

FOOD CONSUMPTION AND GROWTH ENERGETICS OF NESTLING GOLDEN EAGLES

MICHAEL W. COLLOPY¹

ABSTRACT.—Food consumption, energy metabolism, and growth of 12 wild Golden Eagle (*Aquila chrysaetos*) chicks were compared with 4 captive chicks to evaluate the influence of food availability and sibling interaction on growth in wild nestlings. Captive female and male eaglets consumed and assimilated similar amounts of black-tailed jack rabbit (*Lepus californicus*). A linear relationship between age and maximum meal size was used in conjunction with field estimates of crop fullness to refine calculations of daily consumption. Growth of captive chicks was very similar to patterns exhibited by wild nestlings. Among wild nestlings, however, females had significantly heavier asymptotic body weights, but slower growth rates than males. Growth curve inflection points occurred 2.2 days later for females than for males, but the difference was not significant. The energy metabolized (ME) by captive and wild female eaglets showed similar increasing trends throughout the chick-rearing period. ME values for captive and wild males, however, differed substantially. Wild male eaglets had reduced ME values during the sixth week of chick rearing, a time when captive males showed peak consumption rates. This difference may have been due to the presence of sibling competition, principally with females, for food. Received 20 May 1985, accepted 7 Mar. 1986.

Previous work on nesting Golden Eagles (*Aquila chrysaetos*) has focused mainly on diet and nesting biology (see MacPherson 1909, Gordon 1927, Bent 1937, Carnie 1954, Mollhagen et al. 1972, Smith and Murphy 1973). A few studies quantified food requirements using captive (Fevold and Craighead 1958) and wild (Brown and Watson 1964, McGahan 1967) eagles. Several of these nesting studies also reported growth patterns of eaglets, but none concurrently quantified the food consumption of young.

Here I document the food consumption, energy metabolism, and growth rates of captive Golden Eagle nestlings, and compare these values with consumption and growth rates of nestlings in the wild. I also discuss differences between wild and captive chicks in relation to the effects of sibling competition and food availability on the growth of wild eagles.

STUDY AREA AND METHODS

Field study.—The study area was within the Snake River Birds of Prey Area (BPA) and included the Snake River Canyon and surrounding upland desert plateau south of Boise, Idaho, in Owyhee and Elmore counties. The BPA, administered by the Bureau of Land Management, lies within the Great Basin semidesert scrub biome described by Whittaker (1975). Major vegetation types in the area include big sagebrush (*Artemisia tridentata*)

¹ School of Natural Resources, Univ. Michigan, Ann Arbor, Michigan 48104. (Present address: Dept. Wildlife and Range Sciences, 118 Newins-Ziegler Hall, Univ. Florida, Gainesville, Florida 32611.)

associations, shadscale (*Atriplex confertifolia*), and grasses (*Poa* and *Bromus* spp.) (U.S.D.I. 1979).

I observed the offspring of 4 pairs of Golden Eagles in or near the BPA throughout the nesting season in both 1978 and 1979. Because each breeding pair fledged young in 1978, and subsequently nested in the same nests in 1979, I assumed that my presence did not seriously disturb the birds. I monitored the feeding behavior of nestlings from blinds placed 15–40 m away from the nest during 24-h observation periods (noon to noon). At the end of each meal, I estimated the percent fullness of each chick's crop (0, 25, 50, 75, or 100% full). The amount of food consumed by each nestling was calculated using the estimate of crop fullness and the linear relationship describing maximum meal size as a function of age, established with captive male and female chicks (see Results). Estimates of the mean amount of energy metabolized daily (ME) were obtained for male and female nestlings during each week of chick rearing by multiplying the mean daily consumption rates by the efficiency with which black-tailed jack rabbits (*Lepus californicus*) were digested and assimilated (established using captive young). Wild nestlings consumed other vertebrates in addition to jack rabbits, and I assumed their ability to digest and assimilate these prey was similar to that for rabbits.

After each observation period, I climbed to the nest and weighed each nestling, measured its foot-pad length (Kochert 1972), and estimated the percent fullness of its crop and calculated the corresponding biomass in the crop. The corrected body weight of each chick was calculated by subtracting the estimated biomass of food contained in the crop from the total body weight (Collopy 1983). Sex of the study birds was assigned using a discriminant function derived from body weight and foot pad measurements on eagles of known sex (Edwards and Kochert, in press). Measurements of hallux claw length and culmen length (see Bortolotti 1984a) were not taken, so discrimination based on these characters was not possible.

Weight data were analyzed using the Statistical Analysis System's (SAS) nonlinear least squares curve-fitting procedure (NLIN). Logistic and Gompertz growth models were used to fit curves to both male and female weights (Ricklefs 1968). The logistic model best fit the data (Ricklefs, pers. comm.), and I used it to calculate the growth rate constants (K), asymptotic body weights (A), and inflection points (t) of both captive and wild eaglets.

Captive bird study.—In 1978 and in 1979, two Golden Eagle chicks, 10–14 days old, were taken from nests in or near the BPA for use in feeding trials. At the conclusion of the experiments the nestlings were placed in foster nests in the wild from which they fledged successfully. Sex of the nestlings again was assigned based on body weight and foot-pad measurements taken just prior to release; we studied 2 females in 1978 and 2 males in 1979.

The study birds were housed in an unheated, enclosed building 4.0 m long, 1.8 m wide, and 2.5 m high. Each eaglet was isolated in an uncovered wooden cubicle inside the structure. Initially, dimensions were 0.7 m \times 0.9 m. Later, as the birds grew and required more space, cubicle size was enlarged to 1.0 m \times 1.9 m.

Black-tailed jack rabbits, the predominant prey species of Golden Eagles in southwestern Idaho (U.S.D.I. 1979), were used as food in the feeding trials. As the energy content of small mammals can exhibit considerable seasonal variation (Gorecki 1965, Schreiber and Johnson 1975), and as I was attempting to feed the captive chicks a diet normally encountered in the wild, I used jack rabbits that were collected periodically during the feeding experiments. Jack rabbits were collected on 12 April, 7–12 May, and 17 May in 1978, and on 11 April, 25 April, 9 May, and 15 May in 1979. Each whole jack rabbit was weighed, the stomach and intestines removed, and the carcass homogenized using a meat grinder. To guard against possible vitamin and mineral deficiencies, calcium and multiple vitamin supplements were supplied daily to each chick.

Seven consecutive feeding trials were conducted with each captive chick. The duration of each trial ranged from 5 to 7 days. Every morning before the first meal, the birds were weighed on spring scales, and any regurgitated pellets were collected. During each feeding experiment, the study birds were fed approximately the same number of meals daily that I observed wild nestlings of the same age receive (Collopy 1980); however, captive birds were allowed to feed until satiated. The biomass of food consumed at each meal was calculated by subtracting the amount remaining at the end of the meal from the total weight of food presented to the bird. All excrement voided during the course of each experiment was collected from plastic sheeting used to line the cubicles.

The total weights of pellets and excrement obtained during each feeding experiment were determined after oven drying to a constant weight at 65°C. Percent water contained in jack rabbits from each collection was calculated by drying the samples at 65°C and determining the percent weight loss. Fat was extracted from the samples of eagle pellets and excrement with petroleum ether (Soxhlet method; Horwitz 1975), and from samples of all collections of black-tailed jack rabbits. Percent fat in all samples of jack rabbits, eagle pellets, and excrement was determined indirectly by calculating the percentage of material lost following the fat extraction. Energy content (kJ/g) of samples of fat extracted from food, and fat-free extracts from food, pellets, and excrement associated with each feeding trial were analyzed in a Parr adiabatic bomb calorimeter.

Energy ingested (I), egested (E), and metabolized (ME) by each chick during each experiment was calculated from the biomass consumed and the caloric contents of black-tailed jack rabbits, eagle pellets, and excrement. I, E, and ME are expressed in kJ/day. The efficiency with which food was digested and assimilated (i.e., assimilation efficiency, $AE = ME/I$) by each study bird was calculated for each feeding experiment. Percentage data were arcsine transformed prior to statistical analysis to meet the assumptions of the statistical models. All means are presented with standard errors (\pm SE).

RESULTS

Composition and energy content of black-tailed jack rabbits.—A total of 92 black-tailed jack rabbits were collected in the BPA during 1978 and 1979. Between-year comparisons of mean body weights showed that both males ($t = 2.2$, $P = 0.03$) and females ($t = 3.8$, $P = 0.0005$) were significantly heavier in 1979 than in 1978. Energy content of jack rabbits, expressed on a live-weight basis, was 5.54 ± 0.09 kJ/g ($N = 3$) in 1978 and 6.51 ± 0.17 kJ/g ($N = 4$) in 1979 ($t = 4.6$, $P = 0.006$). This difference resulted from the greater percentage fat content in jack rabbits collected in 1979 ($9.0 \pm 0.88\%$) than in 1978 ($3.3 \pm 0.42\%$). The energy content (dry weight) of jack rabbit fat was 39.18 kJ/g ($N = 1$) in 1978 and 43.71 ± 1.93 kJ/g ($N = 4$) in 1979.

Food consumption.—Substantial variation was observed in the amount of food consumed each day by the captive nestlings. Patterns in food consumption were apparent, however, when the amount of food consumed daily by females and males was summarized for each feeding trial (Table 1). For each individual, mean daily food consumption increased steadily during the first three trials, peaked during trials 4 and 5 (28–44 days old), and decreased during the last two trials. A two-way ANOVA

TABLE 1
BIOMASS OF FOOD CONSUMED AND EGESTED BY CAPTIVE MALE AND FEMALE NESTLINGS
DURING EACH FEEDING TRIAL IN 1978 AND 1979

Year	Individual	Feeding trial	Initial		Mean daily biomass consumed		Mean daily biomass egested	
			Age (days)	Weight (g)	Wet weight (g/day)	Dry weight (g/day)	Pellets (g/day dry weight)	Excrement (g/day dry weight)
1978	Female 1	1	15	1012	442	135	8	47
		2	21	1725	541	165	7	59
		3	26	2375	572	174	7	69
		4	32	3225	610	177	9	75
		5	38	3700	522	152	9	68
		6	45	3800	480	139	5	65
		7	51	4000 ^a	561	162	10	71
	Female 2	1	11	322	240	73	4	29
		2	17	800	364	111	3	41
		3	22	1270	385	117	5	46
		4	28	1785	423	123	7	52
		5	34	2175	542	158	7	67
		6	41	2950	479	138	6	65
		7	47	3150 ^b	540	156	8	74
1979	Male 1	1	14	580	249	77	3	33
		2	20	920	370	114	5	49
		3	26	1525	457	141	10	59
		4	32	2050	556	180	10	78
		5	38	2750	531	168	9	74
		6	45	3100	579	195	10	79
		7	51	3300 ^c	375	126	11	50
	Male 2	1	11	395	184	57	7	27
		2	17	670	312	96	4	43
		3	23	1225	408	126	7	50
		4	29	1890	495	160	8	68
		5	35	2550	508	161	7	68
		6	42	3000	456	153	11	63
		7	48	3050 ^d	351	118	6	51

^a Final weight = 4150 g.

^b Final weight = 3500 g.

^c Final weight = 3250 g.

^d Final weight = 3100 g.

comparing captive male and female Golden Eagle chicks showed no significant difference between their mean daily consumption rates during the feeding experiments ($F = 4.08$, $P > 0.20$).

Food consumption during one meal each day tended to be much greater than all others. I assumed that this particular meal was at or close to the

TABLE 2
 MEAN NUMBER OF MEALS PER DAY AND MEAN DAILY FOOD CONSUMPTION BY WILD
 FEMALE AND MALE GOLDEN EAGLE NESTLINGS DURING EACH WEEK OF CHICK REARING IN
 1978 AND 1979

Week of chick rearing	Mean number of meals per day		Mean daily food consumption			
			Female (N = 6)		Male (N = 6)	
	No./day	SE	g/day	SE	g/day	SE
1	4.1	0.7	54	41	40	3
2	3.0	0.8	62	21	139	24
3	3.4	0.8	160	61	277	39
4	2.6	0.5	247	56	349	55
5	2.6	0.7	247	112	336	40
6	3.3	0.8	333	97	276	34
7	3.9	0.5	415	54	376	50
8	4.3	0.6	691	140	381	45
9	4.0	0.9	579	163	366	136
10	2.4	0.7	310	119	245	43

maximum possible for a bird at that stage of development. These maximum meal-size data were subjected to logarithmic transformation prior to analysis, as their variance increased with the age of the chicks. Simple linear regression analyses demonstrated that maximum meal size (Y) and age (X) were significantly related for both captive male and female chicks (males: $\log Y = 1.747 + 0.017X$, $r^2 = 0.82$; females: $\log Y = 1.710 + 0.021X$, $r^2 = 0.83$), and that the slopes of equations derived for female young were significantly steeper ($P < 0.001$) than for males. This indicated that as sexual dimorphism in size increased with age (see also Bortolotti 1984b), females were capable of consuming more food per meal than were males.

I estimated the mean daily food consumption of wild nestlings (Table 2) using the maximum meal size vs age relationship established with captive chicks, the crop fullness following each meal, and the number of meals. Daily food consumption by male and female eaglets varied greatly depending on the number and size of prey delivered by parents. Although females consumed more food than males late in chick rearing, the sexes were not significantly different in the mean amount consumed daily during each week of chick rearing ($F = 0.49$, $P > 0.20$). Furthermore, during the last half of the chick-rearing period, daily food consumption of both wild and captive eaglets was consistently greater than estimates of adult food consumption (Brown and Watson 1964, McGahan 1967).

Growth.—Increases in body weight of male and female Golden Eagle

chicks (Fig. 1) conformed with the growth curves of other captive and wild eaglets (Sumner 1929, 1933; Kochert 1972; Ellis 1979). Although only two male and two female chicks were tested, a comparison of the parameters that describe logistic curves fit to the growth data showed that captive female chicks had asymptotic body weights (A) 518 g heavier than males, while the growth rate constants (K) and inflection points (t) of both sexes were similar (Table 3). Weight gains of captive female chicks showed greater individual variation than those of males (Fig. 2) because one female chick was in relatively poor condition when first acquired.

Growth parameters also were calculated for the wild male and female nestlings (Table 3). Female chicks had asymptotic body weights (A) 636 g heavier than males ($t = -4.73$, $P < 0.001$). Males had significantly faster growth rates (K) ($t = 2.77$, $P < 0.02$). The mean inflection point (t) in the growth curves of males occurred 2.2 days sooner than it did for females, but the difference was not statistically significant ($t = -2.01$, $0.05 < P < 0.10$). A statistical comparison between wild nestlings from single chick broods and captively reared individuals was not possible because of small sample sizes; however, growth rates (K) of these wild male and female eaglets averaged 0.118 ($N = 1$) and 0.112 ($N = 3$), respectively, slightly lower than captive birds of the same sex.

Efficiency of body growth can be expressed as the ratio of biomass production to food consumption (Odum 1959). Captive male and female eaglets both had growth efficiencies that decreased linearly with age (Collopy 1980); however, no significant differences were detected between the regression equations derived for males and females ($F = 0.04$, $P = 0.84$). This inverse relationship reflected the changing pattern of energy allocation to growth during the nestling period. At two weeks of age (feeding trial 1), eaglets converted an average of 27% of the biomass consumed to body weight (Table 1). As the birds approached asymptotic weights, greater proportions of their daily energy budget were allocated to maintenance. This steadily reduced their growth efficiencies to levels below 5% as the birds approached fledging weight.

Metabolism calculations.—Percent fat and energy content of fat-extracted (lean) pellets and excrement were calculated for each feeding trial (Table 4). Energy content of fat was taken from direct measurements of jack rabbit fat. Significantly more fat was found in both the pellets ($t = -5.2$, $P < 0.0001$) and excrement ($t = -8.0$, $P < 0.0001$) of captive eaglets in 1979 (males), than in 1978 (females). Simple linear regression analyses demonstrated that the biomass of fat found in both pellets and excrement was dependent largely on the biomass of fat consumed (Fig. 2). This relationship was not apparent when only the 1978 data were considered, as relatively lean jack rabbits limited variation in the amount

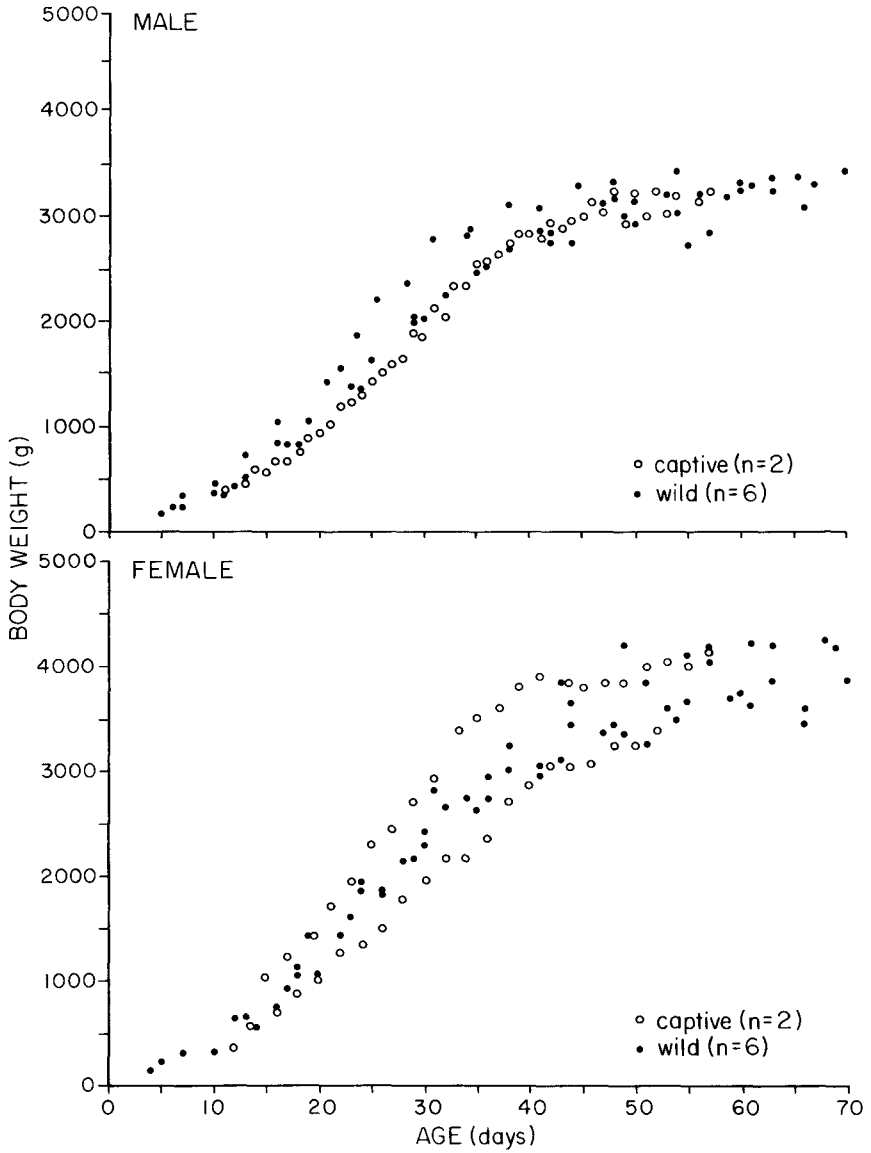


FIG. 1. Body weights of male and female Golden Eagle chicks in relation to age.

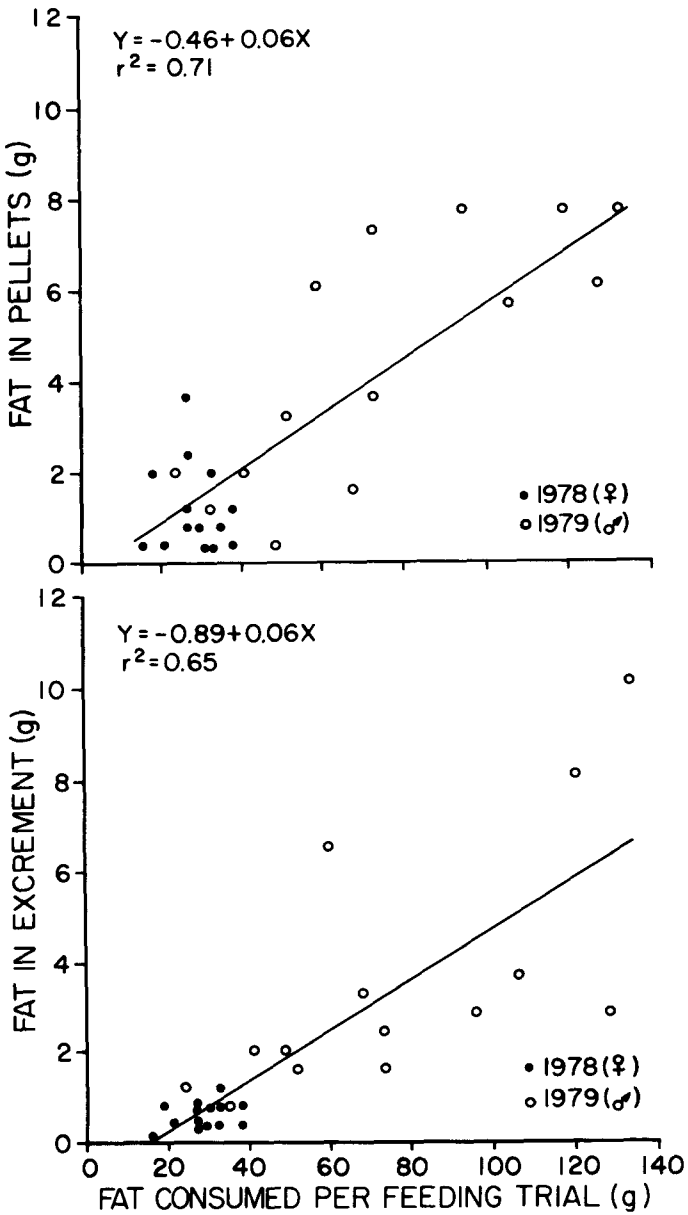


FIG. 2. Cumulative biomass of fat extracted from captive eaglet pellets and excrement collected during each feeding experiment in relation to total biomass of jack rabbit fat consumed.

TABLE 3
LOGISTIC GROWTH PARAMETERS OF FEMALE AND MALE GOLDEN EAGLES MONITORED IN CAPTIVITY AND IN THE WILD DURING 1978 AND 1979

Status	Sex	Asymptotic weight (g)			Growth rate constant (day ⁻¹)		Inflection point (days)	
		N	A	SE	K	SE	t	SE
Wild	Female	6	3834	128	0.119	0.003	26.1	0.5
	Male	6	3198	42	0.139	0.007	23.9	1.0
Captive	Female	2	3779	235	0.127	0.016	26.0	0.8
	Male	2	3261	116	0.138	0.009	26.7	2.7

of fat that the nestlings consumed. In 1979 jack rabbits contained more fat and provided the chicks with an apparent fat surplus in the diet.

Peaks in the amount of energy metabolized daily by captive male and female eaglets occurred at about 2500 kJ/day for both sexes (Fig. 3). Trends in ME for both sexes closely paralleled those of food consumption and were not significantly different ($F = 1.11$, $P > 0.20$). This was due to the relatively constant assimilation efficiencies among the 4 captive birds ($\bar{x} = 74.4\%$, range = 73.9–74.8%). No significant differences in assimilation efficiencies occurred within or between the sexes ($P > 0.50$).

The amount of energy metabolized daily (ME) by wild male and female eagle nestlings during each week of chick rearing was calculated using observed food consumption rates, jack rabbit body composition and energy values, and assimilation efficiencies established using the captive birds (Fig. 3). Although there were no statistically significant differences in ME throughout chick rearing in wild male and female chicks ($F = 0.24$, $P > 0.20$), some differences in the patterns of consumption and metabolism were apparent. Males reached a peak ME value near 1600 kJ/day during weeks 4 and 5, followed by a one-week depression in consumption. ME values once again peaked during weeks 7 and 8 of chick rearing at about 2000 kJ/day. Females showed a consistently increasing trend in ME values, with a peak rate of approximately 3100 kJ/day during week 8 of chick rearing.

DISCUSSION

Studies of captive nestlings frequently are used to estimate the energy requirements of wild birds. To justify the extrapolation of laboratory data to the wild, food consumption and growth patterns of captive and free-living birds must be similar and measured under comparable conditions.

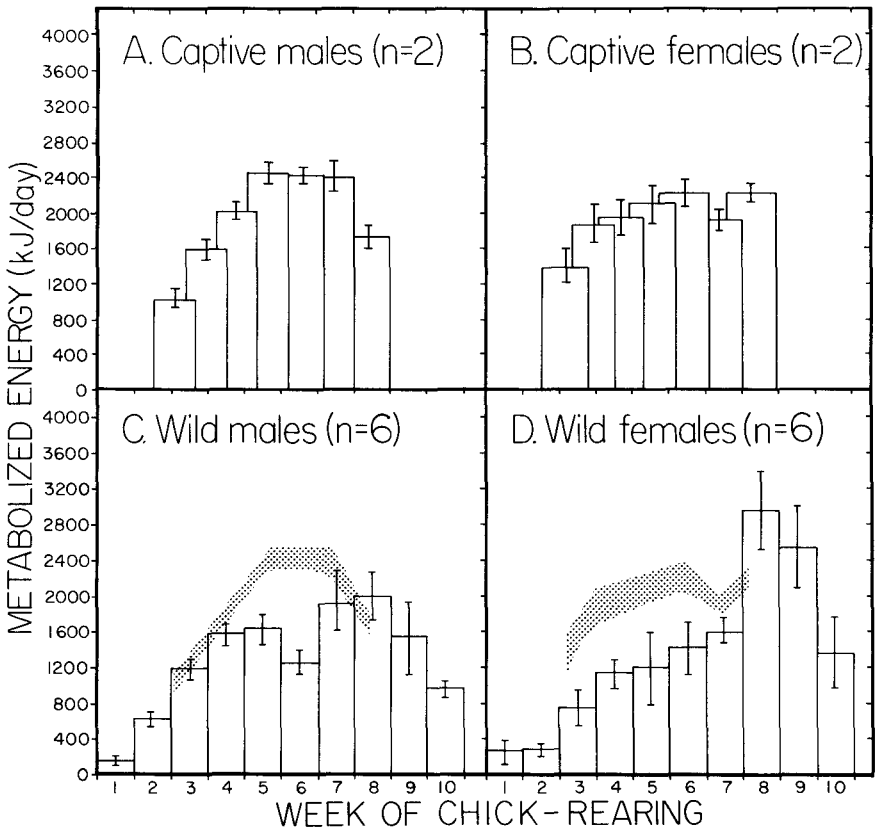


Fig. 3. Mean (\pm SE) daily metabolized energy of captive male (A) and female (B), and wild male (C) and female (D) eaglets in relation to week of chick rearing. Shaded areas on panels (C) and (D) represent \pm SE of the mean for captive male and female eaglets the same age. Overlapping histograms for captive males and females were the result of different-aged eaglets being used in sequential feeding trials.

Some studies have compared the developmental processes of captive and wild nestlings and found no major differences (Junior 1972, Shanholzer 1972, Siegfried 1972). In a study using captive American Kestrels (*Falco sparverius*), however, Bird and Clark (1983) reported that chicks raised by captive parents grew more rapidly and achieved greater size than did hand-reared nestlings. They concluded that lower feeding rates of the hand-reared kestrels limited growth rates.

In this study, Golden Eagle chicks reared in captivity and those monitored in the wild showed little difference in patterns of growth (Fig. 1).

TABLE 4
 PERCENTAGE FAT COMPOSITION AND ENERGY (LEAN) CONTENT OF PELLETS AND
 EXCREMENT PRODUCED BY CAPTIVE FEMALE AND MALE GOLDEN EAGLE CHICKS

	Sex	N	Percentage composition (% dry weight)		Energy content (kJ/g dry weight)		
			Fat	SE	N	Lean	SE
Pellets	Female	14	2.7	0.48	14	16.79	0.42
	Male	14	8.7	1.04	14	17.62	0.29
Excrement	Female	14	0.15	0.01	14	9.54	0.13
	Male	14	0.93	0.14	14	9.25	0.17

There were, however, some differences between the mean daily metabolized energy values of captive male and female chicks and their wild counterparts. Wild female nestlings consistently assimilated slightly less food than captive females during much of the chick-rearing period (Fig. 3). This difference was not surprising as the captive chicks were provided food *ad libitum*, no doubt in excess of the food available to wild nestlings. In contrast, wild male eaglets had reduced ME values midway through chick rearing when captive males showed peak consumption rates (Fig. 3). This decline in the amount of food consumed and assimilated by wild males may have been due to the presence of siblings competing for food, as 5 of the 6 males had siblings.

Dominance among sibling eagles is related to size, with the larger nestling dominating its sibling, particularly at mealtime (Meyburg 1974; Gargett 1978, 1982; Edwards and Collopy 1983; Bortolotti 1986). At the beginning of chick rearing, because of asynchronous hatching, the older nestling typically is dominant, regardless of sex. If the older chick is female it usually dominates its sibling throughout chick rearing. The size advantage associated with hatching first diminishes rapidly, however, if the older sibling is male and the younger is female. Three of the six wild male nestlings monitored in this study had female siblings. In two of these broods the male nestling was older and larger and maintained his dominance over the female chick until approximately the fifth week after hatching. Subsequently, the younger, but larger, female became more aggressive and frequently controlled access to the adult female during mealtime. Presumably, it was this shift in sibling interaction and dominance that caused the depressed ME values among wild males during subsequent weeks of chick rearing.

Recently, Bortolotti (1986) argued that eagle species vary in their patterns of growth, not because of sibling competition for food as proposed

by Werschkul and Jackson (1979), but because of selection to reduce peak energy requirements of nestlings. He also discussed how the growth of eagles in a food-limited situation can result in younger siblings growing at a slower rate. Among Bald Eagles (*Haliaeetus leucocephalus*) Bortolotti found that, regardless of the sex combination in the brood, younger siblings had lower growth rates (K), later inflection points (t), and equal asymptotic weights (A). He attributed these differences largely to the effects of asynchronous hatching and considered the slower growth of the younger chicks phenotypic.

My results suggest that the growth patterns of Golden Eagle nestlings also may be related to gender. In this study, wild male Golden Eagles had higher growth rates (K), earlier inflection points (t), and lower asymptotic weights. Sexual differences in growth patterns occur not only in Golden Eagles, but in seven of nine other species measured by Olendorff (1971). Newton (1979) also reported that in most dimorphic raptor species for which data are available, males fledge earlier than females. If sibling competition, as Bortolotti (1986) suggests, is not a major force in the selection of growth rates, then the sex-specific growth patterns seen among highly dimorphic raptor species should be examined more closely to determine their role in minimizing peak energy requirements.

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