PARENTAL CARE AND FEEDING ECOLOGY OF GOLDEN EAGLE NESTLINGS

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ABSTRACT.—A field study of Golden Eagles (*Aquila chrysaetos*) nesting in and near the Snake River Birds of Prey Area was conducted during 1977–1979. Patterns of parental care differed between female and male eagles during incubation and chick rearing; males consistently captured more food throughout all phases of brood rearing (1.2 vs. 0.6 prey/day), while females typically fed and tended the offspring. During the 7th through 9th week of chick rearing, when the food requirements of nestlings were greatest, the female contributed 43% of the prey biomass. No differences were observed in mean daily capture rates between 1978 and 1979 or between parents of one-chick broods and parents of two-chick broods. Although there were no differences between the sexes in the mean weight of prey captured, there were significant differences among pairs, suggesting differences in prey availability or hunting ability. The daily food consumption of eaglets increased as chick rearing progressed and peaked between the 7th and 9th week. Comparisons between eaglets in different-sized broods revealed that individuals in multiple-chick broods received more food from adults than those in one-chick broods. Late in chick rearing, however, those chicks competing with siblings for food had lower consumption rates. *Received 24 February 1984, accepted 1 May 1984.*

THE general nesting biology of Golden Eagles (*Aquila chrysaetos*) has been described by many naturalists (e.g. MacPherson 1909, Gordon 1927, Bent 1937). Several studies also have been conducted specifically on territory size (Dixon 1937), molt (Jollie 1947), and growth (Sumner 1929, 1933). More recently, research on Golden Eagles has focused on diet and food requirements (e.g. Fevold and Craighead 1958, McGahan 1967, Mollhagen et al. 1972) and nesting success (e.g. Smith and Murphy 1973, U.S.D.I. 1979).

Although these studies contributed greatly to our understanding of eagle biology, none has described the relationship between nestling food consumption and parental care. In this paper, I quantify the division of labor between the sexes of Golden Eagles during breeding and relate these activities to the food consumption of nestlings. The size and total biomass of prey delivered to young by male and female eagles also are considered in relation to theories of sexual size dimorphism and parental investment.

STUDY AREA AND METHODS

The study was conducted along the Snake River Canyon and surrounding upland desert plateau south of Boise, Idaho. This 195,063-ha area, known as the Snake River Birds of Prey Area (BPA), is administered by the Bureau of Land Management and lies within the Great Basin semidesert scrub biome (Whittaker 1975). The major vegetation types in the area include big sagebrush (*Artemisia tridentata*) associations, grasses (*Poa* and *Bromus* spp.), and shadscale (*Atriplex confertifolia*). Approximately one-fifth of the BPA is cultivated. A more detailed description of the vegetation can be found in U.S.D.I. (1979) and Collopy (1980).

Incubation data were collected in 1977–1979 from 11 nesting attempts. Weekly observations at each site were made from a prominent location 150–750 m from the nest, and the amounts of time each parent spent incubating or brooding were recorded. Instances of male eagles providing prey to females when relieving them from incubation also were recorded.

Data during the nestling period were collected at the same four nest sites in 1978 and in 1979. Daylong observations at each study site were made once every 6 days from blinds 15–40 m away. Photographs showing unique plumage characteristics of the breeding adults in 1978 and in 1979 revealed that the same individuals nested at the same sites in both years. The sex of parents was determined from these photographs, from size differences, and from behavior. I identified parents during each nest visit by using these unique plumage characteristics and by comparing photographs of adults taken during each visit. Adults away from the nest were monitored by a second observer, so when identification of the parent on the nest seemed uncertain it was confirmed by accounting for the location and sex of its mate. For a detailed description of nestling diet and nest

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The Auk 101: 753–760. October 1984

observation and visitation procedures see Collopy (1983a).

Parental care of nestlings involved both sheltering and feeding. Sheltering activities included brooding and shading, and both are discussed in this paper. Both the delivery of prey to the nest and its consumption by nestlings were considered feeding activities. The parental care of each adult was analyzed in relation to the age of its offspring. Following each observation period, I measured the body weight and foot-pad size (tip of hallux to tip of middle toe on extended foot) of the chicks (Kochert 1972). Determination of the sex of each chick was made late in the nestling period when size dimorphism became obvious.

All prey delivered to the nest during each observation period were identified to species and assigned to a size class. The estimated proportion of the carcass delivered and sex of the eagle delivering the prey also were recorded. I calculated prey biomass delivered to nests from the estimate of the proportion of the carcasses delivered and the species' weights (Steenhof 1983).

A series of experiments on the food consumption and growth energetics of captive Golden Eagle chicks was conducted concurrently with this study (Collopy 1980). These feeding trials were designed to monitor the consumption rates of eaglets presented black-tailed jackrabbit (*Lepus californicus*) food *ad libitum* and to quantify their growth rates. Because of permit restrictions, the birds were tested only between the ages of 11 and 57 days old. Following the experiments, they were returned to foster eagle nests in the wild, from which they all successfully fledged. During the feeding trials, it was apparent that one meal each day was much larger than all others and that it represented the maximum quantity a chick that age could consume. I quantified this relationship for the two female and two male eaglets tested by expressing the maximum meal size (Y, grams) as a function of age (X, days):

$$\begin{aligned} \text{female: } Y &= -99.96 + 12.31X; \\ R^2 &= 0.87, P < 0.0001; \\ \text{male: } Y &= -20.76 + 7.68X; \\ R^2 &= 0.85, P < 0.0001. \end{aligned}$$

Following each meal, the percentage of the crop of each wild nestling that was full was estimated, and the amount of food consumed was calculated.

Statistical procedures used to analyze data included the Chi-square test, two-sample t-test, and analysis of variance (Remington and Schork 1970). Assumptions of the normality and equal variance of the statistical models were tested; percentage data were arcsine transformed before analysis whenever they were outside the interval between 30 and 70%. All means are reported with standard errors.

RESULTS

Incubation.—A total of 692 daylight hours (56 observation days) of data was collected at 11 Golden Eagle nests during incubation in 1977–1979. At the 10 sites that hatched young, female eagles spent a significantly greater portion of the day incubating (82.6 ± 1.6%) than males did (13.8 ± 1.8%) ($t = -22.90$, $P < 0.0001$). Eggs were left exposed only 3.7 ± 0.4% of the daylight hours. In addition to performing the majority of the daytime incubation, only females incubated at night. Overall, males relieved incubating females 2.1 ± 0.1 times daily and averaged 49.4 ± 4.7 min per incubation bout. Of the 111 male-initiated changeovers, 17 (15.3%) involved food transfers to the female on or near the nest. Eagle behavior away from the nest was not monitored systematically during incubation; females occasionally were observed foraging on their own, however, when males did not provide them with food.

The unsuccessful eagle pair abandoned their nesting effort during the third week of incubation in 1978. The male incubated only once during my 23.4 h of daylight observations and did not deliver any food to his mate. The lower incubation time of the female (67.5% of daylight hours) and the greater exposure time of the eggs (31.6%) suggest that inattentiveness by the male may have forced the female off the nest to forage and ultimately to abandon her effort altogether. No direct evidence exists that the male who successfully bred at this site in 1977 died or was supplanted, but the lack of synchrony between the pair in 1978 suggests that a different male was present.

Brooding/shading nestlings.—A total of 1,248 daylight hours (86 observation days) of data was collected during chick rearing at eight nests in 1978–1979. Chick rearing was defined as the period between the hatching of the first egg and the fledging of the last offspring. Although males regularly landed on nests to deliver prey, they were present only 0.6 ± 0.2% of the observation time. I observed a male brooding and feeding nestlings only once during the study. Clearly, the parental role of males during brood rearing was to provide food, because essentially no time was invested in brooding or feeding young. Several other workers who closely monitored parental behavior at the nest also reported that male eagles rarely brooded or fed young (Hunsicker 1972, Hoechlin 1974, Ellis 1979).

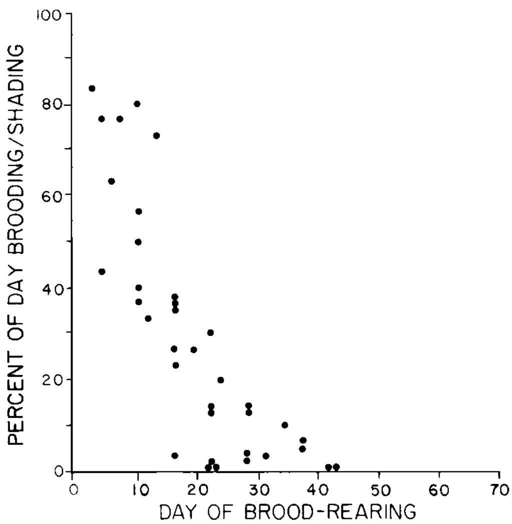

Fig. 1. Percentage of day female Golden Eagles brooded and/or shaded nestlings on the BPA in relation to day of chick rearing in 1978-1979. Zero values for brooding and shading after day 25 are not plotted.

Female eagles averaged 10.9 ± 1.2% of the daylight hours brooding or shading young. The percentage of daylight hours females brooded or shaded their young decreased rapidly, however, as brood rearing progressed (Fig. 1); no chicks were sheltered after 42 days of age. Overall daytime attendance at nests by females averaged 24.0 ± 2.5%, with declines in nest attentiveness paralleling those of brooding and shading as chick rearing progressed. This decrease in attentiveness corresponded with the increased ability of nestlings to thermoregulate, walk, and feed themselves (Collopy 1980). A comparison of female brooding/shading behavior indicated no significant difference among the four sites studied ($F = 0.28$, $P = 0.84$).

As during incubation, only female parents were observed on the nests at dusk; females brooded nestlings nightly until they were an average of 29 days old (range 17-42). After nighttime brooding was suspended, females continued to roost on the nest until the chicks averaged 40 days old (range 17-54 days). Similar patterns of brooding and shading by adult females were reported by Ellis (1979). Precise fledging dates were not obtained, but all nestlings fledged when they were between 66 and 75 days old.

Prey deliveries.—A paired comparison of delivery rates during each week of the breeding season indicated that male Golden Eagles provided significantly more prey items than females did ($t = 3.80$, $P < 0.005$). This was particularly evident during the first 2 weeks of brood rearing, when males delivered 83% of the prey items and over 95% of the prey biomass (Table 1). Females increased their prey deliveries during the third week of chick rearing, when they began spending more time away from the nest. The maximum contribution by females occurred during the 7th through 9th week, when they delivered an average of 43% (range 41-45%) of the biomass received by the nestlings. This 3-week period of hunting by both parents

TABLE 1. Number and biomass of prey deliveries by male and female Golden Eagles to nests on the BPA in 1978-1979 in relation to week of chick rearing.

Week of chick rearing	Number of daylight hours observed	Mean (±SE) number of prey deliveries per 15-h day		Mean (±SE) biomass (g) of prey delivered per 15-h day	
		Male	Female	Male	Female
1	67	1.4 ± 0.38	0.1 ± 0.13	1,251 ± 426.5	7 ± 6.5
2	103	1.2 ± 0.43	0.3 ± 0.19	750 ± 15.6	26 ± 16.9
3	119	0.7 ± 0.27	0.6 ± 0.37	503 ± 295.8	309 ± 166.9
4	134	1.3 ± 0.41	0.0	1,137 ± 372.8	0
5	158	1.1 ± 0.36	0.6 ± 0.27	714 ± 262.7	216 ± 149.2
6	121	1.6 ± 0.46	0.8 ± 0.31	1,184 ± 303.8	286 ± 178.6
7	145	1.3 ± 0.25	1.0 ± 0.38	1,317 ± 556.7	902 ± 313.2
8	122	1.5 ± 0.27	1.5 ± 0.33	1,140 ± 260.8	845 ± 241.2
9	134	0.9 ± 0.23	0.8 ± 0.31	968 ± 359.3	801 ± 315.2
10	145	1.0 ± 0.27	0.5 ± 0.27	1,331 ± 500.6	482 ± 276.2
Overall	1,248	1.2 ± 0.28	0.6 ± 0.44	1,030 ± 284.6	387 ± 270.0

TABLE 2. Mean biomass of prey delivered to nests on the BPA by male and female Golden Eagles in 1978–1979.

	Male			Female			Total		
Nest site	n	Mean prey weight	SE	n	Mean prey weight	SE	n	Mean prey weight[a]	SE
Con Shea	19	989	197	16	992	145	35	990[1]	167
Mudflat	24	1,602	146	7	1,103	356	31	1,489[2]	267
Feedlot	23	1,697	134	4	967	513	27	1,589[2]	306
Indian Cove	33	487	100	28	614	125	61	545[3]	70

[a] Means with different superscripts are significantly different ($P < 0.01$); those with the same superscript are not significantly different ($P > 0.50$).

resulted in peak prey-delivery rates averaging 2,219 g/day, 1,985 g/day, and 1,769 g/day, respectively.

Overall, prey biomass delivered to eagle nests during this study averaged 1,417 g/day (Table 1), considerably more than the 885 g/day delivery rate reported for eagles in Texas (Lockhart 1976). This difference resulted from a greater rate of food delivery (1.8 vs. 0.9 per day) and heavier prey captured (1,153 vs. 947 g) by Golden Eagles in the BPA.

Prey captured by male and female Golden Eagles were not significantly different in mean body weight ($t = 1.35$, $P > 0.10$) (Table 2). Although differences were detected in the size of prey captured at specific study sites (Table 2), I considered these to be the result of different habitats that supported different prey populations (Collopy 1980).

Food consumption.—Prey biomass consumed daily by Golden Eagle nestlings increased during chick rearing, with a peak occurring between weeks 7 and 9 (Fig. 2). This peak corresponded with the period of greatest food consumption and metabolism by captive eaglets fed *ad libitum* (Collopy 1980). During the final week of chick rearing, prey-delivery rates were reduced, and food consumption by young was lower.

The amount of food fed to nestlings by adult females increased from hatching to the 5th week of brood rearing (Fig. 2). During subsequent weeks, however, the relative contribution by females diminished as nestlings became more proficient at feeding themselves. Eaglets were between 34 and 37 days old before they were first observed pulling small quantities of food from prey carcasses. Ellis (1979) also first observed eaglets feeding themselves at 5 weeks of age. Increases in self-feeding during subsequent weeks coincided with the development of the chicks' ability to stand; this enabled nestlings to hold prey with greater proficiency and to tear meat with their beaks.

My limited sample size precluded a statistical analysis of the effects of sex and brood size on daily food consumption of eaglets. Nevertheless, a qualitative comparison between the sexes suggested that female eaglets fed themselves more each day than did males (Fig. 3). Presumably, this resulted from the ability of females to consume more food per meal as they grew older. There was little difference between the sexes in the biomass consumed during adult-fed meals.

The pattern of food consumption by nestlings in one- and two-chick broods differed

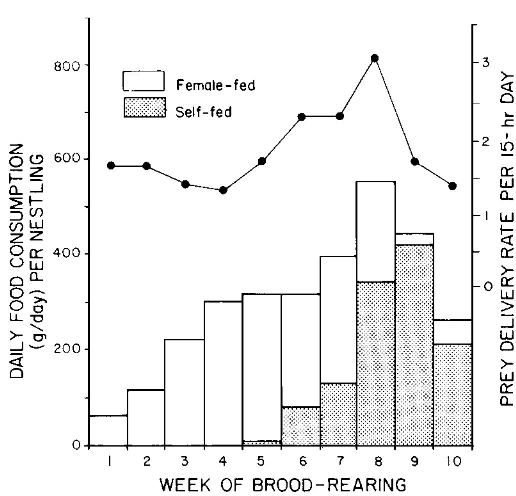

Fig. 2. Mean prey-delivery rates by Golden Eagle parents and daily food consumption by nestlings on the BPA during each week of chick rearing in 1978–1979.

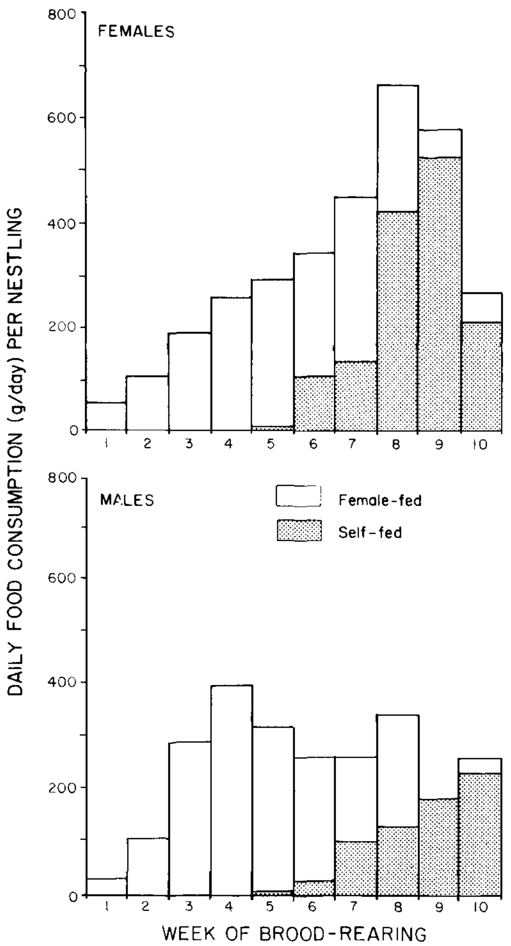

Fig. 3. Mean daily food consumption by female and male Golden Eagle nestlings on the BPA during each week of chick rearing in 1978–1979.

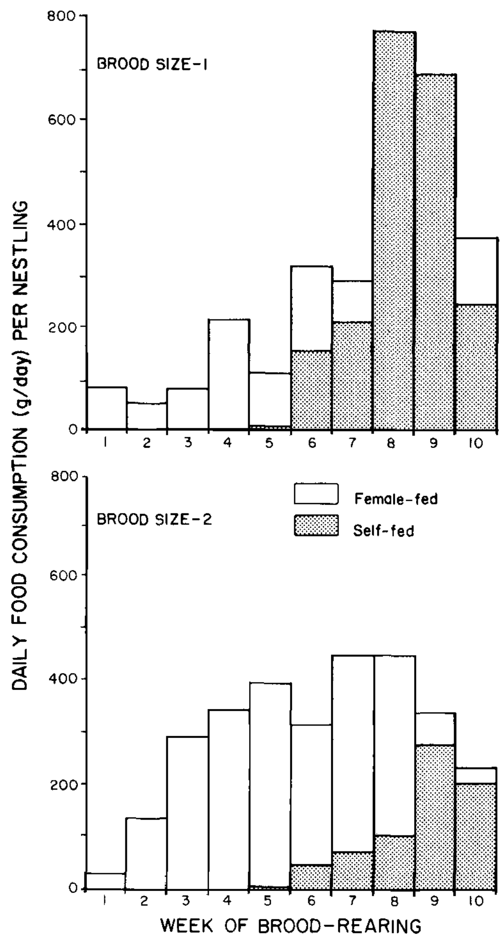

Fig. 4. Mean daily food consumption by chicks in broods of one and two on the BPA during each week of chick rearing in 1978–1979.

substantially because of differences in both adult-fed and self-fed meals (Fig. 4). Individuals in two-chick broods consumed more food during adult-fed meals than did those in one-chick broods. This was because they received significantly more adult-fed meals per day ($F = 14.28$, $P = 0.002$) than did those in one-chick broods. Single chicks, however, had greater consumption rates during self-fed meals than did eaglets in two-chick broods (Fig. 4). Apparently the lack of sibling competition enabled nestlings in one-chick broods to feed themselves more food, particularly because no difference was found in the total biomass of prey delivered to nests with different-sized broods ($t = 0.33$, $P = 0.23$).

Discussion

Incubation.—Newton (1979) characterized three types of division of labor that occur between the sexes in raptors during incubation: (1) no incubation by the male, (2) temporary relief and incubation by the male while the female feeds and rests, and (3) equal sharing of incubation by both sexes. Golden Eagles are typical of the second category, males incubating 14% and females 83% of the daylight hours. Incubation by males can be very important in protecting eggs from chilling or predation when the female is off the nest feeding or resting. The relative contribution of the males varies widely, however, even between congeneric species. For example, data from four Black Eagle (*A. verreauxi*) nests indicated that males incubated approximately 27% of the daylight hours (Rowe 1947; Brown 1952, 1955; Gargett 1977). In contrast, male Wahlberg's Eagles (*A. wahlbergi*) never incubated at the four nests monitored by Brown (1952, 1955).

During the incubation periods at the 10 successful nests monitored in this study, male eagles delivered 17 prey items at a rate of one every 3.3 days. The importance of male prey deliveries was demonstrated at another nest, where the inattentive male was not observed to deliver food to the incubating female. This frequently forced the female off the nest to forage for herself and, in the third week of incubation, to abandon the nesting effort. The delivery rates at Golden Eagle nests in which eggs hatched were similar to the rates (one prey item delivered ever 3.5 days) of male Crowned Eagles (*Stephanoaetus coronatus*) during incubation (Brown 1966). Rettig (1978) reported that a male Harpy Eagle (*Harpia harpyja*) delivered prey to the female once every 7 days during incubation.

Chick rearing.—Parental care exhibited by Golden Eagles during chick rearing is characteristic of large raptors (Brown and Amadon 1968, Newton 1979). Although not often found at the nest, male Golden Eagles play a critical role in breeding success by providing most of the food for the female and young early in, and sometimes throughout, the chick-rearing period. Females are closely associated with the nest early during chick rearing, but, as the young grow and develop thermoregulatory capabilities, females gradually brood and shade less often. By the 5th week, Golden Eagle nestlings are standing and attempting to feed themselves. In subsequent weeks, as the nestlings become more proficient at feeding, females spend less time on the nest and return principally to deliver prey and occasionally to feed the young. It is during this later phase of chick rearing that the female parents capture greater numbers of prey, thus increasing the total amount of food brought to the nest and reducing the relative contribution of the male.

During the first 5 weeks of chick rearing, Golden Eagles in this study delivered an average of 1.5 prey items per day to the nest; males delivered the majority of the prey (1.1 prey items per day), while females primarily brooded and fed the young. During the 6th through 8th weeks of chick rearing, the prey-delivery rate by adult eagles increased to 2.6 prey items per day. Although male eagles contributed to this increase, the 1.1 prey items delivered per day by females accounted for 67% of the increase. During the final 2 weeks of chick rearing, the prey-delivery rate of parents declined to 1.6 prey items per day; male eagles delivered 0.9 and females 0.7 prey items per day. Declines in prey-delivery rates just before fledging appear to be typical of Golden Eagles (Gordon 1927, Brown 1955, Brown and Amadon 1968). In fact, Brown (1955) suggested that parents intentionally reduced their food supply to offspring late during chick rearing and that this reduction facilitated the fledging process.

Similar shifts in the relative proportion of prey items delivered by each parent during chick rearing have been reported for several large raptor species. Prey deliveries by female Crowned Eagles (Brown 1966) and Wahlberg's Eagles (Brown 1955) late during chick rearing exceeded those of the male. In most other species studied, including Ayres' Hawk-eagles (*Hieraaetus dubius*; Brown 1955), Brown Snake Eagles (*Circaetus cinereus*; Steyn 1972), and Harpy Eagles (Rettig 1978), the increased hunting by the female late during chick rearing approached but did not surpass the delivery rate of the male.

The reversed sexual size dimorphism that exists in most raptor species, females being larger than males, often has been interpreted as an adaptation to facilitate the capture of different-sized prey, thereby expanding the food niche and reducing intersexual competition for food (see Selander 1966, Storer 1966, Earhart and Johnson 1970). The direction of this dimorphism recently was interpreted by von Schantz and Nilsson (1981) as an adaptation by which females reduce the relative cost of egg production and increase their ability to capture larger prey. Several other interpretations involving behavioral dominance, nest defense, and energetics also have been proposed (see Newton 1979 for review). Male and female Golden Eagles, although moderately dimorphic compared to other raptors (Brown and Amadon 1968, Snyder and Wiley 1976), did not capture significantly different-sized prey. Although these findings do not support the food-niche hypothesis, it should be noted that this study was conducted during years of average, but increasing, black-tailed jackrabbit densities

(U.S.D.I. 1979). Before any definitive interpretations can be made, it should be determined whether or not male and female eagles exploit different prey during periods of low jackrabbit abundance.

There also was no difference in the amount of food Golden Eagles provided to different-sized broods. Males delivered a fairly uniform supply of prey, which was supplemented by females late during chick rearing when food requirements of the young were greatest. This pattern of food delivery may reflect a limited capacity in the male for prey capture and a need for the female to hunt late in chick rearing. Others also have suggested that the total amount of food captured by adult raptors may be determined primarily by foraging success and not the food requirements of the young (Tinbergen 1940, Snyder and Snyder 1973, Newton 1978).

Even though the capture-success rate of Golden Eagles is not high (20%; Collopy 1983b), it is possible that the prey biomass delivered by males and females may not represent the maximum amount of food they could potentially capture. Instead, it might reflect the level of parental care that is adaptive for that brood. Golden Eagles are long lived and can breed for several years once a territory is established. Consequently, the parental care shown by an adult during a particular reproductive effort should be evaluated in relation to its detrimental effects on future reproduction (Trivers 1972). Inclusive fitness of an adult eagle may actually decrease if the parental care provided during a particular nesting effort sufficiently decreases survivorship or the ability to reproduce successfully in the future (see Williams 1966). Several aspects of their reproductive behavior support the interpretation that Golden Eagles have a conservative parental investment strategy; these include substantial increases in the number of nonbreeding pairs during poor prey years (U.S.D.I. 1979), sensitivity to disturbance during incubation (Fyfe and Olendorff 1976), and lack of aggressive nest defense against humans (Bent 1937).

Acknowledgments

This study was part of the Snake River Birds of Prey Research Project and was funded largely by the Bureau of Land Management. Partial funding also was provided by the National Wildlife Federation, Sigma Xi, and the University of Michigan. Many individuals assisted throughout this study; in particular, I thank my advisor, D. McCullough, and my doctoral committee, R. Storer, G. Fowler, J. Diana, and R. Drobney. M. Kochert, K. Steenhof, A. Bammann, and other BLM employees provided valuable technical assistance. Particular thanks go to T. Edwards and D. Blasdell for their dedicated field assistance. I also wish to acknowledge the critical reviews offered by J. Bednarz, S. Beissinger, K. Bildstein, T. Edwards, D. Ellis, J. Fraser, M. Kochert, and K. Steenhof. This paper is contribution 5417 of the Journal Series, Florida Agricultural Experiment Station, Gainesville, Florida 32611.

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