FOOD CACHING BY FEMALE AMERICAN KESTRELS IN WINTER

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Prey caching is documented for many birds of prey. A review of some raptor species which cache food was provided by Mueller (1974). Additional records of caching among falconiforms were reported by Roest (1957), Gullion (1965) and Balgooyen (1976). Prey caching has also been noted in many owl species (Allen 1924, Lockley 1938, Wallace 1948, Mossman 1955, Jansson 1964, Norburg 1964, Grant 1965, Ligon 1968, Catling 1972). For the purposes of this study, I designated caching behavior as any activity involved in storing or retrieving prey. Storage is that aspect of caching in which a food item is placed in a cache. Retrieval is that aspect of caching in which a stored food item is removed from a cache. Typical prey retrieving behavior which failed to produce a food item is called here an attempt to retrieve.

Most accounts of caching by American Kestrels (*Falco sparverius*) are based on relatively few observations of wild or captive birds (Pierce 1937, Tordoff 1955, Roest 1957). Stendell and Waian (1968) observed a female kestrel store 17 prey items in one cache over a 40-day period. Balgooyen (1976) watched kestrels caching food during the breeding season. He discussed the advantages of caching food, especially during periods when inclement weather is common and while raising young. In the laboratory, Mueller (1974) studied the effects of deprivation interval, time of day, and type of food on the caching behavior of captive kestrels.

The results reported here are from a study I conducted on the behavior of American Kestrels wintering in the Arcata Bottoms, west of Arcata, Humboldt County, California. I observed kestrels for two winter seasons, from October 1972 to March 1973, and from September 1973 to March 1974.

STUDY AREA

The Arcata Bottoms, Humboldt County, California, is bordered on the south by Humboldt Bay, on the west by the Pacific Ocean, on the north by the Mad River, and on the east by the city of Arcata and surrounding redwood (*Sequoia sempervirens*) forest. It consists of extensive pastureland reclaimed from bay tidelands and parts of the Mad River delta.

Wheeler and Harris (1970) described the vegetation in the pastures, dikes, sloughs and intermittent marshes of the Arcata Bottoms. In the pastures they found primarily orchard grass (*Dactylis glomerata*), velvet grass (*Holeus mollis*), fescues (*Festuca* spp.), sedges (*Carex* spp.), and rushes (*Juncus* spp.). On the dikes the vegetation included tufted hairgrass (*Deschampsia caespitosa*), coyote brush (*Baccharis pilularis*), blackberry (*Rubus vitifolius*), mustards (*Cruciferae*), and docks (*Rumex* spp.). In the sloughs and intermittent marshes, stands of one or more of the following were found: cattail (*Typha latifolia*), arrowgrass (*Triglochin maritima*), rushes, horsetail (*Equisetum* spp.), three-square bulrush (*Scirpus americanus*), and saltgrass (*Distichlis spicata*).

MATERIALS AND METHODS

I watched kestrels with a 20× wide-angle spotting telescope and 7× binoculars at distances of 10 to 70 m. For each observation of caching behavior, I recorded the following: species of prey cached, feeding behavior before storing, location of cache, behavior after storing, time of day, and duration of the caching sequence.

RESULTS

The male to female sex ratio of kestrels wintering in the Arcata Bottoms was 1:9 (Koplin 1973). Observations of males were relatively uncommon; therefore, I analyzed data on females only.

I witnessed all aspects of caching behavior during each winter of study (table 1). The frequency of caching behavior was estimated by expressing the total number of caching acts observed each year as a percent of all behavioral acts observed. Caching behavior constituted 1.2% of all behavioral acts observed in 1972–73, and 1.4% in 1973–74. The greater number of caching observations witnessed in 1973–74, therefore, reflect the increased amount of time spent in the field, not actual increases in the rate of caching behavior.

CACHE SITES

I saw 10 kestrels store or retrieve 61 prey items in 64 caches (three prey items were stored a second time). In 14 of these instances, I observed the storing and subsequent retrieval of a particular prey item. Three of the caches were short broken posts, 3 were fence posts, 2 were shrubs, and 56 were grass clumps. Tordoff (1955) reported that a pet kestrel preferred elevated caches and suggested that trees may be preferred in the wild. The general absence of trees in the Arcata Bottoms

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TABLE 1. Number of caching activities by female American Kestrels wintering in the Arcata Bottoms, Humboldt County, California in 1972–73 and 1973–74.

	1972–73	1973–74	Total
Food stored	10	36	46
Food retrieved	9	23	32
Attempts to retrieve	6	6	12
Yearly totals	25	65	90
Total number of behavioral acts observed	2007	4779	6786
Period of observation (hours)	130.5	182.6	313.1

eliminated this possibility. However, kestrels did not use any of the numerous utility poles in the area as caches.

Monthly road censuses (44 km long) conducted in the Arcata Bottoms during the fall and winter of 1972–73 and 1973–74 indicated that relatively large numbers of raptors wintered in the area (Collopy 1975). Combining both seasons, the mean number of kestrels seen was 15.9 per census. The number of other raptors seen, primarily Red-tailed Hawks (*Buteo jamaicensis*), Rough-legged Hawks (*B. lagopus*), and Marsh Hawks (*Circus cyaneus*), averaged 8.4 individuals per census.

The presence of these raptors, and scavengers such as Common Crows (*Corvus brachyrhynchos*), Common Ravens (*C. corax*), gulls (*Larus* spp.), and Turkey Vultures (*Cathartes aura*), increased the probability of losing stored prey if it was too conspicuous (e.g., on utility poles). The use of grass clumps and posts as caches, familiar to kestrels within their hunting territories, apparently provided sufficient orientation for them to find stored prey. These same landmarks probably were less obvious to other less sedentary raptors and scavengers, and tended to conceal stored prey.

PREY SPECIES CACHED

Only vertebrate prey were cached. In 1972–73, 15 (88.2%) of the prey items cached were small mammals; of these, 7 (41.2%) were vagrant shrews (*Sorex vagrans*), 5 (29.4%) were California meadow voles (*Microtus californicus*), 1 (5.9%) was a harvest mouse (*Reithrodontomys megalotis*), and 2 (11.8%) were unidentified. Other prey cached included a common garter snake (*Thamnophis sirtalis*) and a weaver finch (*Passer* spp.). In 1973–74, 30 (68.2%) of the prey items cached were frogs and snakes; of these, 6 (13.6%) were red-legged frogs (*Rana aura*), 15 (34.1%) were Pacific treefrogs (*Hyla regilla*), 6 (13.6%) were unidentified frogs, and 3 (6.8%) were garter snakes. The 14 (31.8%) other prey items cached were meadow voles and shrews.

The shift from caching predominately small mammals in 1972–73 to amphibians and reptiles in 1973–74 reflects the difference in prey captured. In 1972–73, 29 (90.6%) of the vertebrates captured were small mammals. In 1973–74, 34 (73.9%) of the vertebrates captured were frogs and snakes, while the number of small mammal prey decreased to 12 (26.1%). I analyzed the data on capture and storage of prey to determine if selective storing of particular prey items occurred. Because of limited sample size, only data from 1973–74 could be tested. A Chi-square test indicated that the relative proportion of prey type cached corresponded directly with the relative proportion captured ($X^2 = 3.69$, 1 df, $P > 0.05$). Limited data from 1972–73 suggest that this relationship also existed the previous year.

The difference in the proportion of small mammals vs. amphibians and reptiles captured during the two winters of study appears correlated with their relative availability during the two seasons. The absence of frogs from both caching and prey captured in 1972–73, probably reflects a decrease in availability resulting from the relatively dry, cold winter of 1972–73. The warmer, wetter winter of 1973–74 apparently was conducive to poikilothermic activity, resulting in increased vulnerability to predation. Factors related to the observed decrease in small mammal abundance during the winter of 1973–74 are less obvious.

Generally, prey were decapitated before being stored. Of the 17 caches I inspected, 13 (76.5%) contained decapitated prey. On one occasion I found only the inverted pelt of a meadow vole. Stendell and Waian (1968) reported that 14 of 15 (93.3%) small mammals they found in a cache regularly used by a female kestrel, were decapitated.

PREY STORING BEHAVIOR

After killing prey, and feeding on it or not, kestrels flew to a cache. Sites were apparently selected before flight started, since kestrels always flew directly to a spot where prey then was stored. When kestrels used posts or poles as caches, they landed on the structure and stuffed the prey remains in a crack at the top, or wedged it between the post and railing. When storing prey in grass clumps, kes-

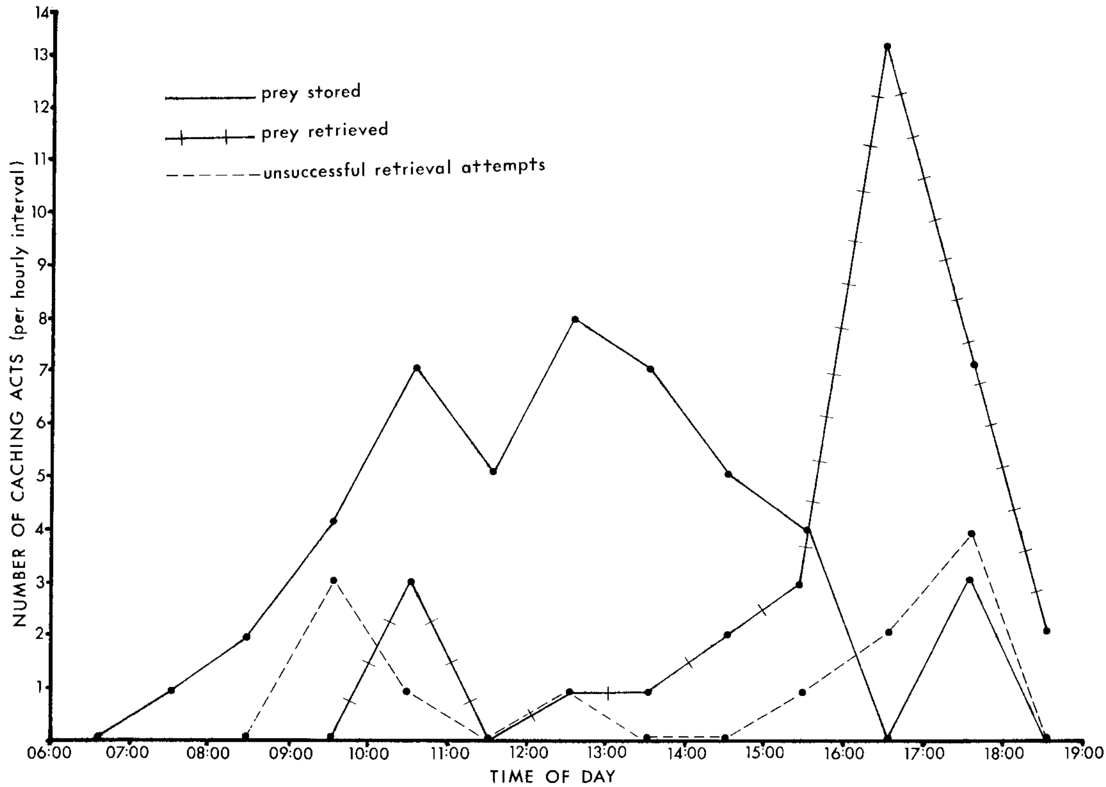

FIGURE 1. Caching activity of female American Kestrels in relation to time of day in the Arcata Bottoms, Humboldt County, California, combined for the winters of 1972–73 and 1973–74. Observations are presented by hourly interval.

trels landed next to the clump, transferred the prey from the talons to the beak (prey usually were carried in the talons during flight, but occasionally smaller prey were carried in the beak), walked to the clump, and attempted to poke the remains between the stems. A kestrel sometimes made several attempts to position prey before it remained in the grass clump. Prey were laid prone, as if to take advantage of their protective coloration. Balgooyen (1976) also observed this phenomenon. Positioning, and the use of inconspicuous caches strongly suggest that specific behavior patterns associated with storing have evolved to minimize the loss of prey to other raptors and scavengers. Kestrels always left the cache immediately after storing prey.

PREY RETRIEVING BEHAVIOR

Kestrels always perched near the cache before attempting to recover stored food. When approaching a typical cache (a grass clump) kestrels either landed beside it or hovered one to three meters above it for three or four seconds. While hovering, they often moved about, looking into several adjacent grass clumps. Once on the ground, kestrels approached the cache and looked into it. Kestrels commonly searched all around the grass clump for prey remains. If unable to locate the stored food, they often walked to adjacent grass clumps to search. When kestrels were unable to find the cache they occasionally abandoned the search. However, the most common response after failing to find cached prey was to return to a nearby perch and resume searching after a few minutes. In an effort to recover a meadow vole, which I had previously collected, a kestrel spent over three minutes on the ground investigating a number of grass clumps.

When a cache was located, kestrels usually picked up prey in their beak, transferred it to their talons, and returned to a feeding perch. If the prey had slipped too far inside the clump to be reached with the beak, kestrels often flew to the top of the clump and landed on it with spread wings. Presumably, this prevented them from falling between the stems. This behavior enabled kestrels to grasp the prey with the talons and remove it.

CACHING BEHAVIOR IN RELATION TO TIME OF DAY

Between 8 and 11% of all behavioral data collected (313 h) was obtained during each

TABLE 2. The behavior of female American Kestrels after caching in relation to feeding behavior before caching; Arcata Bottoms, Humboldt County, California, during 1972–73 and 1973–74.

Feeding behavior before caching	Behavior after caching				
	Continued hunting	Inactive perching	Roosting	Observer departed	Total
1972–73					
Prey fed upon	5	1[a]	0	1	7
Prey not fed upon	2	0	0	0	2
Yearly total	7	1	0	1	9
1973–74					
Prey fed upon	19	1[b]	2	0	22
Prey not fed upon	12	0	0	0	12
Yearly total	31	1	2	0	34
Total	38	2	2	1	43

[a] Inactive for 28 minutes before hunting was resumed.
[b] Inactive for 11 minutes before hunting was resumed.

hourly segment from 08:00 to 17:00. Since field observations were distributed more or less equally throughout the day, the possibility of biasing the temporal distribution of caching activities was minimized. Therefore, I consider figure 1 a representative sample of the time of day in which kestrels stored and retrieved prey. Trends in caching behavior are apparent.

Kestrels tended to store prey throughout the day and to retrieve late in the day. Observations of prey storing were scattered throughout most of the day, with 8 to 17% of all observations occurring during each hourly interval from 09:00 to 16:00. However, most prey retrieval observations (78.1%) occurred after 15:00. This pattern was consistent through both winters, even though the types of prey cached were different.

EFFICIENCY OF PREY RETRIEVAL

Since field observations were evenly distributed throughout the day, I assumed that there was no difference in the probability of observing either prey storing or retrieving behavior. Based on this assumption, I treated the caching data as a representative sample of the relative frequency of prey storing and retrieving. Using the number of prey items I saw stored and retrieved, I calculated a minimum recovery efficiency of 70%. This estimate suggests that 30% of food stored by kestrels was not recovered. Observations of unsuccessful attempts to retrieve prey (13.3% of all caching efforts) indicate that kestrels often were unable to find previously stored food. Presumably, the pirating of stored prey by other raptors and scavengers, and the inability of kestrels to relocate caches contributed to this loss.

BEHAVIOR BEFORE AND AFTER STORING PREY

The behavior of kestrels after storing prey was stratified in relation to presence or absence of feeding prior to storage (table 2). For both winters combined, 67.4% of the prey items cached were partially consumed before storing, while 32.6% were stored without prior feeding. After storing prey, kestrels continued hunting 88.4% of the time. Kestrels continued hunting in all cases where prey were stored without prior feeding. Other behavior after storing included inactive perching (4.7%) and roosting (4.7%).

Observations of kestrels feeding prior to caching suggest that they usually satiate themselves before storing prey. Kestrels have a crop capacity of approximately 12 g, and eat a maximum of 8 to 12 g per meal (J. R. Koplin pers. comm.). This explains why kestrels often were unable to fully consume large prey, especially snakes and voles.

Other observations suggest that kestrels kill and store prey when they are not hungry. In February 1974, I watched a kestrel capture and partially consume a treefrog. After storing the remains in a grass clump, she continued hunting and within 17 min captured another frog. This frog was quickly decapitated and then cached.

DISCUSSION

My findings suggest that caching behavior in kestrels evolved as a behavioral mechanism to maximize food intake and to dampen fluctuations in prey availability (see Balgooyen 1976). The estimated 70% success rate in recovering stored prey illustrates the important role caching behavior can play in storing temporary food surpluses. By hunting immediately after capturing prey, kestrels increase the chance of obtaining food which might not be available later. If this extra food is captured and stored, it can be retrieved later when prey are scarce.

The tendency to store prey throughout the day, but retrieve it in the late afternoon may dampen daily variation in food availability for the diurnal-hunting kestrel. Assuming that vertebrate prey have limited vulnerability throughout the day, kestrels hunting at all times can increase food consumption by storing prey whenever an excessive amount is captured. Late in the day, kestrels have less time to capture the amount of prey required for maintenance through the night. Consequently, they tend to consume more of the prey they capture and to recover stored prey.

My observations agree with Mueller's (1974) data on the caching activities of captive kestrels. He found no apparent correlation between storing prey and the time of day. However, retrieving behavior did appear to correlate with time of day. He reported that "the data suggest a circadian rhythm in the tendency to retrieve stored food; a rhythm which peaks in the late afternoon or evening."

Mueller (1974) also discussed the efficiency of captive kestrels in retrieving prey. He stated that his kestrels attempted to retrieve prey on 65% of the opportunities. For an attempt to be considered successful, he required the kestrels to return directly to the spot where they previously stored food. Also, the time kestrels were allowed to find the cache was limited to five minutes after reintroduction to the feeding area. It is difficult to interpret these results since kestrels in the wild probably lose cached prey to other animals and forget the location of some caches. The time limitation imposed by Mueller probably reduced the number of successful retrieval attempts. Kestrels also had limited area in which to store and retrieve food. This probably increased the likelihood of successful retrieval attempts. These factors affect caching efficiency in different ways and probably confound the results sufficiently to limit their applicability to kestrels in the wild.

After storing food, kestrels normally hunted and killed prey, regardless of feeding behavior before storing (table 2). These observations differ from the laboratory findings of Mueller (1973), in which the predatory behavior of kestrels was directly correlated with the length of time between feedings. Mueller also stated that kestrels never killed another mouse until the mouse already cached was entirely eaten. On three occasions in March 1974, I observed a kestrel sequentially store four frogs in less than five hours. In each case, at least two frogs were not fed upon, or were only decapitated, before being stored. In January, 1973, I also saw a kestrel retrieve and eat two shrews from different caches within 58 minutes. No hunting occurred between the first and second retrieval. Apparently, kestrels may continue to hunt and stockpile prey after they are satiated. They also are able to retrieve several stored prey in succession. These observations suggest that the normal behavior of kestrels studied by Mueller was inhibited by the artificial, laboratory conditions.

The evolutionary significance of caching behavior must be viewed in relation to its effect on the reproduction of kestrels which cache food. Clearly, those kestrels who are most efficient in procuring food for their young, especially during periods of temporary food shortage, will be most successful at raising young. Caching behavior enables kestrels to increase the amount of food they can provide for young, especially during periods of shortage. The caching of food by kestrels during the winter, when prey availability is unpredictable, probably also reduces overwinter mortality.

SUMMARY

Caching behavior by the American Kestrel is described. In 1972–73, I recorded 25 instances of prey caching; of these 10 (40.0%) involved food storage and 9 (36.0%) involved food retrieval. I observed 6 (24.0%) unsuccessful attempts to retrieve prey in 1972–73. In 1973–74, I recorded 65 instances of prey caching, of which 36 (55.4%) involved storage and 23 (35.4%) involved retrieval. I observed 6 (9.2%) unsuccessful attempts to retrieve prey in 1973–74. I witnessed the storage of a single prey item and its subsequent retrieval twice in 1972–73, and 12 times in 1973–74.

Small mammals, birds, snakes, and frogs were the prey items cached. In 1972–73, 15 (88.2%) of the prey cached were small mammals, and in 1973–74, 30 (68.2%) were snakes and frogs.

Prey was cached predominantly in grass clumps (87.5%), but other sites occasionally were used; these included, short broken posts (4.7%), fence posts (4.7%), and shrubs (3.1%).

Kestrels stored prey throughout the day. Between 8 and 17% of all storing observations occurred during each hourly interval from 09:00 to 16:00. Most attempts at retrieval (25; 78.1%) occurred after 15:00.

My findings indicate that kestrels continue hunting immediately after storing prey, regardless of feeding behavior beforehand. Kestrels stockpiled surplus prey items in caches, and retrieved several stored prey in succession.

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LITERATURE CITED

ALLEN, A. A. 1924. A contribution to the life history and economic status of the Screech Owl (*Otus asio*). Auk 41:1–16.

BALGOOYEN, T. G. 1976. Behavior and ecology of the American Kestrel (*Falco sparverius* L.) in the Sierra Nevada of California. Univ. California Publ. Zool. 103:1–83.

CATLING, P. M. 1972. A study of the Boreal Owl in southern Ontario with particular reference to the irruption of 1968–69. Can. Field-Nat. 86: 223–232.

COLLOPY, M. W. 1975. The behavioral and predatory dynamics of American Kestrels wintering in the Arcata Bottoms. M.S. diss. Humboldt State Univ., Arcata, Calif.

GRANT, R. A. 1965. The Burrowing Owl in Minnesota. Loon 37:2–17.

GULLION, G. W. 1965. Ruffed Grouse cached by a raptor. Loon 37:88.

JANSSON, E. 1964. Anteckinger rorande hackande Sparvuggla (*Glaucidium passerinum*). Vår Fågelvärld 23:209–222.

KOPLIN, J. R. 1973. Differential habitat use by sexes of American Kestrels wintering in northern California. Raptor Res. 7:39–42.

LIGON, J. D. 1968. The biology of the Elf Owl (*Micrathene whitneyi*). Univ. Michigan Mus. Zool., Misc. Pub. No. 136.

LOCKLEY, R. M. 1938. The Little Owl inquiry and the Skokholm Storm Petrels. Br. Birds 31: 278–279.

MOSSMAN, A. S. 1955. Experimental studies of fitness as measured by vulnerability to predation. Ph.D. diss. Univ. Wisconsin.

MUELLER, H. C. 1973. The relationship of hunger to predatory behavior in hawks (*Falco sparverius* and *Buteo platypterus*). Anim. Behav. 21:513–520.

MUELLER, H. C. 1974. Food caching behavior in the American Kestrel (*Falco sparverius*). Z. Tierpsychol. 34:105–114.

NORBURG, A. 1964. Studier over Parlugglans (*Aegolius funereus*) Ekologi och Etologi. Vår Fågelvärld 23:228–244.

PIERCE, W. M. 1937. A pet Sparrow Hawk. Condor 39:137–143.

ROEST, A. I. 1957. Notes on the American Sparrow Hawk. Auk 74:1–19.

STENDELL, R. C., AND L. WAIAN. 1968. Observations of food-caching by an adult female Sparrow Hawk. Condor 70:187.

TORDOFF, H. B. 1955. Food-storing in the Sparrow Hawk. Wilson Bull. 67:138–139.

WALLACE, J. G. 1948. The Barn Owl in Michigan, its distribution, natural history and food habits. Michigan State Coll. Agric. Expt. Tech. Bull. No. 208.

WHEELER, R. J., AND S. W. HARRIS. 1970. Duck nesting and production in the Humboldt Bay area of California. California Fish and Game 56:180–187.

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