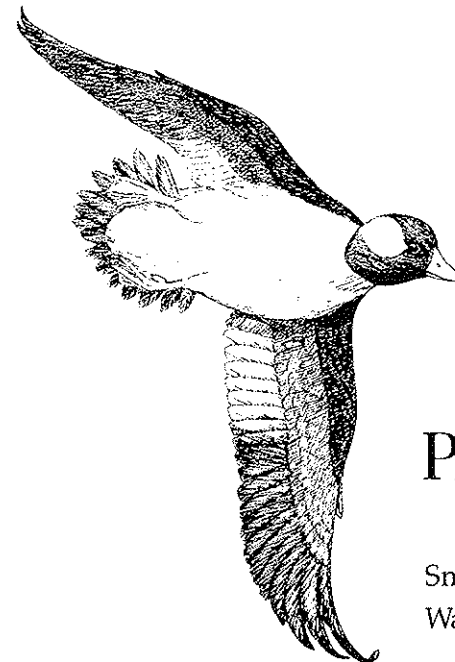


Stooping peregrine falcon and bufflehead

HAWKS, EAGLES, & FALCONS OF NORTH AMERICA

Biology and Natural History



PAUL A. JOHNSGARD

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Dedicated to those who, like King Solomon,

would know the way of an eagle in the sky

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Weights (in grams)

Males (various races) 3550–4400, ave. of 7, 3924; females 4050–5720, ave. of 4, 4692 (Brown and Amadon, 1968). Average of 31 males, 3477; of 18 females 4913, with 4195.5 the best dividing point for judging sex (Edwards and Kochert, 1986). Fifteen males of nominate *chrysaetos* (Eurasian) averaged 3672, and 19 females averaged 5194 (Cramp and Simmons, 1980). Estimated egg weight 138, or 2.9% of female.

Identification

In the hand. The combination of feathered tarsi and a wing length of at least 550 mm serves to separate this species from all other North American raptors.

In the field. Distinction of golden from bald eagle while perched is simple in adult birds; the tawny-colored (rather than pure white) head and neck of the former immediately separates them. However, juvenile and subadult birds are less simple; golden eagles never show any extensive amount of white on the back or underparts, as is typical of immature bald eagles. Young goldens (especially first-year birds) are more likely to exhibit white at the base of the tail than are those bald eagles that still lack any white on the head, and additionally younger bald eagles (to three years) retain dark outer edges on their outermost tail feathers that are lacking in golden eagles.

In flight, golden eagles of all ages exhibit dark wing linings, and most birds show at least lighter (immatures and subadults) if not actually whitish (juveniles) bases to their primaries; subadults and adults also may show a variable degree of lighter and darker mottling or barring on the undersides of their flight feathers. First-year birds also have a white band at the base of the tail (immature bald eagles may also have white at the base of the tail but it is typically much more diffusely sprinkled rather than organized into a definite basal band and thus does not produce such a distinctly half-white, half-black tail). Additionally a diffuse white "window" is sometimes visible at the base of the spread primaries when seen from above, in a pattern similar to that typical of rough-legged hawks. Thus, any flying eagle with dark wing linings and no white on the head can safely be identified as a golden eagle, and any eagle with extensive whitish spotting on the wing linings

and/or underparts, regardless of whether it has any white on the head, can similarly be recognized as a bald eagle. Golden eagles typically but not invariably soar with their wings slightly uptilted (rather than held rigidly horizontal as bald eagles normally do), and they have relatively longer tails than do balds. Golden eagles are generally to be found farther from water than are balds. A buteo-like leisurely soaring over arid rimrock or mountainous country is a typical hunting method. A steep dive to capture prey such as rabbits on the ground is fairly common, but occasionally birds up to the size of geese and cranes are attacked in the air. The wing shape of golden eagles, together with their slightly uptilted flight profile, remind one more of large buteo hawks than do bald eagles, which have seemingly larger heads (owing to their larger and longer bills), although these differences are not easily appreciated unless both are visible simultaneously. Both species are typically silent in flight, but the golden eagle sometimes utters a series of repeated yelping notes when near the nest, especially when carrying prey.

Habitats and Ecology

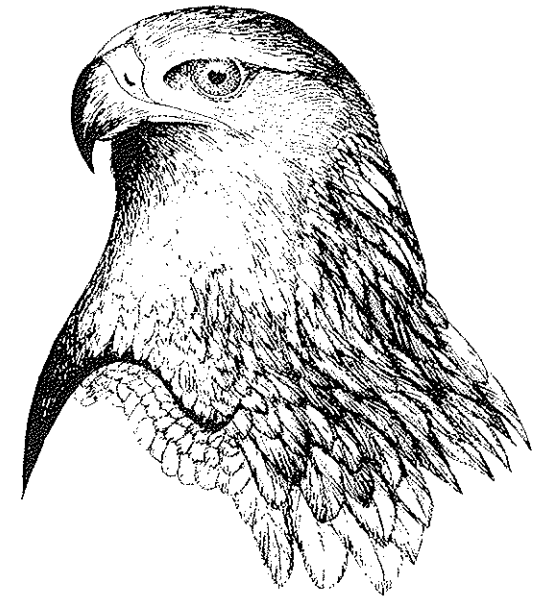
This species occurs in nearly all habitats of the western states, from desert grasslands to above timberline, perhaps avoiding only densely forested areas where hunting is impossible. Generally it occurs in grass-shrub, shrub-sapling, and young woodland growth stages of forested areas, or in forests with open lands nearby for hunting. Essentially, it needs only a favorable nest site (usually in a large tree or cliff), a dependable food supply (mainly of medium to large mammals and birds), and broad expanses of open country for foraging. It especially favors hilly or mountain country over flat habitats, where takeoff and soaring are facilitated by updrafts; deeply cut canyons rising to open or sparsely treed mountain slopes and crags represent ideal habitat (Beebe, 1974).

Wintering habitats of golden eagles in western states tend to be those having available perches plus native shrub-steppe vegetation types (mainly *Artemisia* and similar shrubs), which are habitats that usually have good populations of black-tailed jackrabbits (*Lepus californicus*). Such habitat selection tendencies have been observed in Utah (Fischer, Ellis, and Meese,

1984). In the eastern United States wintering habitats are quite different, and in one survey (Millsap and Vana, 1984), 82 percent of winter records were associated with riverine or wetland systems, mainly steep river valleys or associated reservoirs or wetlands. Estuarine marshlands, barrier islands and associated sounds, and the mouths of major rivers represented the primary coastal habitats.

Breeding densities of golden eagles are relatively low everywhere, as a reflection of territorial spacing and foraging requirements for the species. In Utah, six breeding pairs had home ranges of from 17 to 31 square kilometers, averaging 23 square kilometers, and nesting population densities of from 42 to 52 square kilometers per pair (Smith and Murphy, 1973). There the birds concentrate along high, north-south-oriented ridges and hills, but seem to avoid the intervening broad and flat valleys (Smith and Murphy, 1982). Caminzind (1969) estimated a density of 99–156 square kilometers per pair in his Utah study in the same area. In southern California, 27 year-round home ranges averaged 93 square kilometers (Dixon, 1937), while Spofford (1971) estimated probable winter home ranges of golden eagles ranging from approximately 130 to 260 square kilometers in the Appalachians. One of the highest known breeding densities in North America or anywhere else must be that of the Snake River canyon in southern Idaho, where annual breeding densities in two years ranged from a pair per 5 to 8 kilometers of river, along a 240-kilometer stretch of river that supported up to 56 breeding pairs. There the maximum density is probably a collective function of the availability of suitable nest sites, an adequate prey base, and minimum nesting territory size (Beecham and Kochert, 1975). Differences in population densities in two areas of Sweden (average of 10.2 kilometers between nests in mountains versus 17 kilometers in forests) was attributed to higher hare and grouse prey densities and possibly also topographic and habitat diversity differences in these two areas (Tjernberg, 1985). Average breeding densities in Wyoming have been estimated as 60 square kilometers per pair, and 5.3 kilometers between active nests. The range of nine previous studies from various areas was from 41 to 251 square kilometers per pair (Phillips, McEneaney, and Beske, 1984).

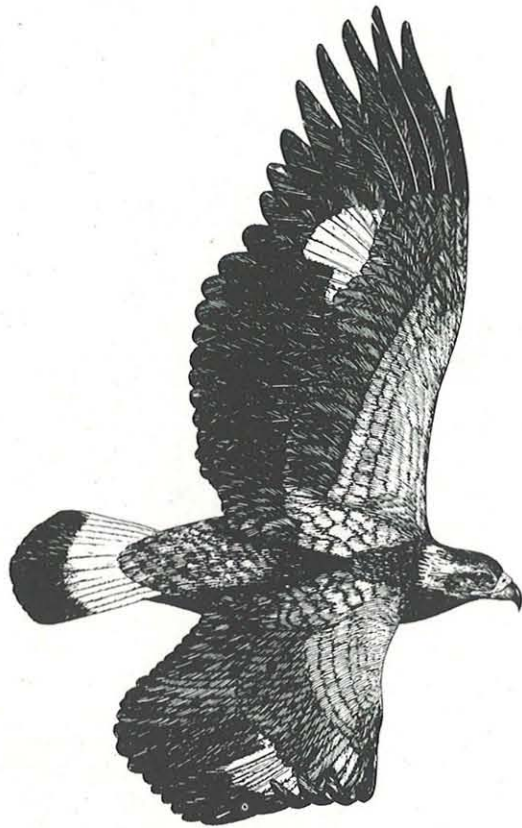
Territoriality probably is an important aspect of spacing and associated limitations to popula-



tion density; it has been studied by Bergo (1987) in a sparse breeding population in Norway. He judged that the regular spacing of nests was probably facilitated and maintained by territorial defense throughout the year, especially by use of aerial activities such as undulating flight displays as well as by soaring and "hanging on the wind." There each pair had a "core area" of their home range that varied from 10 to 35 square kilometers, but this was only a small part of the pair's total hunting range.

Foods and Foraging

A very large amount of information is available on golden eagle foods; Sherrod (1978) listed ten original sources or summaries for the species, seven of which provided a percentage analysis of major food types numerically. In these the mammalian component ranged from 77 to 97 percent of the identified items (unweighted average 82.6 percent), birds ranged from 3 to 28 percent (unweighted average 12.6 percent), and the remainder was mostly comprised of reptiles and fish. Brown and Amadon (1968) suggested that, depending upon locality and prey availability, from 70 to 98 percent of the species's foods on a biomass basis consists of small mammals, mainly



lagomorphs and rodents. This estimate agrees with studies done in the Snake River canyon of southern Idaho, where mammals comprised an estimated 82 percent of prey biomass (and jackrabbits alone about 60 percent), birds comprised 16 percent, and reptiles and fishes occurred in only trace quantities (U.S. Dept. of Interior, 1979).

A comparably large amount of information is available for the Eurasian population of golden eagles, which has been summarized by Cramp and Simmons (1980). These authors commented on the wide range of prey taken, but noted that it consisted mainly of medium-sized mammals, especially lagomorphs (rabbits and hares), and birds, mostly tetraonids (grouse and ptarmigan), with a greater reliance on rodents toward the south, particularly marmots. The most comprehensive of the studies on golden eagle foods in North America was that of Olendorff (1976), who reviewed the entire North American literature

available at that time, representing more than 7,000 identified food items. Of these, there were 52 species of mammals, 48 birds, 5 reptiles, and 2 fish. Lagomorphs comprised 54 percent of the total, marmots, ground squirrels, and prairie dogs 22 percent, game birds 8 percent, wild ungulates 6 percent, passerine birds 3 percent, domestic livestock 1 percent, and mammalian predators 1 percent. In descending frequency of occurrence, the most common prey species were black-tailed jackrabbit (*Lepus californicus*), arctic ground squirrel (*Spermophilus parryii*), white-tailed jackrabbit (*L. townsendii*), desert cottontail (*Sylvilagus audubonii*), and yellow-bellied marmot (*Marmota flaviventris*).

Among the studies that have analyzed prey on a biomass basis is that of Bloom and Hawks (1982), who examined over 1,100 prey items from nests and found that four species (black-tailed jackrabbit, Nuttall's cottontail *S. nuttallii*, yellow-bellied marmot, and chukar *Alectoris chukar*) were the most frequently encountered, accounting for 90 percent of all items, with livestock accounting for less than 1 percent (and some of this probably being carrion). Lagomorphs comprised 91 percent to the total estimated prey biomass. Similarly, six species of jackrabbits, cottontails, ground squirrels, and prairie dogs comprised nearly 90 percent of the prey items found at 41 nests in Texas and New Mexico (Mollhagen, Wiley, and Packard, 1972).

Because of traditional concern by ranchers, especially sheep ranchers, over golden eagle depredation, many papers have been devoted to this controversial topic. The evidence for lamb-killing by golden eagles and ways of reducing such behavior were reviewed by Matchett and O'Garra (1987), who stated that depredation levels vary greatly, depending on natural prey densities, availability of carrion, ranching practices, weather, and a variety of other factors. Probably most lambs are killed by young eagles, and lambs are more often taken during periods of decline in jackrabbit populations or during cold periods when their usual rodent prey are relatively inactive. The use of conspicuous scarecrows, especially in combination with harassment and increased human activity, offers the best means of protecting lambs from eagles according to these authors. Brown and Watson (1964) similarly found that sheep management practices had a great effect on eagle depredation levels, and losses to eagles were infinitesimally small when

compared to those associated with poor management practices.

Eagles hunt largely by soaring-searching techniques, and need either thermals or orographic winds (topography-related updrafts) to help them gain sufficient altitude to hunt and cover the large areas of their foraging ranges. Thus, the birds seek out areas with such updrafts, and avoid areas of downdrafts or dead air. They are unable to take off with any significant amount of prey, possibly even as little as two kilograms, when they are in the center of such downdraft areas (Snow, 1973a). It is unlikely that even an adult eagle can normally take off with more than about three kilograms of prey, although an eagle has been observed in flight carrying a jackrabbit weighing more than 3,170 grams (Kalmbach, Imler, and Arnold, 1964). However, adult black-tailed jackrabbits average only about 2.3 kilograms (Smith and Murphy, 1973). Huey (1962) reported that an adult male eagle is apparently able to carry a load of only about 900 grams easily, or less than 25 percent of its body weight, assuming an average male eagle weight of 4,000 grams. Certainly the amount of wind and the opportunity to take off downslope must greatly influence carrying ability, and even eagles carrying small prey will use wind to assist in this.

Eagles typically hunt by using favorite perches located near an area having regular updrafts that allow them to rise to soaring height, from which they can scan their hunting areas, which are usually upwind. Eagles also prefer to make attacks upwind, in order to have the maximum degree of aerodynamic control and maneuverability, and perhaps also to force the prey to face into the wind while trying to escape. Hatch (1968) has described the cooperative hunting tactics of two golden eagles that worked together in successfully killing a red fox (*Vulpes vulpes*), in which an immature eagle distracted the fox while an adult attacked it from behind. Dekker (1985) likewise observed hunting behavior of golden eagles, reporting that surprise was a basic ingredient in their attacks on ground squirrels. Seven ground squirrels were captured during low flapping flights and eight taken during low, high-speed glides following soaring flights, the low final approach probably helping to screen the attack.

Collopy (1983) found that golden eagles use both solo and tandem-hunting techniques, the

male typically flying in front of the female during tandem hunts and apparently leading the hunt. Overall, 20 percent of 115 hunts he observed were successful, with the smaller and more agile males nearly twice as successful as females during solo hunts. Males also nearly always initiated the attacks during tandem hunts, the female attacking only when the male was unsuccessful. Surprisingly, solo hunts had a higher success rate (29 percent vs. 5 percent) than tandem hunts. However, this statistic is perhaps misleading in that tandem hunting might be mainly directed toward larger and/or more elusive prey than can be caught easily by single birds, as has also been observed in the aplomado falcon.

Social Behavior

More perhaps than to any other bird of prey, people have been inclined to attribute lifelong monogamous pair bonds to eagles, although inadequate evidence is available to support this assertion. Brown (1976a) stated that a bond lasting for the life of any one individual is probably the usual eagle mating pattern, but that if a mate dies the other is likely to try to obtain a new one immediately, even if it is an immature. Such a mate replacement may occur within 10 weeks in a single breeding season (Dixon, 1937), or it may occur by the following season. An unpaired bird may occupy an area for up to two years before obtaining a mate, and it is probable that most pairs are formed only after a territory has been established. Although monogamy is typical, casual bigyny by the male has also occurred (Cramp and Simmons, 1980).

The territories of eagles are extremely large, and perhaps for that reason it is impossible to defend them efficiently. Brown (1976a) suggested that the term "home range" is a better term for the area occupied year-round by eagles, since the birds do not overtly defend this entire area. However, Bergo (1987) studied territoriality in golden eagles in Norway, concluding that territoriality was expressed there in a variety of ways that facilitated spacing of nests. Perhaps the most spectacular of these is the "undulating flight," which has often been interpreted as courtship behavior (Bent, 1937). However, Har-mata (1982) found that over 70 percent of these flights were associated with the appearance of intruders, and Bergo's observations were similar. Bergo did, however, also see undulating flights at

low altitudes when no intruders were apparent, and judged that such flights might have a sexual function as well. Most of the examples of undulating flight that he saw occurred when the performer's mate was in the core area (the males displayed nearly three times as frequently as females, but with fewer undulating "waves" per sequence), and most were performed within a kilometer of the nest. A few undulating flights were intermediate in form between "undulating" and "pendulum" (or figure-eight) in form, but true pendulum flights were also seen twice. Mock attack and evasion between mates was observed several times, and fledged young were also observed to make mock attacks on their own parents. Bergo believed these mock attacks to have sexual significance when performed between pairs.

Other aerial activities commonly observed by Bergo that might constitute territorial advertisement included slow glides (such as "hanging on the wind") and soaring, plus much less frequent fast glides, flapping flights, and diving. Conspicuous and inconspicuous perching were also frequently seen but of uncertain significance in territorial advertisement. "Exposed perching" (use of the highest and most exposed available perch) and calling were probably not a part of advertisement behavior, at least in this population.

Additional data on territoriality were provided by Collopy and Edwards (1989) and by Tjernberg (1985); Tjernberg concluded that the distributional pattern of nests in Sweden was affected more by spacing behavior than by a shortage of suitable nest sites. There was a high stability in size and spacing of pairs, with territories typically occupied annually although not all pairs bred every year. Further, no new territories were formed in between existing territories, although in five cases where one member of a pair disappeared a new mate was present the following breeding season. Smith and Murphy (1973) found that three of five pairs occupied territories during all four years of their study, while the other two occupied territories for three years, although the majority of specific nest sites were used only a single year (perhaps because of human disturbance). Brown (1976a) stated that the average number of golden eagle nest sites per territory in his experience is 2.6, but the known range is 1–11.

Ellis and Powers (1982) described the occurrence of copulatory behavior in golden eagles at times when fertilization was clearly not a functional part of the behavior, such as during the incubation and fledging periods, and judged that such behavior might serve as a territorial display, help maintain pair bonds or synchronize reproductive readiness, or serve as displacement behavior in conflict situations.

Breeding Biology

The first phase of nesting biology probably involves the choice of nest site, which is likely to be either the nest used the previous year or a fairly nearby location. Nest building can be done at almost any time of year; indeed Brown (1976a) suggested that the only times it is not likely to be done are when the sites are snow-covered or the pair have a brood in the nest or just out of it, and are thus occupied by hunting. In Scotland perhaps 95 percent of the sites are on cliffs, and some of the pairs with three nests also have rock sites that they sometimes use. On the other hand, all but one of 21 nests in a western Washington study were in Douglas fir (*Pseudotsuga menziesii*) trees, with the other on a cliff, and most were at forest edges or in small stands near clear-cuts or open fields (Bruce, Anderson, and Allen, 1982).

Caminzind (1969) noted that 87 percent of 31 nests he observed in Utah were on cliffs, while the rest were on the ground or some artificial structure. More than half of this total faced west, and only 4 percent faced east, although Caminzind did not believe this to provide any evidence for or against the sun's possible effect in influencing nest site selection. McGahan (1968) noted that 62 percent of 92 nests in Montana were on cliffs, and most of the rest were in large-limbed trees such as Douglas fir. Of the cliff nests, nearly half faced south, while only about 10 percent faced north, which McGahan attributed to possibly advantageous warming effects in early spring. Similarly, 37 Alaska nests were mostly oriented toward the south or south-east, and all but one were on cliff faces (Ritchie and Curatolo, 1982). Data from these and other areas suggest that directional exposure of nests may be related to a strong sensitivity to thermal stress in young eagles (Mosher and White, 1976).

In the area of plains, hills, and buttes in

northeastern Wyoming nearly 90 percent of the eagles nested in trees, with a preference shown for larger trees. Ground nests there tended to be on butte tops, while tree nests were found close to watercourses. Both deciduous trees and ponderosa pines were used, with the nests usually placed in the upper one-third of the tree in either case (Menkens and Anderson, 1987).

Brown (1976a) judged that from 10 to 25 percent of eagle pairs do not lay during any given year in Scotland, but only scant evidence exists that nonbreeding is more common in years of poor prey supply. Caminzind (1969) reported that 13 percent of 31 nests in his study area during two years had no eggs present. While nest abandonment for various reasons may account for some such cases, probably some of these nonlaying pairs involve immature birds that may nonetheless form pairs, defend territories, and construct nests. However, Teresa (1980) reported a case of a nesting pair in which one bird was in subadult plumage but which nevertheless fledged two young. She stated that about 2 percent of 564 observed nesting attempts had one pair member (probably the male) a subadult, and that such pairs had an estimated breeding success rate of 80 percent. Similarly, Steenhof, Kochert, and Doremus (1983) found that about 5 percent (17) of 340 territorial pairs of eagles in Idaho included one subadult bird, three of which failed to lay eggs. Of six subadults for which the sex was known, four were males.

Eggs are laid at intervals of about 90–120 hours, with the clutch size typically two or three, but sometimes only one and rarely four (Brown, 1976a). Of 82 Scotland clutches, the average size was 1.91, with 72 percent of the nests having two eggs (Cramp and Simmons, 1980). Similar or slightly higher clutch sizes seem typical for western North America, with Caminzind (1969) reporting an identical average of 1.91 eggs in 23 clutches in Utah, Beecham and Kochert (1975) an average of 2.04 for 89 clutches in Idaho, and McGahan (1968) an average of 2.1 eggs for 20 clutches in Montana. Three-egg clutches rarely comprise more than about 10 percent of the total in any of the available samples; Jenkins and Joseph (1984) estimated that of 267 clutches from North America and Scotland a collective average of 9.7 percent of the nests had three-egg clutches. Furthermore, for 1,309 successful nestings, only 16 of the pairs (1.01 percent) successfully fledged

three young, with unusually high numbers in 1981 (9 of the 16 cases) apparently being associated with extremely high jackrabbit densities that year.

Incubation is done by the female for the most part, but cases have been known of males taking an almost equal share (Brown, 1976a). Although some early literature suggests incubation periods of as short as 35 days (summarized by Brown and Amadon, 1968), most recent observations indicate a minimum 41-day (Caminzind, 1969; Olendorff, 1973) or 43- to 45-day incubation period (Brown, 1976a; Cramp and Simmons, 1980; Hobbie and Cade, 1962). Because of the fairly long egg-laying interval, the young are often substantially different in size and age. This may frequently lead to the older nestling killing the younger (Brown and Amadon, 1968), although the incidence of this is probably quite low, and the rare fledging of "triplets" in nests would suggest that the younger birds sometimes can hold their own in defending themselves and in competition for food. Collopy (1981, 1984) suggested that intense sibling competition for food during periods of low jackrabbit abundance may produce a differential mortality among the sexes (females surviving better than males). He found no differences in the food-provisioning rates of one-chick broods and two-chick broods, although different pairs provisioned their broods at significantly differing rates. Most of the food for chicks was captured by the male, while the females typically fed and tended the offspring.

The fledging period is about 72–84 days, but the young remain largely dependent upon their parents for as much as about 11 weeks afterward, may remain within their parents' territory for several more weeks thereafter, and at least in one case wintered on the edge of the parents' home range (Walker, 1987; Hobbie and Cade, 1962).

Breeding success in golden eagles tends to be fairly variable, often following fluctuations in primary prey populations such as jackrabbits. Thompson, Johnstone, and Littlefield (1982) found annual reproductive success rates to parallel jackrabbit abundance closely in Oregon, with a 15-year mean of 1.08 young fledged per breeding territory, 1.7 young fledged per successful nest, and 51 percent of the nests successful. Beecham and Kochert (1975) estimated a similar average of 1.1 young fledged per nesting attempt, 1.8 young fledged per successful nest, and 65 percent of the

nests successful over a three-year study. McGahan (1968) found a slightly higher average number of young fledged per nest (1.4) in a three-year study, while Caminzind (1969) estimated a two-year average of 1.13 young hatched per nest and 0.84 fledged per nesting attempt. Over a six-year period, productivity in New Mexico, Colorado, and Wyoming remained fairly constant, with annual averages of from 1.2 to 1.5 birds fledged per nest (of 264 total nests), and with 82–95 percent of the hatched young fledging annually (Boeker and Ray, 1971). In the Snake River Birds of Prey Natural Area of Idaho the average clutch size over eight years was 1.98 eggs for 365 nests, and the estimated hatching success was 69 percent. The average number of hatched young was 1.4 for all nests, and 1.77 for all successful nests, while the average number of fledged young was 1.03 for all nests and 1.62 for all successful nests (U.S. Dept. of Interior, 1979). Breeding success in Scotland has been found to depend largely on the degree of human interference as well as relative food supplies and extent of pesticide usage (Cramp and Simmons, 1980).

Evolutionary Relationships and Status

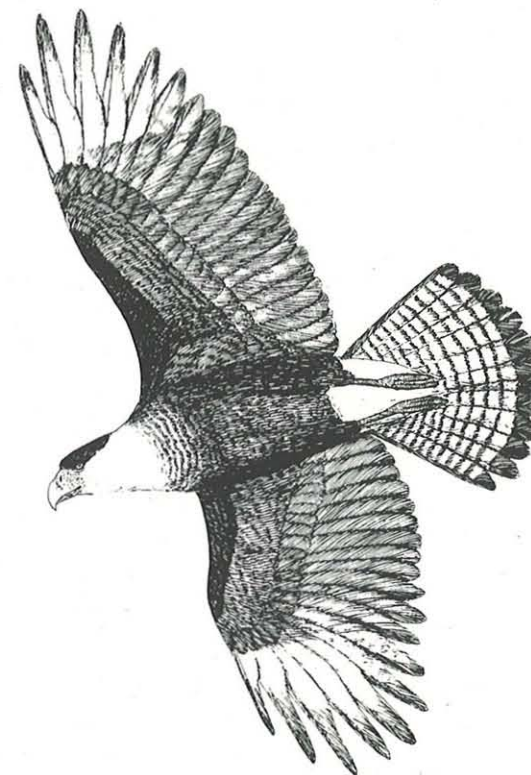
The golden eagle is one of a number of similar "booted eagles" that all have feathered tarsi and are placed in the genus *Aquila*. Brown and Amadon (1968) suggested that the golden eagle along with *verreauxi* (the Verreaux's eagle of Africa), *audax* (the wedge-tailed eagle of Australia) and *gurneyi* (Gurney's eagle of New Guinea) may all have been derived from the same ancestral

stock. Stresemann and Amadon (1979) suggested that *chrysaetos*, *audax*, and possibly *gurneyi* form a superspecies.

In a general review, Snow (1973a) presented unpublished data of L. G. Huegely suggesting that at least 16,000 golden eagles were resident in eight western states, including Wyoming (3,063), Colorado (2,600), Montana (2,433), New Mexico (2,050), Nevada (1,833), Oregon (1,600), Idaho (1,383) and Utah (1,367). My very similar estimates of 1986 winter populations, based on the Audubon Society's Christmas Bird Count data, are of 18,520 birds for the whole of North America except Alaska and the Canadian territories, with the largest populations occurring in Wyoming (3,140), Colorado (2,120), Montana (1,985), Nevada (1,400) and Utah (1,115). Oakleaf (1985a) believed that Wyoming alone may support over 4,000 breeding pairs. There do not appear to be any good estimates for Canadian or Alaskan breeding populations. Snow (1973a) suggested that the total North American population may be at least 50,000 birds, and Braun, Hamerstrom, and White (1975) judged that as many as 100,000 may be present, but it is difficult to imagine where all of these birds might be breeding. Palmer (1988) recently estimated a North American population of about 70,000 birds, which seems to me to represent the upper numerical limits of probability.

A recent and extensive bibliography of the golden eagle and other members of the genus *Aquila* is available (LeFranc and Clark, 1983). Palmer (1988) noted that he consulted over 700 sources on this species, and cited 242 of these.

Family Falconidae (Caracaras and Falcons) Tribe Polyborini (Caracaras)



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Note: Most citations to journal article titles have been abbreviated to conserve space. Such shortened titles are indicated by parentheses.

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