAVIOR

Mating system and sex ratio. Usually monogamous, but 2 males copulated with 1 female in central California, and the trio successfully raised young (G. Hunt pers. comm.). Several reports of trios in Norway (Bergo 1988), Sweden (Laistal 1966 cited in Watson 1997), and Scotland (Dennis 1983). Few data on mate fidelity. Some pairs stay together for several years; a mated pair stayed together for ≥ 3 seasons in sw. Idaho (USGS unpubl.). Often assumed to mate for life, but research is needed to verify this assumption (Watson 1997). In sw. Idaho, following an unsuccessful breeding season, 1 adult female left her mate from the previous year to mate successfully with a male from another territory (Marzluff et al. 1994). One adult female and 2 adult males switched territories in California (G. Hunt pers. comm.). Lost mates replaced within a few days in 5 cases in Wyoming (Phillips et al. 1984), within 2–10 wk (Dixon 1937, USGS unpubl.), and within 3 d in California (Hunt et al. 1999); rapid replacement of mates may indicate surplus of non-breeders in population (Haller 1982, Phillips et al. 1984, Tjernberg 1985; see Demography and populations: population regulation, below). No data on population sex ratio.

Pairbond. In nonmigratory (resident) populations, appear to maintain pair bond year-round (Harmata 1982, Bergo 1987); no information on maintenance of pair bond in migrants. Pairs in w. Norway spent more time together during autumn, winter, and the pre-laying period than during nesting season (Bergo 1987). Pre-nesting activities consisted of territorial defense, mutual stimulation by aerial displays, carrying materials to nest, and vocalizing (Hickman 1968). Copulation most frequent before egg-laying (Palmer 1988), but occurs year-round and may function in pair-bond maintenance outside breeding season (Gordon 1968, Ellis and Powers 1982, Harmata 1982). Copulation usually occurs on a conspicuous perch (Bergo 1987) or at the nest (Palmer 1988) and may be followed and/or preempted by mutual soaring, rolling and foot-touching, cliff-racing, and extended periods of perching close together (Harmata 1982); occasionally accompanied by food transfer (Ellis 1979). Undulating flight by male sometimes follows copulation (Gordon 1939). Prior to copulation, female leans forward with bill in line with body axis and nearly touches substrate; vocalizes prior to, during, and after coition. Droops wings laterally, possibly to balance; often deflects tail slightly to one side. Male either alights on female from flight or climbs upon her back from behind; drops to tarsi with feet closed and lowers tail under female's for cloacal contact. Male usually flaps wings to maintain balance but does not vocalize. Average time for copulation 11 s; occasionally followed by preening and Ruffle-Shaking (Ellis 1979). In Montana, copulated several times/d from beginning of Mar

until 55 d after completion of clutch at a nest (Ellis and Powers 1982). Other courtship behaviors may include undulating flight by 1 or both pair members, chases, dives, mock attacks, presenting talons, mutual soaring, and circling (Ross 1941, Wood 1941).

Extra-pair copulations. No information.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Typically solitary or in pairs (Watson 1997). Occasionally bathes in groups (Brandt 1951, Spofford 1964) and roosts communally in unique circumstances (rarely; e.g., extremely cold weather and abundant prey); maximum of 124 roosted along a stretch of 85 power poles on a very cold night in e. Idaho (Craig and Craig 1984a; see Spacing, above). Immatures in Utah often associate with one another during winter (Edwards 1969), and immatures also may roost with Bald Eagles during winter, sometimes on the same branch (Edwards 1969, T. and E. Craig unpubl.).

Before independence, social behavior of fledglings and adults nonaggressive; fledgling pairs may mutually preen or nibble when perched together and often follow one another or fly together (O'Toole et al. 1999). In California, 4 generations of 6 related individuals flew together without aggression on 6 separate occasions (D. Bittner pers. comm.). This suggests that related Golden Eagles may tolerate one another for extended periods of time; adult male in Arizona transferred prey to 8-mo-old juvenile (Palmer 1988). Related individuals staying with family groups may explain "trios" during nesting season, but further research is needed (see Breeding: fledgling stage, below).

Play. Individuals and pairs engage in behavior that involves repeatedly carrying an object (e.g., moss or dead prey) to great height, dropping it, then diving after it (Gordon 1955, Davies 1982). Both adult and young carry sticks, drop them, and then retrieve them again while in flight (Coomber 1977, Hardey 1977, Palmer 1988). One such sequence was followed by mutual undulating display of a male and female (Hardey 1977), possibly in the context of courtship.

Nonpredatory interspecific interactions. Often harassed by corvids and other raptor species, particularly near nests of the smaller species (Palmer 1988, USGS unpubl.). Occasionally smaller raptors (e.g., Prairie Falcons) will drive eagles to the ground (MNK). Typically ignores attacks from smaller species, but will roll and extend talons toward chasing individual without displaying predatory behavior (MNK); physical contact sometimes ends in injury or death of attacking species (Walker 1983). Interspecific interactions sometimes related to competition for food. Aggressive behavior toward Ferruginous Hawk in Montana involved undulating flight and aggressive chasing flight (Harmata 1982). Sometimes attacks

coyotes in defense of prey (Bowen 1980, Jordheim 1980). Wintering Bald and Golden eagles fed together at carcasses in Utah; no aggressive behavior observed (Edwards 1969). Dominated Bald Eagles at carcasses in Idaho (T. and E. Craig unpubl.), California Condors in California (Snyder and Schmitt 2002), and White-tailed Eagles (*Haliaeetus albicilla*) in Norway through threat displays; no physical contact (Halley and Gjershaug 1998). Distances from eagle nests to Common Raven, Gyrfalcon, Peregrine Falcon, and Rough-legged Hawk (*Buteo lagopus*) nests suggest interspecific competition for nest sites or space and imply these species avoided Golden Eagle nesting sites in the central Canadian Arctic (Poole and Bromley 1988).

PREDATION

No records of predation on eggs; predation on nestlings and adults is rare. Wolverines (*Gulo gulo*) preyed on nestlings in sw. Alaska (Petersen et al. 1991), and grizzly bears (*Ursus arctos*) killed and ate nestlings in Denali National Park, AK (L. and D. Keeler pers. comm.). A wolverine caught and killed a nesting adult during incubation in n. Sweden (Björvall and Franzen 1986).

Nest defense is mainly passive. Rarely defends nest against other avian species (USGS unpubl.), but agonistic encounters with corvids and other raptors common during the nesting season (Collopy and Edwards 1989). Killed and did not eat 3 Great Horned Owls in Utah (J. R. Murphy in Palmer 1988) and 1 Ferruginous Hawk in Wyoming (Buhler et al. 2000), possibly as territorial or nest defense. Nesting adult in Alaska vocalized and dove repeatedly on intruding grizzly bears, sometimes striking adult bear on back of head and neck with talons and feet (L. and D. Keeler pers. comm.). Not normally aggressive toward human intruders in nesting area; often leaves nest unseen and does not return to area for hours (Camenzind 1969); attacks on humans rare (Bent 1937, Gordon 1955).

BREEDING

PHENOLOGY

Pair formation. In temperate areas, where pairs remain on nesting territory year-round, new pairs form throughout the year soon after lost mates are replaced ($n = 13$; Dixon 1937, Hunt et al. 1997, USGS unpubl.). Pair formation begins upon return to breeding areas in Denali National Park, AK, from late Feb to mid-Apr (CLM). Courtship and nest selection can last >1 mo (MNK). In sw. Idaho, aerial displays, stick-carrying, and vocalizing started in late Jan, with a peak in mid-Feb (Hickman 1968). Resident pairs in the Diablo Range, CA, participate in courtship and nest-building from Dec to Jan (Hunt et al. 1997).

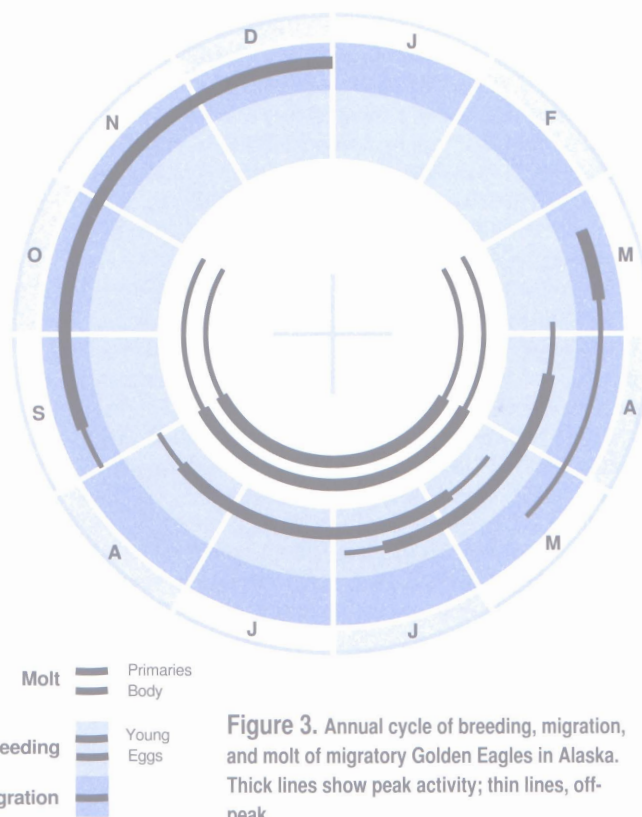


Figure 3. Annual cycle of breeding, migration, and molt of migratory Golden Eagles in Alaska. Thick lines show peak activity; thin lines, off-peak.

Nest-building. Residents add material to nests year-round; may begin refurbishing nests in autumn, with activity peaking from late Jan to early Mar (Watson 1997). In s. California, nest construction began in fall and continued through winter (Dixon 1937). Nest-building began in Dec in Oklahoma and Jan in Texas (Palmer 1988). Duration of nest-building varies, and is probably longer for residents than migrants. Nest construction usually begins 1–3 mo prior to egg-laying; nest-building began 95 d prior to incubation in Japan (Aoyama et al. 1988). Bowl construction (see Nest, below) is the last phase of nest-building and occurs in the last 3–4 wk before egg-laying (CLM).

First/only brood per season. Only 1 brood/season, but will reneest when eggs fail to hatch (see Eggs, below). Laying dates vary among populations (Appendix 2) and among years (Hickman 1968, Camenzind 1969, Beecham and Kochert 1975, USGS unpubl.). Laying begins as early as late Jan and early Feb in sw. Idaho and s. California (Dixon 1937, Hickman 1968) and as late as late Mar–early May in central and n. Alaska (McIntyre 1995, Young et al. 1995; Fig. 3). Latitude and elevation may account for variation in laying dates among populations (Baglien 1975); eggs laid later at more northern latitudes and higher elevations (Appendix 2). Along Front Range of Rocky Mtns. in Wyoming, Colorado, and New Mexico, lays earlier in south and at lower elevations (Boeker and

Table 1. Heights (m) of nests and nesting cliffs used by Golden Eagles in various parts of their range. Data shown as mean \pm SD (*n*).

Location	Cliff height	Nest height	Source
Central Canadian Arctic	22.8 \pm 8.2 (41)	13.0 \pm 5.7 (41)	Poole and Bromley 1988
E. Hudson Bay	71.9 \pm 26.5 (17)	37.2 \pm 19.0 (31)	Morneau et al. 1994
Sw. Idaho	25.5 \pm 14.8 (86)	17.6 \pm 11.8 (86)	USGS unpubl.
N. Utah	21.7 \pm 12.8 (7)	15.1 \pm 9.7 (7)	Peterson 1988
Overall mean	35.5 \pm 24.3 (4)	20.7 \pm 11.1 (4)	

Ray 1971). In w. Arizona, laying dates may be synchronized with rainfall patterns and reproductive periods of prey (Millsap 1981). In sw. Idaho, hatching dates related to both winter severity and jackrabbit abundance; eagles hatched earlier when rabbits were abundant and later after severe winters (Steenhof et al. 1997). Hatching dates range from 10 Mar to 25 Jun in w. North America (Appendix 2). Young usually fledge when 45–84 d old (see Fledgling stage, below); young in nest from early May to late Aug in central and n. Alaska (McIntyre 1995, Young et al. 1995; Fig. 3). Postfledging dependence period varies (see Fledgling stage and Immature stage, below). Nesting chronology in Denali National Park, AK, closely parallels chronology of arctic ground squirrel populations: Eagles arrive at nesting areas before ground squirrels emerge from hibernation, but brood-rearing coincides with peak abundance of ground squirrels; onset of migration coincides with onset of hibernation in ground squirrels and hoary marmots (*Marmota caligata*) in Sep (CLM).

NEST SITE

Selection process. Unknown which sex selects nest site; females may have selected nest sites in San Diego Co., CA (Dixon 1937).

Microhabitat. Usually nests on cliffs; also in trees (Menkens and Anderson 1987), on ground (Menkens and Anderson 1987), clay cliffs (Houston 1985), river banks (Phillips and Beske 1990), and human-made structures, including windmills, observation towers (Camenzind 1969), nesting platforms (Phillips and Beske 1990), abandoned gold dredges (Petersen et al. 1991), and electrical transmission towers (Steenhof et al. 1993, Hunt et al. 1999). Many nests have a wide view of surrounding area (Beecham 1970) or are on prominent escarpments (Bates and Moretti 1994). Proximity to hunting grounds an important factor in nest-site selection (Camenzind 1969). In northern areas, weather conditions at beginning of nesting season are a critical factor in choice of nest-site location (Morneau et al. 1994). Average annual snowfall may limit distribution of nest sites; in sw. Montana, nests usually built below areas receiving >500 cm of snow (Baglien 1975).

Cliff nests are built on several rock substrates including sandstone, shale, granite gneiss, limestone, basalt, and granite (Schmalzried 1976, USGS unpubl., CLM). Usually avoids building nests on loosely cemented materials such as breccias, conglomerates, or agglomerate sluff (Baglien 1975).

Cliff nests most common throughout most of North America; trees nests more common in ne. Wyoming (Menkens and Anderson 1987, Phillips and Beske 1990), central Coast Range in California (Hunt et al. 1999), and coastal Washington (Eaton 1976, Bruce et al. 1982). Nests in a wide variety of trees, including ponderosa pine (*Pinus ponderosa*; Phillips and Beske 1990), several oak species, California laurel (*Umbellularia californica*), eucalyptus (*Eucalyptus* sp.), California sycamore (*Platanus racemosa*; Hunt et al. 1995), Douglas fir (*Pseudotsuga menziesii*; McGahan 1968), Fremont cottonwood (*Populus fremontii*; Bates and Moretti 1994), and white spruce (*Picea glauca*; Ritchie and Curatolo 1982, CLM). In n. Wyoming, prefers large pines rather than cottonwoods (Phillips and Beske 1990). Nesting trees usually the largest or one of the largest trees in a stand (Menkens and Anderson 1987), isolated or on the fringe of small stands of timber (Baglien 1975), and <500 m from large clearcuts or open fields (Bruce et al. 1982). In w. Washington, nests near clearcuts <10 yr old; may benefit from openings in dense timber formed by fire and logging (Thomas 1977, Servheen 1978, Anderson and Bruce 1980). Avoids building nests in dense stands (Phillips and Beske 1990). In Wyoming, nests usually in upper one-third of nest tree (Schmalzried 1976, Menkens and Anderson 1987, Phillips and Beske 1990). Larger trees may improve nest stability and longevity, and placement in upper portion of tree may improve accessibility for adults (Menkens and Anderson 1987).

Heights of nesting substrates range from 0 to 107 m. At 4 study areas, nesting cliffs averaged 35.5 m, height of cliff nests 20.7 m (Table 1). Nest-tree heights ranged from 38 to 72 m in w. Washington, with nests ranging from 20 to 64 m high (*n* = 6; Anderson and Bruce 1980). Occasionally nests on the ground where cliffs and trees are scarce, primarily in Nevada (Seibert et al. 1976), Wyoming (Menkens and Anderson 1987),

and N. Dakota (Ward et al. 1983). Ground nests tend to be on hillsides (Ward et al. 1983).

Tree nests were close to water courses in ne. Wyoming (Menkens and Anderson 1987); nests in n. Wyoming and se. Montana were in large trees in the bottom of isolated drainages (Phillips et al. 1990). Cliff nests 9.1–60.9 m above Noatak River, AK (mean 37 m, $n = 25$; Amaral and Gardner 1986). All nests on Porcupine River, AK, were within 400 m of the river, with 84% within 100 m of the river ($n = 37$; Ritchie and Curatolo 1982). Nests 0.05–1.2 km from water in se. Wyoming (mean 0.3 ± 0.05 SE [$n = 30$]; MacLaren et al. 1988), 1.2–8.1 km from water in w. Washington ($n = 6$; Anderson and Bruce 1980), and 1.6–8.0 km from water in n. Utah (mean 2.1 ± 2.9 SD [$n = 7$]; Peterson 1988). In s. California, trees on slopes provide panoramic views of foraging habitat and may provide wind lift for flight; trees on valley floors rarely used as nest sites (Dixon 1937). Tree nests in w. Washington were on slopes ranging from 30 to 88% ($n = 6$; Anderson and Bruce 1980, Bruce et al. 1982).

NEST

Construction process. See Phenology, above. Usually refurbishes and reuses existing nests; from 1980 to 2000, only 9.5% of breeding pairs nesting on Snake River Canyon cliffs used new nests each year (range 0–18, $n = 841$ nesting attempts). New nests may or may not be used the year constructed (Dixon 1937, MNK); some nests in sw. Idaho not used for up to 6 yr after construction (USGS unpubl.). Nest construction is sometimes rapid, but usually prolonged; nest-building took 4–6 wk in Texas (Palmer 1988). Brings sticks and branches to ≥ 1 nests in autumn and winter; approximately 1 mo before egg-laying, brings softer materials to a selected nest to form a "bowl" within the nest (Watson 1997). Sometimes adds material to alternate nests prior to laying eggs (Bergo 1987, MNK). Nest-building in San Diego Co., CA, usually occurred 10:00–13:00, or after morning hunt completed (Dixon 1937); nest-building in Texas occurred between dawn and 11:00 (Palmer 1988). Both sexes participate nearly equally in nest-building prior to incubation (Bergo 1987, Aoyama et al. 1988), and both sexes add fresh vegetation (greenery) to nest throughout nesting season; female makes most deliveries during brood-rearing (Bergo 1987, Aoyama et al. 1988). In sw. Idaho and se. Oregon, 50% of sites contained fresh nesting material during latter stages of nesting cycle (Hickman 1968). All sites in Denali National Park, AK, during brood-rearing stage ($n = 189$) contained fresh nesting material (CLM).

Structure and composition matter. Wide variety of vegetation for nest-building; usually reflects flora of immediate vicinity (Hickman 1968, CLM). Individual pulls at base of vegetation, breaking it off; uses a technique similar to tearing prey. Carries sticks and

other vegetation to nest in bill or feet, depending on size of item. Often weaves sticks into existing nest structure. Less frequently uses animal bones, shed antlers (Ellis and Bunn 1998), and human-made objects, including wire and parts of fence posts (Schmalzried 1976), as nesting materials. Bowl lined with a wide variety of vegetation types, including shredded yucca (*Yucca* spp.), grasses, dry yucca leaves (Slevin 1929, Dixon 1937), strips of inner bark, dead and green leaves, soft mosses and lichens (Gabrielson and Lincoln 1959), and Douglas fir and pine boughs (Jollie 1943).

Dimensions. In Arizona and w. Washington, smaller than Bald Eagle nests. Arizona nests ($n = 12$; Grubb and Eakle 1987): 175.7 cm long (range 121.9–264.2), 119.8 cm wide (range 83.8–203.2), and 65.0 cm high (range 12.7–200.7). Lined portions of 8 nests 93.6 cm long (range 53.3–185.4), 79.0 cm wide (range 38.4–160.0). Tree nests in w. Washington: 0.9 m deep with 1.2–1.5 m diameters ($n = 6$; Anderson and Bruce 1980). Sticks in 12 Arizona nests: 58.4 cm long (range 7.6–177.8), 1.2 cm diameter (range 0.4–5.3); weighed 64.2 g (range 5–820). Largest nest on record, in Sun River, MT, was 6.1 m tall and 2.59 m wide (Ellis 1986).

Microclimate. Nest-site exposure may be a factor in nest-site selection (Mosher and White 1976); certain exposures may protect nests from prevailing inclement weather (Watson and Dennis 1992, Morneau et al. 1994), minimize intense (direct) sunlight that puts nestlings at risk of overheating (Mosher and White 1976, Watson and Dennis 1992), reduce exposure to cold (Mosher and White 1976, Poole and Bromley 1988), avoid prevailing winds (MacLaren et al. 1988, Poole and Bromley 1988), and minimize exposure to down-drafts (Eaton 1976). Usually nests on south-facing cliffs in northern areas ($>60^\circ\text{N}$). Of 714 nests in Alaska (Mosher and White 1976, Ritchie and Curatolo 1982, CLM), Yukon (Hayes et al. 1980, Yukon Dept. Renew. Resour. 1982), Northwest Territories (Poole and Bromley 1988), and Quebec (Morneau et al. 1994), 54% were on south-facing cliffs, 18% on west-facing cliffs, 14% on north-facing cliffs, and 14% on east-facing cliffs. Pairs farther south less likely to select south-facing sites; of 423 nests in Montana (McGahan 1968, Baglien 1975), Wyoming (Schmalzried 1976), Idaho (Hickman 1968, USGS unpubl.), Oregon (Hickman 1968), and Nevada (Seibert et al. 1976), 37% on south-facing cliffs, 22% on north-facing cliffs, 21% on east-facing cliffs, and 20% on west-facing cliffs. Nest orientations can differ within study areas, with more south-facing nests at higher elevations (Craig and Craig 1984b). In many study areas, all exposures were used (McGahan 1968, Lockhart 1976, Seibert et al. 1976).

May use south-facing sites at northern latitudes simply because they are the only nesting habitat free of snow when territories are first occupied in spring

(Amaral and Gardner 1986). Alternatively, selection for south-facing cliffs may be a strategy to minimize exposure of incubating birds to cold (Mosher and White 1976, Poole and Bromley 1988). Early in breeding season, south-facing sites in central Canadian Arctic benefit from direct radiation and high reflectance radiation, while being in the lee of prevailing northerly winds (Poole and Bromley 1988). Later in nesting season, nestlings in these poorly protected nest sites may be exposed to high temperatures unless the nest is provided with shade (Poole and Bromley 1988). Parents may spend more time brooding or shading to protect young from overheating in unshaded south-facing nests. In temperate areas, appears to select nest sites that avoid direct sunlight to protect nestlings from overheating and to decrease brooding time required of adults (Mosher and White 1976). Of 418 nests in the Snake River Canyon, ID, 12.7% had 5–25% shading, and 54.8% had 25–100% shading (USGS unpubl.). In Boulder Co., CO, no nest was in direct sunlight for >2–4 h/d (Jollie 1943), and 33% of nests in sw. Montana had exposures that provided shade from hot afternoon sun (McGahan 1968).

Sixteen of 30 nests (53.3%) in e. Hudson Bay had overhangs (Morneau et al. 1994). Percentage of nest covered by overhang averaged 38.3% at 41 nests in the central Arctic (Poole and Bromley 1988) and only 3.7% at 7 nests in n. Utah (range 0–20; Peterson 1988). Although overhangs protect nests from sun, rain, snow, and ice formation (Kochert 1972, Poole and Bromley 1988), falling rocks or soil can kill incubating or brooding eagles or nestlings (Phillips et al. 1990). Avoids building nests in areas with major downdrafts; selection of slopes with updrafts may conserve energy and thereby enhance reproductive success (Eaton 1976). Most nests inaccessible to humans and mammalian predators (requiring either a ladder or ropes to be reached by humans): 80.2% in sw. Idaho (USGS unpubl.) and 87.3% in Denali National Park, AK (CLM).

Maintenance or reuse of nests, alternate nests. Often constructs alternate nests. Number of supernumerary nests/territory ranges from 1 to 14, usually 2 or 3 (MNK). In a 2-yr study in Utah, 11 of 21 pairs had >1 nest (Camenzind 1969), and 20 of 36 pairs had alternate nests in a 5-yr study in Montana (McGahan 1968). All 65 pairs nesting on cliffs in the Snake River Canyon used >1 nest/territory during 30 yr (USGS unpubl.). Alternate nests can be separated by <1 m or >5 km (McGahan 1968); number of nests and distances between them may be related to terrain features and proximity of other nesting pairs (Boeker and Ray 1971). Some pairs use same nest every year but repair and add material to alternate nests until eggs are laid (McGahan 1968, Boeker and Ray 1971, USGS unpubl.). Other pairs switch nest sites from year to year; reuse of nests not apparently associated with previous

year's success (Boeker and Ray 1971, USGS unpubl.).

EGGS

Shape. Short-ovate to ovate or rarely elliptical-oval (Bent 1937).

Size. Mean length 74.5 mm (range 67.5–85.7); mean breadth 58.0 mm (range 49.4–64.3, $n = 63$ eggs; Steinbeck 1884, Bent 1937); 20 clutches averaged 74.4 mm ± 3.40 SD \times 57.3 mm ± 1.63 SD (Palmer 1988).

Mass. Averaged 141.4 g (range 113.9–176.6, $n = 30$; Hanna 1930).

Color. Base color varies from white to "cream-buff" or pinkish white. Usually evenly marked small blotches, spots, or fine dots unevenly distributed or concentrated at one end. Some are evenly sprinkled with small dots. Colors of markings are "bay" and various shades of browns. Some eggs have large blotches of drabs overlaid with browns (Bent 1937).

Surface texture. Rough.

Eggshell thickness. Thickness of eggshells collected pre-1947 differed little from those collected during the post-DDT era; mammal-feeding habits (see Food habits: diet, above) resulted in little biomagnification of organochlorine pesticides and minimal eggshell-thinning (Anderson and Hickey 1972, Kochert 1972). Shell thickness of pre-1947 clutches from w. North America averaged 0.583 mm ± 0.003 SD ($n = 290$). Shell thickness of eggs collected during the 1960s and 1970s (Reynolds 1969, Beecham 1970, Anderson and Hickey 1972, Kochert 1972) averaged 0.593 mm for Idaho ($n = 51$), 0.637 mm for Montana ($n = 7$), 0.580 mm for Alaska ($n = 4$), 0.605 mm for California ($n = 9$), and 0.623 mm for Utah ($n = 17$).

Mean empty shell weight, 13.04 g (range 11.02–14.30) based on 1,083 eggs (Reynolds 1968, Anderson and Hickey 1972, Kochert 1972).

Clutch size. Typically 1–3, rarely 4 (DeGroot 1928, Ray 1928, Gordon 1955). A California nest contained 5 eggs, but 1 egg apparently laid prior to the others (DeGroot 1928). Number of eggs averaged 1.99 in 332 clutches from 8 studies in 5 western states (n. California, $n = 21$; n. Colorado $n = 52$, central Utah, $n = 49$; sw. Idaho, $n = 160$; sw. Montana, $n = 50$); 14% contained 1 egg, 76% 2 eggs, and 10% 3 eggs (Slevin 1929, Jollie 1943, Camenzind 1969, Reynolds 1969, Arnell 1971, Olendorff 1973, USGS unpubl.). Clutches with 3 eggs most common in years when prey is abundant (USGS unpubl.). No clinal variation in clutch size. Clutch size not related to laying date in sw. Idaho ($n = 115$; USGS unpubl.). No data on whether age of female affects clutch size.

Egg-laying. In captivity, eggs laid at mostly 3- to 4-d intervals (mean 3.5 d, $n = 35$), with 2 cases of 7 and 10 d between second and third egg (Kish 1970, 1972; Hamerstrom 1971, Grier 1973). Laying intervals in the wild range from 3 to 5 d ($n = 4$; Gordon 1955, Aoyama

et al. 1988). Incubation begins with first egg, leading to asynchronous hatching (Watson 1997). Renesting occurred in only 0.01% of 674 nesting attempts in sw. Idaho (USGS unpubl.), and in 1.0% of 200 attempts in Scotland (Watson 1997); average of 24 d after failure of first clutch (range 19–30, $n = 13$; Dixon 1937, Camenzind 1969, Morrison and Walton 1980, Dennis 1983).

INCUBATION

Onset of broodiness and incubation in relation to laying. No information.

Incubation patch. Present in both sexes; more developed and conspicuous in females (R. Jackman pers. comm.).

Incubation period. Female settles in incubation posture on nest before first egg is laid (Ellis 1979). Estimated average incubation period 42.4 d (range 41–45, $n = 11$ clutches; Abbott 1924, Gordon 1955, Mitchell 1968, Camenzind 1969, Reynolds 1969, Beecham 1970, Aoyama et al. 1988, Watson 1997).

Parental behavior. In sw. Idaho, females did all nocturnal and 82.6% of diurnal incubation ($n = 11$ nesting attempts); males relieved incubating females 2.1 times daily ± 0.1 SE. Male incubation bouts averaged 49.4 min ± 4.7 SE; 17 of 111 male-initiated changeovers (15.3%) involved food transfers to the female on or near the nest (Collopy 1984). Inattentiveness by male may force female off eggs to forage and ultimately abandon nesting effort (Collopy 1984).

Hardiness of eggs against temperature stress; effect of egg neglect. Eggs can tolerate cooling, but the precise amount is unknown. At least 1 egg hatched from a clutch of 2 in sw. Idaho after being exposed to snowy and cold conditions (0° C) for at least 1 to 5 h during late incubation (MNK).

HATCHING

Hatching asynchronous (Watson 1997); hatching interval between first and second eggs 96.5 h ($n = 1$; Aoyama et al. 1988). From Ellis 1979 ($n = 1$): Chick vocalizations (chirping) begin up to 53 h before hatching. First heard calling from egg 15 h 10 min before pipping; individual egg hatching may last >36 h. Eaglet activity increased from 26 h 50 min after pipping until emergence. Female may assist hatching by caving and separating egg. Eaglet surged against shell every few seconds at 35 h after pipping, and egg was broken completely around a belt about a third from the blunt end 35 h 15 min after pipping. Wing emerged at 35 h 19 min, ends of shell separated at 36 h 30 min, and nestling free 37 h 20 min after pipping.

YOUNG BIRDS

Condition at hatching. Average 110.6 g (range 105–115, $n = 7$) within 1 d of hatching in the wild (Sumner 1929a, 1929b; Ellis 1973). Down dries within 2 h of hatching (Watson 1997). At hatching, covered

with short grayish-white “pre-pennae” down (Brown and Amadon 1968). Ear holes open, beak black, egg tooth prominent, feet and legs pale flesh colored, talons white to flesh colored (Sumner 1929a, 1929b; MNK). Capable of limited locomotion; weak and feeble, eyes partially open, unable to detect movement (Sumner 1929a, 1929b). Altricial; must be fed by parent.

Growth and development. Increases in mass follow a general sigmoid growth pattern (Ellis 1979, Collopy 1986). Mass ranges from about 100 g at hatching to about 500 g at 10 d. From then growth is linear, reaching asymptote at 40–45 d. Female nestlings had slower growth rates but significantly higher asymptotic weights (mean 3,803 g; $n = 102$) than males (mean 3,233; $n = 85$; Collopy 1980, 1986). Nestlings attain maximum body mass at approximately 50–60 d after hatching (Collopy 1986).

Growth of alar, caudal, humeral, spinal, ventral, capital, crural, and femoral feather tracts linear with no apparent difference between sexes ($n = 3$ [Ellis 1979]; $n = 23$ [Collopy 1980]). Seventh primary 269 to 316 mm and left center rectrix 191 to 253 mm at 65 d. Alar and caudal tracts continue to grow to full length after fledging (Ellis 1979). Foot-pad growth linear between 6 to 31 d; reaching asymptote between 31 and 35 d ($n = 23$; Kochert 1972). Mean foot-pad size differed significantly between male and female nestlings beginning at 21–25 d. Foot-pad size averaged 148.6 mm for female and 134.9 mm for male nestlings 46–59 d old ($n = 107$; Kochert 1972).

Depends on parents to regulate body temperature (i.e., brooding and shading) for first 20 d after hatching (Watson 1997). Prone to heat stress and death in extreme conditions; responds to heat stress by moving to cool objects or shaded portions of nest, or by panting (Ellis 1979). Droops wings to dissipate heat and spreads wings to absorb radiant energy, dry plumage, or dissipate heat (Ellis 1979). Wing spread first seen around 7 wk of age.

Behavior. See Ellis 1979 for details on preening, scratching, defecation, and casting of pellets. Inter-sibling conflicts occur frequently and occasionally result in siblicide, particularly when food is limited (Edwards and Collopy 1983, Watson 1997). When attacked by sibling, subordinate chick turns away, partially spreads tail, lowers head, and remains still to suppress aggression; aggressive interactions wane between 10 and 13 d, but continue sporadically to late brood-rearing (Ellis 1979). Late-season agonistic behavior related to lack of food (Ellis 1979). Larger, most aggressive chick, typically a female, receives most food (Collopy 1980). Subordinate chick is sometimes starved or forced from nest (Sakaguchi and Chiba 1988). Probability of siblicide depends on sex and order of hatching sequence, with siblicide more than likely to occur when a female hatches before a male in the brood (Edwards and Collopy 1983, Bort-

olotti 1989). In sw. Idaho, aggression occurred in all nests with 2-chick broods observed from blinds, and resulted in 1 death in 3 (43%) of 7 broods (Collopy 1980). Siblicide accounted for 7% of 41 nestling mortalities in sw. Idaho (Beecham and Kochert 1975) and 6 (40%) of 15 nestling losses in central Europe (Kropil and Majda 1996).

From Ellis 1979. Aggressive interactions with parents increase with nestling age. Nonaggressive billing of adults begins around 20 d of age, but is aggressive by day 40 and continues until fledging. As fledging age approaches, regularly engages in rush attacks (running and flapping wings) when parents enter nest; occasionally foot-stabs parents. Mantles prey to protect food from parent and nest mate, beginning about 40 d of age. Occurred in all nests with >1 young ($n = 3$ nests) and is associated with development of self-feeding.

Locomotion. From Ellis 1979 ($n = 4$ chicks) and Collopy 1980 ($n = 12$). Able to distinguish objects at 7 d, but probably incapable of acute visual discrimination at <10 d (Sumner 1929a, Ellis 1979). During first week, spends >95% of the day in lie position; subsequently, proportion of day spent lying decreases. Begins sitting at 1 d old; begins to stand at 17–20 d. No difference between male or female chicks in development of lying, sitting, or standing. Wing-flapping, performed while sitting, first seen about 9–10 d old. Performed while standing, as chicks grow older. Flapping begins to increase during week 5, with frequency increasing linearly until fledging. Males developed flapping at a significantly greater rate than females. See Ellis 1979 and Collopy 1980 for details.

PARENTAL CARE

Brooding. Males in Idaho spent 74% of perched time at locations away from nest. Male almost never broods; female broods and shades young from hatch to about 45 d of age (observed once at 50 d; Ellis 1979, Collopy 1984). Time spent brooding to 19 d related to wind chill (Ellis 1979). Percentage of day brooding/shading decreases linearly from >80% at 1–10 d of age to <5% at 40 d (Collopy 1984). Female broods young nightly until 17–42 d after hatch (mean 29) and roosts on nest until 17–54 d (mean 40; Collopy 1984).

Feeding. From Ellis 1979 and Collopy 1984. Both parents bring prey to nest, but male rarely feeds young directly. Adults may not feed young on hatch day; mean number of adult-fed meals/d increased rapidly during week 1 and decreased significantly during the nesting season ($n = 10$ broods). Biomass fed directly by female increased until fifth week; then decreased with linear increase of self-fed meals by young. Young begin self-feeding at 34–37 d old, and successfully tear carcasses at 45–55 d; by week 8, young consume more by self-feeding than fed by adults; increases in self-feeding coincide with devel-

opment of standing behavior. No direct feeding after fledging.

Meal size increases throughout the nesting season; estimated morsel size fed ranged from 6 mm at hatching to 15 mm at fledging (Ellis 1979; Collopy 1980). Although chicks in multiple-chick broods received more food from adults than 1-chick broods, they had lower consumption rates from self-fed meals during late brood-rearing (Collopy 1984). Adult exhibits no chick bias in apportioning food, but dominant chick usually receives food first by intimidating subordinate chick (Collopy 1980, Edwards and Collopy 1983).

From Collopy 1984. Both sexes hunt throughout brood-rearing period. Over entire nesting season, males delivered significantly more prey/d (1.2 deliveries ± 0.28 SE; 1,030 g/d ± 284.6 SE; $n = 8$) than females (0.6 deliveries ± 0.44 SE; 387 g/d ± 270 SE; $n = 8$). Male provided almost all food during first 2 wk (83% of deliveries and 95% biomass). Female increased prey deliveries in third week of brood-rearing, with maximum contribution in seventh–ninth weeks (43% of biomass); similar delivery rates for sexes during weeks 7–10. Prey size did not differ between male and female, but differed among nests.

Overall prey-delivery rates averaged 1.8 items/d in sw. Idaho (range 1.0–3.1) and 0.9/d in w. Texas during brood-rearing (Lockhart 1976, Collopy 1984). Delivered larger prey in Idaho (1,153 g) than in Texas (947 g). Mean delivery rates in sw. Idaho increased from 1.5/d during first 5 wk of brood-rearing to 2.6/d during sixth–seventh weeks, then decreased to 1.6/d during final 2 wk; delivery rates did not differ between 1- and 2-chick broods (Collopy 1984).

Nest sanitation. Young expel feces several centimeters outside nest cup as early as 1 d, and consistently defecate over nest rim by 30 d (Ellis 1979). Food accumulates at nests, and nests may contain prey in various stages of decomposition (MNK). Adults sometimes remove or consume prey remains uneaten by young (Macpherson 1910, Hunsicker 1972, Hoechlin 1974), but uneaten prey not removed in 1,012 h of observation of 8 broods in Idaho (Collopy 1983a). May remove dead nestlings <3 wk old (Palmar 1954, USGS unpubl.). Brings in green plant material throughout the season to cover debris or perhaps repel ectoparasites (Wimberger 1984, Watson 1997). Ectoparasites can be abundant in nest material (see Demography and populations: disease and parasites, below). Several species of nonparasitic arthropods occur in eagle nests (Hickman 1968). Most have no effect on eagles, but Ellis (1979) reported retarded growth and weight loss of nestlings from a Montana nest where dermestid beetle larvae (*Dermestes* sp.) consumed prey items in the nest.

Carrying of young. Reports of parents carrying fledging-age young are rare and anecdotal ($n = 4$;

Palmer 1988). Not recorded during intensive studies of fledging behavior (Dunstan et al. 1978, Ellis 1979, Collopy 1980, Walker 1987, Bahat 1992, O'Toole et al. 1999).

COOPERATIVE BREEDING

Occasional reports of trios (see Behavior: sexual behavior, above).

BROOD PARASITISM

None reported.

FLEDGLING STAGE

Departure from nest. For several weeks prior to fledging, nestlings flap wings and hop in practice flights; intensity increases as fledging approaches (see Young birds, above). Young leave nest as early as 45 d of age (USGS unpubl.) and as late as 81 d (Gordon 1955). In sw. Idaho, 101 chicks from 61 broods averaged 64.4 d (range 45–77) old at departure from nest (USGS unpubl.). Mean age at first flight was 10.1 wk ($n = 28$) in w. North Dakota (O'Toole et al. 1999). Departure from nest includes falling, jumping, walking, or flying. Departure can be abrupt, with young jumping off and using a series of short, stiff wing-beats to glide downhill or being blown out of nest while wing-flapping; often includes a short flight on unsteady wings followed by an uncontrolled landing (Camenzind 1969, CLM). Many departures before capable of flight are associated with chicks exposed to thermal stress or nest parasite infestations (USGS unpubl.). Occasionally young fledge unsuccessfully and are grounded; in most cases, parents feed and care for grounded young (Hickman 1968, MNK, CLM). No evidence, other than an anecdotal report (Miller 1918), that adults force young out of nests to encourage fledging. Adults may facilitate fledging by decreasing prey deliveries during last few weeks of brood-rearing (Collopy 1984). Self-sustained flight not usually achieved until >64 d of age (Brown and Amadon 1968).

Growth. During post fledging, muscle mass of juveniles develops, and flight feathers reach full growth (Jollie 1947). Because mass and skeletal growth reaches asymptote prior to fledging (Collopy 1980), mass fluctuates depending on food intake, and skeletal growth and development are minimal during post-fledging (M. Collopy pers. comm.).

Association with parents or other young. Associates with parents and siblings for varying times after fledging; migrants may break association sooner than residents. Young stay with parents 1–6 mo after fledging (USGS unpubl.). At 1 nest in United Kingdom, fledglings stayed ≤70 m from nest for 2 wk, and male delivered food at safe perches near nest (Walker 1987). Females rarely provided food to fledged young in sw. Idaho; females made <5% of prey deliveries during postfledging period (M. Collopy pers. comm.).

Siblings moved together after fledging in w. North Dakota, and usually stayed within 300 m of each other up to 121 d postfledging (O'Toole et al. 1999). Before independence, fledglings exhibit nonaggressive social behavior (O'Toole et al. 1999). Fledglings mutually preen or "nibble" when perched together (Ellis 1979), display "play" catching and plucking of prey together (O'Toole et al. 1999), and stoop, talon-touch, and talon grapple (Grant and McGrady 1999). Agonistic interactions between parents and offspring or between siblings rare, except just before or after fledglings gain independence (Walker 1987, 1988; Bahat 1992; Watson 1997; Grant and McGrady 1999; O'Toole et al. 1999).

Ability to get around, feed, and care for self. Flying ability develops slowly, partly a consequence of incomplete flight-feather growth (Walker 1987). In Israel, females developed flying skills, flew longer distances, and moved farther from nest site sooner than males (Bahat 1992). Distance of fledglings from their nest increased significantly with time in w. North Dakota, but sexes did not differ in distance moved (O'Toole et al. 1999). Movements >5 km not observed until >29 d after fledging; movements >10 km not observed until >98 d after fledging in N. Dakota (O'Toole et al. 1999). First hunting attempts 28–68 d after fledging in Alaska, Israel, and England (Walker 1987, Bahat 1992, CLM). Fed at carcasses 35 d after fledging, and bathed 30 d after fledging (Walker 1987). Juveniles seek shade or lie prostrate in the sun with wings open and tail fanned during exceptionally hot weather (Walker 1987).

IMMATURE STAGE

In United Kingdom, independence estimated 75–85 d after fledging, when adults began territory defense displays toward their young (Walker 1988). Dependency on parents probably reduced to ≤2 mo at northern end of range in Alaska (Brooks Range and Seward Peninsula; Kessel 1989). Fledgling dispersal and independence 32–70 d (mean 56 d) after fledging in Denali National Park, AK, and coincided with initiation of migration. Most fledglings left natal areas in Denali within 20 d of one another ($n = 48$), but no evidence that young accompanied parents at onset of autumn migration or that siblings moved together (CLM).

Annual movements of first-year eagles from Denali averaged >5,500 km, with individuals migrating south to w. Canada and w. U.S. in autumn and north to w. Yukon and Alaska in spring (CLM). First-year eagles from Denali remained on wintering areas longer than adults and returned to northern latitudes 5–12 wk after adults (CLM). Most first-year eagles from Alaska showed tenacity to wintering areas; most did not wander once they reached the end of autumn migration (CLM). First-year eagles from Alaska returned to

Alaska and Yukon during their second summer, but did not return to their natal areas (CLM).

Postindependence movements at temperate latitudes involve nonlinear wandering beyond the natal area (O'Toole et al. 1999). First-year eagles banded in Snake River Canyon, ID, dispersed from natal areas in nearly all directions (Steenhof et al. 1984). Most individuals did not move beyond boundaries of adjacent states; 78% of encounters were <100 km, and 1% of encounters were >1,000 km from banding locations (Steenhof et al. 1984). First-year eagles from sw. Idaho did not move significantly farther than older birds; 8 of the 9 most distant (>500 m) encounters were of birds >1 yr old (Steenhof et al. 1984). Subadults in the Altamont Pass area, CA, tend to be sedentary, showing only local or intrarange movements during the year (Hunt et al. 1999).

Radio-telemetry and banding data from Scotland suggest that as subadults reach breeding age, they tend to return to natal areas (Grant and McGrady 1999). May gain territories by killing territory holders (Hunt et al. 1995, Grant and McGrady 1999).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding. Six eagles marked as nestlings in sw. Idaho were 4–7 yr old when first detected on breeding territories (Steenhof et al. 1984). Generally breeds after attaining adult plumage, which is usually acquired in fifth summer, but capable of breeding earlier (see Distinguishing characteristics, above, and Appearance, below). In sw. Idaho, 0–13% of nesting pairs had 1 subadult (≤ 4 yr old) from 1970 to 1981; percentage of pairs with subadults related inversely to adult densities in preceding winter (Steenhof et al. 1983). In Denali National Park, AK, percentage of nesting pairs with subadults averaged 2% per year (range 0–6, $n = 14$ yr); all 7 breeding subadults were females (CLM). In central California, 1 pair had 2 subadults; percentage of pairs with ≥ 1 subadults ranged from 0 to 6% between 1996 and 2000 (G. Hunt pers. comm.). However, 51% of pairs in Norway had ≥ 1 subadult members (Bergo 1984). Territorial adults usually prevent subadults from nesting; most subadults nest in territories with high disturbance and high turnover rates (Steenhof et al. 1983) or where persecution has been high (Bergo 1984).

Clutch. See Breeding: eggs, above. Renests rarely when first clutch is destroyed (Watson 1997). No records of pairs producing >1 brood/yr.

Annual and lifetime reproductive success. Long-term (≥ 10 yr) annual reproductive success (number of young reared to nest-leaving/pair): 0.78 in Montana and Wyoming (Phillips et al. 1990), 0.79 in sw. Idaho (Steenhof et al. 1997), 0.80 in Scotland (Watson 1957),

0.82 in Utah (Bates and Moretti 1994), 1.08 in Oregon (Thompson et al. 1982), and 0.66 in Alaska (McIntyre and Adams 1999). Annual reproductive success varies with prey abundance and weather in sw. Idaho: percentage of females that lay eggs each year related positively to jackrabbit abundance and inversely to winter severity; percentage of laying females successful related positively to rabbit abundance and inversely to frequency of hot spring days, when nestlings are susceptible to heat stress; see Causes of mortality, below (Steenhof et al. 1997). Prey abundance also influences annual reproductive rates in Utah, Alaska, and Europe (Smith and Murphy 1979, Tjernberg 1983, Bates and Moretti 1994, Watson 1997, McIntyre and Adams 1999).

Populations at northern end of range have smaller broods and produce fewer fledglings than those in temperate areas; mean brood size 12% lower in northern populations ($n = 4$ study areas) compared to temperate latitudes ($n = 5$ study areas; 1.38 vs. 1.56 fledglings/successful pair); population productivity 25% lower for northern populations ($n = 2$ study areas) compared to temperate latitudes ($n = 3$ study areas; 0.66 vs. 0.87 fledglings/occupied nesting area; McIntyre and Adams 1999). See Population regulation, below.

From Steenhof et al. 1997 and McIntyre and Adams 1999. Percentage of pairs that lay eggs each year was the most variable reproductive component in both sw. Idaho and interior Alaska, varying from 38 to 100% in Idaho (mean $79\% \pm 15.5$ SD [$n = 22$ yr]) and 33–90% in Alaska (mean $62\% \pm 8.7$ SD [$n = 10$ yr]). Percentage of laying pairs successful ranged from 32 to 80% in sw. Idaho (mean $60\% \pm 13.9$ SD [$n = 23$ yr]) and 42–82% in Alaska (mean 71%, $n = 10$ yr). Mean brood size at fledging ranges from 1 to 2 and averaged 1.56 ± 0.22 SD in sw. Idaho ($n = 23$ yr) and 1.43 in Alaska. Broods of 3 at fledging are relatively uncommon and occur mainly in years of high prey abundance (Jenkins and Joseph 1984, USGS unpubl.).

Percentage of eggs that hatch: 57% in central Utah ($n = 87$ eggs, 44 clutches; Smith and Murphy 1979), 65% in sw. Idaho ($n = 282$ eggs, 145 clutches; USGS unpubl.), and 86% in s.-central Montana ($n = 28$ eggs, 14 clutches; Reynolds 1969). Percentage of nestlings that survive to leave nest: 77% in sw. Idaho ($n = 302$ young, 168 broods; USGS unpubl.), 80% in central Utah ($n = 50$ young, 35 broods; Smith and Murphy 1979), and 46% in s.-central Montana ($n = 24$ young; Reynolds 1969).

Few data on lifetime reproductive success. A marked male began occupying a nesting territory in Snake River Canyon, ID, at age 4; continued to occupy it for 14 consecutive years, was successful in 10 yr, and produced a total of 15 young (USGS unpubl.).

LIFE SPAN AND SURVIVORSHIP

Varies with age and geographic area. Postfledging mortality in Denali National Park, AK, estimated at 2%, and first-year survival after independence estimated at 18–46%, based on satellite telemetry ($n = 48$; CLM). Near a wind turbine facility in w.-central California, estimated survival rates, based on conventional telemetry of 257 individuals, were $84\% \pm 4$ SE for first-year eagles, $79\% \pm 2$ SE for 1- to 3-yr-olds and adult floaters, and $91\% \pm 2$ SE for breeders; no difference in survival rates between sexes (Hunt 2001). Regression analysis of banding data suggested 50% of eagles in the Rocky Mtns. lived 3 yr, 25% lived 6 yr, 5% lived 13 yr, and 1% lived 20 yr (Harmata 2002).

Longevity record in North America, determined via banding encounters: 23 yr 10 mo (Klimkiewicz 1997). In Europe, life span 46 yr in captivity (Gordon 1955) and 32 yr in the wild (Staav 1990). Average life expectancy of adults in wild estimated at 39.5 yr in w. Scotland and 12 yr in Germany (Watson 1997).

DISEASE AND BODY PARASITES

Diseases. Bacterial infections include avian cholera (*Pasteurella multocida*; Rosen et al. 1973), tuberculosis (*Mycobacterium avium*; Waterston 1959, Wilson and MacDonald 1965), and erysipelas (*Erysipelothrix insidiosa*; Bigland 1957). Cholera affects eagles that ingest waterfowl that have died from the same infection (Rosen et al. 1973). Although bacterial infections cause individual mortalities, their significance at the population level is unknown. At least 1 viral disease, avian pox (*Avipoxvirus*; Moffatt 1972), and 1 fungal disease, aspergillosis (*Aspergillus*), affect Golden Eagles. Pox is apparently rare, but 13% of 30 Golden Eagles presented for treatment at the University of Minnesota had symptoms of aspergillosis (Redig 1981). Most eagles with aspergillosis have some other debilitating injury or illness (P. Redig pers. comm.).

Infectious protozoans include hematozoa (*Leucocytozoon*; Stabler and Holt 1965), intestinal coccidia (*Isospora buteonis*; Mathey 1966), and flagellates (*Trichomonas gallinae*). Cysts from benign protozoan (*Sarcocystis* spp.) occur frequently on necropsy specimens (P. Redig pers. comm.). Trichomonads cause the most well-known and widespread protozoan infections. Eagles become infected with *Trichomonas* after feeding on pigeons and doves. Symptoms of trichomoniasis, or "frounce," include yellow, caseous lesions in the oral cavity (Stabler 1941) that can block the esophagus and cause starvation. Four of 10 dead fledglings examined in Idaho died from trichomoniasis (Beecham and Kochert 1975); deaths from frounce affected at least 4% of 107 young that fledged from sw. Idaho in 1970 and 1971 (Kochert 1972).

Capillariasis, a disease caused by nematode worms, has been documented only in Scottish Golden Eagles (Watson 1997), but strongeid trematodes and nema-

todes were found in a dead eagle from Washington (Mathey 1966).

Body parasites. Ectoparasitic arthropods that occur in nests include 2 species of ticks (*Ornithodoros concanensis* and *Haemaphysalis leporispalustris*; Hickman 1968, Knight and Marr 1983), 3 species of cimicids (Mexican chicken bugs [*Haematosiphon inodorus*]; Lee 1954, McFadzen et al. 1996; human bed bugs [*Cimex lectularius*]; and cliff swallow bugs [*Oeciacus vicarius*]; Hickman 1968), and a biting midge (*Leptoconops hertszii*; Hickman 1968). As many as 48 ticks were on a single eaglet, primarily around eyes and ears (Hickman 1968). Neither ticks nor cimicids seem to cause significant problems for eagles, but chicks in nests heavily infested by *H. inodorus* sometimes fledge prematurely (MNK). Ears and nostrils of nestlings sometimes infested by bird blowfly, *Protocalliphora* (Diptera: Calliphoridae), larvae that live in nest material and periodically suck blood of nestlings (Hill and Work 1947, Hill 1948); infestations appear as black crusts in and around ear openings and usually subside before eagles fledge, as larvae pupate; eagle mortality rarely results (Kochert 1972).

Feather lice (Phthiraptera) infect adults, primarily on head and neck (Pfaffenberger and Rosero 1984). Parasitic trombidiform mite larvae (*Harpyrhynchus*) also can cause progressive feather loss on head and neck (Schulz 1990).

CAUSES OF MORTALITY

Most recorded deaths result from human-related causes (Franson et al. 1995; see Conservation and management, below). Starvation was the most common cause of death among instrumented juvenile Golden Eagles from Denali National Park after postfledging period (CLM). Some eagles killed by intraspecific aggression in California and Scotland (Grant and McGrady 1999, Hunt et al. 1999). Some deaths result from injuries sustained when attacking porcupines (*Erethizon dorsatum*; Bortolotti 1984b).

Exposure. Susceptible to thermal stress during first 6 wk after hatching (Mosher and White 1976; see Breeding: nest site, above). Heat stress a significant mortality factor for nestlings in Idaho (Beecham and Kochert 1975). Nesting success and brood size at fledging inversely related to number of days with temperatures $>32^{\circ}\text{C}$ during brood-rearing (Steenhof et al. 1997).

RANGE

Initial dispersal from natal site. Few data. See Breeding: immature stage, above. Known distances between hatching site and breeding area in the Snake River Canyon, ID, ranged from 6.7 to 64.7 km (1–12 territory widths) and averaged $39.6 \text{ km} \pm 24.1 \text{ SD}$ ($n = 4$; Steenhof et al. 1984, USGS unpubl.). Males may be more likely to breed near their natal areas than females

are; 5 of 6 eagles marked as nestlings in Snake River Canyon and later encountered there as breeders were males (Steenhof et al. 1984, USGS unpubl.).

Fidelity to breeding site and winter home range. Generally faithful to breeding site; one individual remained on same nesting territory for ≥ 12 yr in Idaho (Snake River Canyon; USGS unpubl.).

Both residents and migratory individuals show fidelity to wintering areas. Ten eagles wintering in central Idaho were recaptured within 1.6 km of sites where they were first captured 1–5 winters earlier (T. and E. Craig unpubl.). Three of 4 immatures from Denali National Park wintered in the same areas in Alberta, Washington, and Montana in 2 consecutive winters (CLM), and adult migrants from Montana ($n = 1$ male) and Alaska ($n = 1$ female) returned to their respective wintering sites in Idaho for ≥ 2 consecutive years (T. and E. Craig unpubl., L. Schueck and J. McKinley unpubl.).

Dispersal from breeding site. Few data. A radioed female used nesting territories 15 km apart in consecutive years in Snake River Canyon (USGS unpubl.). Three individual radio-tagged breeders (1 female, 2 males) switched territories in California; settled in different territories within 8 km of their old ones 10 d–3 mo after leaving their original territories; construction of a new reservoir may have precipitated the female's move (G. Hunt pers. comm.).

Home range. In w. U.S., forages over home ranges that average 20–33 km² during breeding season. Year-round home range size, based on radio telemetry, averaged 20.4 km² \pm 7.1 SD (range 21.7–27.9) for 8 nesting pairs in ne. Wyoming and 32.5 km² \pm 20.0 SD (range 15.1–61.3) for 4 pairs in se. Wyoming (Phillips and Beske 1982, Platt 1984); breeding-season range size varied from 26.1 to 54.0 km² for 5 pairs in n. Wyoming (Tyus and Lockhart 1979). Nesting-season range size averaged 23.1 km² \pm 2.2 SE (range 16.9–30.2) in n.-central Utah, based on observations of 6 unmarked pairs (Smith and Murphy 1973).

Most comprehensive information on home range comes from Snake River Birds of Prey National Conservation Area in sw. Idaho. Breeding-season home range averaged 25.5 km² \pm 22.0 SD (range 1.9–83.3) for 17 pairs in 13 territories during 3 studies conducted between 1975 and 1994. Range size for each study averaged 28.6 km² \pm 20.5 SD (range 4.9–48.7, $n = 4$ radioed pairs; Dunstan et al. 1978), 32.8 km² \pm 17.7 SD (range 11.8–49.0, $n = 1$ radioed pair, 3 unmarked pairs; Collopy and Edwards 1989), and 20.8 km² \pm 25.3 SD (range 1.9–83.3, $n = 9$ radioed pairs; Marzluff et al. 1997). Home-range boundaries at 4 territories remained fairly consistent over >20 yr; ranges in 1970s and 1990s were similar in size and configuration (Marzluff et al. 1997). Some pairs, however, expanded their ranges into neighboring vacant territories; the home range of a pair radio-tagged in

sw. Idaho (Marzluff et al. 1997) included 90% of the former home range of its neighboring territory, determined by radio telemetry before the territory became vacant (Dunstan et al. 1978, Collopy and Edwards 1989).

Resident pairs maintain home range year-round with shifts in intensity of use from breeding season to winter (Dunstan et al. 1978, Marzluff et al. 1997). Although some pairs used smaller ranges in winter (mainly within nesting season home range), others used much larger winter ranges. A pair in se. Wyoming used a 13.6-km² area in winter compared to 24.0 km² in nesting season (Platt 1984), and 3 pairs in sw. Idaho used a mean winter range of 8.9 km² \pm 7.4 SD (range 3.3–17.3) compared to 32.0 km² for nesting (Dunstan et al. 1978). Range sizes of 8 resident pairs in sw. Idaho varied during nonbreeding season but were about 10 times larger than breeding-season range (mean 304.8 km² \pm 599.1 SD [range 13.8–1,760.0]; Marzluff et al. 1997). These larger ranges resulted from periodic excursions outside core areas; 95% harmonic-mean ranges that excluded these excursions were similar in size to other reported home ranges (Marzluff et al. 1997). These excursions represent searches for breeding and foraging opportunities. A female in sw. Idaho included a territory 15 km from her nest (a move of 3 territories) in her excursions 1 winter; she settled and bred in the new territory the next spring (Marzluff et al. 1997, USGS unpubl.).

Individuals do not use all areas within their home range but instead concentrate activity within core areas (Platt 1984, Marzluff et al. 1997). Core areas contained 95% of locations of radio-tagged eagles but only 14.4% \pm 3.1 SE of the breeding-season home range and 25.3% \pm 5.8 SE of the nonbreeding-season range in sw. Idaho ($n = 9$; Marzluff et al. 1997). Ranges of neighboring pairs in sw. Idaho overlapped only slightly in the breeding season (mean 3.7% \pm 1.7 SD; $n = 10$) but overlapped more during nonbreeding season (mean 22.1% \pm 9.4 SE; Marzluff et al. 1997). Distance traveled from nest did not differ among years or between sexes, but mean distance traveled during breeding season (1,047 m \pm 367 SE) was significantly less than during nonbreeding season (3,036 m \pm 241 SE; Marzluff et al. 1997). Breeding-season range size was similar for males and females of a pair (Dunstan et al. 1978) and tended to increase with total number of young fledged (Marzluff et al. 1997).

Wintering migrants sometimes occupy large areas and may wander nomadically. Juvenile males ($n = 3$) from central Alaska tracked via satellite telemetry occupied wintering areas in w. U.S. that ranged from 1,700 to 262,000 km²; 5 juvenile females used 2,200–59,000 km² (CLM). Average 90% core use areas based on a combination of locations from conventional radio and satellite telemetry of migrants differed signifi-

cantly between adults and immatures during 2 winters in sw. Idaho: $43.6 \text{ km}^2 \pm 31.0 \text{ SD}$ for 6 adults and $248.1 \text{ km}^2 \pm 96.6 \text{ SD}$ for 3 immatures (L. Schueck et al. unpubl.). These ranges did not include long excursion flights made by tagged individuals. Size of area used by males and females did not differ. Winter home ranges of adults overlapped considerably (mean $36.3\% \pm 15.7 \text{ SE}$ in 1993 and $58.3\% \pm 12.8 \text{ SE}$ in 1994). One adult female used same home range (100% overlap) in 2 successive winters.

POPULATION STATUS

Density. Amount of area/nesting pair varies from 29 to $251 \text{ km}^2/\text{pair}$ in w. U.S. habitats. Densities are highest in Denali National Park, AK: $28 \text{ km}^2/\text{pair}$ (McIntyre and Adams 1999); total area/pair ranges from 34 to $89 \text{ km}^2/\text{pair}$ (mean 60) in Wyoming (Phillips et al. 1984), 100–119 km^2/pair in Utah (Camenzind 1969, Edwards 1969), $66 \text{ km}^2/\text{pair}$ in sw. Idaho (Kochert 1972), 65–192 km^2/pair in Montana (Reynolds 1969), and 252 km^2/pair in Nevada (Page and Seibert 1973). Densities in Hudson Bay much lower than in w. U.S.: $961 \text{ km}^2/\text{pair}$ (Morneau et al. 1994).

Year-round densities vary by state. Government biologists reported the following number of eagles encountered/1,000 km driven from 1970 to 1972: Wyoming, 10.4; Utah, 5.0; Colorado, 3.3; New Mexico, 1.6; Arizona, 1.2; Texas, 0.3; Oklahoma, <0.1 (Boeker 1974). Note: Watson (1997) converted these data incorrectly and misreported them as aerial-survey results.

Winter densities along aerial transects were greater in parts of New Mexico ($0.2\text{--}3.5/100 \text{ km}^2$) than in the Trans-Pecos region of Texas ($0.16\text{--}1.4/100 \text{ km}^2$), 1963–1968 (Boeker and Bolen 1972). New Mexico counts were more variable during winter, reflecting arrival and departure of migrants. Mean densities along aerial transects in 6 western states averaged 5.5/100 km^2 from 1973 to 1979 (yearly range 4.8–7.3/100 km^2). Wyoming and nw. Colorado had greatest densities (up to 18/100 km^2), followed by Utah, Montana, Idaho, and New Mexico (USFWS 1981). Winter densities in s. Idaho correlate strongly with black-tailed jackrabbit abundance (Kochert 1980, Craig et al. 1984).

Numbers. Up to 100,000 individuals in North America during the 1970s (Braun et al. 1975). Between 2,000 and 10,000 breeding pairs in Canada (Kirk and Hyslop 1998). Few data on abundance in U.S. since mid-1980s. Olendorff et al. (1981) estimated 63,242 wintering individuals in 16 w. U.S. states. Estimated number of breeding pairs: 3,381 in Wyoming (Phillips et al. 1984), 1,200 in Nevada (Herron et al. 1985), and 500 in California (Thelander 1974). Number of known territories, 1977–1986: Wyoming, 804; Oregon, 506; Colorado, 500; Nevada, 430; Washington, 190; Idaho, 156; and Montana, 50 (Harlow and Bloom 1989).

Trends. Long-term surveys show declines in nesting populations in w. U.S. but not Alaska or Canada (Kochert and Steenhof 2002). Number of occupied nesting territories declined significantly from 35 to 29 (average annual change: -0.71%) in Snake River Canyon between 1971 and 1994 (Steenhof et al. 1997); declines associated with loss of shrubs and jackrabbit habitat due to widespread fires (Kochert et al. 1999). Nesting populations in San Diego Co., CA, decreased from an estimated 85 pairs in 1900 to 40 occupied territories in 1999 due to extensive residential development (D. Bittner and J. Oakley unpubl.). Number of nesting pairs in a Colorado study area declined from 10 in 1972 to 7 in 1990 (Leslie 1992). Number of nesting pairs in ne. U.S. declined from 8 pairs in 1951 (Todd 1989) to 2 pairs in 1999 (C. Todd pers. comm.). Nesting populations and productivity in Canada likely stable (Kirk and Hyslop 1998).

Breeding Bird Surveys (BBS) and Christmas Bird Counts (CBC) have limited value for detecting trends because of few routes in Golden Eagle habitat and low number of individuals counted. BBS data show no trend for nesting Golden Eagles either on a regional or continental scale (Sauer et al. 2001); CBC data suggest Golden Eagles increased significantly at 2.8%/yr throughout U.S. and Canada from 1955 to 1999 (J. Sauer and W. Link unpubl.).

Migration counts in e. U.S. and e. Canada suggest a decline in Golden Eagle passage rates from 1930s to early 1970s, with stable or increasing trends since early 1970s (Bednarz et al. 1990, Titus and Fuller 1990, Hussell and Brown 1992, Hawk Mountain Sanctuary unpubl., L. Goodrich pers. comm.). No significant trends at migration sites in w. North America since mid-1980s, but increases in adult detection rates and a decrease in migratory immatures may indicate lowered reproduction in parts of w. U.S. in response to habitat changes (J. Smith pers. comm.).

POPULATION REGULATION

Availability of food and nesting sites ultimately determines nesting density (Hunt et al. 1995). Territorial behavior apparently limits number of nesting pairs in stable environments (Brown and Watson 1964, Watson and Langslow 1989). Most populations include nonterritorial adults known as "floaters," individuals that cannot nest because all suitable territories are occupied; floaters fill vacancies as they occur and thereby contribute to population stability (Hunt et al. 1995). Number of territorial pairs in sw. Idaho and interior Alaska did not fluctuate with annual changes in prey abundance and weather (Steenhof et al. 1997, McIntyre and Adams 1999), but long-term habitat change may affect number of pairs that an area can support. Some pairs abandoned territories after wildfires destroyed jackrabbit habitat adjacent to Snake River Canyon; remaining pairs

expanded their ranges and subsumed neighboring vacant territories, resulting in a smaller nesting population (Kochert et al. 1999).

Reproductive rates fluctuate with prey densities and weather conditions (Smith and Murphy 1979, Tjernberg 1983, Bates and Moretti 1994, Steenhof et al. 1997, McIntyre and Adams 1999). Jackrabbit abundance limited reproduction in sw. Idaho during 15 of 23 yr, and weather influenced how severely reproduction declined in those years. Annual reproductive output is influenced most strongly by proportion of pairs that lay eggs (Steenhof et al. 1997). Many pairs do not lay eggs during periods of low prey abundance (Smith and Murphy 1979, Steenhof et al. 1997, McIntyre and Adams 1999). Laying rates related to conditions prior to nesting season. Females lay eggs if they are able to gain body mass and mobilize reserves for egg production; insufficient food supplies and/or increased energy needs due to cold weather will prevent egg-laying (Tjernberg 1983). Well-fed eagles can withstand cold better than food-stressed individuals (Stalmaster and Gessaman 1984). Percentage of pairs laying eggs in sw. Idaho was related positively to black-tailed jackrabbit abundance and inversely to winter severity (Steenhof et al. 1997). Migratory populations that nest in northern parts of range produce smaller broods and fewer fledglings than resident eagles in temperate regions, possibly due to energetic costs of migration and a combination of severe climate and low prey diversity on breeding grounds (McIntyre and Adams 1999). Spring weather may affect survival of nestlings in more southern areas: young are susceptible to thermal stress during first 6 wk after hatching (Mosher and White 1976). Nesting success and brood size at fledging were related positively to jackrabbit abundance and inversely to frequency of hot spring days in sw. Idaho; inadequate food interacted with high temperatures to cause nestling mortality in years with low rabbit populations (Steenhof et al. 1997). Frequent interactions between floaters and territory holders in areas of the Swiss Alps with high floater densities apparently reduce reproductive success of territorial pairs (Haller 1996), but no evidence for this in North America.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Humans cause >70% of recorded deaths, directly or indirectly (Franson et al. 1995). Accidental trauma (collisions with vehicles, power lines, or other structures) is the leading cause of death (27%), followed by electrocution (25%), gunshot (15%), and poisoning (6%; Franson et al. 1995).

Shooting and trapping. Traditionally shot in parts of North America where depredation of domestic

sheep was suspected. Unregulated aerial hunting of eagles began in California as early as 1936, with >200 killed that winter. From 1941 to 1961, 20,000 may have been shot from airplanes in southwestern states (Spofford 1964). Hunting clubs in w. Texas shot nearly 5,000 from 1941 to 1947; shooting may have reduced number of breeding pairs in parts of Texas and New Mexico (Phillips 1986). In 1971, >500 killed in Colorado and Wyoming by helicopter gunmen hired by sheep ranchers (Beans 1996). Illegal shooting continues to occur; no information on recent trends or levels.

Incidentally trapped and poisoned throughout w. North America by attempts to bait and kill mammalian carnivores (Bortolotti 1984b). At least 10 died in 1971 from eating thallium sulfate-laced antelope set out by sheep ranchers in Wyoming; despite public outcries, poisoning by sheep ranchers continued into 1980s (Beans 1996). Attracted to exposed bait associated with snares, leg-hold traps, and strychnine sets designed to catch or kill wolves (*Canis lupus*), foxes, bobcats, and coyotes. Most trapping/poisoning deaths have occurred in winter; females more susceptible to incidental trapping/poisoning than males, possibly due to spatial/geographic segregation of sexes in winter (Bortolotti 1984b).

Native Americans have harvested young Golden Eagles for religious purposes in southwestern states for many years (Fewkes 1900, Hough 1971); harvest was widespread historically (Palmer 1988). Members of the Hopi tribe remove nestlings from nests in Apr, raise them in captivity, and sacrifice them when they are fully feathered in Jul. Since 1986, the U.S. Fish and Wildlife Service has issued a permit to the Hopi to legally conduct these activities. Reported take has varied from 3 to 28 each year (J. Bart pers. comm.).

Pesticides and other contaminants/toxins. Less susceptible than most raptors to organochlorine pesticides because of mammal-feeding habits. Eggs collected after 1946 had shell thicknesses similar to (<10% difference) those collected in earlier years (Anderson and Hickey 1972). From 1964 to 1975, when many organochlorine pesticides were still legal, DDE and dieldrin levels in eggs and tissues from Golden Eagles in w. North America were below thresholds known to cause reproductive problems (see Reynolds 1969, Kochert 1972, Reidinger and Crabtree 1974, Noble et al. 1993 for exact levels). From 1990 to 1993, 48% of migrant eagles in w.-central Montana had detectable levels of DDE in their blood, but maximum concentration was <0.021 ppm wet weight (Harmata and Restani 1995). No dieldrin detected.

Secondary poisoning occurs when individuals consume prey killed or sickened by chemicals used to protect crops or kill rodents. Golden Eagles susceptible to phorate (Mineau et al. 1999), carbofuran (Mineau 1993), strychnine (Littrell 1990), and anticoagulant rodenticides (Stone et al. 1999). From 1977 to 1980, 3

dead in Oregon had lethal (>8 ppm) levels of heptachlor epoxide; poisoned eagles apparently ate prey that had eaten heptachlor-treated seed (Henny et al. 1984). From 1990 to 1993, heptachlor epoxide levels in plasma of vernal migrants in w.-central Montana were <0.039 ppm wet weight (Harmata and Restani 1995).

Mercury contamination occurs infrequently and at low levels. Mercury detected at low levels (<1 ppm) in only 22% of 77 migrants sampled in Montana, 1985–1992 (Harmata and Restani 1995), and no wintering eagles sampled in Idaho from 1990 to 1995 had elevated mercury levels (Craig and Craig 1998). Eggs collected in Canada from 1968 to 1975 contained mercury at levels too low (<0.35 mg/kg) to affect reproduction ($n = 22$; Noble et al. 1993). Mercury residues in eggs and tissue from Idaho were below lethal levels (<1 ppm), but some nestlings from agricultural areas had elevated mercury residues in feathers, apparently because they ate Ring-necked Pheasants that had eaten seed treated with methyl mercury (Kochert 1972).

Ingestion of lead. Elevated blood-lead levels (>0.20 ppm) occurred in 36% of 162 eagles from s. California, 1985–1986 (Pattee et al. 1990), 46% of 281 wintering eagles from Idaho, 1990–1997 (Craig and Craig 1998), and 56% of 86 spring migrants in Montana, 1985–1993 (Harmata and Restani 1995). Sources of lead have not been definitively documented; likely ammunition in hunter-killed upland game birds and mammals (Wayland and Bollinger 1999), particularly deer (Pattee et al. 1990) and ground squirrels (Harmata and Restani 1995), with waterfowl as a secondary source. Blood-lead levels vary with season (Pattee et al. 1990). Eagles that consume prey items contaminated with lead may experience only temporary elevations in blood lead (Harmata and Restani 1995). However, blood-lead levels of recaptured wintering individuals in Idaho did not decrease over 1–5 yr, suggesting repeated or continual exposure to lead in the environment (Craig and Craig 1998). Chronic subclinical lead exposure may weaken eagles and predispose them to injury, predation, starvation, disease, or reproductive failure (Kramer and Redig 1997, Craig and Craig 1998). Mortality from ingested shot and bullet fragments occurs occasionally (P. Redig pers. comm.). Four of 31 dead eagles from Canadian Prairie Provinces (13%) had been lead poisoned from 1990 to 1996 and 3 (10%) were sublethally exposed to lead (Wayland and Bollinger 1999). In Idaho, 7 of 16 eagles necropsied between 1977 and 1986 were lead-poisoned (Craig et al. 1990).

Collisions/electrocutions. Killed by collisions with cars, fences, wires, and wind turbines. Nearly 1,000 killed on highways near Rock Springs, WY, in winter 1984–1985 (Phillips 1986). At least 28–43 killed annually by turbine blade strikes in the Altamont Pass

Wind Resource Area, CA. Of 61 mortalities in the Diablo Range, CA, 1994–1997, 37% were turbine strikes, 5% car strikes, 3% fence collisions, and 16% electrocutions (Hunt et al. 1999).

Vulnerable to electrocution when landing on power poles. Less-adept immatures are most susceptible. Risk increases when inclement weather hampers flight or when wet feathers increase conductivity (Avian Power Line Interaction Committee 1996). Most mortalities occur during winter in western states where natural perches are lacking; poles with cross arms diagonal or parallel to prevailing winds are most lethal (Benson 1981, Harness and Wilson 2001). From 1986 to 1996, ≥ 272 electrocution deaths occurred in w. North America; 3-phase and single-phase transformers caused most electrocutions (Harness and Wilson 2001). See Management, below, for information on efforts to reduce electrocutions.

Degradation of habitat. Fires since 1980 have caused large-scale losses of shrubs and jackrabbit habitat in areas used by eagles throughout the Intermountain West. Wildfires that burned $>40,000$ ha of shrublands between 1981 and 1987 in the Snake River Birds of Prey National Conservation Area affected nesting populations adversely. Nesting success at burned territories in Snake River Canyon declined after major fires. Abandoned burned territories have been subsumed by neighboring pairs, resulting in a decreased number of nesting pairs (Kochert et al. 1999).

Mining and various types of energy development occur in eagle nesting and wintering habitat. Surface coal mines threaten limited nesting sites in Wyoming (Phillips and Beske 1984). Mine high walls provide new nesting habitat, but reclamation laws require that high walls be eliminated (Fala et al. 1985). Nests with broods have been relocated up to 1.4 km in Wyoming to move young from proposed mining areas or existing mine high walls scheduled for elimination (Postovit et al. 1982, Fala et al. 1985). Pairs at relocated nests have been successful for >20 yr (H. Postovit pers. comm.).

Urbanization and human-population growth have made areas historically used by eagles unsuitable, particularly in s. California (Scott 1985) and the Colorado Front Range (Boeker 1974). Extensive agricultural development reduces jackrabbit populations and makes areas less suitable for nesting and wintering eagles (Beecham and Kochert 1975, U.S. Dept. of the Interior 1979, Craig et al. 1986).

Disturbance at nest and roost sites. Recreation and other human activity near nests can cause breeding failures, but most evidence is anecdotal or correlative. Nesting success in Scotland was related inversely to human disturbance around nests (Watson 1997). Adults spent less time at nests and fed young less food less frequently when observers camped 400

versus 800 m from nests in Alaska (Steidl et al. 1993). Abandoned territories in San Diego Co., CA, had more dwellings within 1.6 km and higher human populations within 4.8 km than territories that continued to be occupied (Scott 1985). Not particularly sensitive to sonic booms or low-level jets in Arizona ($n = 1$ nesting pair; Ellis et al. 1991).

Direct human/research impacts. Climbers sometimes kill eggs/young when they: (1) spend too much time at nest and cause parents to abandon eggs or young; (2) keep parents off nest long enough to subject eggs or young to overheating or cooling; (3) flush an adult, who kicks an egg or young out of nest; (4) cause a nest to collapse; or (5) cause young to fledge prematurely. These cases are rare and can be avoided with proper precautions (USGS unpubl.). Nestlings in Montana experienced loss of mass when parents temporarily abandoned nests following a prolonged visit to nest by researchers, but all nestlings later fledged at or above normal weights (Ellis 1973). Pairs whose young were banded in 3 Rocky Mtn. states ($n = 23$) were more likely to move to alternate nests or not breed the following year than pairs whose young were not banded ($n = 53$; Harmata 2002).

Fixed-wing aircraft surveys of nests in Rocky Mtns. caused no desertions or mortalities; attempts to drive eagles from nests during low passes were unsuccessful (Boeker 1970). Close approaches with fixed-wing aircraft and helicopters never caused adults or nestlings to flush from Montana cliff nests (DuBois 1984). During 906 helicopter passes by nests with incubating adults in sw. Idaho and interior Alaska ($n = 20$ yr), only 11 adults flushed from nests. Adults perched off nests were more likely to flush: 121 of 227 adults observed perched near sw. Idaho nests flushed during helicopter checks throughout nesting season. No young fell or flushed prematurely from nests during 778 helicopter checks of nests with young in sw. Idaho and Denali National Park, AK (USGS unpubl., CLM).

Wing markers had no adverse effects on individuals marked as nestlings in sw. Idaho (Kochert et al. 1983), and adults wearing colored wing markers in Wyoming ($n = 6$) exhibited normal reproductive behavior and above-average reproductive success (Phillips et al. 1991a). In sw. Idaho, 9 nesting pairs with adults wearing backpack radio transmitters had similar productivity and success rates as control pairs ($n = 3$ yr; Marzluff et al. 1997).

MANAGEMENT

Adults, young, eggs, and nests protected since 1962 in U.S. by Bald and Golden Eagle Protection Act. Amendments passed in 1978 authorize and regulate "taking" of unoccupied nests on resource development sites. Federal regulations outlawed use of aircraft to kill eagles in U.S. in fall 1962. Protected in Canada,

Mexico, and U.S. by Migratory Bird Treaty Act. Used for falconry by a few individuals; rigorous standards limit the number taken from the wild (USFWS 1987). U.S. Fish and Wildlife Service authorizes permits to allow Native Americans to take and possess eagles and their parts for religious purposes (see Effects of human activity, above).

Biologists, engineers, and government officials have cooperated in developing and publicizing power-pole designs that reduce raptor electrocutions. Since early 1970s, utility companies have modified poles to prevent eagle electrocutions; some new power lines in nonurban areas have been built to raptor-safe construction standards (Avian Power Line Interaction Committee 1996).

Hacking techniques used to establish or re-establish populations in parts of the range. Hacking involves placing 6- to 8-wk-old nestlings in artificial cages. Humans care for young until they are 12 wk old, when the cage is open and birds are allowed to leave and begin feeding themselves; fledglings continue to be fed at hack sites for 4–6 wk until young achieve independence. Efforts to establish breeding populations in the s. Appalachians began in 1981 at the Pisgah National Forest, NC (Hammer and Reed 1983). Eagles subsequently reintroduced to Kansas (May and Weigel 1989), Tennessee (B. Anderson pers. comm.), and Georgia (Touchstone 1997), using both captive bred birds and young from nests in Wyoming and Colorado. At least 1 individual hacked in Georgia later successfully fledged 7 young between 1991 and 2000, 5.4 km from the hacking site (T. Touchstone pers. comm.), and another successfully fledged 4 young between 1993 and 1996 in Tennessee >200 km from the hacking site (B. Anderson pers. comm.).

Occasionally responsible for losses of young domestic sheep in several western states during lambing season (Phillips et al. 1991b), particularly in cool, wet springs when rabbit populations are low (Matchett and O'Gara 1987). Federal agents assist livestock operators by trapping and relocating eagles suspected of killing livestock. In 1975, 145 eagles were trapped and relocated (USFWS 1982). Most residents returned to their original territories after relocation (Phillips et al. 1991b). Relocation of migratory eagles as far as 322 km was successful in reducing depredation on a short-term basis (Waite and Phillips 1994), but translocations are expensive and may only transplant the problem (Matchett and O'Gara 1987). Scarecrows, combined with harassment, may be another way to protect lambs from eagles (Matchett and O'Gara 1987).

Management of healthy eagle populations requires maintaining prey habitat in foraging areas. In shrub-steppe habitats, this involves sustaining native shrub communities, which are prime habitat for black-tailed jackrabbits (Marzluff et al. 1997, Kochert et al. 1999).

Shrub communities should be protected within 3 km of nests, and communities can be maintained primarily through active fire suppression and secondarily by restoring shrubs in burned areas (Kochert et al. 1999).

APPEARANCE

MOLTS AND PLUMAGES

Hatchlings. Mostly covered in down at hatching. Prepennae down short, pale gray with dark tips (Jollie 1947) or white (Hoechlin 1974); patches of skin exposed along vertebrae and ventral surface (Jollie 1947). Down darker on nape, back, and upper surface of wings. Dark down around eye and edge of eyelid; short, thick, white down rims ear (Jollie 1947, Nakajyo et al. 1983). Long, white, preplumulae down emerges about day 6, progressively obscuring prepennae down by about day 15 (Jollie 1947). Preplumulae down grows for about 30 d, forming dense, nearly waterproof covering on chick (Palmer 1988).

Juvenal plumage. Primaries break skin around 15 d, followed by secondaries, scapulars, and rectrices at 18 d (Sumner 1929a, Ellis 1979, Watson 1997). Primaries rupture sheaths at 21 d followed by secondaries, scapulars, and rectrices. Greater upper wing-coverts break skin between 22 and 25 d and burst sheaths around 27 d (MNK). Dorsal and ventral tracts emerge through skin between 22 and 28 d and break sheaths 29–35 d (Seidensticker 1968). Capital, femoral, and crural tracts break skin between 29 to 35 d and rupture sheaths between 36 and 42 d (Seidensticker 1968). Capital feathers continue to rupture sheaths until about 49 d. At about 56 d, preplumulae down begins to be replaced by plumules of Juvenal plumage (Jollie 1947). Juvenal feathering essentially complete about 60 d (Watson 1997). Full feather growth complete by 80–105 d (Jollie 1947, Nakajyo et al. 1983).

Juvenal plumage retained about 9 mo. Distinctive because all feathers same age, show same amount of wear, and are uniform in color, shape, and length (Bent 1937, Jollie 1947); exception is possible replacement feathers, which usually are not at molt centers, or molted symmetrically (P. Bloom and W. Clark unpubl.). All feathers dark brown with the following exceptions: Lanceolate feathers on head and nape often golden brown and contour feathers dark brown to blackish on recently fledged eagles (Bent 1937, Watson 1997). Primaries dark brown; inner primaries occasionally have white at base. Secondaries usually have white bases which always lack grayish marbling (Jollie 1947, Palmer 1988). Occasionally some upper wing-coverts also white (Johnsgard 1990), and some also have small white "epaulet" at upper end of scapulars (Spofford 1961). Rectrices predominantly white with dark terminal band of varying width;

distinct border between white and dark part of feather (Jollie 1947, Tjernberg 1988). Dark flecks or grayish lines sometimes present in white area, particularly near irregular border between white and dark (Jollie 1947, Watson 1997). Under tail-coverts paler than remaining underparts, but feathered tarsi may also be paler approaching whitish (Jollie 1947, Clark and Wheeler 1987). Sexes similar.

MOLT PATTERNS AFTER FLEDGING

After Jollie 1947, Watson 1997, P. Bloom and W. Clark unpubl., and others as noted. Annual molt is incomplete, with 2–3 yr required to replace complete set of feathers. Molt usually occurs from Mar/Apr through Sep/Oct, and transition from one plumage class to another occurs during this time. Molt usually suspended during winter and migration, but occasionally 1 or 2 feathers grow during this period. First molt (Prebasic I) begins at 10–12 mo, continues through summer, and resumes the following summer. Replacement of all Juvenal feathers usually complete by end of third molt. From then on, molt proceeds in a continuous cycle in which there are ≥ 3 ages of feathers: fresh, the previous molt, and the molt before that. These different ages of feathers are recognizable by their color and wear. Juvenal secondaries and rectrices narrower, longer, and more pointed than replacement feathers in subsequent molts.

Molt occurs in predictable pattern, but rate may vary among individuals, depending on environmental factors and physiological conditions. Body molt usually begins before flight-feather molt and generally proceeds anterior to posterior; begins at head and neck, progressing to back and belly. Head, neck, back, throat, scapular tracts, and alulae usually replaced each year. Molt of flight feathers begins with primaries, starting with P1 and progresses outward, usually stopping at P4 or P5 by end of first molt. Next molt continues from where it left off previous year and proceeds in subsequent molts in a progression of waves; third molt usually begins at innermost primary again, at the same time that remaining outermost primaries are replaced. Molt of secondaries begins sometime in midsummer (May–Jul), well after primary molt has begun. Usually 3 different molt centers in secondaries, all molting simultaneously; generally starting with S1 and molting inward, S4 or S5 and molting inward (but occasionally outward), and S14 and molting outward. From second molting season onward, normally has at least 3 ages of secondaries, with molt proceeding from where it left off the previous year. Tail molt often begins with R1 and continues symmetrically outward, but variation in order of rectrix molt common. As many as 9 rectrices may be replaced annually; some are molted every year and others every 2 yr. Tail-feathers replaced more frequently than secondaries and primaries.

Size of white area in wings and tail once thought to be indicator of relative age, with white decreasing over time (Bent 1937). However, this character is highly variable among individuals (Tjernberg 1988); age cannot be determined solely by amount of white in flight feathers (Clark and Wheeler 1987).

An alternative method to age individuals in the hand through the fourth year is based on pattern of molt in remiges and rectrices. Most eagles reach adult plumage soon after they are 4 yr old, but some may still retain some white in the tail through the fifth or sixth molt; differences in plumage characteristics are subtle after the fourth year (Tjernberg 1988). Individuals vary in plumage and rates of molt; variation in molt increases with age, making it more difficult to assign age reliably, particularly beyond the second summer. General patterns of molt for an "average" eagle have been identified and are described in the following plumage classes (Jollie 1947, P. Bloom and W. Clark unpubl.). Because n. Alaskan birds fledge later than eagles in the lower 48 states, they may not fit molt categories described below.

Basic I plumage. Usually attained by end of second summer of life. Characterized by 2 ages of feathers: new ones dark and shiny; old ones faded and worn. Older primaries appear lighter at the base than new ones; P1-6 may be new. New rectrices retain extensive white areas, have grayish marbling in the dark tip, and are shorter and blunter than the pointed Juvenal feathers. Border between white base and dark tip often less defined than in Juvenal plumage. Two to 9 rectrices new; usually includes R1 and R2. New secondaries at 3 molt centers are darker and wider and have more blunt tips and varying amounts of grayish marbling toward the base than Juvenal feathers. Usually replaces 1-6 secondaries, but some eagles don't molt secondaries the first molt. Median and lesser upper wing-coverts are light colored and evenly worn; under wing-coverts begin to be replaced in this plumage and have a characteristic rusty-brown color. May have somewhat mottled appearance caused by new body-feathers.

Basic II plumage. Usually attained by the third summer and characterized by 3 ages of primaries; 1 or both P10s usually old (retained Juvenal). Molt of primaries appears as a wave proceeding outward on the wing; newest feathers outermost. Most secondaries have been replaced at least once and have grayish marbling with dark tips; may still have some white at the base. Most secondaries usually replaced, although 1-5 Juvenal secondaries may be retained; S9 often replaced last. Normally 2 ages of non-Juvenal rectrices with gray marbling and white bases; shorter and wider than Juvenal rectrices. Border between white and dark in tail more diffuse and jagged than in younger birds. Molt pattern for rectrices irregular for this and subsequent age classes; asymmetrical molt

common. Some may have a few adult-type remiges and rectrices. Most upper wing-coverts dark, but with scattered, light, older feathers or groups of feathers.

Basic III plumage. Attained during fourth summer. Three ages of feathers: both P10s new. Most secondaries "adult" with grayish marbling and dark tips; usually lack white at base. Juvenal secondaries usually no longer present. White pattern under wing, if present, divided by dark primaries and secondaries. New rectrices have marbling in dark areas, lack white, or have reduced white areas at base; others may still show extensive white areas. Tail typically has dark central "pillar" where "adult-type" R1 and R2 have grown in; still suggests Juvenal tail at a distance. Upper wing-coverts predominantly faded but interspersed with groups of new, dark feathers.

Definitive Basic plumage. Usually attained during fifth summer. Adult plumage characterized by 3 ages of feathers. Entire plumage dark brown except area encompassing rear crown, postocular region, nape (extending forward to rear border of to ear-coverts), and sides of lower neck golden brown; rear underparts (mainly under tail-coverts) and some upper wing-coverts paler and buffier (Watson 1997). Paler wing-coverts usually mainly include median-coverts, larger lesser-coverts and innermost 1 or 2 greater-coverts. All flight feathers marbled with dark tips. Usually lack white areas on bases of tail or flight feathers. Feather-tips form dark band on trailing edge of wing. Rectrices marbled with wide, black terminal band; may have uniform gray base or dark bars on dark gray; background rarely white or light gray (Tjernberg 1988, Watson 1997). A few individuals retain some white in base of tail for many years (T. and E. Craig unpubl.).

Sexes similar in coloration. Suspected sexual differences in pattern and number of bands on tails of adults (Wheeler and Clark 1995) not verified by studies; may not be a reliable method for distinguishing sexes (W. Clark pers. comm.).

Aberrant plumages. A few cases of partial albinism have been reported (Clark and Wheeler 1987), and a melanistic specimen (taxidermy mount) has been described (Aiken 1928).

BARE PARTS

Bill and cere. Bill and cere tricolored (Clark and Wheeler 1987); bill black at tip, lightening to bluish gray at base. Cere fleshy, yellowish white in nestlings and yellow in juveniles and adults (Brown and Amadon 1968).

Iris. Dark brown in juveniles. Eyes of adults vary from dark brown, hazel, or light yellow to flecked gold and brown; a few even appear white (D. Bittner pers. comm.); uniform colors of brown or hazel are most common (T. and E. Craig unpubl.).

Bare skin on head. Orbital-ring yellow.

Legs and feet. Feet yellow, but lighter in nestlings (Brown and Amadon 1968). Legs feathered to toes. Talons black to blackish slate colored.

MEASUREMENTS

LINEAR

Sexes differ significantly in length of wing-chord, tail, culmen, middle toe, foot pad, and hallux claw; females larger in all respects (Appendix 3). Foot pad accurately sexed 100% of the sample, males <138.5 mm; females >138.5 mm (Edwards and Kochert 1986). Combination of culmen and hallux talon lengths accurately sexed 97% of adults and 100% of immatures; wing-chord and body mass alone are not reliable predictors of sex (Bortolotti 1984a, Edwards and Kochert 1986).

Hallux claw significantly longer in adults than in immatures, and tails significantly longer in immatures than adults (Appendix 3). Differences in adult and immature culmen and wing-chord lengths equivocal; significantly longer for only adult males (Bortolotti 1984a). Age-class differences in tail and wing not as great as for Bald Eagles and other sea eagles (Amadon 1980, Bortolotti 1984a). See Bortolotti 1984a for eighth-primary and first-secondary lengths and bill depth, width, and length; see Friedmann 1950 for tarsus width. Geographic variation in size not documented in North American populations (Bortolotti 1984a).

MASS

From necropsy of adults and immatures from Idaho: 31 males averaged $3,477 \text{ g} \pm 101.0 \text{ SE}$ (range 2,495–4,281), and 18 females averaged $4,913 \text{ g} \pm 163.9 \text{ SE}$ (range 3,374–6,124; Edwards and Kochert 1986). Masses of adults/immatures trapped in sw. Idaho ranged from 3,000 to 4,475 g (mean $3,900 \pm 335 \text{ SD}$) for 34 males and from 4,075 to 5,280 g (mean $4,627 \pm 420 \text{ SD}$) for 14 females (USGS unpubl.). See Breeding: fledging stage, above, for mass of nestlings at fledging.

PRIORITIES FOR FUTURE RESEARCH

Development of a population monitoring strategy should be a priority for the western United States, where population declines are suspected. In addition, factors that influence population trends are not well understood. Information on effects of environmental contaminants (for example, heavy metals) and habitat alteration on populations is lacking for both breeding and wintering grounds. More information is needed on population dynamics to answer questions raised by pending proposals to harvest this species for Native American religious ceremonies; for example, if and

how survival rates vary across geographic areas and whether human-caused mortality is additive or compensatory. The size of the floating segment of populations needs to be estimated more accurately, and additional information is needed on how floaters interact with territorial breeders. To determine if there is interchange among nesting populations, more data are needed on natal and breeding dispersal. Genetic analyses could provide insights on relatedness of individuals from different regions.

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Appendix 1. Proportion of major prey taxa in diets of Golden Eagles during the breeding season in w. North America, based on proportion of individual items.

Location	Number of years	Number of items	Percent of total prey items		Source
			Leporidae ¹	Sciuridae ²	
Alaska	4	196	51 ³	32	Ritchie and Curatalo 1982, Mindell 1983, Petersen et al. 1991
Central Alaska	13	2,569	18 ³	68	CLM
Central Montana	6	1,989	58	17 ⁴	McGahan 1968, Reynolds 1969
Se. Montana, n. Wyoming	2	312	15	58 ⁵	Lockhart and Phillips 1976, Lockhart et al. 1977
Se. Wyoming	4	721	41	42 ⁶	Schmalzried 1976, MacLaren et al. 1988
N.-central Colorado	3	231	89	2	Craig 1974, Olendorff 1973
E. Washington	6	315	3	46 ⁷	Knight and Erickson 1978, Marr and Knight 1983
Sw. Idaho	11	2,203	62	12 ⁴	USGS unpubl.
Se. Oregon	2	209	61	4 ⁴	Hickman 1968
Ne. California, nw. Nevada	6	1,156	85	3 ⁴	Bloom and Hawks 1982
Central Utah	2	844	92	2	Arnell 1971, Smith and Murphy 1973
Central California	7	842	17	47	Carnie 1954, Hunt et al. 1995
New Mexico, w. Texas	3	1,396	74	16 ⁸	Mollhagen et al. 1972, Lockhart 1976
Arizona	1	39	37	16	Eakle and Grubb 1986

¹Jackrabbits and cottontail rabbits unless otherwise noted.²Ground squirrels unless otherwise noted.³Snowshoe hares.⁴Ground squirrels and yellow-bellied marmots.⁵Prairie dogs.⁶Prairie dogs (21%), ground squirrels, and yellow-bellied marmots.⁷Yellow-bellied marmots.⁸Ground squirrels and prairie dogs.**Appendix 2.** Golden Eagle laying and hatching dates by geographic region in w. North America. Data shown as mean (range, n).

Location	Laying	Hatching	Source
Ne. Alaska	16 Apr (28 Mar–14 May, 25)	28 May (9 May–25 Jun, 25)	Young et al. 1995
Ne. Alaska	(13 Apr–14 May, 8)	(25 May–25 Jun, 8)	Ritchie and Curatalo 1982
N. Northwest Territories	24 Apr (13 Apr–4 May, 19)	5 Jun (25 May–15 Jun, 19)	Poole and Bromley 1988
S.-central Alaska	15 Apr (27 Mar–5 May, 170)	27 May (8 May–16 Jun, 170)	McIntyre 1995
Se. Washington	(13 Mar–20 Mar, 4)	(24 Apr–1 May, 4)	Monk 1976
Ne. Wyoming	14 Mar (27 Feb–13 Apr, 86)	25 Apr (10 Apr–25 May, 86)	Phillips and Beske 1990
Se. Wyoming	(20 Mar–4 Apr, 7)	(2 May–31 May, 7)	Schmalzried 1976
Se. Oregon	5 Mar (16 Feb–26 Mar, 22)	16 Apr (30 Mar–7 May, 22)	Hickman 1968
Sw. Idaho	25 Feb (28 Jan–24 Mar, 60)	8 Apr (10 Mar–5 May, 60)	Hickman 1968
Sw. Idaho	1 Mar (3 Feb–17 Apr, 1,026)	12 Apr (17 Mar–29 May, 1,026)	USGS unpubl.
Ne. Colorado	(10 Mar–1 Apr, 11)	(21 Apr–13 May, 11)	Olendorff 1973
N.-central Utah	(25 Feb–11 Apr ¹ , 9)	(12 Apr–16 Apr, 9)	Camenzind 1969
N.-central Utah	7 Mar (21 Feb–2 Apr, 14)	18 Apr (3 Apr–14 May, 14)	Smith and Murphy 1973
W.-central California	27 Feb (5 Feb–15 Mar, 51)	9 Apr (19 Mar–26 Apr, 51)	Hunt et al. 1995

¹Includes reneest.

Appendix 3. Selected linear measurements (mm) of North American Golden Eagles. Data shown as mean (range, *n*).

Variable/age class	Male ¹	Female ¹	Source ²
Wing-chord (unflattened) ³			
Adult	595.0* (569–619, 23)	640.4 (601–674, 27)	Bortolotti 1984a
Immature	585.9* (559–636, 26)	632.2 (601–665, 31)	
Tail length			
Adult	286.5* (267–310, 22)	307.2** (290–330, 24)	Bortolotti 1984a
Immature	297.7* (269–341, 23)	322.0** (285–375, 30)	
Culmen length ⁴			
Adult	40.6* (36.9–43.5, 23)	44.2 (41.7–47.5, 27)	Bortolotti 1984a
Immature	39.4* (36.2–42.6, 26)	43.3 (39.9–50.0, 31)	
Foot pad			
Adult/immature	131.6 (120–137, 31)	145.4 (139–153, 18)	Edwards and Kochert 1986
Hallux-claw length			
Adult	49.4** (45.9–52.9, 23)	55.7* (49.8–63.4, 26)	Bortolotti 1984a
Immature	47.8** (44.9–51.3, 24)	54.0* (49.7–58.2, 30)	

¹Within age class, sexes differ significantly ($p < 0.01$) for all variables reported by Bortolotti (1984) and Edwards and Kochert (1986).
²All measurements from museum skins except Edwards and Kochert 1986, which were from necropsied birds.
³Within variables, significant differences between age classes denoted as * for $p \leq 0.05$ and ** for $p < 0.01$.
⁴Measured from cere.

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