Nesting of Subadult Golden Eagles in Southwestern Idaho

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Age at first breeding is an important factor in the population dynamics of avian species (Lack 1968, Henny et al. 1970, Newton 1979). In species that delay breeding 3 or more years, age at first breeding often varies between individuals and sometimes is determined by local conditions (Lack 1968). Deferred maturity is common among Falconiformes (Newton 1979). In many raptor species with delayed maturation, individuals wear distinctive predefinitive feathering (Palmer 1972) until the typical age at first breeding. Breeding by birds in these "subadult" plumages, however, has been recorded in at least 28 species of Falconiformes (Newton 1979: 345). The selective advantage of wearing subadult plumage beyond the age of reproductive maturity has been investigated in passerines (Selander 1965, Rohwer 1978, Rohwer et al. 1980) but not in raptors. According to Newton (1979: 122), nesting by subadult raptors is usually associated with one of two conditions. Raptors may breed at a younger age when prey populations are especially abundant, as has been observed in some accipiters (McGowan 1975, Newton 1976). Alternatively, subadults may nest when human persecution artifically depletes adult numbers, as has been observed in Peregrine Falcons (*Falco peregrinus*, Ratcliff 1980: 276) and in *Aquila* populations in Europe (Valverde 1960, Novelleto and Petretti 1980). The former situation implies that nesting by subadults is limited by food resources, while the latter implies that territoriality limits nesting.

Golden Eagles (*Aquila chrysaetos*) are long-lived raptors that typically do not breed until their 4th or 5th year (Brown and Amadon 1968). Until their 4th year, eagles wear predefinitive feathering that is recognized easily in the field (Jollie 1947). Nesting by these subadult Golden Eagles has been reported at several locations in Europe and North America (Sandeman 1957; Watson 1957; Besson 1964, 1967; Bates 1976; Ellis 1979; Novelletto and Petretti 1980; Teresa 1980). This paper reports the frequency and success of subadult Golden Eagles nesting in southwestern Idaho over an 11-yr period. Environmental circumstances associated with subadult nesting are examined to determine: (1) whether nesting by subadult eagles is directly limited by food resources or territorial behavior, and (2) whether or not our observations can suggest a selective advantage for retention of subadult plumage beyond the age of reproductive maturity.

We studied nesting Golden Eagles in southwestern Idaho from 1970 to 1981 along a 240-km stretch of the Snake River Canyon that includes the Snake River Birds of Prey Area (U.S. Dept. of Interior 1979). Occupied nesting territories were located on the basis of territorial activity, courtship, brood-rearing activity, presence of eggs or young, or other conspicuous field signs. We examined some nests for eggs, eggshell fragments, or other signs of reproductive activity but observed other nests only from a distance.

We considered a territorial pair to be breeding if it laid at least one egg. A breeding attempt was confirmed by observing an incubating adult, eggs, young, or any field sign that indicated that eggs had been laid. To standardize our results, we considered a breeding attempt as successful if one or more young reached 52 days, which is 80% of the average age at which most young normally leave the nest. In addition, pairs were considered successful if at fledging time no dead young were found in or within 50 m of a well-worn nest with new nesting material, fresh prey remains, and much fecal matter on and below the nest.

From 1973 to 1981, Golden Eagle wintering populations were censused along 20 aerial transects randomly distributed along the Snake River floodplain. Transects were flown each January following the procedures of Boeker and Bolen (1972) over a 17,920-km^2 area that encompassed the nesting study area. The population sampled probably consisted of resident territorial pairs, resident nonterritorial birds, and migrants; it probably represented the pool from which new territorial pairs were recruited.

We classified eagles seen on both the nesting and wintering surveys as subadults if any white was observed on the tail or wings (Jollie 1947), and we classed all other birds as adults. Most birds classed as subadults were probably less than 3.5 yr old, but individual variation in plumage development (J. R. Murphy pers. comm.) precludes accurate aging. Sex was assigned to nesting birds only if copulation was observed or if one bird (presumably the female) spent more time incubating or brooding during several observations (Ellis 1979, Collopy 1980).

Black-tailed jackrabbits (*Lepus californicus*), the principal prey of eagles, were censused using a combination of spotlighting transects and counts by raptor survey crews (U.S. Dept. of Interior 1979). Jackrabbit abundance estimates for each nesting territory were based on the habitat composition of the territory and habitat-specific jackrabbit densities (U.S. Dept. of Interior 1979). Habitat and densities were tabulated in a 22-km^2 circle around each nest, the average home range size of radio-tagged eagles in the area (U.S. Dept. of Interior 1979). Human activity at nesting territories was assessed in the same circular areas from maps and aerial photos. All differences were evaluated at the 0.10 level of significance.

During the 11-yr study, we observed 670 occupied nesting territories (up to 63 in a single year). Of these, 330 could not be used in the analysis, because both members of the nesting pair were not observed. Of the remaining 340 territorial pairs, 17 (5%) included one subadult. We did not observe pairs in which both members were subadults. Four of the nesting subadults were males, 2 were females, and 11 were not sexed.

Three of the 17 pairs with subadults (18%) failed to lay eggs. The sex of the subadult was unknown in all three cases. This rate of nonbreeding was not significantly different ($\chi^2 = 0.10$, $P = 0.747$) from the overall rate of pairs with two adults (15%). Of the 14 pairs with subadults that bred, 6 (43%) successfully raised young that fledged. This success rate was significantly lower ($\chi^2 = 6.56$ Fisher exact one-tail, $P = 0.015$) than the rate for breeding pairs with two adults (74%). At least two of the eight failures by pairs with subadults may have been associated with the subadult's age or lack of experience. One clutch of eggs laid by a pair with a subadult male was infertile, and another clutch was abandoned by a pair with a subadult of unknown sex.

The proportion of pairs with subadults varied from 0 to 13% per year during the 11-yr study (Table 1). The frequency of subadult nesting was highest when winter adult densities were lowest (Table 1), and subadult nesting was inversely correlated with winter adult densities ($r = -0.63$, $P = 0.069$) during the 9 yr when data were collected on wintering populations. In contrast, the incidence of subadult nesting was not correlated with either density of wintering subadults ($r = -0.15$, $P = 0.667$) or yearly jackrabbit abundance ($r = 0.10$, $P = 0.787$). The total number of occupied territories did not increase either when subadult nesting was high or when rabbits were abundant.

In the year preceding occupancy by subadults, 7 territories had successful breeders, 7 had unsuccessful breeders, and 2 had nonbreeding pairs. Only one subadult appeared at a territory that had been vacant the previous 2 yr. The only territory that was reoccupied after having been vacant for more than 2 yr was occupied by a pair of which both were adults. These findings contrast with Sandeman's (1957) and Bates' (1976) observations that subadults in Scotland usually secure territories that have been vacant in previous years.

Subadults appeared at some southwestern Idaho territories significantly more often than expected (Poisson Goodness-of-Fit Test, $\chi^2 = 9.4$, $P < 0.005$). Three territories had subadults present in 2 yr, and one had subadults in 3 breeding seasons. It is unlikely, however, that the same individuals were observed in subadult plumage in different years, because subadults were seen at the same territory in consecutive years only once; in this case the bird seen the second year had significantly more white in the tail and wings than did the bird observed the year before.

TABLE 1. Proportion of subadults in the Golden Eagle nesting population in relation to jackrabbit abundance and winter eagle populations.

Year	Percentage of nesting pairs with subadults	Jackrabbit density (n/100 km^2)	Winter Golden Eagle densities (n/1,000 km^2)	
			Adult	Subadult
1970	4	—	—	—
1971	3	8,980	—	—
1972	0	—	—	—
1973	4	1,769	32	33
1974	6	1,434	22	10
1975	0	1,099	17	8
1976	6	1,319	23	8
1977	3	1,911	19	1
1978	6	2,131	18	4
1979	9	3,690	16	5
1980	13	4,798	9	7
1981	3	5,786	22	19

The 12 territories used by pairs with subadults had more evidence of human activity than did the 52 used only by adults (Table 2). There were significantly more kilometers of low-voltage-distribution powerlines within a 2.65-km radius of the nests used by subadults ($t = 3.10$, $P = 0.003$). In addition, subadults tended to nest in intensively farmed areas (Table 2) more often than expected by chance ($\chi^2 = 4.36$ Fisher exact one-tail, $P = 0.043$). Distances from nests to nearest human habitation and roads were also shorter in territories used by subadults, but the differences were not statistically significant ($t = 1.24$, 0.46; $P = 0.220$, 0.641). Although sample sizes were too small to allow statistical comparison, the territories used by subadults in more than one year appeared to have the highest level of human activity.

Prey densities were available for only 40 of the 64 territories. Jackrabbit densities at the 10 of these territories used by pairs with subadults did not differ significantly from those at the 30 territories used only by adults ($t = 1.71$, $P = 0.104$). Differences in territory quality apparently were not related to our earlier finding of lower nesting-success rates for subadults. When territories used by subadults were occupied by pairs of which both were adults, success rates did not differ significantly ($\chi^2 = 2.5$, $P = 0.114$) from those in territories used exclusively by adults.

The southwestern Idaho Golden Eagle population appears to be similar to other avian populations in which territorial behavior limits breeding density and the individuals prevented from breeding are often young birds (Carrick 1963, Ficken and Ficken 1967, Brown 1969, Newton 1979). Unlike the situation in

TABLE 2. Characteristics of nesting territories in relation to their use by subadult Golden Eagles (95% confidence intervals in parentheses).

	Territories not used by subadults ($n = 52$)	Territories used by subadults ($n = 12$)
Kilometers of powerlines	4.5 (3.4-5.6)	9.1 (4.7-13.6)
Distance from nest to nearest road (m)	523 (387-658)	452 (203-701)
Distance from nest to nearest human habitation (m)	2,272 (1,868-2,675)	1,712 (934-2,488)
Percentage of territories intensively farmed[a]	27% (15-39)	58% (30-86)

[a] Intensively farmed territories had more than 20% of the 22-km² area surrounding the nest farmed.

accipiters (McGowan 1975) and kestrels (Village 1979), subadult nesting in Golden Eagles did not coincide with periods of food abundance. Instead, subadults apparently nested only when there was an available slot in one of the relatively stable territories. The inverse correlation between winter adult densities and the frequency of subadult nesting suggests that territorial openings were most often filled by subadults when nonterritorial adults were not available. When eagle populations were high, birds in adult plumage were more likely to fill territorial slots than were subadults.

The type of territories used by subadults provides additional evidence that territoriality rather than food limits their nesting. Unlike young Sparrowhawks (*Accipiter nisus*), which nested mainly in areas with high prey densities (Newton 1976), subadult Golden Eagles used territories that had prey densities similar to those in all territories surveyed. Territories used by subadults did not appear to be inferior from the standpoint of rearing young, but they did show signs of increased human activity. The most likely explanation for the use of disturbed territories by subadults is higher turnover rates among the pairs occupying them. Higher turnover rates could be caused by either mortality or emigration and would result in more frequent mate replacement and increased chances for subadult nesting. The presence of humans could increase both mortality and emigration through shooting, chemical contamination, electrocution, or stress. These situations parallel the conditions facing European *Aquila* populations and further verify the significance of territoriality in Golden Eagles.

Existing theories that attempt ot explain the retention of subadult plumage beyond the age of maturation have been developed for passerines and are based on cryptic feathering (Selander 1965) and female mimicry (Rohwer 1978, Rohwer et al. 1980). Subadult plumages in Golden Eagles are neither cryptic nor female-mimicking. Golden Eagles also differ from passerines in that territories are usually occupied year-round, there is a prolonged period of parental care, and both sexes have deferred maturity and subadult plumages. Although the existing hypotheses are inadequate to account for subadult plumages in Golden Eagles, aspects of both Selander's and Rohwer's explanations appear relevant to Golden Eagle breeding biology.

Distinctive plumages probably facilitate age-class discrimination both by birds selecting mates and by those competing for territories. Subadult plumage may offer young birds protection against aggression from competitive adults. Brown and Watson (1964) and Kochert (1972) observed that territorial eagles seemed less aggressive toward subadults that enter their territories. The mechanism for this reaction might be explained by a modification of Rohwer's mimicry hypothesis. In a species with prolonged parental care, selection would favor individuals that do not react aggressively to their own young. The white wings and tail of first-year eagles may be the stimuli that suppress aggressive behavior. Older eagles with plumages that resemble first-year birds are also unlikely to elicit aggressive responses from adults. Thus, by mimicking younger birds, subadult eagles can obtain the same advantages that passerines obtain by mimicking females. Reduced aggression would allow eagles access to food resources in and near territories. Unlike the situation in passerines, however (Rohwer 1978), the reduced aggression probably does not enhance opportunities for breeding by subadult eagles. Our observation that subadults rarely nested when adult densities were high suggests that subadults were not acquiring territories deceptively (Rohwer 1978). The same signals that reduce aggressive encounters between eagles probably also reduce an individual's chance of obtaining a territory and mate. Newton et al. (1981) observed that Sparrowhawks mate selectively by age/plumage. Indeed, our data on differences in breeding success by plumage class may indicate a possible selective advantage for territorial eagles that do not mate with subadults. The advantage, then, in retaining subadult plumage would be protection from aggression and access to food resources. The disadvantage that would preclude "cheating" would be failure to breed except when adult densities are low.

Additional research needed to verify these hypotheses would include determining whether or not territorial adult eagles do, in fact, respond less aggressively to subadults, territorial birds actively choose mates wearing definitive feathering, and other raptors with delayed maturation and prolonged periods of parental care show similar strategies. More information is also needed on eagle mortality rates, particularly in relation to areas of human activity.

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Foraging Behavior and Success of Golden Eagles

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Quantitative data on the predatory behavior and capture success of free-living birds of prey are difficult to obtain. Consequently, most studies have assessed predation indirectly from prey remains found on nests (e.g. Craighead and Craighead 1956, Smith and Murphy 1973) or by observing prey delivery rates to nests (e.g. Snyder and Wiley 1976, Newton 1978, Collopy 1983). For most species, however, available information remains qualitative (Bent 1937, Brown and Amadon 1968, Brown 1977). The purpose of this paper is to describe the hunting behavior and capture success of Golden Eagles (*Aquila chrysaetos*).

The study area, known as the Snake River Birds of Prey Area (BPA), is located along the Snake River Canyon in the cold desert plateaus south of Boise, Idaho. Vegetation and topography of the area are described by USDI (1979) and Collopy (1980).

Each of four pairs of nesting Golden Eagles was observed approximately once every 6th day during incubation, brood-rearing, and post-fledging periods at four sites in 1978 and 1979 (Collopy 1980). I directly observed adults away from the nest by means of focal animal sampling (Altmann 1974). In 1978, 961.6 h of daylight observations were made at study sites during 72 24-h sampling periods; in 1979, 1,107.7 h of daylight observation were made at sites during 78 24-h sampling periods. The amount of time individual eagles were observed varied, depending on their behavior and on the local topography. A second observer simultaneously observed nests during the brood-rearing period from blinds located 15-40 m away, which allowed the identification of the prey and the sex of the adult. Individual recognition of adults at the nest was facilitated by photographs showing unique plumage characteristics. I readily distinguished one male by the radio-telemetry transmitter that had been attached to it by an earlier researcher (Dunstan et al. 1977). When both eagles hunted together or in the same vicinity, sex was assigned based on relative body size (females are larger than males). All capture attempts by eagles of unknown sex were excluded from consideration.

Golden Eagles were observed to hunt and capture prey while foraging alone (solo-hunt) and in pairs (tandem-hunt). Each predatory attack (e.g. pounce or stoop) directed at potential prey was considered a capture attempt. The percentage of success was calculated as the proportion of capture attempts with known outcomes that were successful. All capture attempts with undetermined outcomes were excluded from analysis. Overall, 10 of 92 (10.9%) attempts by males and 3 of 36 (8.3%) attempts by females were of unknown capture success due to distance from observer and/or local topography.

Chi-square contingency tests (Remington and Schork 1970) were used to detect significant differences ($P < 0.05$) in capture success due to mode of hunting and sex.

Male Golden Eagles attempted significantly more prey captures when solo-hunting than when tandem-hunting ($\chi^2 = 19.2$, $P < 0.0005$); females used both foraging methods equally ($\chi^2 = 1.0$, $P > 0.30$) (Table 1). This difference in hunting mode between the sexes was due to the fact that males had fewer opportunities to tandem-hunt early during the nesting season when females were brooding young and not hunting. The eagles tandem-hunted primarily late in brood-rearing when nestlings were left unattended for most of the day (Collopy 1980). Fisher (1893), Willard (1916), and Gordon (1955) have also reported tandem-hunting in Golden Eagles.

Overall, 26 tandem-hunts were recorded. Pairs frequently were observed systematically quartering the ground below cliffs along talus slopes. The eagles typically were oriented into the wind, which enabled them to course slowly over vegetation and attack any potential prey from relatively close quarters. During tandem-hunts the male was always in front of the female and appeared to lead the direction of the hunt. Males also flew at greater heights than females on 23 (88%) of the hunts. Frequently during a hunt, the male circled back, with the female following, to revisit a particular area on the slope. Solo-hunting eagles foraged in the same areas, searching with the same low coursing flight.

Twenty (77%) of the tandem-hunts resulted in cap-