ACTIVITY BUDGETS, ENERGY EXPENDITURES, AND ENERGY INTAKES OF NESTING FERRUGINOUS HAWKS

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ABSTRACT.—Daily energy expenditures of two pairs of nesting Ferruginous Hawks were estimated from activity budgets, and were compared with energy intakes determined from observed prey captures. In 1974 and 1975 respectively, the adult males expended 330.9 ± 37.8 (SD) and 374.3 ± 18.1 kcal/day, whereas the adult females expended 265.3 ± 28.3 and 294.6 ± 34.5 kcal/day. The total daily energy expenditures of adults and young (approximately 995.8 and 967.1 kcal/day in 1974 and 1975, respectively) were more than balanced by their gross intakes (1,337.8 ± 308.2 and 1,393.2 ± 236.7 kcal/day, respectively). The adult males had foraging efficiencies (kcal gathered/kcal expended in hunting) estimated at 7.56 ± 2.17 in the first year and 7.31 ± 1.80 in the second. Estimates of energy intake and foraging efficiency are maxima due to the likely under-representation of small prey items in regurgitated pellets. *Received 18 August 1977, accepted 4 April 1978.*

BECAUSE of technical difficulties associated with the direct measurement of daily metabolism in free-living birds, indirect methods of measurement are usually employed (Gessaman 1973, King 1974). One such technique is to convert an animal's observed daily activity budget to an approximate energy budget, using estimates of the energetic cost of various activities derived from laboratory studies (Pearson 1954, Schartz and Zimmerman 1971, Stiles 1971, Utter 1971, Wolf and Hainsworth 1971, Utter and LeFebvre 1973, Calder 1975, Wolf 1975). Another method is to estimate an animal's daily energy intake by combining an observed feeding rate with a measurement of the caloric density of food items (Gibb 1956, Graber 1962, Schmid 1965, Mosher and Matray 1974). Never have the two methods been combined so that one estimate could be compared with the other.

In conjunction with a field study of the foraging behavior of Ferruginous Hawks (*Buteo regalis*) (Wakeley 1978a, b), I collected detailed activity data on two nesting pairs of hawks. I also determined their feeding rates by directly observing prey captures made by the two adult males. From these data, I have estimated the hawks' average daily energy balance, taking into account both energy intake and expenditures.

STUDY AREA AND METHODS

The study area was in Curlew Valley, Idaho, about 8 km north of Snowville, Utah. A detailed description and map of the study area were given by Wakeley (1978b). Briefly, the area consisted of a patchwork of cultivated fields, old fields, and land used to graze livestock. In topography, it was essentially flat and provided excellent viewing of raptor behavior over long distances. Both pairs of hawks nested in solitary Utah juniper (*Juniperus osteosperma*) trees near the western edge of the study area.

Activity budgets of nesting Ferruginous Hawks were determined by direct observation during the nesting seasons of 1974 and 1975. Male 1 and Female 1 were observed in 1974; Male 2 and Female 2 in 1975. Observations were made between 0600 and 2100 MDT. More than 160 h of data on each bird were recorded during a 4-week period in each year. Observations were made from a blind in 1974 and from the cab of a pickup truck in 1975. Observations began on 19 May in 1974 and on 26 May in 1975,

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when the birds' nestlings were slightly less than 1 and 2 weeks old, respectively. The hawks had three young in the first year and two in the second. To allow biologically meaningful comparisons between years when observations started on different dates, all data are presented in terms of approximate nestling age.

Observations of the birds' behavior were made during sampling hours that were scattered throughout each day and throughout each week in an effort to sample all time periods with about equal intensity. Instantaneous samples (Altmann 1974) of the hawks' ongoing behavior were made at 5-min intervals during each sampling hour. The percentage of time the hawks devoted to each activity was estimated from the percentage of samples in which each activity was observed. Percentages were later converted to number of hours to facilitate the estimation of energy expenditures. Activity budgets are presented initially in terms of a 15-h day because data were collected only during the daylight hours. Energy budgets were calculated for a 24-h day by assuming a 9-h nighttime resting period.

The following behavioral categories were recognized. An adult hawk sitting over and in contact with the young was "brooding" them. When "perched on the nest" a bird was standing on the nest, but not in contact with the young. There were no other perches in the nest trees except the nests themselves. A hawk was "perched near the nest" if less than 500 m from the nest tree, and "far from the nest" if more than 500 m away. The hawks showed two types of flight behavior. Low-altitude (active) flights involved almost constant wing beating with only brief periods of gliding, and usually occurred below 30 m altitude. High-altitude (soaring) flights usually took place well above 30 m.

Prey captures were observed directly or were inferred when additional prey were brought to the nests. Prey items generally could not be recognized at the time of capture, so the species composition of the prey eaten by the hawks was determined by examination of pellets cast during the observation periods. Bones and teeth within the pellets were used to identify prey species. No attempt was made to identify hair.

The conversion of daily activity budgets to estimates of energy expenditure required several assumptions that will be considered below. In all cases, means ±SD were calculated from four weekly estimates.

RESULTS AND DISCUSSION

ACTIVITY BUDGETS

The adult males.—The male hawks were similar in their average daily activity budgets, and their activities changed little through the 4-week observation period in each year. On the average, both hawks spent more than one-third of the daylight period perched on the scattered juniper trees within 500 m of each nest tree (Table 1). Each male hawk spent less than 1% of the day at the nest itself, and then only when carrying prey. In contrast, Angell (1969) reported that, at one nest, a male Ferruginous Hawk did much of the brooding of the young. Preliminary observations in 1974 showed that Male 1 occasionally assisted in incubation, but the bird spent little time at the nest after the eggs had hatched.

The average number of hours that the male hawks devoted to various activities changed considerably with time of day (Table 1). The birds were similar in the distribution of time spent in low-altitude flight and in perching far from the nest. Both activities were more common in the morning and evening, and declined in midday. High-altitude flights were limited mostly to the hours between 0900 and 1800, and probably were related to the presence of suitable air currents.

The time each bird spent away from the nest was devoted largely to foraging, which included searching for, killing, eating, and carrying prey. Almost no hunting activity was observed in the vicinity of the nests. The hawks hunted either (1) from the ground, (2) from a perch, (3) from low-altitude (active) flight, or (4) from high-altitude (soaring) flight (Wakeley 1978a). Soaring flights were more frequent than expected from the prey captures they produced and might have functioned in exploration, territorial signaling, or thermoregulation, as well as in foraging (Wakeley 1978a).

TABLE 1. Number of hours devoted to various activities by adult male Ferruginous Hawks during daylight hours, according to time of day and week of observation

Activity	3-h interval	Week of observation in terms of approximate nestling age					Mean
		1–2	2–3	3–4	4–5	5–6	
Brooding	All	0.0 (—)[a]	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	— (0.0)	0.0 (0.0)
Perched on nest	0600–0900	0.1 (—)	T (0.0)	0.0 (0.0)	0.0 (0.0)	— (T)	T (T)
	0900–1200	T (—)[b]	T (0.0)	0.0 (0.0)	0.0 (0.0)	— (0.0)	T (0.0)
	1200–1500	0.0 (—)	0.0 (0.0)	0.0 (0.0)	T (T)	— (0.0)	T (T)
	1500–1800	T (—)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	— (0.0)	T (0.0)
	1800–2100	T (—)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	— (0.0)	T (0.0)
	15-h total	0.2 (—)[c]	0.2 (0.0)	0.0 (0.0)	T (T)	— (T)	0.1 (T)
Perched near nest	0600–0900	1.9 (—)	1.8 (2.2)	0.8 (2.0)	1.2 (1.4)	— (0.6)	1.4 (1.6)
	0900–1200	0.9 (—)	0.8 (0.6)	1.0 (0.1)	1.1 (0.7)	— (0.6)	1.0 (0.5)
	1200–1500	0.5 (—)	1.1 (0.8)	1.0 (1.1)	2.1 (0.0)	— (0.3)	1.2 (0.6)
	1500–1800	1.0 (—)	0.6 (1.1)	0.7 (0.4)	0.7 (2.3)	— (0.6)	0.8 (1.1)
	1800–2100	1.0 (—)	1.3 (2.0)	0.7 (2.7)	0.7 (2.5)	— (1.2)	0.9 (2.1)
	15-h total	5.4 (—)	5.6 (6.7)	4.0 (6.4)	5.8 (6.9)	— (3.3)	5.2 (5.8)
Perched far from nest	0600–0900	0.7 (—)	0.9 (0.4)	1.1 (0.6)	1.0 (0.5)	— (1.7)	1.0 (0.8)
	0900–1200	0.9 (—)	0.8 (0.2)	0.4 (0.5)	1.1 (0.3)	— (0.9)	0.8 (0.5)
	1200–1500	1.1 (—)	0.5 (T)	0.1 (0.1)	0.5 (0.2)	— (1.0)	0.6 (0.2)
	1500–1800	1.4 (—)	0.4 (0.4)	0.8 (0.4)	0.9 (0.1)	— (0.5)	1.0 (0.3)
	1800–2100	1.7 (—)	1.2 (0.7)	1.3 (0.1)	1.7 (0.2)	— (1.0)	1.5 (0.5)
	15-h total	5.7 (—)	3.7 (1.7)	3.7 (1.7)	5.3 (1.3)	— (5.1)	4.7 (2.5)
Low-altitude (active) flight	0600–0900	0.3 (—)	0.3 (0.3)	1.0 (0.4)	0.8 (1.1)	— (0.7)	0.6 (0.6)
	0900–1200	0.2 (—)	0.1 (0.2)	0.3 (0.5)	0.1 (0.9)	— (0.4)	0.1 (0.3)
	1200–1500	0.2 (—)	0.1 (T)	0.0 (0.1)	0.0 (0.1)	— (0.1)	0.1 (0.1)
	1500–1800	0.2 (—)	0.1 (0.1)	0.1 (0.4)	0.5 (0.2)	— (0.3)	0.3 (0.3)
	1800–2100	0.3 (—)	0.2 (0.6)	0.5 (0.1)	0.4 (0.3)	— (0.7)	0.3 (0.3)
	15-h total	1.1 (—)	0.9 (1.0)	2.0 (1.4)	1.8 (2.5)	— (2.3)	1.4 (1.8)
High-altitude (soaring) flight	0600–0900	0.0 (—)	0.0 (0.1)	0.1 (0.0)	0.0 (0.0)	— (0.0)	T (T)
	0900–1200	1.0 (—)	1.3 (2.0)	1.3 (1.8)	0.7 (1.2)	— (1.1)	1.1 (1.6)
	1200–1500	1.3 (—)	1.2 (2.1)	1.9 (1.7)	0.4 (2.7)	— (1.6)	1.1 (2.1)
	1500–1800	0.4 (—)	1.9 (1.5)	1.4 (1.8)	0.9 (0.4)	— (1.7)	1.0 (1.4)
	1800–2100	T (—)	0.3 (T)	0.5 (0.2)	0.1 (0.1)	— (0.0)	0.2 (0.1)
	15-h total	2.7 (—)	4.7 (5.6)	5.1 (5.5)	2.1 (4.3)	— (4.4)	3.6 (5.0)

[a] Male 1 (1974) without parentheses; Male 2 (1975) within parentheses
[b] T denotes < 0.05 h
[c] Due to rounding errors, numbers may not total exactly

TABLE 2. Rates of prey capture (prey items/h) by adult male Ferruginous Hawks according to time of day and week of observation

Bird and year	3-h interval	Week of observation in terms of approximate nestling age					Mean
		1–2	2–3	3–4	4–5	5–6	
Male 1 (1974)	0600–0900	0.44 (8)[a]	1.11 (7)	0.55 (8)	1.05 (10)	—	0.79
	0900–1200	0.44 (11)	0.50 (11)	0.83 (11)	0.17 (12)	—	0.48
	1200–1500	0.37 (12)	0.47 (15)	0.70 (10)	0.61 (6)	—	0.56
	1500–1800	0.44 (9)	0.81 (9)	0.33 (3)	0.50 (10)	—	0.52
	1800–2100	0.33 (10)	0.75 (10)	0.50 (6)	0.69 (13)	—	0.57
	Mean	0.40	0.73	0.58	0.60	—	0.58
	Prey items per 15-h day	6.06	10.92	8.73	9.06	—	8.69
Male 2 (1975)	0600–0900	—	0.56 (16)	1.08 (10)	0.92 (12)	0.67 (12)	0.81
	0900–1200	—	0.72 (11)	1.00 (7)	0.33 (9)	0.67 (10)	0.66
	1200–1500	—	0.94 (8)	0.81 (10)	1.00 (7)	0.33 (6)	0.77
	1500–1800	—	0.17 (9)	0.67 (9)	0.50 (8)	1.03 (9)	0.59
	1800–2100	—	0.17 (12)	0.17 (7)	0.00 (12)	0.33 (6)	0.17
	Mean	—	0.51	0.75	0.55	0.61	0.60
	Prey items per 15-h day	—	7.68	11.19	8.25	9.09	9.05

[a] Sample size (h) in parentheses

TABLE 3. Number of hours devoted to various activities by adult female Ferruginous Hawks during daylight hours, according to time of day and week of observation

Activity	3-h interval	Week of observation in terms of approximate nestling age					Mean
		1–2	2–3	3–4	4–5	5–6	
Brooding	0600–0900	3.0 (—)[a]	1.0 (1.8)	0.3 (0.1)	0.0 (0.0)	— (0.0)	1.1 (0.5)
	0900–1200	0.8 (—)	0.2 (0.4)	0.0 (0.0)	0.0 (0.0)	— (0.0)	0.2 (0.1)
	1200–1500	0.4 (—)	0.0 (0.7)	0.0 (0.0)	0.0 (0.0)	— (0.0)	0.1 (0.2)
	1500–1800	0.1 (—)	0.0 (1.4)	0.0 (0.0)	0.0 (0.0)	— (0.0)	T (0.3)[b]
	1800–2100	1.2 (—)	0.2 (1.4)	0.0 (0.0)	0.0 (0.0)	— (0.0)	0.3 (0.4)
	15-h total	5.6 (—)[c]	1.4 (5.7)	0.3 (0.1)	0.0 (0.0)	— (0.0)	1.8 (1.4)
Perched on nest	0600–0900	0.0 (—)	1.4 (0.9)	0.7 (0.7)	0.5 (0.2)	— (0.0)	0.6 (0.4)
	0900–1200	1.7 (—)	1.7 (1.2)	1.8 (1.2)	1.0 (0.2)	— (0.0)	1.5 (0.7)
	1200–1500	2.3 (—)	2.3 (1.8)	1.5 (0.4)	2.6 (0.6)	— (0.0)	2.2 (0.7)
	1500–1800	2.6 (—)	2.2 (1.1)	1.0 (1.2)	0.6 (0.0)	— (0.0)	1.6 (0.6)
	1800–2100	1.8 (—)	2.3 (1.2)	0.3 (0.2)	0.2 (0.3)	— (0.0)	1.1 (0.4)
	15-h total	8.4 (—)	9.9 (6.3)	5.1 (3.8)	4.8 (1.2)	— (0.0)	7.1 (2.8)
Perched near nest	0600–0900	0.0 (—)	0.6 (0.3)	1.8 (2.2)	2.5 (2.8)	— (2.9)	1.2 (2.1)
	0900–1200	0.5 (—)	1.0 (1.0)	1.2 (1.0)	1.2 (2.5)	— (2.9)	1.0 (1.8)
	1200–1500	0.2 (—)	0.6 (0.1)	1.5 (1.1)	0.0 (1.6)	— (2.8)	0.6 (1.4)
	1500–1800	0.3 (—)	0.7 (0.2)	1.8 (1.3)	1.9 (2.8)	— (2.1)	1.2 (1.6)
	1800–2100	T (—)	0.5 (0.3)	2.5 (2.3)	2.8 (2.7)	— (3.0)	1.4 (2.1)
	15-h total	1.1 (—)	3.5 (2.0)	8.9 (7.8)	8.4 (12.5)	— (13.7)	5.4 (8.9)
Perched far from nest	0600–0900	0.0 (—)	0.0 (0.0)	0.0 (0.0)	T (0.0)	— (0.1)	T (T)
	0900–1200	0.0 (—)	0.0 (0.0)	0.0 (0.0)	T (0.0)	— (0.0)	T (0.0)
	1200–1500	0.0 (—)	0.0 (0.0)	0.0 (T)	T (0.0)	— (0.1)	T (T)
	1500–1800	0.0 (—)	0.0 (0.0)	0.0 (0.1)	T (0.0)	— (0.0)	T (T)
	1800–2100	0.0 (—)	0.0 (T)	0.0 (0.0)	0.0 (0.0)	— (0.0)	0.0 (T)
	15-h total	0.0 (—)	0.0 (T)	0.0 (0.1)	0.1 (0.0)	— (0.2)	T (0.1)
Low-altitude (active) flight	0600–0900	0.0 (—)	0.0 (T)	0.1 (0.0)	T (T)	— (0.0)	T (T)
	0900–1200	0.0 (—)	0.0 (T)	0.0 (0.1)	0.4 (0.0)	— (0.0)	0.1 (T)
	1200–1500	T (—)	T (0.0)	0.0 (0.0)	0.0 (0.0)	— (0.1)	T (T)
	1500–1800	0.0 (—)	T (0.1)	0.1 (0.0)	T (0.1)	— (0.2)	T (0.1)
	1800–2100	0.0 (—)	0.0 (T)	0.0 (0.1)	T (T)	— (0.0)	T (T)
	15-h total	T (—)	T (0.1)	0.2 (0.1)	0.5 (0.1)	— (0.2)	0.2 (0.1)
High-altitude (soaring) flight	0600–0900	0.0 (—)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	— (0.0)	T (0.0)
	0900–1200	0.0 (—)	0.1 (0.3)	T (0.7)	0.4 (0.3)	— (0.1)	0.1 (0.4)
	1200–1500	0.1 (—)	0.1 (0.4)	T (1.5)	0.3 (0.8)	— (0.1)	0.1 (0.7)
	1500–1800	0.0 (—)	0.1 (0.3)	0.1 (0.5)	0.4 (0.2)	— (0.8)	0.2 (0.4)
	1800–2100	0.0 (—)	0.0 (T)	0.2 (0.4)	T (0.0)	— (0.0)	0.1 (0.1)
	15-h total	0.1 (—)	0.3 (1.0)	0.5 (3.1)	1.2 (1.3)	— (1.0)	0.5 (1.6)

[a] Female 1 (1974) without parentheses; Female 2 (1975) within parentheses
[b] T denotes < 0.05 h
[c] Due to rounding errors, numbers may not total exactly

The male hawks foraged throughout the day, as indicated by each bird's average rate of prey capture during various time intervals (Table 2). The hawks rarely caught and ate a prey item without carrying a portion back to the nest. Thus, Table 2 includes essentially all captures the birds made each day, not just those that I was able to observe directly. Males 1 and 2 were remarkably similar in their average daily capture rates: 8.69 ± 2.00 and 9.05 ± 1.54 prey items per day, respectively. Capture rates did not change significantly either by time of day or by week of observation ($P > 0.05$; Friedman 2-way analysis of variance by ranks). In contrast to a report by Angell (1969), these Ferruginous Hawks never used a food cache.

During the last week of observation in 1974, Male 1 spent a larger proportion of the midday time period perched near the nest than he had during any previous week (Table 1). This change in the bird's activity pattern was associated with midday temperatures in excess of 32°C for four consecutive days (U.S. Weather Bureau data for Snowville, Utah). During that time, Male 1 often drank from irrigation ditches and breathed with his beak open even after short flights. These observations suggest that the hawk was under heat and water stress that curtailed his midday activities. In the following year, Male 2 showed no evidence of heat stress. However, temperatures that year never exceeded 32°C. The tendency for other desert birds to become relatively inactive during the hottest part of the day, apparently to avoid excessive heat loading, has been noted by Dawson (1954), Calder (1968), and Ricklefs and Hainsworth (1968).

The adult females.—Activity budgets of the female hawks changed considerably during the observation periods (Table 3). The number of hours each bird spent brooding the young declined rapidly through the season, and the time each hawk spent perched near the nest generally increased as time spent actually on the nest declined. Active feeding of the young continued, but at a declining rate, until the young were 4–5 weeks old.

Both female hawks spent significantly less time away from the nest areas than did the males ($P < 0.05$; Mann-Whitney U-test). Neither female hunted during the 4-week observation period in each year, unlike the nesting female observed by Angell (1969). In 1975, Female 2 caught her own prey on two occasions, but only after the main observation period, a few days before the fledging of her young.

During the final week of observation in 1974, Female 1 spent an unusually large proportion of the time interval from 1200 to 1500 perched on the nest (Table 3). She devoted nearly all of this time to shading the young, which she accomplished by standing on the nest rim with her back to the sun and her wings partially spread. This activity was seen often in the early parts of both seasons, but rapidly declined in frequency as the young grew older. The reappearance of the behavior in Female 1 apparently was another result of high ambient temperatures during the last week of observation in 1974. Angell (1969) reported shading behavior in a male Ferruginous Hawk, but I saw this activity in females only.

Energy Expenditures

Activity budgets can be converted to energy budgets only if the metabolic cost of various activities is known or can be estimated. At the present time, there is so little information on the cost of activities in free-living birds that one must rely on the limited number of measurements made in laboratory studies, and use reasonable guesses to supply missing figures. I have followed the common practice of expressing energy costs in terms of multiples of a bird's standard metabolic rate (SMR).

To estimate the hawks' standard metabolic rates, I used the regression equations provided by Aschoff and Pohl (1970). Because the Ferruginous Hawks had not been weighed, I used in the equations the mean body weights of two adult males (1,237 g) and three adult females (1,983 g) determined by Imler (1937). The predicted standard metabolic rates for the males were 4.44 kcal/h during the assumed 15-h active phases of their normal 24-h cycles, and 3.59 kcal/h during the 9-h resting phases of their daily cycles. For the female hawks, the corresponding figures were 6.26 and 5.08 kcal/h, respectively.

Utter (1971) estimated the cost of daytime resting at 2.0 SMR for Purple Martins (*Progne subis*) and for Mockingbirds (*Mimus polyglottos*). The value of 1.5 SMR was preferred by Utter and LeFebvre (1973). Wolf and Hainsworth (1971) calculated that a resting hummingbird (*Eulampis jugularis*) expended energy at a rate of 1.7 SMR at the field temperature. I have adopted the average figure of 1.7 SMR to

TABLE 4. Estimated average daily energy expenditures by nesting Ferruginous Hawks

Birds	Activity	Estimated energy cost (kcal/h)	Average number of hours per day		Estimated energy expenditure per bird per day (kcal)	
			1974	1975	1974	1975
Adult ♂♂	Resting (night)	6.1	9.0	9.0	54.9	54.9
	Perched on or near nest (resting)	7.6	5.3	5.8	40.3	44.1
	Perched far from nest (sit-and-wait hunting)	11.1	4.7	2.5	52.2	27.8
	Low-altitude (active) flight	51.1	1.4	1.8	71.5	92.0
	High-altitude (soaring) flight	31.1	3.6	5.0	112.0	155.5
	TOTAL	—	24.0	24.1	330.9	374.3
Adult ♀♀	Brooding or resting (night)	8.6	9.0	9.0	77.4	77.4
	Brooding (day)	10.6	1.8	1.4	19.1	14.8
	Perched (resting)	10.6	12.5	11.8	132.5	125.1
	Low-altitude (active) flight	72.0	0.2	0.1	14.4	7.2
	High-altitude (soaring) flight	43.8	0.5	1.6	21.9	70.1
	TOTAL	—	24.0	23.9	265.3	294.6

estimate the costs of nighttime resting, inactive perching, and brooding by Ferruginous Hawks. This value is probably conservative because it may not cover such additional costs as thermoregulation and specific dynamic action.

When perched far from the nests, the male hawks usually were engaged in sit-and-wait hunting (Wakeley 1978a). The metabolic cost of that activity included the small cost of the seven or eight attempts to capture prey the birds made per hour. Strikes lasted only a few seconds each, so their contribution to the energetic cost of sit-and-wait hunting was not great. In my previous paper, I used what I thought to be a generous estimate of the cost of that hunting technique (3.5 SMR). For this analysis, the cost of alert perching, expanded by the cost of occasional strikes, is assumed to be 2.5 SMR.

A number of measurements of the cost of active flight in nonpasserine birds (tabulated by Wakeley 1978a) average about 12.5 SMR. Because the Ferruginous Hawks in low-altitude (active) flight occasionally glided for brief periods, 11.5 SMR seems a more reasonable estimate of their energy expenditure. The energetic cost of soaring flight was assumed to be 7.0 SMR, halfway between the estimates for sit-and-wait hunting and for low-altitude flight.

Using these estimates of the energetic cost of the birds' activities, I calculated the total daily energy expenditures for the adult Ferruginous Hawks (Table 4). The average number of hours per day devoted to each activity was taken from Tables 1 and 3. In each case, I assumed a 9-h nighttime rest period. The hawks' total daily energy expenditures were estimated to be 330.9 kcal/day for Male 1, 374.3 kcal/day for Male 2, 265.3 kcal/day for Female 1, and 294.6 kcal/day for Female 2. Standard deviations, calculated from four weekly estimates, were 37.8, 18.1, 28.3, and 34.5 kcal/day, respectively.

Information reviewed by King (1974) suggests that the ratio of daily energy expenditure to standard metabolic rate (DEE/SMR) averages about 3.5 for most birds. My figures for the male hawks (3.34 for Male 1 and 3.78 for Male 2) agree reasonably well with that generalization. However, for the female hawks, which did not forage for themselves and which led very sedentary lives, the ratios were 1.90 and 2.11,

TABLE 5. Determination of mean weight of prey items found in hawk pellets

	Year		Estimated mean prey weight (g)[a]
	1974	1975	
Number of pellets examined	30	26	—
Prey species found:			
Thomomys talpoides	13	30	89.9
Spermophilus townsendi	5	4	204.5
Microtus montanus	6	0	41.0
TOTAL	24	34	—
Estimated average prey weight (g)	101.5	103.4	—

[a] See text

respectively. These results suggest that DEE may not be a simple function of body weight, as King (1974: 39) suggests, but rather may depend quite heavily upon the behavior of the individual bird and the stage of the annual cycle.

During most of the time they spent away from the nests, the male hawks were actively foraging. In a previous paper, I concluded that the hawks devoted approximately one-half of the time they spent soaring to purposes other than food gathering (Wakeley 1978a). Therefore, by assuming that the birds foraged continuously when away from the nests (except for half of the time spent soaring), I estimate that the male hawks in 1974 and 1975 spent an average of 33 and 28% of their daily (24 h) cycles gathering food, respectively. In terms of energetic cost, Males 1 and 2 expended approximately 179.7 ± 27.8 and 195.5 ± 37.0 kcal/day foraging. Thus, foraging activity accounted for 54 and 52% of their total daily expenditures, respectively.

To balance the energy gathered by the male hawks in the form of prey with that expended by the families they supported, it was necessary to estimate the energy expended by the birds' nestlings. Hatching dates for the hawks' young were known to within 3 days, but the sex of the birds was not determined. An even sex ratio was assumed. From growth curves calculated by Howard (1975), the nestlings' average weights during the observation periods were estimated at 900 g in 1974 and 1,050 g in 1975. Standard metabolic rates for the nestlings were predicted from Aschoff and Pohl's (1970) equations, and the birds' energy expenditures were assumed to be 1.7 SMR throughout the day. Their total daily energy expenditures were estimated to be 133.2 kcal/day/bird in 1974 and 149.1 kcal/day/bird in 1975.

Combining the expenditures for each family of hawks (i.e. adult male + adult female + nestlings), I estimated that the birds used 995.8 kcal/day in 1974 and 967.1 kcal/day in 1975. There were three nestlings in 1974 and only two in 1975, yet the total energy expenditures were about equal. This was due both to the greater average age of the young observed in 1975 and to their parents' higher level of activity compared to the adults in the previous year (Table 4).

ENERGY INTAKE

Analysis of pellets cast by the hawks during the observation periods revealed only three prey species: the northern pocket gopher (*Thomomys talpoides*), Townsend's ground squirrel (*Spermophilus townsendi*), and the mountain vole (*Microtus montanus*) (Table 5). Mean weights for pocket gophers were calculated from measurements of 116 individuals of mixed age and sex captured by Tryon (1947) during

TABLE 6. Foraging efficiencies (kcal gathered/kcal expended) of adult male Ferruginous Hawks, according to time of day and week of observation

Bird and year	3-h interval	Week of observation in terms of approximate nestling age 1–2	2–3	3–4	4–5	5–6	Mean
Male 1 (1974)	0600–0900	9.63	20.43	4.02	9.28	—	10.84
	0900–1200	6.06	6.96	9.22	2.83	—	6.27
	1200–1500	4.01	6.98	10.50	25.98	—	11.87
	1500–1800	6.74	9.07	4.29	4.77	—	6.22
	1800–2100	4.76	12.47	4.95	7.23	—	7.35
	15-h mean[a]	5.85	10.61	6.17	7.61	—	7.56
Male 2 (1975)	0600–0900	—	11.63	19.48	6.87	5.51	10.87
	0900–1200	—	7.78	7.52	2.32	6.39	6.00
	1200–1500	—	12.46	11.98	9.26	3.62	9.33
	1500–1800	—	2.50	6.11	15.12	10.58	8.58
	1800–2100	—	3.22	9.82	0.00	3.16	4.05
	15-h mean	—	7.60	9.74	6.05	5.83	7.31

[a] Daily mean is weighted according to the amount of energy expended during each interval

summer in Montana. Weights of 26 individuals trapped during May and June by Scheffer (1941) were used to calculate an average weight for *Spermophilus townsendi*. The mean weight for *Microtus* was determined from four individuals caught in the study area. The average size of a prey item contained in the hawk pellets was 101.5 g in 1974 and 103.4 g in 1975 (Table 5). Because of the close agreement of these two estimates, the samples were combined and the average figure of 102.6 g was used in subsequent calculations.

I was able to identify only a few prey items at the time they were captured and carried to the nests. Among these were several deermice (*Peromyscus maniculatus*), the only known prey animal not found in the pellets. Their absence from the pellets suggests that small prey items may be under-represented due to the more complete breakdown of their remains. The mean weight of 314 *Peromyscus* trapped in the study area was 20.2 ± 4.7 g. In the following calculations, I have used the estimated mean prey weight (102.6 g) derived from the pellet analysis. However, I regard that estimate as an absolute maximum due to the likely under-representation of small prey items.

The male Ferruginous Hawks captured 8.69 ± 2.00 and 9.05 ± 1.54 prey items per day in 1974 and 1975, respectively. Given that prey items averaged 102.6 g, the hawks caught an estimated 891.9 ± 205.4 and 928.8 ± 157.8 g of prey per day. Using Górecki's (1967) measurement of the caloric density of small mammals (1.50 kcal/g live weight), I have calculated that the hawks captured as much as 1,337.8 ± 308.2 and 1,393.2 ± 236.7 kcal of prey per day in 1974 and 1975, respectively.

BALANCING ENERGY INTAKE AND EXPENDITURE

Male 1 gathered no more than 1,337.8 kcal/day, which supported two adult and three nestling hawks whose total expenditures were approximately 995.8 kcal/day. Similarly, Male 2 collected 1,393.2 kcal/day while he, his mate, and his two nestlings expended 967.1 kcal/day. In 1974 and 1975, the hawks' intakes exceeded their expenditures at most by 34 and 44%, respectively.

In terms of metabolizable energy (King 1974), the hawks' intakes must have been somewhat lower than my estimates. To calculate energy assimilated by the birds, one must subtract energy lost to egestion (i.e. pellet formation) and to excretion. I had no way to estimate these losses. However, if my estimates of energy expenditures are correct, approximately 70% of the gross energy of prey items eaten must have been metabolized by the hawks.

Foraging Efficiency

Each day, the two male hawks captured enough prey to feed themselves, their mates, and their young. To accomplish this, each hawk must have gathered far more energy than he expended foraging. An animal's foraging efficiency can be quantified as the ratio of daily energy uptake to daily foraging cost (Wolf 1975, Wolf et al. 1975). Using the foraging costs estimated previously, I have calculated that the average foraging efficiencies of the two male hawks were 7.56 ± 2.17 in 1974 and 7.31 ± 1.80 in 1975 (Table 6). That is, the hawks gathered 7.31–7.56 kcal of prey for every kcal they expended foraging. There were no significant differences in foraging efficiencies either by time of day or week of observation ($P > 0.05$; Friedman 2-way analysis of variance).

Using much more limited activity data, Wolf (1975) calculated somewhat lower foraging efficiencies, 4.35 ± 0.44 (SE) and 3.43 ± 0.35, for two male Malachite Sunbirds (*Nectarinia famosa*). Wolf observed these nectar-feeding birds only for 2- or 3-h periods at roughly the same time in the morning and evening; his observations did not cover the entire day. Therefore his estimates of foraging efficiency may not be directly comparable to mine because they do not represent daily averages, and because the birds could have foraged with different efficiencies during portions of the day they were unobserved. Furthermore, Wolf's figures may be too low because he was unable to account for energy consumed in the form of insects. My own estimates are likely to be too high due to biases in the calculation of mean prey size. Foraging efficiencies reported here also differ conceptually from those of Wolf (1975) in that the energy gathered by the male hawks was divided among the families they supported and was not consumed entirely by the forager.

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A National Workshop on Mitigating Losses of Fish and Wildlife Habitats (**The Mitigation Symposium**) will be held at Fort Collins, Colorado, 16–20 July 1979. The losses of fish and wildlife habitat that occur as a result of development projects of many kinds and of land use changes constitute a major national environmental problem. This symposium proposes to assess the magnitude of this problem and to develop strategies and recommendations for acheiving better mitigation, in the public interest. Sessions will deal with the problem in coastal as well as terrestrial and fresh water environments, and with all regions of the country. The event is sponsored by the American Fisheries Society, The American Society of Civil Engineers, The Wildlife Management Institute, and The Wildlife Society. Additional information is available from **Dr. Gustav A. Swanson, Program Director, The Mitigation Symposium, Fishery and Wildlife Biology, Colorado State University, Fort Collins, Colorado 80523.**

The second **North American Conference on Common Loon Research and Management** will be held at Syracuse University January 14–16, 1979, under the sponsorship of the National Audubon Society, the U.S. Fish and Wildlife Service, and Syracuse University. Requests for further information should be directed to **Judith W. McIntyre, Biology Department, Syracuse University, Syracuse, New York 13210.**