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PREY DELIVERY, CACHING, AND RETRIEVAL RATES IN NESTING PRAIRIE FALCONS

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Abstract. From 1984–1987, 48 nesting attempts of Prairie Falcons (*Falco mexicanus*) were observed for 568 days (8,397 hr) in southwestern Idaho. Observations started 1–5 weeks prior to incubation until the young were 35 days old or a nesting attempt failed. I investigated prey delivery, caching, and retrieval rates during the nesting season; relationships between prey delivery rates, hatching date, the number of young fledged per pair, and the physical condition of the young were assessed. The main prey item was the Townsend's ground squirrel (*Spermophilus townsendii*), which accounted for 37% of all delivered prey items (n = 1,742 items). Males delivered 97.5, 95.3, and 70.2% of all prey items during the preincubation, incubation, and brood-rearing stages, respectively. Overall, males delivered 76.6% of all prey. Prey delivery rates by a pair were three to four times higher during brood rearing than during preincubation and incubation. The prey delivery through the day was bimodal in frequency and may have reflected the diurnal aboveground activity pattern of the falcon's main prey item, the Townsend's ground squirrel. Diurnal caching patterns followed delivery patterns. Prey delivery rates per pair/hour decreased with progressively later hatching dates, resulting in a decrease in productivity. Prey delivery rates per pair/hour and the proportion of Townsend's ground squirrel in a falcon pair's diet increased with the number of young fledged per pair. Caching and retrieval rates peaked during the first 2 weeks of brood rearing and then declined. Retrieval rates did not differ from caching rates. Prey retrievals peaked in the early morning and late afternoon hours. Caching was considered an important behavioral mechanism to maximize food intake and to dampen fluctuations in prey availability.

Key words: Caching; diet; diurnal pattern; Falco mexicanus; *Idaho; nesting; Prairie Falcon; prey delivery; productivity.*

INTRODUCTION

Snyder and Wiley (1976) hypothesized three distinct stages in the food needs of nesting raptors: egg laying, incubation, and brood rearing. Females require additional food prior to and during egg laying, as has been demonstrated with the Eurasian Kestrel, *Falco tinnunculus* (Cavé 1968, Dijkstra et al. 1982), Eurasian Sparrowhawk, *Accipiter nisus* (Newton et al. 1983, Newton and Marquiss 1984, Newton 1986), and Cooper's Hawk, *A. cooperii* (Snyder and Snyder 1973). Therefore, food intake in raptors is likely to be higher during egg laying than during incubation. During incubation, food intake is hypothesized to remain stable. During the nestling stage, food intake is expected to rapidly increase over the period of rapid growth of the young (6–25 days for most birds, Ricklefs 1968) and to decline when asymptotic growth has been reached. Considerable information is available on prey delivery rates in raptorial birds during the nesting stage (Newton 1979, p. 168–171), but few studies have examined food requirements over the whole nesting season (Tinbergen 1940, Green 1976, Masman 1986). Prey deliveries may be associated with caching behavior, i.e., the deliberate hiding of food items for later use (Oliphant and Thompson 1976). Caching behavior has been reported in a number of raptors, notably the American Kestrel, *F. sparverius* (Mueller 1974, Nunn et al. 1976, Collopy 1977), Eurasian Kestrel (Rijnsdorp et al. 1981), Merlin *F. columbarius* (Oliphant and Thompson 1976), Gyrfalcon *F. rusticolus* (Poole and Boag 1988), Peregrine Falcon *F. peregrinus* (Palmer 1988), Eleonora's falcon *F. eleonorae* (Walter 1979), and Prairie Falcon *F. mexicanus* (Oliphant and Thompson 1976, Sitter 1983, Palmer 1988). Raptors may cache food to dampen changes in supply due to fluctuating prey availability (Rijnsdorp et al. 1981, Sitter 1983, Palmer 1988), or unfavorable hunting conditions (Nunn et al. 1976, Palmer 1988, Poole and Boag 1988). Thus, food caching is a means to reconcile prey availability and food

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requirements. Removing a stored food item from a cache is referred to as food retrieval (Collopy 1977). Here I report on prey delivery, caching, and retrieval rates of the Prairie Falcon through the entire nesting season. Specifically, I examine whether prey delivery rates, i.e., the frequency with which prey items are delivered to the nesting territory by an adult falcon, follow the predictions made by Snyder and Wiley (1976). Also, I investigate relationships between prey delivery rates, hatching date, the number of young fledged per pair (productivity), and their physical condition (i.e., weight).

METHODS

From 1984–1987, I studied 48 nesting attempts of Prairie Falcons in the Snake River Birds of Prey Area (SRBOPA) in southwestern Idaho for 568 days (8,397 hr). The study area is part of the Western Intermountain Sagebrush Steppe, characterized by cold winters and hot, dry summers (U.S. Department of Interior 1979, West 1983). Each nesting falcon pair was observed, on average, once every 6 days. A nesting territory was a confined locality where aeries were found, usually in successive years, and where no more than one pair bred at one time (Newton 1979). An observation day started 30 min before sunrise and was terminated 30 min after sunset. Observations were usually made from blinds placed at distances ranging from 82–250 m ($\bar{x}$ = 150 m) from an aerie by two observers, each on a half-day shift. They used 10–45 × Bushnell telescopes and 7 × 35 or 10 × 50 binoculars. The observers were systematically rotated through all observed falcon pairs to minimize bias. The falcons were not individually marked. Sex of the focal bird was determined by its relative size (female's are about one-third heavier than males [Palmer 1988]) and sex-specific behavior (e.g., position of the falcon during copulation, food begging). Observations usually started 1–5 weeks prior to incubation and continued until the young were 29–35 days old (just before their first flight; Enderson 1964), or the nesting attempt failed. Productivity (young fledged per pair) was determined by counting the number of young per occupied territory that reached 30 days of age (sensu Steenhof 1987). Young were aged with a photographic aging key (Moritsch 1983). Hatching dates were calculated by using the estimated age of the young. Laying dates were based on a 34-day incubation period (Burnham 1983). I categorized observation days (OD) in 6-day intervals labelled by midpoints (preincubation, OD = 91: days −51, −45, −39, −33, −27, −21, −15, −9, −3; incubation, OD = 246: days 3, 9, 15, 21, 27, 33; and brood rearing, OD = 231: days 34, 39, 45, 51, 57, 63, and 69). Day 34 was included when falcons had recently hatched young (i.e., <4 days old).

Prey delivered to the nesting territory was classified as mammal, bird, reptile, or unidentified. Mammalian prey items were further subdivided if possible. Items that were positively identified as Townsend's ground squirrels (*Spermophilus townsendii*) were assigned to a separate category. All other mammals were lumped into the small mammal category. Biomass estimates for delivered prey items were not attempted, because the observer distance to the aeries was too great. In 1986 and 1987, 65 young were weighed to provide an index of physical condition of the young, using a 1,000-g Pesola spring balance. Crop fullness was estimated in increments of 25% and weight of young adjusted accordingly (U.S. Bureau of Land Management, unpubl. data). Young were an average 31 ± 2 (range = 25–35) days old when weighed. Their sex was determined by morphological measurements and weight (Holthuijzen 1988). The weights of young were not adjusted for age, because Prairie Falcons reach their asymptotic weight when they are about 25 days old (Fowler 1931, Sitter 1983). Frequency data were square root transformed (Sokal and Rohlf 1981). Statistical analyses were evaluated at $P = 0.05$. Variation is expressed in standard deviations, unless otherwise noted.

RESULTS

DIET

Mammals comprised at least 64.1% (range = 54.9–74.7%) of all freshly killed prey items (n = 1,742) delivered to the nesting territory (Table 1). Townsend's ground squirrels occurred most frequently in the Prairie Falcon's diet (37.0% of all delivered prey), followed by small mammals not identified as Townsend's ground squirrels (27.1%), birds (4.0%), and lizards (0.7%). Differences in prey categories between the sexes were found for 1986 (χ^2 = 12.37, df = 3, P = 0.006), but not for other years (1984: χ^2 = 6.36, df = 3, P = 0.09; 1985: χ^2 = 6.40, df = 3, P = 0.09; and 1987: χ^2 = 1.15, df = 3, P = 0.76). Overall, differences between the sexes were slight (χ^2 =

TABLE 1. Diets of nesting Prairie Falcons, 1984–1987. Numbers in parentheses are percentages of total number of prey items delivered to the nesting territories each year.

Year	Sex	Prey category					Total
		Unidentified	Small mammal	Townsend's ground squirrel	Bird	Lizard	
1984	Male	110 (34.2)	56 (17.4)	87 (27.0)	7 (2.2)	0 (0.0)	260 (80.7)
	Female	25 (7.8)	6 (1.8)	28 (8.7)	3 (0.9)	0 (0.0)	62 (19.3)
	Total	135 (42.0)	62 (19.2)	115 (35.7)	10 (3.1)	0 (0.0)	322 (100.0)
1985	Male	108 (20.4)	131 (24.8)	121 (24.8)	24 (4.5)	9 (1.7)	393 (74.3)
	Female	48 (9.1)	45 (8.5)	41 (5.8)	2 (0.4)	0 (0.0)	136 (25.7)
	Total	156 (29.5)	176 (33.3)	162 (30.6)	26 (4.9)	9 (1.7)	529 (100.0)
1986	Male	97 (28.7)	105 (31.1)	57 (16.9)	22 (6.5)	1 (0.3)	282 (83.4)
	Female	27 (8.0)	10 (2.9)	17 (5.0)	1 (0.3)	1 (0.3)	56 (16.6)
	Total	124 (36.7)	115 (34.0)	74 (21.9)	23 (6.8)	2 (0.6)	338 (100.0)
1987	Male	90 (16.3)	84 (15.2)	217 (39.2)	7 (1.3)	1 (0.2)	399 (72.2)
	Female	38 (4.8)	35 (6.3)	77 (14.0)	4 (0.7)	0 (0.0)	154 (27.8)
	Total	128 (23.1)	119 (21.5)	294 (53.2)	11 (2.0)	1 (0.2)	553 (100.0)
Total	Male	405 (23.2)	376 (21.6)	482 (27.7)	60 (3.4)	11 (3.4)	1,334 (76.6)
	Female	138 (8.0)	96 (1.1)	163 (9.3)	10 (0.6)	1 (0.6)	408 (23.4)
	Total	543 (31.2)	472 (27.1)	645 (37.0)	70 (4.0)	12 (0.7)	1,742 (100.0)

8.15, df = 3, $P = 0.04$); females delivered fewer birds than males.

Prey categories changed over the years (Table 1). Prey items identified as Townsend's ground squirrels decreased from 35.7% in 1984 to 30.6% in 1985, and further declined to 21.9% in 1986 (Table 1). In 1987, however, 53.2% of the diet was composed of Townsend's ground squirrels. Interpretation of these data is limited, however, because of the large percentage of unidentified items (31.2%).

For each nesting pair of falcons, the percentage of Townsend's ground squirrels delivered to the nesting territory was calculated for the brood-rearing stage and regressed on productivity. Productivity increased significantly with the percentage of Townsend's ground squirrels in the falcon's diet (t-test slope, $b = 0.08$, $t = 3.77$, $P = 0.0006$) (Fig. 1).

PREY DELIVERIES

Significant differences in prey delivery rates per pair/hour were found among years, stages, and nesting pairs (ANOVA, $F = 26.21$, df = 3 and 518, $P < 0.0001$; $F = 402.54$, df = 2 and 518, $P < 0.0001$; and $F = 3.17$, df = 44 and 518, $P < 0.0001$, respectively). Prey delivery rates were high in 1984, 1985, and 1987 (0.24 ± 0.17, 0.21 ± 0.19, and 0.22 ± 0.21 items/hr, respectively); the lowest rate was recorded for 1986 (0.13 ± 0.12 items/hr) (Duncan's multiple range test [DMR], $P = 0.05$). Prey delivery rates peaked during brood rearing (0.37 ± 0.16 items/hr, OD = 231) and were significantly higher than during the preincubation stage (0.10 ± 0.08 items/hr OD = 91) (Table 2). The lowest delivery rates were observed during the incubation stage (0.08 ± 0.07 items/hr, OD = 246) (DMR, $P = 0.05$).

Males delivered 76.6% of all prey to the nesting territories at a rate of 0.15 ± 0.14 items/hr or 2.30 ± 2.11 items/day (OD = 568) over the entire nesting cycle (Table 2). Males delivered an average 0.10 ± 0.08 items/hr (OD = 91; 97.8% of all delivered prey items) during preincubation, decreasing to 0.07 ± 0.07 items/hr (OD = 246; 95.3% of all delivered prey items) during incubation. They rapidly increased the number of prey delivered immediately after hatching (Fig. 2) from a rate of 0.18 ± 0.12 items/hr when young were 0–3 days of age (OD = 14) to a peak of 0.32 ± 0.16 items/hr when young were 8–14 days of age. Prey delivery rates for males then decreased and remained at about 0.24 items/hr for the rest of the brood-rearing stage.

Females delivered few prey items to the nesting territory during both preincubation and incubation (Fig. 2). During brood rearing, however, prey delivered by the female rapidly increased from 0.02 ± 0.03 items/hr (OD = 14) when young were 0–3 days of age to a peak of 0.19 ± 0.11 items/hr (OD = 41 days) when young were 21–27 days of age, about 2 weeks after the peak in prey deliveries by the male. Prey delivery rates of female subsequently declined to 0.13 ±

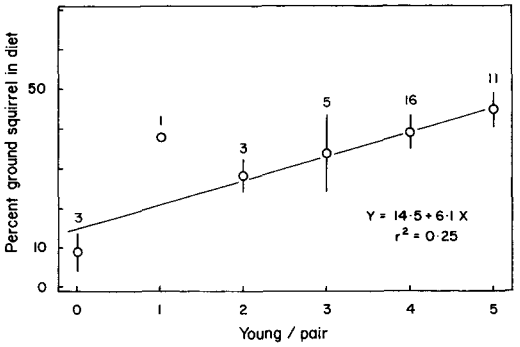

FIGURE 1. Townsend's ground squirrel as a percentage of the Prairie Falcon's diet ($\bar{x} \pm$ SE) during brood rearing regressed on young fledged/pair, 1984–1987. Numbers above SE bars refer to the number of nesting pairs.

0.10 items/hr. The number of prey delivered through the combined activities of the male and the female falcon showed a steady increase following hatching and peaked when the young stabilized in weight at 21–27 days of age.

The frequency distribution of prey deliveries during an observation day showed a bimodal pattern (Fig. 3). The first peak was in late morning (2–5 hr after sunrise) and the second in late afternoon (12–13 hr after sunrise). A stronger bimodal pattern was demonstrated for males than for females, but this was probably a reflection of sample size, because males delivered 75% of all prey.

RELATIONSHIPS BETWEEN PREY DELIVERY RATES, PRODUCTIVITY, HATCHING DATE, AND WEIGHT OF YOUNG

No significant differences were found among years when the average number of prey delivered per pair/hour during brood rearing was regressed on productivity (ANCOVA, slopes $F = 2.27$, df = 3 and 35, $P > 0.10$; intercepts $F = 2.14$, df = 3 and 35, $P > 0.10$). Therefore, prey delivery data were combined for all years. The average prey delivery rate per pair/hour significantly increased with the number of young fledged per pair (Fig. 4).

The average prey delivery rate per pair/hour during brood rearing decreased significantly with progressively later hatching dates for 1985 and 1986 ($b = -0.01$, $t = -2.83$, df = 1, $P = 0.02$; and $b = -0.004$, $t = -3.35$, df = 1, $P = 0.01$), but not for 1984 and 1987 ($t = -1.48$, df = 1, $P = 0.18$; and $t = -1.34$, df = 1, $P = 0.21$). Differences among years were not significant

TABLE 2. Numbers of prey items delivered, cached, and retrieved per hour by Prairie Falcon pairs, 1984–1987 (OD refers to observation days).

Stage	Sex	Prey items/hr						Prey items/day					
		Delivered		Cached		Retrieved		Delivered		Cached		Retrieved	
		$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Preincubation (OD = 91)	Male	0.10	0.08	0.01	0.03	0.01	0.03	1.37	0.11	0.16	0.37	0.15	0.42
	Female	0.00	0.01	0.02	0.04	0.02	0.05	0.04	0.18	0.22	0.49	0.33	0.62
	Total	0.10	0.08	0.03	0.05	0.03	0.06	1.41	1.10	0.38	0.68	0.48	0.81
Incubation (OD = 246)	Male	0.07	0.07	0.01	0.03	0.01	0.03	1.06	1.00	0.15	0.40	0.15	0.43
	Female	0.01	0.02	0.01	0.03	0.02	0.04	0.06	0.24	0.20	0.50	0.22	0.52
	Total	0.08	0.07	0.02	0.05	0.03	0.05	1.12	1.03	0.35	0.66	0.37	0.73
Brood rearing (OD = 231)	Male	0.26	0.14	0.03	0.05	0.03	0.06	3.99	2.15	0.39	0.81	0.52	0.97
	Female	0.11	0.10	0.07	0.08	0.07	0.08	1.66	1.60	1.10	1.23	1.13	1.28
	Total	0.37	0.16	0.10	0.10	0.10	0.11	5.65	2.57	1.49	1.58	1.65	1.69
All stages (OD = 568)	Male	0.15	0.14	0.02	0.04	0.02	0.05	2.30	2.11	0.25	0.61	0.30	0.73
	Female	0.05	0.08	0.04	0.06	0.04	0.07	0.71	1.30	0.57	0.98	0.61	1.01
	Total	0.20	0.18	0.06	0.08	0.06	0.09	3.01	2.85	0.82	1.26	0.91	1.37

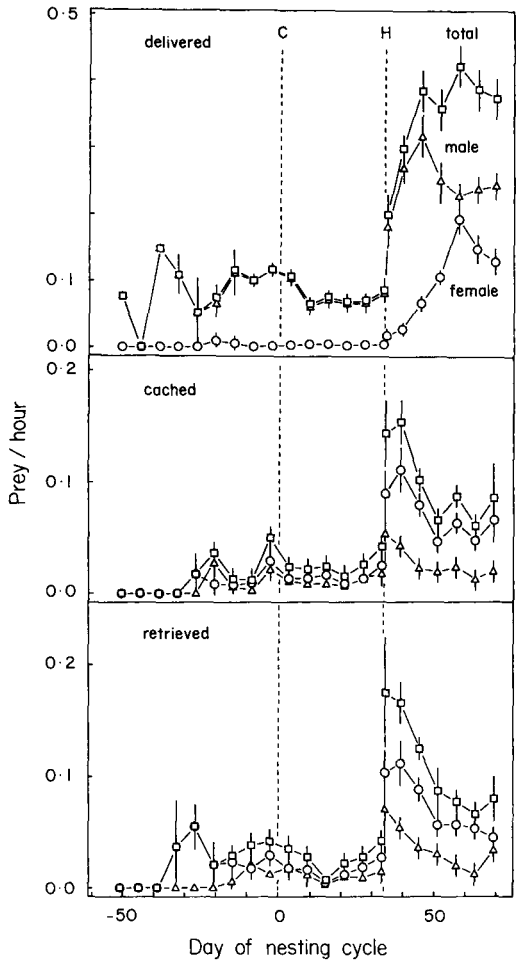

FIGURE 2. Number of prey items ($\bar{x} \pm$ SE) delivered to the nesting territory, cached, and retrieved per hour, by Prairie Falcon nesting pairs, for each sex, 1984–1987. C = clutch completion; H = hatching.

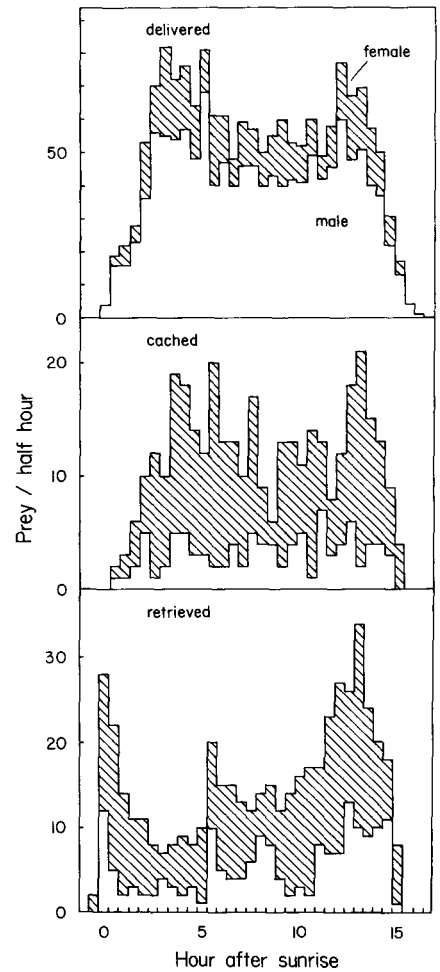

FIGURE 3. Diurnal frequency distribution of prey items delivered, cached, and retrieved per half-hour by Prairie Falcon nesting pairs (568 observation days), and for each sex, 1984–1987.

(ANCOVA, slopes: $F = 1.34$, df = 3 and 33, $P > 0.10$; and intercepts: $F = 1.46$, df = 3 and 33, $P > 0.10$). When the data were pooled for all years, again a decrease was found in prey delivery rates with hatching taking place later in the nesting season (Fig. 5). This coincided with a decrease in productivity (t-test slope, $b = -4.93$, $t = 46.67$, $P = 0.0001$, $r_s = 0.33$) (Fig. 6).

Weights of both male and female young showed a weak, but nonsignificant increase with prey delivery rates per pair/hour (males: Pearson's product moment correlation coefficient $r_s = 0.49$, $n = 13$, $P = 0.09$; and females: $r_s = 0.47$, $n = 17$, $P = 0.06$, respectively).

CACHING AND RETRIEVAL

Prairie Falcons cached prey items in clumps of grass (*Poa* spp.), big sagebrush (*Artemisia tridentata*), or other brushy vegetation, on ledges, and in small cavities in the nesting territory. Male and female falcons used separate caching sites within a general caching area. The falcons were very alert when caching. Just before storing a prey item, they would stand upright with their necks craned, observing their surroundings sometimes for several minutes. The prey would then be transferred from the talons to the bill and pushed into the vegetation or a crevice. After scanning the environment, the falcon would fly

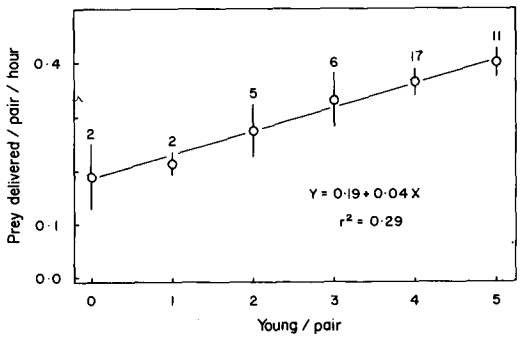

FIGURE 4. Average number of prey items delivered per Prairie Falcon pair/hour during brood rearing ($\bar{x}$ ± SE) regressed on young fledged/pair, 1984–1987. Numbers above the SE bars refer to the number of nesting pairs.

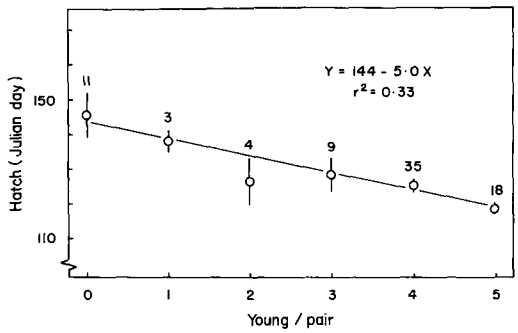

FIGURE 6. Julian hatching date ($\bar{x}$ ± SE) regressed on the number of Prairie Falcon young fledged/pair, 1984–1987. Numbers above the SE bars refer to the number of pairs observed.

off. A falcon would immediately retrieve a prey item when watched by its mate, other raptors, or ravens (*Corvus corax*). Potential cache robbers were chased off before the falcon would cache prey.

Caching rates per pair/hour showed significant differences among years, stages, and nesting pairs (ANOVA, $F = 4.62$, df = 3 and 518, $P = 0.0003$; $F = 65.11$, df = 2 and 518, $P > 0.0001$; and $F = 2.51$, df = 44 and 518, $P > 0.0001$, respectively). High caching rates were observed in 1987 (0.07 ± 0.11 items/hr, $n = 163$ days), 1984 (0.06 ± 0.08 items/hr, $n = 89$ days), and 1985 (0.05 ± 0.07 items/hr, $n = 162$ days), which were all higher than in 1986 (0.04 ± 0.06 items/hr, $n = 154$ days) (DMR, $P = 0.05$). A greater number of prey items were cached during brood rearing (0.10 ± 0.11 items/hr, $n = 231$ days) than during either preincubation (0.03 ± 0.06 items/hr, $n = 91$ days) or incubation (0.03 ± 0.05 items/hr, $n = 246$ days) (DMR, $P = 0.05$) (Table 2). Caching rates were high during the first week of brood rearing (0.14 ± 0.13 items/hr, $n = 14$ observation days, young 0–3 days old), then decreased to 0.07 ± 0.07 items/hr ($n = 40$ days) when young were 14–20 days and remained at this level for the rest of the brood-rearing stage (Fig. 2). Female falcons cached most prey items (77.7%). Males only cached prey when the female did not accept the prey, the female was absent, or the young did not consume the prey. The diurnal frequency distribution pattern of prey caching closely followed the pattern described for delivered items with higher numbers of prey cached in the early morning and late afternoon (Fig. 3).

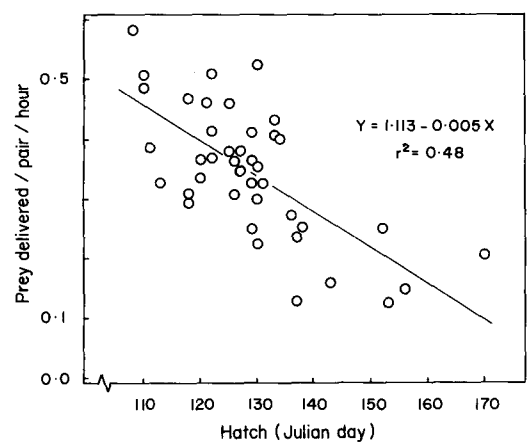

FIGURE 5. Average number of prey delivered per pair per hour during brood rearing regressed on Julian hatching date, 1984–1987.

Retrieval rates per pair/hour did not show differences among years, but differed significantly among stages and nesting pairs (ANOVA, $F = 2.37$, df = 3 and 518, $P = 0.07$; $F = 64.25$, df = 2 and 518, $P > 0.0001$; and $F = 1.73$, df = 44 and 518, $P = 0.003$, respectively). The lowest retrieval rate was found for 1986 (0.05 ± 0.08 items/hr, OD = 154); the retrieval rates for 1984, 1985, and 1987 (0.07 ± 0.11, OD = 89; 0.06 ± 0.08, OD = 162; and 0.07 ± 0.10 items/hr, OD = 163, respectively) were not significantly different, but all were higher than for 1986 (DMR, $P = 0.05$). During brood rearing, retrieval rates/hour were significantly higher (0.10 ± 0.11 items/hr, OD = 231) than during both the preincubation and incubation stages (0.03 ± 0.06, OD = 91, and 0.03 ± 0.05 items/hr, OD = 246,

TABLE 3. Pearson's product moment correlation coefficients between prey delivered, cached, and retrieved per hour by Prairie Falcon pairs, 1984–1987. OD refers to observation days.

Stage	Behavior	Behavior	
		Cached	Retrieved
Preincubation (OD = 91)	Delivered	0.30*	0.002 (ns)
	Cached		0.19 (ns)
Incubation (OD = 246)	Delivered	0.47**	0.17*
	Cached		0.45**
Brood rearing (OD = 231)	Delivered	0.18*	−0.08 (ns)
	Cached		0.61**
All stages (OD = 568)	Delivered	0.46**	0.30**
	Cached		0.63**

* $P < 0.01$, ** $P < 0.0001$.

respectively; DMR, $P = 0.05$) (Table 2). Like caching rates, retrieval rates were highest during the first week of brood rearing (0.17 ± 0.17 items/hr, OD = 14, young 0–3 days old) then declined to 0.09 ± 0.11 items/hr (OD = 41) when young were 14–20 days of age and stayed at this level for the remainder of the brood-rearing stage (Fig. 2). Females retrieved most prey (73.7%), especially early in the brood-rearing stage. Retrieval of prey items during the day was high in the early morning hours (0–1 hr after sunrise), then rapidly declined, reaching its lowest level when prey deliveries peaked in late morning (Fig. 3). Prey items were steadily retrieved during the afternoon. A second peak occurred in late afternoon-early evening (11.5–13.5 hr after sunrise) followed by a rapid decline. Both sexes showed a similar diurnal pattern in prey retrieval.

When prey delivery rates were high, more prey was cached during each stage, as well as for all stages combined (Table 3). Correlations between prey delivery rates and retrieval rates per day were weak or nonsignificant. High caching rates were strongly associated with high retrieval rates for the incubation and brood-rearing stages and for all stages combined (Table 3). Prairie Falcons retrieved on average as many prey items as they cached during each of the stages and for all stages combined (t-tests, P's < 0.10).

DISCUSSION

Newton (1979) divided studies of diurnal raptors into two groups based on pattern of food consumption. For the first group, that included the Peregrine Falcon, Osprey (*Pandion haliaetus*), and several harrier species (*Circus* spp.), total food consumption increased during the nestling period and with the number of young. Also, the female did not hunt before the young had fledged. In the second group, which included several accipiters, food consumption did not increase with age and the number of young; the female started hunting before the young had fledged. In Prairie Falcons, total prey deliveries increased during the nestling stage and with the number of young. Females procured prey throughout incubation, although at a very low rate, and continued to provide prey in increasing numbers during the brood-rearing stage. Apparently, Prairie Falcons do not belong to either group, but occupy a position along a continuum with the two groups at the extremes.

The Prairie Falcon's diet in the SRBOPA, as determined by direct observation, generally agreed with earlier findings based on prey collections (U.S. Department of Interior 1979, Steenhof and Kochert 1988). For instance, I found that at least 64% of the prey items were mammalian, whereas 67.3% mammalian prey (percentage of individuals) was estimated using prey collections (U.S. Department of Interior 1979). The Townsend's ground squirrel represented the single most important prey item of Prairie Falcons and comprised at least 22–53% of all delivered prey. Similar findings were reported in the same area by Steenhof and Kochert (1988).

Prey delivery rates of Prairie Falcons closely followed the hypothetical food intake curve as proposed by Snyder and Wiley (1976). Prey deliveries during preincubation were higher than during incubation, particularly during egg laying (0–12 days prior to clutch completion) when the female needs additional food. Female Prairie Falcons lay four to five eggs (Palmer 1988), which

represents an estimated 22–27% of the bird's body weight, assuming that the fresh egg weight of a Prairie Falcon is about the same as that of a Peregrine Falcon (45 g; Ratcliffe 1980). During these stages most of the prey is delivered by the male (97.8% and 95.3%) so that the female can accumulate large body reserves for use in incubation and nestling periods, conserve energy to produce eggs, and reduce the risk of damage to the eggs through hunting activities (Newton 1979). Occasionally, females would procure prey that was taken to the nesting territory and was either consumed or cached. In most instances, however, prey was not taken to the nesting territory, but was apparently consumed away from the canyon, because females returned with extended crops and blood on their talons or lower abdomen. Males usually perched in the nesting territory or incubated during the females' hunting trips. During brood rearing a rapid increase in prey delivery rates occurred. During the first 2 weeks male Prairie Falcons still delivered most prey items. As the young required less brooding, females increased their contribution to the food supply, which peaked when young stabilized in weight at about 24 days of age (Fowler 1931, Sitter 1983). Thus, prey delivery rates closely paralleled the growth rate of the nestlings, as was found for other avian species (Ricklefs 1968, Newton 1979, Poole and Boag 1988).

Prairie Falcons demonstrated higher prey delivery rates with increasing brood size. However, this does not mean that Prairie Falcons adjust their delivery rate to the number of young. The prey delivery rate is more likely to be determined by the availability of prey, especially the Townsend's ground squirrel. This is illustrated by data for the 1986 and 1987 nesting seasons. In 1986, Townsend's ground squirrel density was low compared to 1987 (Peterson and Yensen 1986, Quinney et al. 1987). The falcons spent two to three times as much time procuring prey than in 1987. Prey delivery rates for 1986 were significantly lower than for 1987, as was productivity (Holthuijzen, unpubl. data). Also, productivity was positively associated with the percentage of Townsend's ground squirrel in the falcon's diet (Ogden and Hornocker 1977, U.S. Department of Interior 1979, Steenhof and Kochert 1988), again emphasizing the importance of the availability of this species to nesting falcons. More likely, pairs provided prey at the maximum possible rate after their young hatch, as was found for other raptor species, e.g., accipiters (Snyder and Snyder 1973, Newton 1978).

The bimodal pattern in prey deliveries of Prairie Falcons may to some extent reflect the diurnal availability of the Townsend's ground squirrel. From late winter through early spring, Townsend's ground squirrels restrict their activities aboveground to the warmer midday hours after emergence in late February (Johnson et al. 1977). As the season progresses, aboveground activity becomes more bimodal with a morning and late afternoon peak. Thus, Prairie Falcons may synchronize their hunting activities with the activity pattern of their main prey species. Similar relationships were found for other raptors in relation to small mammal activity during the day (Rijnsdorp et al. 1981, Raptor Group RUG/RIJP 1982).

The ability of the male to provide prey to the female during the preincubation stage, and prey abundance, are known to affect laying date and therefore hatching date and clutch size of a number of raptors (Cavé 1968; Newton 1979, 1986; Dijkstra et al. 1982; Newton et al. 1983; Newton and Marquiss 1984; Simmons et al. 1986; Barnard et al. 1987). In 1986, prey delivery rates by male Prairie Falcons during the preincubation stage regressed on hatching date showed a significant negative relationship, but this relationship was not found for other years. Possibly, in 1986, early nesting only took place when the male provided more than the average numbers of prey during preincubation, i.e., the more proficient males were associated with early nesting. This has been observed in the Eurasian Sparrowhawk (Newton 1986) and in nonraptorial birds (Newton 1979, 1980). Also, low Townsend's ground squirrel numbers in 1986 may have induced late nesting, resulting in later average hatching dates for 1986 as compared to other study years. In addition, late-nesting Prairie Falcons were confronted with decreasing prey availability due to the gradual estivation of Townsend's ground squirrels from May through July (U.S. Department of Interior 1979, Smith and Johnson 1985). The net result was a decrease in productivity of progressively later-nesting falcons.

As can be expected, caching and retrieval rates were high when peak numbers of prey were delivered, particularly during early brood rearing, when the small falcon young need to be fed frequently and at regular intervals, but cannot consume much food (Ratcliffe 1980). The diurnal retrieval pattern again showed the importance of

caching as a mechanism to maximize food intake and dampen fluctuations in prey availability. Retrieval rates peaked in the early morning hours just after sunrise, when the young had been without food during the night. In the afternoon, retrieval rates remained moderately high, when prey deliveries declined, and peaked again during late afternoon to early evening.

Poole and Boag (1988) reported a similar pattern in Gryfalcons, although caching was observed only after the eggs had hatched. The caching rates were high when the young were small, then declined, and caching was not observed after the nestlings were 29 days of age. Prairie Falcons, however, continued to cache prey throughout the brood-rearing stage, possibly due to the activity pattern of the Townsend's ground squirrel. Rijnsdorp et al. (1981) found that the Eurasian Kestrel also exploited prey with a distinct availability pattern, which in turn induced a diurnal rhythm in caching behavior.

The adaptive value of caching is determined by the ability of the bird to successfully store the prey in a suitable site without losing it to potential cache robbers and to identify the cache site at a later time to retrieve the item. Collopy (1977) calculated a 70% success rate for free-ranging American Kestrels retrieving prey, and Mueller (1974) reported a success rate of 65% for captive birds. Prairie Falcons appear to have a higher success rate, because the number of caches and retrievals on a daily basis were not significantly different. However, these calculations are based on the number of caches and retrievals, not individual prey items, so that the actual success rate may be lower. Prairie Falcons usually cached in restricted locations and systematically checked all preferred sites for cached prey. This may suggest that the falcons did not remember the exact caching location. Free-living American Kestrels approached caching sites more directly than Prairie Falcons (Collopy 1977), and captive American Kestrels could accurately locate a caching site (Mueller 1974). Merlins (Oliphant and Thompson 1976), however, had to search for the location of a cache, much like Prairie Falcons.

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