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Energetics of the American Kestrel (*Falco sparverius*) During Three Seasons in Northern Utah

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ENERGETICS OF THE AMERICAN KESTREL (FALCO SPARVERIUS) DURING THREE SEASONS IN NORTHERN UTAH

by

Lucinda Haggas

A thesis submitted in partial fulfillment
of the requirements for the degree

of

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in

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Lucinda Haggas

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ABSTRACT

Energetics of the American Kestrel (Falco sparverius) during three seasons in northern Utah

by

Lucinda Haggas, Master of Science

Utah State University, 1985

Major Professor: Dr. James A. Gessaman
Department: Biology Ecology

Behavioral activities and predatory behavior of 18 American Kestrels (Falco sparverius, 9 males and 9 females) were observed for 350+ hours during 3 seasons (nonbreeding = Jan-Feb, breeding = mid-Mar-Apr, and postbreeding = late-Aug-Sept) in northern Utah. Daily energy expenditure (DEE) of male and female kestrels was estimated with a model that incorporated flight activity data from free-living birds and laboratory measurements on daytime and nighttime metabolic rates and energy costs of tissue production derived from captive kestrels. Production costs were included in the DEE for breeding and postbreeding kestrels.

The energy cost of gonadal growth for males (0.02 kcal/day) and females (0.20 kcal/day) was added to the DEE of breeding kestrels. Breeding females expended an estimated 10.13 kcal/day for producing an average clutch of 4.5 eggs. The energy costs of fat deposition (2.27 and 4.39 kcal/day for males and females, respectively) and molt (2.38

and 2.72 kcal/day for males and females, respectively) were added to the DEE of postbreeding kestrels. In addition to the DEE, the model predicted nonflight energy expenditure (NFEE) and flight energy expenditure (FEE) during the day, and energy expenditure during the night (NEE).

DEE of nonbreeding birds is generally higher (47.71 kcal/day) than those from the breeding (44.89 kcal/day) and postbreeding (42.42 kcal/day) seasons. DEE of females (48.69 kcal/day) is higher than males (41.31 kcal/day) primarily because females averaged 15.5% heavier than males during all 3 seasons, and females have higher costs of production. Kestrels are heaviest during the nonbreeding season and the amount of metabolizable energy available is highest. DEE is lower during the breeding and postbreeding seasons because thermoregulatory demands have decreased which may allow energy to be metabolized for production.

NFEE accounts for most (48.5%) of the DEE. Flight costs are relatively small because kestrels allocate an average 3% of the photoperiod (25.6 min/day) to flight activities. Egg production accounts for 20% of the DEE of breeding females. The energy cost of fat deposition and molt accounts for 11.6 and 15.9% of the DEE for postbreeding males and females, respectively. These reproductive and tissue production costs may also elevate the DEE of breeding and postbreeding females to that of nonbreeding females.

(97 pages)

INTRODUCTION

An assessment of the amount of daily energy expended by an animal may elucidate its functional role in energy transfer within an ecosystem. An animal's time and energy requirements can be summarized within a daily energy budget that can be briefly defined as the cost of daily energy expenditure and the energy costs of tissue production. A daily energy budget can be helpful in postulating on the evolution of adaptive strategies (King 1974) and behavioral roles, or providing information on the geographical distribution of species and migration. Apparently, seasonal changes in daily energy expenditure occur in some species but not in others (King 1974). An animal may modify its energy budget during different seasons by the temporal separation of energy demanding events that are associated with the annual cycle. Mobilization of energy by migratory birds for such requirements as thermoregulation, foraging, reproduction, molt, and fat deposition will result in an optimum energy budget specifically adapted to local environments (Orians 1961). The seasonal mobilization of energy allows species to adapt to different environments, or habitats, and is an indicator of the nature of its ecological niche (Pianka 1974).

Direct observation on the activity of free-living birds from a high trophic level such as Falconiformes, can facilitate an analysis of energy flow: however, activity studies on this avian predatory group are few. The amount of energy that can be mobilized for the energy needs of an animal is also influenced by the abiotic environment. Hayes and Gessaman (1980) examined the combined effects of air temperature, solar radiation and wind speed on the energy metabolism of captive raptors, and determined that small raptors, i.e. American Kestrels, were affected more by these environmental variables than Red-tailed Hawks (Buteo jamaicensis) and Golden Eagles (Aquila chrysaetos). Daily energy expenditure has been predicted from flight activity data collected in the field and laboratory determinations of metabolic rate for nonbreeding (wintering) American Kestrels and White-tailed Kites (Elanus leucurus, Koplin et al. 1980) and nonbreeding Bald Eagles (Haliaeetus leucocephalus, Stalmaster 1981). This technique has also been used to estimate daily energy expenditure of Ospreys (Pandion haliaetus, Levenson 1976), Ferruginous Hawks (Buteo regalis, Wakeley 1978), Black-shouldered Kites (E. caeruleus, Tarboton 1978), and Am erican Kestrels (Rudolph 1982) during the breeding season but bioenergetic studies on free-living raptors over several seasons are lacking.

American Kestrels are ideal field subjects for a study on seasonal energy relationships because they are common (Hayward et al. 1976), conspicuous, and migratory throughout most of their range (Bent 1938), and many of their metabolic requirements have been well studied in the laboratory (Gessaman and Findell 1979, Hayes and Gessaman 1980, and Gessaman 1982). The objectives of the present study were to determine if male and female kestrels undergo variations in daily energy expenditure during the nonbreeding, breeding and postbreeding seasons, and if the mobilization of energy for behavioral activity and tissue production by males and females can be related to their ecological role.

METHODS AND MATERIALS

Study area

I studied free-living kestrels in the vicinity of Logan in northern Utah (Fig. 1). Logan is situated in a mountain valley (elev. = 1370 m), locally known as Cache Valley. The valley (773 km^2) is partly surrounded by 3 mountain ranges and Wasatch-Cache National Forest lands. These include the Bear River Range to the east and south, and the Wellsville and Clarkston Mountains to the west. The northern border is defined by the Idaho state line. The valley is predominantly a rural agricultural area, characterized by flat, open country with scattered windbreaks around farms. The landscape includes a variety of habitats such as irrigated cropland, dry pasture, wet fields and open water as part of the Bear River system and associated wetlands. Most of the settlements are located on the periphery of the valley and agricultural interests, wetlands, and several unincorporated villages are located in the interior. Brushy areas are scarce and are confined to water courses. The mountain slopes are dominated largely by sagebrush-forb communities with Bigtooth maple (*Acer grandidentatem*), Rocky Mountain maple (*Acer glabrum*) and Curl-leaf mountain mahoghany (*Cercocarpus ledifolius*) and Utah juniper (*Juniperus osteosperma*, L. M. Schultz pers. comm.) in the canyons and aspen-spruce-fir complexes at higher elevations.

Daily time budget

Kestrels make ideal subjects for a time-energy study because they are conspicuous, easy to observe, and occupy relatively small home ranges (average maximum diameter=0.97 km, present study) in open country (Behle and Perry 1975). I recorded data from 18 adults (9 males, 9 females) for 352.5 hrs with the Focal-Animal and Instantaneous Sampling Techniques of Altmann (1974) during the nonbreeding (Jan-Feb), breeding (mid-Mar-Apr, including the egg laying and incubation phases) and postbreeding (late-Aug-Sept) seasons in 1978. Single birds were observed for half-day periods during the nonbreeding and breeding seasons, and from dawn to dusk during the postbreeding season. Observation hours were distributed fairly evenly among each season, sex, and time of day to obtain a representative sample of kestrel activity. Thirteen study sites were located in open country within 15 km of Logan. All sites were relatively free of disturbances, such as vehicular traffic and human activities.

I monitored kestrel behavior at close range (8-30 m, occasionally to about 60 m) from within a vehicle, which served as a moveable blind. A few birds were color marked with Testor's yellow model paint to facilitate identification, and I distinguished other individuals by characteristics such as roost site selection and feather deletions. Recorded field observations were of two types: (1) elapsed time and hour (MST) of behavioral activities including flight, interactions with other conspecifics, preening, and copulatory activity, and (2) predatory behavior including hunting method, prey provisioning, predatory efficiency, and caching and retrieving. Behavioral data were used to construct daily time budgets for kestrels during the nonbreeding, breeding and postbreeding seasons. Data on flight activities also were used in a model to predict daily energy expenditure (DEE) for kestrels during 3 seasons. Since individual bouts of directional and hovering flight, and preening often occur in rapid succession, I cumulatively recorded each of these behaviors from single kestrels in hourly intervals. Timed behavioral activities are described as follows:

Flight behavior

Time allocated to total flight activities was divided into 3 categories:

Directional flight: flapping flight employed in all traveling and perch exchanges, and gliding to the ground for prey. The majority of kestrel flight was included in this category. I also recorded the number of complete flights (flights where take-off and landing were observed) made by kestrels during the postbreeding season.

Hovering flight: rapid wing flapping while remaining stationary over a fixed point. Kestrels may "kite" under certain wind conditions and remain motionless for brief periods with their wings outstretched.

Species Interactions: escape-type flight evoked by an aggressive interaction with another bird, or, attack-type flight directed toward another bird. I also tallied the number of interactions between kestrels and other avian species.

Nonflight behavior

Preen: grooming behavior includes feather maintenance and rearrangement, and stretching.

Copulation: includes mounting and mating.

Perch-hunt: sitting and hunting from a perch position. I did not distinguish between "sitting" and "hunting" from a perch position, because I observed kestrels instantaneously convert from an inactive sitting-type posture to one of active flight and hunting. This change in activity occurred without an obvious difference in their outward appearance.

All flight, preening and copulatory behavior was recorded to the nearest second. Perch hunting was estimated by subtracting all timed behavioral activities from the total observation time recorded from each kestrel.

Daily energy expenditure

I estimated the daily energy expenditure (DEE) of free-living male and female kestrels during the nonbreeding, breeding and postbreeding seasons largely from an energetics model derived from wintering raptors (Koplin et al. 1980, Table 1). The DEE is the summation of energy expended during the day and night (nighttime energy expenditure or NEE) and the energy expended in tissue production. Kestrels are diurnal and the energy expended during the day includes nonflight energy expenditure (NFEE) and flight energy expenditure (FEE). The tabular account of these energy costs is referred to as a daily energy budget (DEB).

Inputs to the model include data on daily flight and nonflight behavior (as a proportion of the photoperiod), body weight, and meteorological condition, e.g. air temperature, wind speed, solar radiation and photoperiod. Seasonal weight data were obtained from 119 kestrels (84 males, 35 females) that were live-trapped in Cache Valley with a balchatri trap as described by Mueller and Berger (1959). Average daily air temperature and wind speed were obtained directly from the National Climatic Center (NOAA). Since kestrels roosted in cavities throughout the study period, they were exposed to temperatures which were slightly higher than nocturnal temperatures outside the cavity as suggested by Kendeigh (1961). I added an average of 4.3°C to the average daily temperature recorded by the Weather Service to account for the microclimate of the cavity (Kendeigh 1961). Measurements on direct solar and diffuse sky radiation for Cache Valley were obtained from the Department of Soil Science and Biometeorology at Utah State University (I. Dirmhirn pers. comm.). Photoperiods were calculated by adding one hour (to account for twilight) to the elapsed time between sunrise and sunset recorded at Ogden, UT (Gale Research Co. 1977). The error accrued from the 72 km distance between Ogden and Logan is less than 5 minutes (Gale Research Co. 1977).

I modified the model of Koplin et al. (1980) by replacing the equations for existence and standard metabolism (Kendeigh et al. 1977) with data that were derived from kestrels studied at Utah State University (Hayes 1978, Gessaman and Findell 1979, Table 2). Units conversion factors used in the metabolism equations are listed in Table 3. Throughout this paper, the terms basal (BMR) and standard (SMR) metabolic rate are used as defined by Kendeigh et al. (1977): resting metabolic rate (RMR, Hayes and Gessaman 1980) is included in the DEE model as nonflight metabolic rate during the day (J. A. Gessaman pers. comm.).

The model includes the metabolic costs of productive events associated with the breeding and postbreeding seasons (Table 2). Gonadal recrudescence costs for both sexes during the breeding season are small, 0.1% (BMR) for males and 1.0% (BMR) for females (J. A. Gessaman pers. comm.). The cost of egg production was added to the DEE model for breeding females and was calculated as follows: The average clutch size (4.5, A. Woyda unpublished data) is multiplied by the weight of an average egg at laying (15g, R. Atkins unpublished data) times the energy content of an egg (1.05 kcal/g, King 1973). Hence,

$$4.5 \times 15g \times 1.05\ kcal/g = 70.88\ kcal.$$

This was divided by the efficiency of egg production (King 1973) to give the total energy cost of egg production:

70.88 kcal/0.7 = 101.25 kcal.

The female requires about 10 days to produce this clutch since eggs are laid approximately every 2 days. Thus, the daily cost of egg production is 10.13 kcal/day. Although incubation is not a productive event, I increased NFEE and NEE of breeding females by 3% to account for the energy cost of incubation (Gessaman and Findell 1979). No incubation costs were derived for males.

I added the energy costs of fat deposition and molt to the DEE model for postbreeding kestrels. These costs were largely taken from the literature, but data based on kestrels were used when possible. I determined the energy cost of fat deposition as follows: Body fat is rapidly deposited in kestrels during September (30 days) and was measured by Gessaman (1979) as,

males: 4.4g
females: 8.5g.

These values were multiplied by the energy content of fat production (Moen 1973),

males: 4.4g x 9.3 kcal/g fat = 40.9 kcal
females: 8.5g x 9.3 kcal/g fat = 79.1 kcal,

and divided by the efficiency of fat production (Connell 1959). Then,

males: 40.9 kcal/0.6 = 68.2 kcal
females: 79.1 kcal/0.6 = 131.8 kcal,

and the daily cost is:

males: 68.2 kcal/30 days = 2.3 kcal/day

females: 131.8 kcal/30 days = 4.4 kcal/day.

I used the procedure outlined in Kendeigh et al. (1977) to calculate the energy cost of molt. The cost of molt is related to the cost of the new plumage and body weight in the following way:

wt. of new plumage = (P) = $0.09(W)^{0.95}$ (Turcek 1966),

where W = 103.1g (males) and 119.0g (females). Then P = 7.4g (males) and P = 8.4g (females). Kendeigh et al. (1977) estimate that the cost of molt for a carnivorous bird is 57.0 kcal/g of feathers. Then, the energy cost of molt for each sex is:

males: 7.4g x 57.0 kcal/g = 419.5 kcal

females: 8.4g x 57.0 kcal/g = 480.7 kcal.

Additionally, the energy cost of molt is reduced according to ambient temperature (27.5% at 17°C, average daily air temperature May-Sept in Cache Valley, National Climatic Center (NOAA), Kendeigh et al. 1977). This better reflects the actual cost of molt to the bird. The reduction is:

males: 419.5 kcal x 0.275 = 115.4 kcal

females: 480.7 kcal x 0.275 = 132.2 kcal, and the average daily cost of molt to the bird, based on a 128 day molt period from mid-May to mid-Sept (L. Haggas, J. S. Kirkley, and L. R. Jones, unpublished data) is:

males: 419.5 kcal - 115.4 kcal = 304.1 kcal/128 days = 2.4 kcal/day

females: 480.7 kcal - 132.2 kcal = 348.5 kcal/128 days = 2.7 kcal/day.

I assembled 24 daily activity records (4 daily activity records x 2 sexes x 3 seasons) for the energy budget analysis. Sixteen complete daily activity records were composed from observations collected during half-day periods during the nonbreeding and breeding seasons. Data recorded during half-day periods for kestrels that were of the same sex and reproductive phase, and during similar weather conditions, e.g. air temperature, solar radiation and wind velocity were integrated into one daily activity record. Most of the observations assimilated into daily activity records were derived from half-day recordings that were separated by 3 calendar days. During the postbreeding season, eight complete daily activity records were collected from dawn to dusk observations on individual birds.

Statistical analyses

A 3-way analysis of variance (Cochran and Cox 1966) was performed on all timed behavioral activities. Variables included in the analysis were: total flight activity including directional and hovering flight, and species interactions, preening, and copulatory activities. All units were in min/hr. Data were stratified by 3 main effects, e.g. observation season, sex of the bird, and hour of the day. These data were further stratified into 3 seasons, e.g. nonbreeding (Jan-Feb), breeding (mid-Mar-Apr), and postbreeding (late-Aug-Sept), 2 sexes, e.g. male and female, and 15 1-hr intervals, e.g. 0500-2000 hr. Data on kestrel encounters with other species were also analyzed by a 3-way design. Variables included the interaction time (min/day), and the number of interactions with each species (no./day). Data were stratified by 3 observation seasons, sex of the kestrel, and 10 avian species.

The DEE and DEB analyses were completed with a 2-way analysis of variance. Variables included were: DEE, NFEE, FEE, and NEE, and meteorological condition. Data were stratified by 2 main effects, e.g. observation season and sex of the bird. These data were further stratified into 3 seasons and 2 sexes as previously described.

Two independent sample T-tests and multiple comparison tests, utilizing Fisher's LSD, were used as required (Ott 1977). Significance was recorded at the 0.05 level unless specified otherwise. All data on predatory behavior were analysed by 2 x 3 chi-square contingency tables, and chi-square goodness-of-fit tests (Ott 1977, D. White pers. comm.).

RESULTS

Daily time and activity budget

Flight

Kestrels are diurnal, and their activity is marked by departure from and arrival to the roost usually within 20-30 min of sunrise and sunset. Flight activity increases steadily after morning arousal, remains dynamic for most of the day, and then sharply decreases until the bird retires to roost. I did not observe kestrels entering roost cavities during the day, except when they were inspecting potential nest sites, incubating eggs, or caring for young during the breeding season.

Flight of kestrels is characterized by short, direct flapping and gliding movements lasting from several seconds to a few minutes. Kestrels hover conspicuously over fields while frequently changing their vertical and lateral position. Soaring is rare, but I observed 1 male soaring upward for 13 min before he was lost from view. Kestrels allocated an average 20.6-53.3 min/day (2.3-5.9% of the photoperiod) to total flight activities while the remainder of the photoperiod (10-14 hrs) was spent in nonflight behavior that is mostly perch-hunting (87.6-94.9%, Table 4). The average time spent in flight activities differs between the sexes and time of the year. I composed daily flight patterns from the average amount of time alloted to total flight activities according to season, sex and hour (Fig. 2). The dynamic nature of kestrel daily activity is illustrated as periods of relatively high activity alternate with low periods. Kestrels were usually active from 0500-2000 hr during the breeding and postbreeding seasons, but reduced their flight activity from 0500-0700 hr, and from 1800-2000 hr during the nonbreeding season to correlate with the shorter photoperiod.

There is a significant relationship between time allocated to total flight activities and hour of the day ($p<0.01$, Table 5). An array of 15 means (LSD=1.42) representing flight activity (min/hr) was not clearly separated, but kestrels tended to fly more from 1200-1800 hr, than from 0600-1200 hr. Flight activity is generally lowest during the crepuscular hours, i.e. 0500-0700 hr and 1800-2000 hr. The combined interaction between observation season and sex of the bird was a significant influence on total flight activity ($p<0.01$, Table 5). Breeding males allocated significantly more time to flight activities (min/hr) than breeding females and nonbreeding and postbreeding kestrels (LSD=0.90). Mean flight levels for males were twice as high as females during the breeding season. Although average flight levels for breeding males are significantly greater than nonbreeding and postbreeding males, seasonal differences in flight levels among females were not apparent. Males and females during the nonbreeding and postbreeding seasons allocated similar amounts of time to flight activities ($p<0.05$, Table 5).

Directional flight

Directional flight is the largest component of total flight and kestrels allocated an average 19.3-42.9 min/day (2.8-4.8% of the photoperiod) in this activity (Table 4). Time partitioned to directional flight activities as a proportion of daily total flight was as follows: nonbreeding males (90.2%) and females (89.6%): breeding males (80.5%) and females (93.4%): and postbreeding males (96.6%) and females (91.0%). There is a significant relationship between time allocated to directional flight activity and hour ($p<0.01$, Table 6). An array of 15 means (LSD=1.09) was not well separated but kestrels generally partitioned more time to flight from 1100-1200 hr and from 1400-1700 hr, than from 0800-1100 hr and 1200-1400 hr. Directional flight was usually lowest during the crepuscular hours, from 0500-0700 hr, and from 1800-2000 hr.

The combined interaction of observation season and sex of the bird is a statistically significant influence on directional flight activity ($p<0.01$, Table 6). Breeding males exhibited higher levels of directional flight activity than breeding females, and nonbreeding and postbreeding kestrels (LSD=0.69). Intersexual comparisons within seasons, and intrasexual comparisons among seasons were identical to those previously described for total flight.

Number and duration of flights

I recorded 1183 complete flights (570 and 613 for males and females, respectively) made by kestrels during the postbreeding season. The mean number of flights for males (142.5/day) and females (139.5/day) was similar, based on a 15-hr daily flying period. The highest average number of flights for males (16.5/hr) occurred at 1100-1200 hr, and for females (21.2/hr) at 1300-1400 hr (Fig. 3). The mean total time in flight activities for males was 1.44 min/hr (Fig. 3), and individual flights averaged 0.13 min. Females allocated a similar amount of time to flight as males (1.74 min/hr, $p>0.05$, Fig. 3), but spent significantly more time in single flights (0.20 min/flight, $p<0.05$). The number of flights per hour may indicate the amount of time spent in flight. There is a direct relationship between the mean number of flights (no./hr) and mean total flight time (min/hr) for each sex (Fig. 4). Both relationships have a significant correlation coefficient ($r=0.93$, $p<0.05$: $r=0.67$, $p<0.05$, for males and females, respectively).

Although the time allocated to total flight activities by males and females during the postbreeding season was similar (Table 4), I observed different flight patterns from 2 females during 2 afternoon thunderstorm events. These data were obviously biased and were not included in the data analysis. The mean number of flights made by these females flying during the thunderstorms (11.1/hr) was similar to the average number of flights recorded from postbreeding males

(9.5/hr) and females (9.3/hr, $p<0.05$, Fig. 3): however, the females flying during the storm events allocated significantly more time to flight activities (6.20 min/hr) than other postbreeding males and females (1.44 min/hr and 1.74 min/hr, respectively, $p<0.01$, Fig. 3). The mean number of flights (no./hr) recorded from these 2 females during the storms was not significantly correlated with mean total flight time (min/hr, $r=0.73$, $p<0.05$). Evidently the storms have influenced flight activity, and specifically, hovering flight. These data are presented in the next section.

Hovering

Kestrels allocated an average 0.6-10.1 min/day (0.1-1.1% of the photoperiod) to hovering flight (Table 4). Hovering time represented as a proportion of total flight activities was as follows: nonbreeding males (7.9%) and females (9.5%): breeding males (18.9%) and females (5.1%): postbreeding males (2.9%) and females (2.9%). There were no apparent differences in hovering times recorded from males and females during the 3 seasons and among the observation hours ($p>0.05$). However, I recorded 86.7% of the total time allocated to hovering flight by postbreeding females from two females whose elevated flight activity coincided with 2 separate afternoon thunderstorms as described below.

On 7 Sept a storm event occurred from 1300-1600 hr: average wind speed was 6.17 m/sec and gusts were recorded to 10.8 m/sec. I recorded 85.4% (3.7 min) of the total daily time allocated to hovering

(4.3 min) from 1 female during this thunderstorm activity. I collected similar data from another female on 19 Sept. This storm event occurred from 1430-1830 hr and the average wind speed was 4.63 m/sec. I recorded 91.2% (20.4 min) of the total daily time allocated to hovering (22.3 min) during the storm. The average time allocated to hovering by these females during both storms (2.41 min/hr) was significantly higher than the mean value recorded from males (0.04 min/hr) and females (0.05 min/hr) that hovered on other days ($p<0.01$, Fig. 5). The average wind speed during the days that the storms occurred exceeded the average value recorded from the other 7 days of the postbreeding season ($p<0.05$).

Species interactions

Kestrels allocated relatively little time, from 0.1-1.7 min/day (0.01-0.20% of the photoperiod) to species interactions (Table 4). Time partitioned to encounter activities as a proportion of daily total flight was as follows: nonbreeding males (1.9%) and females (0.9%): breeding males (0.6%) and females (1.6%): and postbreeding males (0.5%) and females (6.1%). Kestrels instigated 68 of 80 interactions with conspecifics and 9 other avian species. Encounters were usually brief, ranging from 0.03-2.50 min., and averaging 0.20 min. A kestrel attack generally consists of single and or repeated pendulum-type stoops at an intruder. Direct contact is rare, although I witnessed 2 aggressive in-flight collisions which will be related later. Stoops are accompanied by a typically incessant and rapid "killy" call (Bent 1938, Willoughby and Cade 1964) that persists until the intruder departs.

Time allocated to species encounters was significantly influenced by the combined interaction of observation season and sex of the bird ($p<0.05$, Table 7). Postbreeding females partitioned more time to species interactions than postbreeding males and other kestrels during the nonbreeding and breeding seasons (LSD=0.62). There is a significant relationship between the number of kestrel interactions and the combined influence of observation season and avian species ($p<0.01$, Table 7). A histogram of 16 means (LSD=0.70) indicated that kestrels were generally involved in more interactions with Red-tailed Hawks during the nonbreeding season, and European Starlings and conspecifics during the breeding season than with other species (Fig. 6). Kestrels had significantly more conflicts with conspecifics than with other species during the postbreeding season.

The longest and most aggressive interaction that I observed involved 2 kestrel pairs during the breeding season, where one pair attempted to usurp another's territory. The event lasted approximately 2 hrs but was broken up by several rest periods. The resident pair based their defense from the tree containing their nest cavity, and from an adjacent Lombardy poplar (Populus nigra var. italica, L. M. Schultz pers. comm.) where the male roosted. The resident female was incubating 3 eggs at this time. Most of the conflict involved the resident male and the intruder female, and included spectacular diving flights, constant vocalizations, and 2 mid-air collisions as the resident male attacked the intruder female. This incident was excluded from the data analysis because I did not have the opportunity to collect similar data from breeding females.

Preening

Kestrels allocated an average 10.8-55.6 min/day (1.6-6.3% of the photoperiod) to preening activities (Table 4). The total daily preening time varied during the seasons: breeding and postbreeding kestrels preened significantly more than nonbreeding birds (LSD=0.64, $p<0.05$, Table 8). The average daily preening time was significantly affected by the combined influence of observation season and hour ($p<0.05$, Table 8). A plot of 45 means (LSD=2.47) according to season generally indicated that preening activity is concentrated within a 4-hr morning period (Fig. 7). With the exception of breeding females, these hours were from 0800-1200 hr during the nonbreeding season, and from 0600-1000 hr during the breeding and postbreeding seasons. Intersexual variations in the average daily preening time within seasons were similar ($p<0.05$).

Daily patterns of preening activity between sexes are similar in phase and intensity during the nonbreeding and postbreeding seasons. Preening patterns of males and females during the breeding season are closely in phase, but differ in intensity during most of the day. Preening activity of breeding females is high in the early morning, but they have 2 additional preening periods in the afternoon (1200-1400 hr and 1800-1900 hr) before abruptly ending for the day

(Fig. 7).

Copulatory activity

On the average, kestrels copulated 16.4 times (Fig. 8), and apportioned 2.0 min/day (0.2% of the photoperiod) to mating activities during the breeding season (Table 4). I recorded a total of 148 copulations but 75% of these were from 1 kestrel pair. Copulation occurs throughout the day, but the average number and duration of these copulatory acts is greatest from 0800-0900 hr (Fig. 8). The highest number of copulations that I recorded from a single pair was 7.0 (no./hr), and the longest event lasted 1.1 min.

Kestrels engage in copulatory activity most frequently during the breeding season, although I observed 2 isolated acts, one each during the nonbreeding (20 Jan) and postbreeding seasons (30 Aug). Cloacal contact appeared doubtful on both of these occasions. Copulation is a noisy event and is accompanied by continual vocalizations from both partners. I did not observe any promiscuous behavior among kestrels in my study.

Predatory behavior

Kestrels are sit and wait predators and search for prey from a conspicuous, elevated perched or hovering position. They usually hover over open areas where suitable perches are lacking. Perch and hover hunting techniques were utilized to obtain vertebrate and invertebrate prey during the entire study period. Hawking, or aerial invertebrate capture, was employed during the postbreeding season. Kestrels obtained most of their prey by perch-hunting (89.5%): hawking and hovering accounted for 6.0 and 4.5%, respectively (Table 9). I observed 691 attempts to capture prey (133, 83 and 475 during the nonbreeding, breeding and postbreeding seasons, respectively), and of these, 382 strikes (55.3%) were successful (27.8, 39.9 and 65.7% during the nonbreeding, breeding and postbreeding seasons, respectively).

During the nonbreeding and postbreeding seasons, males and females hunt for themselves and are often within close proximity to each other. Prey were acquired by direct capture from hunting, by retrieval from a cache, or by an unobserved method. During the breeding season, females confine their activities to the vicinity of the roost and rely heavily on their mates to provision them with prey. Food provisioning behavior was unidirectional, i.e. from males to females, and unique to the breeding season.

Vertebrate prey were captured, quickly killed on the ground and usually transferred to a perch for eating. Voles (<u>Microtus</u> sp.) were the major prey species and teeth fragments of the montane vole (M. montanus) were found in kestrel pellets. Most remains could not be identified to the species level, but many were also probably from the meadow vole (M. pennsylvanicus, E. C. Oaks pers. comm.). Most vertebrate prey acquired by hunting, or by retrieval from a cache, were eaten immediately (Table 10). Other prey were subjected to different predatory actions before they were lost from my view. Predatory actions utilized by kestrels for prey handling included: partially eating the prey, caching prey, transferring prey from males to females, or unobserved action. Several predatory actions were often sequentially performed on the same prey (Table 10).

Few invertebrates were captured during the nonbreeding and breeding seasons, but kestrels supplemented their vole diet with orthopterans during the postbreeding season. Kestrels hawked acridids after sighting them from a perch. Most of the invertebrate prey were not identifiable from my observation distance and all were consumed immediately after kestrels returned to a perch. I collected several regurgitated pellets during June and July, 1977, that contained mandibles and body fragments of field crickets (Gryllidae, E. M. Coombs pers. comm.). Most of these were probably Acheta assimilis (W. J. Hanson pers. comm.). Other grasshopper pieces that I found discarded around feeding perches were identified as Melanoplus packardii (J. A. MacMahon pers. comm.).

Kestrels often cache freshly killed or partially eaten prey near the point of capture. Small mammals that are cached are usually decapitated and placed in a prone position with the ventral side down. The cache and retrieve process is most likely a short-term food storage event because I observed prey being retrieved the same day they were captured, as well as during the next day.

I did not observe kestrels feeding on carrion or pirating prey from other avian species. On 3 occasions, I recorded kestrels releasing captured prey in the presence of a non-conspecific. The behavioral signals exchanged between the kestrel and the other bird were very subtle, but in all cases, kestrels vocalized an alarm after releasing the prey which was immediately pounced upon by the other bird. Food piracy occurred twice on one afternoon between a male kestrel and a male Northern Harrier during the nonbreeding season. Another incident involved a breeding female kestrel and a Black-billed Magpie.

Hunting

Nonbreeding and postbreeding kestrels, and breeding males, acquired most of their prey by direct capture ($p<0.05$, Table 10). Breeding females received most of their prey from males: these data are presented in the following section on prey provisioning. Nonbreeding males and females captured 31 voles and 6 invertebrates (Table 9). More vertebrates were taken from perch-hunts than hover-hunts ($p<0.05$), and all invertebrates were captured by perch-hunting. Although the total number of prey caught by each sex was similar ($p<0.05$), males caught more vertebrate prey than females

(22 and 9, respectively, $p<0.05$). Captures made while hovering were restricted to males, and these prey were obtained between 1300-1400 hr (Fig. 9). Total captures made by females were distributed throughout the day: however, males caught significantly more prey during the afternoon (1300-1700 hr) than the morning (0800-1300 hr, 17 and 5 prey, respectively, $p<0.05$). Kestrels handled prey differently during the nonbreeding season than other seasons (Table 10). Males tended to consume prey directly after capture rather than caching or eating a portion and caching the remains ($p<0.05$). This pattern is partially true for females: females consumed more prey directly after capture than they cached ($Z=7.17$).

Kestrels were observed catching 28 voles, 1 deer mouse (*Peromyscus* sp.), and 4 invertebrates during the breeding season (Table 9). Like the nonbreeding season, more vertebrates were caught from perch-hunts than from hover-hunts, and all invertebrates were obtained by perch-hunting ($p<0.05$). Unlike the other seasons, males caught significantly more vertebrate prey than females ($p<0.05$). Both sexes caught a similar number of invertebrates. Males and females caught vertebrates throughout the day (Fig. 9), but all hovering captures were made between 1100-1700 hr. Intersexual differences in prey handling are described later in the section on prey provisioning behavior.

Postbreeding kestrels obtained 18 voles and 294 grasshoppers during the 9-day observation period (Table 9). Males and females obtained significantly more total prey during the postbreeding season than during the other 2 seasons because of the heavy predation on acridids which represented 94.2% of the diet ($p<0.05$, Table 9). Males and females caught a similar number of each prey type ($p<0.05$) and averaged 2 voles and 32.7 grasshoppers per day. All voles were acquired by perch-hunting. More grasshoppers were caught by perch-hunting (89.9%) than from hawking or hovering ($Z=11.40$), and hawking captures exceeded hovering ones ($Z=2.76$). Males and females appeared to catch a similar number of prey from perch-hunting and hawking ($p<0.05$), and from hovering. Both sexes caught voles throughout the day (Fig. 9). Hovering kestrels caught grasshoppers only from 1400-1900 hr, and more prey were hawked between 1200-1500 hr than during any other 3-hr interval between 0600-1800 hr ($p<0.05$, Fig. 10). Methods of prey handling were similar between males and females (Table 10).

Prey provisioning

Males and females captured similar numbers of total prey during the nonbreeding and postbreeding seasons; however, breeding males captured significantly more prey than breeding females ($p<0.05$, Table 9). Breeding males also secured significantly more vertebrate prey than nonbreeding and postbreeding males ($p<0.05$, Table 10). Breeding males may supply a large proportion of the female's diet, as females acquired significantly more prey from males than they secured on their own ($p<0.05$). Apparently, these males capture more prey so they can provision their mates. Females do not undergo these seasonal fluctuations in prey capture levels ($p<0.05$). Breeding males sometimes hunted away from the nest site for several hours while females usually remained in the roost area. Often, males vocalized their return with prey while still some distance away. At this point, some females left their perches, met the males in flight, and grabbed prey from their talons. At other times, males dropped prey for females to catch in flight, however, most prey transfers occurred in the immediate vicinity of the roost area as follows: a male would perch adjacent to his mate, offer prey and transfer it from his beak to her beak. Females whined in anticipation of food and often snared prey quickly as soon as they were within reach. Only vertebrate prey were transferred from males to females.

Although no differences were evident between the number of prey retained by males and the number transferred to females ($p<0.05$), there may be a difference in food quality. Males provisioned females with significantly more fresh kills than with stored carcasses that had been retrieved from caches ($p<0.05$, Table 10). Males were persistent in supplying their mates with food, and often brought prey when females were already eating. I noted one male retrieve a food item and offer it to his mate after she had dropped it to the ground. Apparently, the urge to provision females can overide a male's own hunger as described in the following account: I observed a male transfer prey to his mate who was already eating. She took the prey, ate most of the food and cached the remainder. The male retrieved this cached prey and presented it to the female, whereupon she took and recached it in a new location. Again the male retrieved this prey and offered it to the female. She took and ate a portion, and then cached the remains and roosted. The male retrieved this same prey for the third time and ate all that remained.

Predatory efficiency

The efficiency of kestrel predation, i.e. number of successful strikes/total number of strike attempts, varied with the observation season and the sex of the bird (Table 11). Although hawking was the most successful method of prey capture (82.1%), followed by perch-hunting (56.3%) and hovering (30.4%), most prey were acquired by perch-hunting (89.5%), and the number of prey obtained from hawking and hovering was substantially less (6.0 and 4.5%, respectively).

Nonbreeding males hunted as efficiently from perches as from hovers ($p>0.05$), but 91.3% of the prey captures were from a perched position (Table 11). Females perch-hunted about as effectively as males ($p>0.05$) and secured all prey by this method. I observed 1 hovering attempt by a female, and this was unsuccessful (Table 9). Breeding males were about twice as successful at hover-hunting than perch-hunting, but, like nonbreeding males, most of their prey (70.4%) were obtained from perch-hunts (Table 11). Breeding males were more efficient at hovering than nonbreeding and postbreeding males ($p<0.05$), and they obtained a larger proportion of their prey by hovering than males during other seasons ($p<0.05$). Breeding females caught all their prey while perch-hunting (Table 11) and were considerably less efficient at this capture technique than males (Table 11, $p<0.05$). I did not observe any hovering attempts from these females.

Males and females were more successful at prey capture during the postbreeding season than the other 2 seasons ($p<0.05$, Table 11). Both sexes were more efficient at hawking and perch-hunting than hovering ($p<0.05$). Although hawking grasshoppers was as efficient as perch-hunting for voles and other invertebrates ($p>0.05$), both sexes perch-hunted to obtain most of their prey (Table 11).

Cache and retrieve activity

I observed kestrels caching 49 prey and retrieving 27 food items throughout the study period (Fig. 11). Only vertebrate prey were cached. Since all retrieved prey originated from caches, I combined cache and retrieve data for each sex within each season and based the analysis on the number of cached prey. Cache and retrieve activity was highest during the breeding season, and lowest during the nonbreeding season ($p<0.05$). There were no significant intersexual differences in cache and retrieve activity within seasons ($p>0.05$). Kestrels recovered 35.6% (number retrieved/total number cached) of their cached prey; differences between sexes were not evident. Kestrels cached 75% of their prey from 0800-1400 hr, but appeared to retrieve prey throughout the day (Fig. 12).

Vertebrate prey were caught 1 at a time with up to 2 voles caught per hr on a few occasions. However, I observed unusual predatory behavior from 1 male who captured 5 mammals from the same vicinity in 56 min. All were cached near each other on the ground along a fence line. These prey were small, and the kestrel may have been raiding a nest.

Kestrels usually flew directly to the cache for prey storage and retrieval. I observed 4 kestrels recover prey that they had stored earlier in the day, and 6 others who retrieved a food item, ate a portion, and then recached the prey. Some of these were restored to the original cache. I combined data on cache locations for both sexes because males and females appeared to choose similar sites. Sixty-four caches were found and categorized as follows: ground sites (often within conspicuous grass clumps): natural arboreal sites (tree crotches and cavities): and artificial sites (utility poles and fence gates, Fig. 13). Two unusual caches included an old metal can on the ground and an inactive Northern Oriole nest. Seasonal differences in cache site selection may exist during the breeding and postbreeding seasons ($p<0.05$). Breeding kestrels stored significantly more prey on the ground and in natural sites than in artificial ones ($p<0.05$) whereas postbreeding kestrels chose ground caches more often than natural or artificial sites ($p<0.05$). Although these data are few, the majority of caches (57%) made during the nonbreeding season were also on the ground.

Daily energy budget

Daily energy expenditure

There is a significant relationship between the combined influence of observation season and sex of the bird and the daily energy expenditure of nonbreeding, breeding and postbreeding kestrels ($p<0.05$, Table 12). DEE of nonbreeding kestrels, egg-producing females during the breeding season, and postbreeding females that had accrued costs of fat deposition and molt were significantly higher than breeding and postbreeding males (LSD=3.99). DEE of egg-producing females and nonbreeding females was statistically similar and was significantly higher than all other kestrels in this study. DEE of nonbreeding and postbreeding kestrels, breeding males and breeding females who have already produced eggs and are incubating a clutch (DEE=42.37 kcal/day), is significantly influenced by the separate effects of observation season and sex of the bird ($p<0.05$). DEE of nonbreeding kestrels (47.73 kcal/day) was significantly higher than breeding (39.38 kcal/day) and postbreeding (42.41 kcal/day) kestrels (LSD=2.8) while mean DEE of breeding and postbreeding kestrels was similar. During all seasons DEE of females (45.64 kcal/day) was significantly greater than males (40.70 kcal/day, LSD=2.3); females average 15.5% heavier than males.

Breeding females expended 10.1 kcal/day (19.6% of the DEE) for egg production which is a significant addition to the DEE ($p<0.05$, Table 12). The cost of incubation is small (1.13 kcal/day or 2.7% of the DEE) and does not significantly alter the DEE of breeding females ($p>0.05$). The average costs of fat deposition (2.27 and 4.39 kcal/day for males and females, respectively) and molt (2.38 and 2.72 kcal/day for males and females, respectively) together account for 11.6 and 15.9% of the DEE for males and females, respectively. These energy demands are a statistically significant addition to the DEE of postbreeding females ($p<0.05$, Table 12), but not for males ($p>0.05$).

Meteorological conditions

Average daytime ambient temperature (Ta), solar radiation (Qs), and average nocturnal air temperature (Tna) were significantly lower during the winter (nonbreeding season), than the spring (breeding season), or fall (postbreeding season, $p<0.05$, Table 13). An array of means indicated that daytime and nighttime air temperatures and solar radiation during the breeding and postbreeding seasons was similar (LSD=2.57, 2.05, and 0.29, respectively, Table 13). The length of the photoperiod (P) varies significantly during all 3 seasons ($p<0.05$) the longest light period occurs during spring (breeding season), and the shortest in winter (nonbreeding season). The opposite is true for the nocturnal period (1-P) as the longest night time period occurs during winter, and the shortest in spring. Wind speed did not vary significantly during all 3 seasons.

Daily nonflight energy expenditure

Daily nonflight energy expenditure (NFEE) is a product of the time allocated to nonflight behavior (NFA) and the resting metabolic rate (RMR, Table 1). Kestrels expended 18.9-24.6 kcal/day (44.1-52.2% of the DEE) to NFEE during the nonbreeding, breeding and postbreeding seasons (Table 12).

There is a significant relationship between NFEE and the separate influences of observation season and sex of the bird ($p<0.05$, Table 12). Although the mean NFEE levels are not well separated, NFEE is generally higher among nonbreeding kestrels, and females have higher levels of energy expenditure than males (LSD=3.17).

Daily flight energy expenditure

Daily flight energy expenditure (FEE) is a product of the time allocated to flight activity (FA) and a multiple of basal metabolic rate (BMR, Table 1). Kestrels expended 3.2-7.1 kcal/day (6.7-19.6% of the DEE) in flight during the nonbreeding, breeding and postbreeding seasons (Table 12).

FEE and flight activity are statistically affected by the combined influence of observation season and sex of the bird ($p<0.05$, Tables 12 and 13, respectively). Breeding males allocated significantly more time to flight activity (LSD=0.02), and expended significantly more energy to flight (LSD=2.24) than breeding females, and nonbreeding and postbreeding kestrels. Flight activity levels and mean FEE levels among breeding females, nonbreeding and postbreeding kestrels were statistically similar.

Nighttime energy expenditure

Nighttime energy expenditure (NEE) is a product of the duration of the nighttime period (1-P) and standard metabolic rate (SMR, Table 1). The NEE of kestrels was 11.0-22.0 kcal/day (25.5-44.0% of the DEE) during the nonbreeding, breeding and postbreeding seasons (Table 12). NEE is significantly affected by the separate influences of observation season and the sex of the bird ($p<0.05$, Table 12). NEE is significantly higher during the nonbreeding than the breeding and postbreeding seasons (LSD=0.75) and is significantly higher among females than males (LSD=0.61).

DISCUSSION

Sensitivity analysis of the DEE model

The relative importance of each variable and each component of energy expenditure, nonflight energy expenditure (NFEE), flight energy expenditure (FEE) and nighttime energy expenditure (NEE), on DEE was identified with a sensitivity analysis and is expressed as a sensitivity ratio (percent change in DEE/percent change in each variable). Body weight had the highest sensitivity ratio during all 3 seasons, probably because it is the basis of all the metabolic components in the model. Sensitivity ratios for energy expenditure were consistent during all 3 seasons; NFEE was the highest, and FEE was the lowest value. Although FEE undergoes the most percentage change in value, the energy expenditure due to flight activities has a relatively small effect on DEE because kestrels allocated a small proportion of the day to flight.

Effect of variables and components of energy expenditure on the DEE

Average daily air temperature and solar radiation are inversely related to DEE and generally DEE was more sensitive to these variables than all the other variables during the 3 seasons. Weight, flight activity and photoperiod are directly related to DEE. An average 15.2% increase in weight, which is the difference between females and males during each season increases DEE by about 9.0%. Flight activity has its greatest impact on DEE of males during the breeding season (19.2%). Photoperiod had a negligible effect on DEE. The relationship between wind speed and resting metabolism (NFEE, J. A. Gessaman pers. comm.) is non-linear (Hayes and Gessaman 1980): wind speeds recorded in this study had a moderate effect on kestrel DEE. The effect of average nocturnal air temperature on DEE was slight.

The components of energy expenditure are directly related to DEE. NFEE changed DEE more than FEE and NEE during all 3 seasons: FEE has its greatest influence on DEE during the breeding season and the effect of NEE is highest during the nonbreeding season. NFEE and FEE are significantly affected by environmental and behavioral influences, respectively, whereas NEE is significantly affected by the season of observation and sex of the bird.

Daily energy expenditure

Seasonal variation of energy occurs in kestrels, and in general DEE of nonbreeding birds is higher than those from the breeding and postbreeding seasons. During the nonbreeding season, kestrel weight is high, and average daily and nocturnal air temperature, solar radiation and photoperiod are low relative to the other seasons; consequently, NFEE and NEE are correspondingly high. These meteorological conditions place increased thermoregulatory demands on kestrels during the nonbreeding season and 92% of the DEE is for NFEE and NEE. This scenario is reversed during the breeding and postbreeding seasons as body weight is lower and average daily and nocturnal air temperature, and solar radiation are relatively high: consequently, NFEE and NEE are lower but still account for about 82% of the DEE. Energy demands for thermoregulation have decreased and productive activities may correspond with the warmer months of the year because kestrels can mobilize energy more easily for these events than during colder months. Kestrels are expending energy for reproduction during the breeding season, and for fat deposition and molt during the postbreeding season, and may be seasonally mobilizing their metabolizable energy to those events that are most demanding for the season.

Generally, the DEE of females is higher than males because they are heavier: thus, their average NFEE, FEE and NEE are correspondingly higher. The energy requirement for egg production increases the DEE of breeding females by 24.4%. Although this DEE is statistically similar to that expended by nonbreeding females, the time period that this high level of energy expenditure is sustained is short. Breeding females lay an average clutch of 4.5 eggs in 10 days (A. Woyda unpublished data).

Kestrels are cavity nesters and lay their eggs in a small depression usually consisting of wood chips and leaves. Cavities are well insulated and are characterized by lower air temperatures during the day, but slightly higher temperatures at night (Kendeigh 1961). Cavities also receive lower levels of incoming and reflected solar radiation and light compared to the outside environment (McComb and

Noble 1981). Since little daily energy (1.13 kcal/day) is required for incubation and the eggs appear to be well insulated, the cost of incubation may be satisfied through metabolic heat production. Vleck (1981) reported that Zebra Finches (Poephila guttata) incubating at temperatures within the zone of thermalneutrality did not expend energy above the resting rate. Ambient air temperatures inside kestrel nest cavities were often within the thermalneutral zone (ca. 20°C, J. A. Gessaman pers. comm.), and when temperatures were below this level, kestrels may have expended about 3% of their NFEE and NEE for incubation (Gessaman and Findell 1979). Although both sexes develop brood patches (Cade 1982) and share incubation duties, I observed females doing most of the incubating during the day, and all of the incubating at night. Males relieved females for short periods totalling about 3-4 hr daily. Females are heavier and can potentially supply more heat to the eggs than males. Some males may incubate at night (Roest 1957, Gessaman 1979) but females are probably more energetically favored for incubation at night than males.

Production costs of fat deposition and molt each increase the DEE of postbreeding males by 6-7%. Postbreeding females accumulate more fat than males and their DEE is increased by about 19%. The cost of molt to postbreeding females is relatively smaller and increases the DEE by 7.3%. Gessaman (1979) found that body fat levels in kestrels increased from the end of the breeding season to the beginning of fall migration with the period of most rapid fat deposition occurring in September. This pattern is similar to other migratory species that deposit body fat presumably as an energy source for migration (King and Farner 1965). The energy cost of molt includes biosynthesis and weight of the new feathers, and may be reduced with increasing ambient temperature (Kendeigh et al. 1977). The daily cost that I estimated represents an average for the entire period. Feathers are dropped slowly at the beginning and end of the molt period, but more rapidly in the middle (C. Henny pers. comm.). Although molting birds will lose body heat faster than non-molting ones because heat conductance increases with feather loss, the molt period of kestrels coincides with those months of the year when ambient temperature and solar radiation are high. The molt period can extend from the time after the clutch is completed to the time of migration, but usually molt does not overlap with migration (Kendeigh et al. 1977). If wild kestrels are similar to captive ones, and feathers drop when the clutch is complete (Willoughby and Cade 1964) then this may occur as early as 15 May (A. Woyda unpublished data). Kestrels leave Cache Valley about mid-September when a major southward migration of kestrels has been observed in the Wellsville Mtns (Fig. 1, Hoffman and Potts 1980).

Daily nonflight energy expenditure

Although NFEE is significantly influenced by the combined statistical interaction of observation season and sex of the bird, the breeding and postbreeding season data merit an explanation so that this apparent relationship between males and females is not misinterpreted. The seasonal effect on NFEE for nonbreeding and postbreeding kestrels, and breeding males, is clear. NFEE is higher during the nonbreeding season than the other seasons because kestrel weight is high, and daily air temperature and solar radiation is low. NFEE of breeding males and postbreeding kestrels is correspondingly low because body weight is low, and daily average temperature and solar radiation is high compared to the nonbreeding season.

However, the disparity in NFEE recorded from males and females during the breeding and postbreeding seasons does not correspond with the inherent differences that are attributed to body weight. NFEE for breeding females is 22.8% higher than breeding males and NFEE levels for postbreeding males are 1.1% higher than postbreeding females (Table 12). These anomolies can be explained when meteorological data collected from the days that each sex was observed are compared. Conditions of daily average temperature and solar radiation collected from days observing breeding males were higher than the seasonal averages for these variables while temperature and solar radiation during days spent observing breeding females were more similar to these averages. High temperature and solar radiation, coupled with the lighter weight of males, depressed NFEE to a level lower than expected given the difference in weight between sexes. NFEE from postbreeding males is greater than postbreeding females because daily average temperature on days observing males was below the seasonal average; daily average temperature during observations of females was identical to the seasonal mean. Solar radiation during days spent observing females were higher than the seasonal mean, while those recorded when males were observed were more similar. Consequently, NFEE is slightly higher than expected for postbreeding males, and correspondingly lower, for postbreeding females.

Daily flight energy expenditure

Breeding males are allocating about twice as much time to flight activities as breeding females, and nonbreeding and postbreeding males. Since the time allocated to flight activities is directly related to FEE, breeding males are expending significantly more energy in flight activities than breeding females, and nonbreeding and postbreeding kestrels. Although the energy cost of flight is actually greater for females since they are heavier than males, males have increased the overall cost of flight by partitioning more time to this activity. Flight activity levels between males and females are significantly different during the breeding season, and the increased flight activity of breeding males is apparently related to a behavioral division of labor within the breeding pair. This will be discussed in a later section.

Nighttime energy expenditure

NEE of nonbreeding kestrels is significantly higher than breeding and postbreeding birds because body weight is high and photoperiod and nocturnal air temperature are low during the nonbreeding season. Females are heavier than males and consequently have higher levels of

NEE.

Energy conserving measures on metabolism

Kestrels commonly reside in open country and usually choose unshaded conspicuous sites as hunting perches. Hayes and Gessaman (1980) measured energy metabolism of kestrels, Red-tailed Hawks and Golden Eagles under the combined influence of air temperature, radiation, and wind speed, and determined that kestrels, due to their small size, were influenced more by these environmental conditions than the larger raptors. Heat absorption from incident solar radiation may alleviate some of the kestrel's thermoregulatory demand during the winter when air temperatures are low, and NFEE is high (Kendeigh et al. 1977). Hayes and Gessaman (1980) reported that solar radiation decreased metabolism at all wind speeds, and predicted that kestrels could save 13.4% of their hourly metabolic rate at solar noon on 1 January in Logan, UT. Utah receives an average 53.3 and 62.9% of possible sunshine during January and February, respectively (National Climatic Center, NOAA, 1968-1978), but the opportunity for energy gain from solar radiation must be balanced with the effects of a short photoperiod and the low solar angle at Logan (41° 45' N. L.). Under the solar conditions that I recorded during the 1978 winter, DEE was reduced by 3.6 and 3.3% for males and females, respectively. During late summer kestrels may experience heat stress under high radiation loads, and I observed them panting and seeking shade on several hot, dry afternoons in late September (L. Haggas unpublished data).

Kestrels may also save energy at night by selecting cavities as roost sites. I observed kestrels roosting exclusively in cavities during the winter (nonbreeding season), whereas they roosted within trees with foliage in addition to cavity sites during the fall (postbreeding season, L. Haggas unpublished data). Wood is a good insulator, and cavities provide a warm and protected microclimate compared to the outside environment (Kendeigh 1961, McComb and Noble, 1981). By roosting in cavities, kestrels reduce NEE and lower their DEE by 4.4%.

Thermal effects of solar radiation and cavity roosting enable wintering kestrels to operate at a lower level of energy expenditure and reduce their DEE by about 8%. These energy savings may help extend the northern range of wintering males and allow these individuals to occupy a territory all year. Cade (1955) reported that kestrels maintain territories during the nonbreeding season in California. I observed a male kestrel in January stooping on and driving off a Prairie Falcon perched in the tree containing the kestrel's roost cavity. Wintering males in Cache Valley outnumber females by about 3:1 (Gessaman 1982). These males may gain a reproductive advantage by remaining on their territories and attracting females earlier than migratory males (East 1982).

Comparison of DEE values with other estimates of kestrel energy metabolism

Comparable studies on kestrel energetics are few. DEE calculated for nonbreeding kestrels in northern Utah averages 14.5% lower than those estimated from free-living, nonbreeding kestrels in California (Koplin et al. 1980). Additionally, my estimates of kestrel DEE are about 5% lower than those predicted from the model of Koplin et al. (1980) during the breeding and postbreeding seasons.

Rudolph (1982) estimated daily energy expenditure from free-living, breeding kestrels in central California by combining a time budget with multiples of standard metabolic rate (King 1974). Although Rudolph's estimate of the energy expenditure of males (39.2 kcal/day) is similar to that of northern Utah males (36.4 kcal/day), DEE for breeding males in my study is low because daily temperature and solar radiation were above average. Energy expenditure of females in California (31.6 kcal/day, Rudolph 1982) is lower than that in northern Utah (41.2 kcal/day, excluding the cost of reproduction), but it is also lower than the energy expended by California males which does not agree with the observed differences in weight between sexes (Roest 1957, Balgooyen 1976, Yanez et al. 1980, Wieck 1980, Cade 1982) and the direct relationship between weight and metabolism (Aschoff and Pohl 1970).

DEE (excluding costs of flight metabolism and production) estimated from free-living kestrels can be used as an approximation of the daily energy metabolism of captive kestrels measured by Gessaman (1980). Mean DEE (39.9 kcal/day) predicted from the energetics model in this study averaged 3.8% higher than the daily energy metabolism estimated from food consumption trials of captive birds (38.4 kcal/day), and 7.1% higher than those estimated from the heart rate method (37.2 kcal/day). My estimates of kestrel energy expenditure utilizing the time-energy approach average 37.8% lower than the daily energy expenditure predicted from King's (1974) equation. King's (1974) equation, based solely on the weight of the bird, was derived mostly from passerines and includes only 1 raptor, which was an owl. Thus, this relationship may not be suitable for computing kestrel energy metabolism. However, King (1974) suggested that since the ratio of daily energy expenditure and basal metabolic rate of several birds and mammals was within a narrow range (2.0-4.0), the daily energy expenditure may be a function of body weight. DEE/BMR ratios obtained from Koplin et al. (1980), Gessaman (1980), Rudolph (1982), and this study are within the range predicted by King (1974). Additionally, my average ratio (DEE/BMR) for a breeding female kestrel producing eggs (3.2) is within the range recorded from egg-laying domestic fowl and Lapland Longspurs, an arctic passerine (2.4 to 4.0, King 1974).

Time, energy and behavioral roles

Studies on time budgeting and its relationship to energy mobilization to various activities between sexes and among different seasons are few. Kestrels in northern Utah are seasonally partitioning time to different activities and mobilizing energy to satisfy these demands. Generally, male and female kestrels partitioned their time budgets similarly to flight, preening and perch-hunting behavior during the nonbreeding and postbreeding seasons. Differences between sexes were evident regarding the amount of time allocated to flight activities by breeding males, and to species interactions by postbreeding females.

Breeding kestrels alter their behavior to accomodate reproductive activities. A division of labor was created as males significantly increased their flight activity and females remained relatively sedentary in the vicinity of the roost. Breeding males allocated about twice the time to total and directional flying activities as breeding females and nonbreeding and postbreeding kestrels. Breeding males expended 19% of DEE to FEE, compared to 8-9% that was expended by nonbreeding and postbreeding birds. The increased flying time is associated with foraging and males caught more prey during the breeding season than the other seasons. Since food provisioning behavior was also frequently observed, it is likely that breeding males have assumed a food provider role and provide most, if not all, of the energy needs of the female. This behavior has been documented in many raptors (Newton 1979) and also in most of the British members of the family, Paridae (Perrins 1979). Provisioning behavior was observed only during the breeding season, and was unidirectional from males to females. Males supplied females with more fresh uneaten carcasses than stored prey, which suggests that there may be some qualitative difference between these food items. Females restricted their hunting activities during the breeding season and exhibited higher levels of nonflight behavior than breeding males and nonbreeding and postbreeding kestrels. Since females obtained more of their food from their mates than they secured on their own, they appeared to rely on males to obtain prey. By restricting flight activities and relying on males to provide food, females may conserve energy that could be mobilized for egg production.

Although this increased activity of the male kestrel causes a substantial increase in flight energy expenditure, the impact on the DEE is low because the time allocated to flight is only 3-5% of the photoperiod; consequently, costs for FEE are low. A small male expends more energy per gram of body weight than the larger female, but operates on less total energy and will have a lower DEE. Males can execute a high-activity food providing role at a smaller cost than females. Differences in energy expenditure between the sexes may be related to the evolution of reversed sexual dimorphism (females being larger than males), and allow the pair to operate at a lower energy budget than if kestrels were traditionally dimorphic (males larger than females), or monomorphic (Balgooyen 1976). Levenson (1979) reported that breeding male Ospreys allocated more time to flight activities than females during the incubation and nestling periods prior to the postfledging period. This flight activity was associated with foraging and supplying the female with fish. He also related that this division of labor between male and female Ospreys may be more energetically favorable for the pair and allow them to operate on less total energy so that they may have more energy available to provide for the young. Such a divison of labor between sexes during the breeding season has also been reported in other birds. East (1982) found that the time budgets of European Robins (*Erithacus rubecula*) were generally similar during the postbreeding season, but different during the breeding season.

Time budgets of postbreeding male and female kestrels also differed regarding the amount of time allocated to interactions with other species. Postbreeding females allocated more time to species interactions than postbreeding males and also nonbreeding and breeding kestrels. Many of these interactions involved the young of the pair: the reason for this behavior is unknown.

Seasonal mobilization of energy

Generally, the amount of energy expended by kestrels corresponds to the weight of the bird, and is greater during the nonbreeding than the breeding or postbreeding seasons. Kestrels are about 10% heavier in winter and can potentially metabolize more energy during the nonbreeding season compared to the other 2 seasons. DEE estimated from males during the nonbreeding season are 25.0 and 13.1% higher than those from the breeding and postbreeding seasons, respectively. DEE of nonbreeding females averages 3.2% lower than breeding females, and 12.1% greater than the DEE from postbreeding females. DEE of breeding and postbreeding males differ by 10.5% while breeding females expend 15.6% more daily energy than postbreeding females. Kendeigh (1973) reported that midwinter DEE levels (27.9 kcal/day) of caged house sparrows in Illinois were 40.2% higher than those estimated in midsummer (19.9 kcal/day).

Intra- and intersexual comparisons of energy mobilization among and within seasons can be made when each component of energy expenditure is expressed as a percentage of DEE. The range of each component expressed as a percentage of DEE is as follows: NFEE (44.1-51.1%), NEE (25.5-44.1%), and FEE (6.7-19.2%). Energy expended in production ranged from 0.5-20.1%, but was only included in the DEE during the breeding and postbreeding seasons. Seasonal fluctuations in energy costs are greatest for NEE, flight activities of males and production activities of females. NFEE constitutes most (average=48.3 kcal/day) of DEE and is largely dependent on daily air temperature and the bird's need to thermoregulate. Thus, when thermoregulatory demands are high, energy may not be available to support production or higher activity levels. Conversely, when thermoregulatory demands are low, energy may potentially be mobilized to support production and greater activity, including egg production in breeding females and fat deposition and molt in postbreeding birds, and the increased flight activity of breeding males.

CONCLUSIONS

1. Generally, male and female kestrels apportion time similarly to flight behavior, preening and interactions with conspecifics during the nonbreeding, breeding and postbreeding seasons in northern Utah. Exceptions occur during the breeding season when males allocate more time to flight in order to provide for the food requirements of females. Postbreeding females spent more time in species interactions that were directed toward their young. Preening activity was at its lowest level during the nonbreeding season. Wind may be important in determining the amount of time spent in flight as evidenced by the flight activities of 2 females during thunderstorm events.

2. Kestrels acquire most vertebrate and invertebrate prey by perch-hunting, and utilize hawking techniques to prey heavily on acridids. Breeding females acquire more of their prey from males than they captured by themselves. Of the 3 hunting methods utilized, hawking was the most efficient, but perch-hunting was employed to capture most prey. Cache and retrieve activity is a short term food storage event: this activity is greatest during the breeding season. Kestrels usually select ground sites as caches, but natural sites are also selected during the breeding season.

3. Kestrel daily energy expenditure (DEE) depends largely on the body weight of the bird and ambient temperature. DEE of kestrels in northern Utah varies seasonally and averages 19.1% higher during the

nonbreeding season than the breeding and postbreeding seasons. Kestrels average 10% heavier during the nonbreeding season and average daytime and nighttime air temperature is significantly lower than during the breeding and postbreeding seasons. Consequently, thermoregulatory costs are large during the nonbreeding season and kestrels may only be able to mobilize energy for tissue production during the warmer months when thermoregulatory requirements have decreased. DEE for females is generally higher than males because they average 15.5% (17.2g) heavier than males during all 3 seasons. DEE of breeding and postbreeding females is similar to that of nonbreeding kestrels because of the added energy costs of tissue production. Breeding females expend energy for egg production and postbreeding females accrue energy costs for fat deposition.

4. The largest component of the DEE is daily nonflight energy expenditure (NFEE) and the smallest is the energy expended in flight activities (FEE). Although the cost of flight is relatively expensive (12.5 x BMR), kestrels only allocate about 3% of the photoperiod (23.5 min/day) in flight related activities. Breeding males allocated significantly more time to flight behavior (53 min/day) than breeding females, and nonbreeding and postbreeding kestrels, but the increase in time was not a significant addition to the total amount of time available for diurnal flight. Hence, the energy cost of the increased flight activity of breeding males was not a significant addition to the DEE.

5. Kestrels may reduce their daily energy ependiture by 8% during the nonbreeding season by 2 behavioral adaptations: they may remain perched in an unsheltered site an absorb incident solar radiation and they may conserve energy at night by selecting cavities as roost sites.

6. Although the differences in DEE between breeding males and females is due to the associated costs of weight and egg production, the fact that a behavioral role change occurs suggests that males are more energetically favored to assume a food providing role while females reduce their activity, and conserve energy for egg production. Smaller males require less total energy and may reduce the energy expenditure of the pair compared to the DEE levels output if both kestrels were of the same size and had similar energy requirements.

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APPENDIX

Table 1. A model (after Koplin et al. 1980) predicting the daily energy expenditure (DEE) of kestrels during 3 seasons (nonbreeding = Jan-Feb, breeding = Mar-Apr, and postbreeding = Aug-Sept) in northern Utah. NFEE = nonflight enrgy expenditure, FEE = flight energy expenditure, NEE = nighttime energy expenditure, PR = production.

$$DEE = NFEE + FEE + NEE + PR$$

$$DEE = [(NFA \times P)RMR] + [(FA \times P)(BMR \times FC)] + [(1-P)SMR] + (PR)$$

Symbol	Description	Units
DEE	daily energy expenditure	kcal/day
NFA	non-flight activities	proportion of the diurnal period
RMR	resting metabolic rate as a function of weight, temperature, solar radiation and wind speed	kcal/day
SMR	standard metabolic rate as a function of nocturnal air temperature	kcal/day
1-P	nocturnal period	proportion of the 24 hr day
FA	flight activities	proportion of the diurnal period
BMR	basal metabolic rate	kcal/day
FC	flight coefficient (12.5)	dimensionless (Gessaman 1980)
P	diurnal period	proportion of the 24 hr day
PR	production: gonadal growth (G), egg production (EP), fat deposition (FD) and molt (MT)	kcal/day

Table 2. Explanation of model inputs and equations used for predicting kestrel daily energy expenditure (DEE) during 3 seasons (nonbreeding=Jan-Feb, breeding =Mar-Apr, postbreeding=Aug-Sept) in northern Utah. Symbols and other model inputs (FA, NFA, P, 1-P) are defined in Table 1. M = male, F = female.

Symbol	Description	Units	Source
RMR	$RMR = 24.9926 - 0.0489(W) - 0.3068(Ta) - 4.7724(Qs) + 1.1688(U)^{0.5}$	cal/g/hr	Hayes (1978)
SMR	$SMR = -0.264(Tna) + 13.31$	cal/g/hr	Gessaman and Findell (1979)
BMR	$BMR = 0.5916(W)^{0.729}$	kcal/day	Aschoff and Pohl (1970)
W	weight	g	L. Haggas, J. S. Kirkley, and L. R. Jones (unpub. data)
Ta	average daytime air temperature	°C	Natl. Climatic Center (NOAA)
Tna	average nocturnal air temperature	°C	Natl. Climatic Center (NOAA)
Qs	solar and diffuse sky radiation	$cal/min/cm^2$	I. Dirmhirn (pers. comm.)
U	wind speed	m/sec	Natl. Climatic Center (NOAA)
GR	gonadal growth	(M) 0.02 kcal/day (F) 0.20 kcal/day	J. A. Gessaman (unpub. data)
EP	egg production	10.13 kcal/day	A. Woyda (unpub. data) R. Atkins (unpub. data), King (1973)
INC	incubation	1.13 kcal/day	Gessaman and Findell (1979)
FD	fat deposition	(M) 2.27 kcal/day (F) 4.39 kcal/day	Moen (1973), Connell (1959), and Gessaman (1979)
MT	molt	(M) 2.38 kcal/day (F) 2.72 kcal/day	Turcek (1966), Kendeigh et al. (1977)

Table 3. Units conversion factors used in metabolism equations. W = kestrel weight (g).

Season	W	cal/g/hr to kcal/day
nonbreeding		
males	119.1	2.858
females	138.0	3.312
breeding		
males	107.8	2.587
females	124.1	2.978
postbreeding		
males	110.7	2.657
females	127.0	3.048

Table 4. Mean daily budget of behavioral activities (min/day) for kestrels during 3 seasons (nonbreeding =Jan-Feb, breeding = Mar-Apr, postbreeding = Aug-Sept) in northern Utah. Behaviorial acivity as a percent of the photoperiod is in parentheses. Dashes refer to less than 0.1%. Asterisks indicate significance (p<0.05) across rows.

	nonbreeding				breeding				postbreeding			
Behavioral Activity	Male		Female		Male		Female		Male		Female	
Flight												
Directional	19.3	(2.8)	20.7	(3.2)	42.9*	(4.8)	24.0	(2.7)	19.9	(2.2)	25.3	(2.8)
Hovering	1.7	(0.3)	2.2	(0.3)	10.1	(1.1)	1.3	(0.1)	0.6	(0.1)	0.8	(0.1)
Interaction	0.4	(0.1)	0.2	---	0.3	---	0.4	---	0.1	---	1.7*	(0.2)
Subtotal	21.4	(3.2)	23.1	(3.5)	53.3*	(5.9)	25.7	(2.8)	20.6	(2.3)	27.8	(3.1)
Non-flight												
Preen	12.5	(1.9)	10.8	(1.6)	55.6	(6.3)	55.6	(6.3)	50.1	(5.6)	39.6	(4.4)
Copulation	0.0	(0.0)	0.0	(0.0)	2.0	(0.2)	2.0	(0.2)	0.0	(0.0)	0.0	(0.0)
Perch-hunt	626.1	(94.9)	626.1	(94.9)	789.1	(87.6)	816.7	(90.7)	829.3	(92.1)	832.6	(92.5)
Subtotal	638.6	(96.8)	636.9	(96.5)	846.7	(94.1)	874.3	(97.2)	879.4	(97.7)	872.2	(96.9)
Total	660.0	(100.0)	660.0	(100.0)	900.0	(100.0)	900.0	(100.0)	900.0	(100.0)	900.0	(100.0)

Table 5. Mean time (min/hr) allocated to flight by kestrels during 3 seasons (nonbreeding = Jan-Feb, breeding = Mar-Apr, postbreeding = Aug-Sept) in northern Utah. Data are stratified by hour (LSD=1.42) and by the combined interaction of season and sex (LSD=0.90).

hour	min	season	sex	min
1400-1500	2.93	breeding	males	3.53
1600-1700	2.75	postbreeding	females	1.74
1100-1200	2.55	breeding	females	1.68
1700-1800	2.49	nonbreeding	females	1.53
1200-1300	2.49	nonbreeding	males	1.39
1500-1600	2.38	postbreeding	males	1.36
0900-1000	2.34			
1300-1400	2.33			
1000-1100	2.11			
0800-0900	1.98			
0700-0800	1.64			
0600-0700	1.15			
1800-1900	0.79			
0500-0600	0.12			
1900-2000	0.08			

Table 6. Mean time (min/hr) allocated to directional flight by kestrels during 3 seasons (nonbreeding = Jan-Feb, breeding = Mar-Apr, postbreeding = Aug-Sept) in northern Utah. Data are stratified by hour (LSD=1.09) and by the combined interaction of season and sex (LSD=0.69).

hour	min	season	sex	min
1600-1700	2.54	breeding	males	2.86
1100-1200	2.51	postbreeding	females	1.69
1400-1500	2.38	breeding	females	1.60
1500-1600	2.25	nonbreeding	females	1.38
0900-1000	2.17	nonbreeding	males	1.32
1200-1300	2.15	postbreeding	males	1.29
1000-1100	2.04			
1300-1400	1.95			
0800-0900	1.90			
1700-1800	1.68			
0700-0800	1.64			
0600-0700	1.15			
1800-1900	0.79			
0500-0600	0.12			
1900-2000	0.08			

Table 7. Mean number (no./day) and mean time (min/hr) allocated to species interactions by kestrels during 3 seasons (nonbreeding = Jan-Feb, breeding = Mar-Apr, postbreeding = Aug-Sept) in northern Utah. Data are stratified by the combined interactions of season and species (LSD=0.70) and by season and sex (LSD=0.62).

season	species	no	season	sex	min
postbreeding	American Kestrel	1.80	postbreeding	females	0.12
breeding	European Starling	1.35	breeding	females	0.03
nonbreeding	Red-tailed Hawk	1.21	breeding	males	0.02
postbreeding	Black-billed Magpie	1.03	nonbreeding	males	0.02
breeding	American Kestrel	0.95	nonbreeding	females	0.01
breeding	Northern Flicker	0.40	postbreeding	males	0.01
nonbreeding	Rough-legged Hawk	0.40			
nonbreeding	Northern Harrier	0.38			
postbreeding	Red-tailed Hawk	0.20			
breeding	Northern Harrier	0.20			
nonbreeding	European Starling	0.17			
nonbreeding	Black-billed Magpie	0.15			
breeding	Black-billed Magpie	0.13			
nonbreeding	Western Meadowlark	0.13			
postbreeding	Brewer's Blackbird	0.10			
breeding	Short-eard Owl	0.10			

Table 8. Mean time (min/hr) allocated to preening by kestrels during 3 seasons (nonbreeding = Jan-Feb, breeding = Mar-Apr, postbreeding = Aug-Sept) in northern Utah. Data are stratified by hour (LSD=1.43) and by season (LSD=0.64).

hour	min	season	min
0900-1000	5.42	breeding	3.71
0600-0700	4.99	postbreeding	3.00
0700-0800	4.01	nonbreeding	0.78
0800-0900	3.83		
1100-1200	3.25		
1200-1300	3.09		
1300-1400	2.12		
1700-1800	1.95		
1400-1500	1.93		
1000-1100	1.90		
1600-1700	1.70		
1500-1600	1.47		
1800-1900	1.27		
0500-0600	0.42		
1900-2000	0.04		

Table 9. Total prey caught by kestrels utilizing 3 hunting methods during 3 seasons (nonbreeding = Jan-Feb, breeding = Mar-Apr, postbreeding = Aug-Sept) in northern Utah. V = vertebrate, I = invertebrate, Uns = no. unsuccessful strikes.

	Perch			Hover			Hawk		Total	
	V	I	Uns	V	I	Uns	I	Uns	V	I
<u>non-breeding</u>										
males	20	1	48	2	0	4	-	-	22	1
females	9	5	43	0	0	1	-	-	9	5
<u>breeding</u>										
males	16	3	29	8	0	1	-	-	24	3
females	5	1	20	0	0	0	-	-	5	1
<u>post-breeding</u>										
males	10	147	66	0	1	2	8	2	10	156
females	8	117	59	0	6	31	15	3	8	138
total	68	274	265	10	7	39	23	5	78	304

Table 10. Total number of vertebrate prey acquired and processed by kestrels during 3 seasons (nonbreeding = Jan-Feb, breeding = Mar-Apr, postbreeding = Aug-Sept) in northern Utah. Sequential predatory actions on single prey are coded as follows: E=Eat, C=Cache, P=Pirate, T=Transfered from male to female, U=Unobserved.

	Method of Acquisition																					
Predatory action	**Hunt**								**Retrieved**					**Unobserved**								
	E	E C	E P	E T U	C	P	T U	U	E	E C	E U	T E C	T U	E	E C	E P	C	T E	T E C	T C	T U	
Season																						**Total**
non-breeding																						
males	14	3	1	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22
females	9	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	12
breeding																						
males	7	1	0	6	4	0	6	0	5	2	1	1	1	0	0	0	1	1	2	3	3	44
females	3	2	0	6	0	0	6	0	7	3	0	1	1	1	5	1	1	1	2	3	3	46
post-breeding																						
males	3	2	0	0	5	0	0	0	2	1	0	0	0	1	1	0	0	0	0	0	0	15
females	1	4	0	0	1	0	0	2	2	1	0	0	0	0	0	0	1	0	0	0	0	12
total					92						29							30				151

Table 11. Prey captured (%) and predatory efficiency (%) of kestrels utilizing 3 hunting methods during 3 seasons (nonbreeding = Jan-Feb, breeding = Mar-Apr, post-breeding = Aug-Sept) in northern Utah. Data from Table 9.

	Prey Captured			Predatory Efficiency		
	Perch	Hover	Hawk	Perch	Hover	Hawk
non-breeding						
males	91.3	8.7	--	30.4	33.0	--
females	100.0	0.0	--	24.6	0.0	--
breeding						
males	70.4	29.6	--	39.6	88.9	--
females	100.0	0.0	--	23.1	0.0	--
post-breeding						
males	94.6	0.6	4.8	70.4	33.0	80.0
females	85.6	4.1	10.3	67.9	16.2	83.3
average	89.9	4.5	6.0	56.3	30.4	82.1

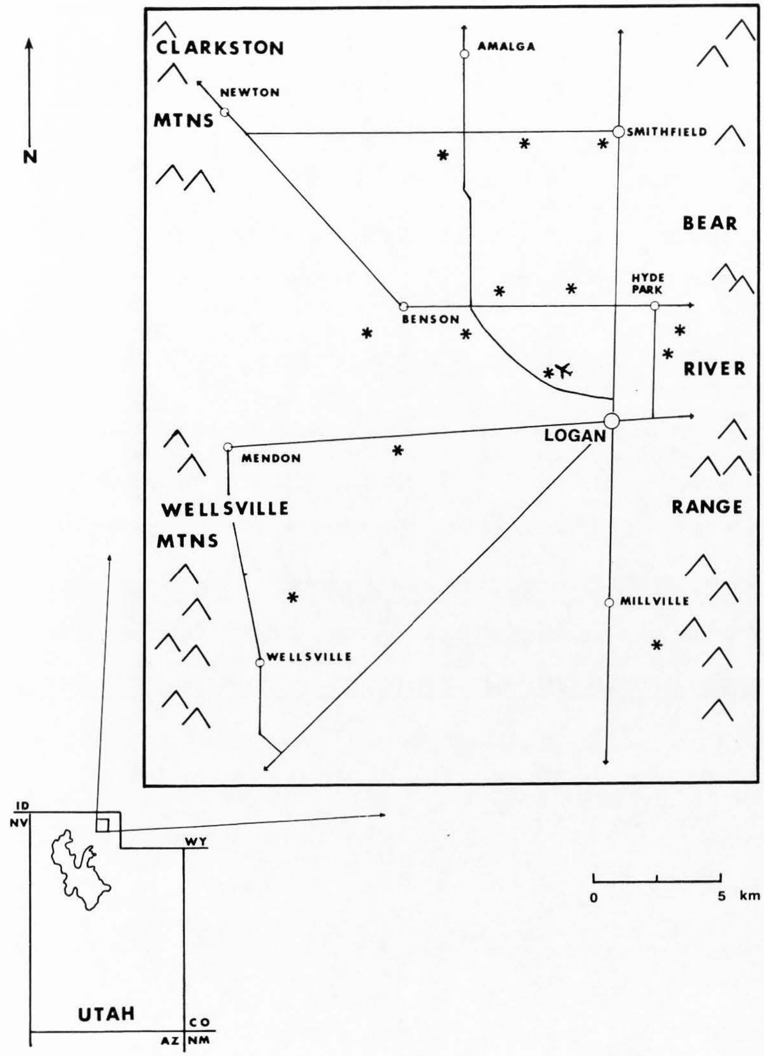
Table 12. Mean levels of nonflight energy expenditure (NFEE), nighttime energy expenditure (NEE), flight energy expenditure (FEE) and daily energy expenditure (DEE) predicted from a model for kestrels (see Table 1) during 3 seasons (nonbreeding = Jan-Feb, breeding = Mar-Apr, and postbreeding = (Aug-Sept) in northern Utah. Production (PR) values are explained in Table 2. All units are in kcal/day. Significance is indicated by different letters down columns. Standard error (SE) follows in parentheses.

season	NFEE	NEE	FEE	PR	DEE	(SE)
non-breeding						
males	22.39bc	19.32cA[1]	3.79a	0.00	45.50b	(1.06)
females	24.25c	21.99cB	3.68a	0.00	49.92c	(0.70)
breeding						
males	20.04a	11.01aA	7.13b	0.02	38.20a	(2.28)
females	24.61c	13.15aB	3.48a	10.33	51.57c	(1.16)
post-breeding						
males	19.87ab	12.50bA	3.21a	4.65	40.23a	(2.93)
females	19.66ab	13.32bB	4.50a	7.11	44.59b	(2.04)

[1] lowercase letters indicate main effect due to season
uppercase letters indicate main effect due to sex

Table 13. Mean input variables to a model predicting daily energy expenditure (DEE) of kestrels during 3 seasons (nonbreeding = Jan-Feb, breeding = Mar-Apr, and postbreeding = Aug-Sept) in northern Utah. Symbols are defined in Table 2. Units for P and FA are proportions of the 24 hr day and the photoperiod, respectively. Significance is indicated by different letters down columns.

season	W (g)	Ta (^{o}C)	Qs (cal/min cm^2)	U (m/sec)	Tna (^{o}C)	P	FA
non-breeding							
males	119.1a	2.9a	0.274a	0.53	2.9a	0.461a	0.0340a
females	138.0b	2.8a	0.246a	0.00	3.3a	0.466a	0.0296a
breeding							
males	107.8a	12.7b	0.729b	0.96	9.6b	0.606c	0.0527b
females	124.1b	10.8b	0.530b	1.12	9.1b	0.595c	0.0233a
post-breeding							
males	110.7a	12.2b	0.573b	0.46	9.7b	0.563b	0.0252a
females	127.0b	15.6b	0.614b	0.37	11.9b	0.571b	0.0312a


N
CLARKSTON
MTNS
NEWTON
AMALGA
SMITHFIELD
BEAR
HYDE PARK
BENSON
RIVER
LOGAN
MENDON
WELLSVILLE
MTNS
RANGE
MILLVILLE
WELLSVILLE
ID
NV
WY
UTAH
CO
AZ
NM
0
5 km

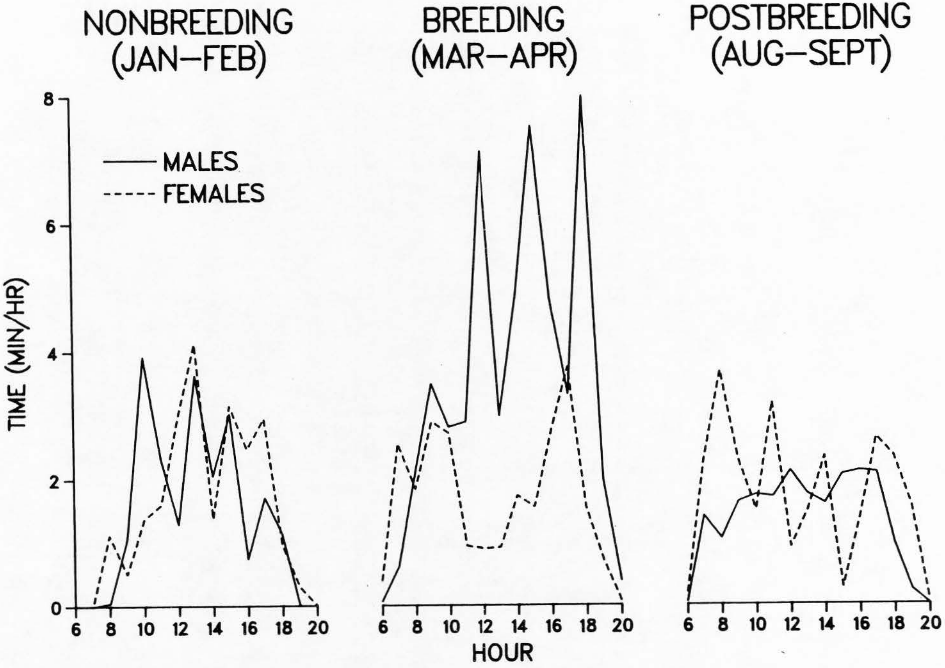
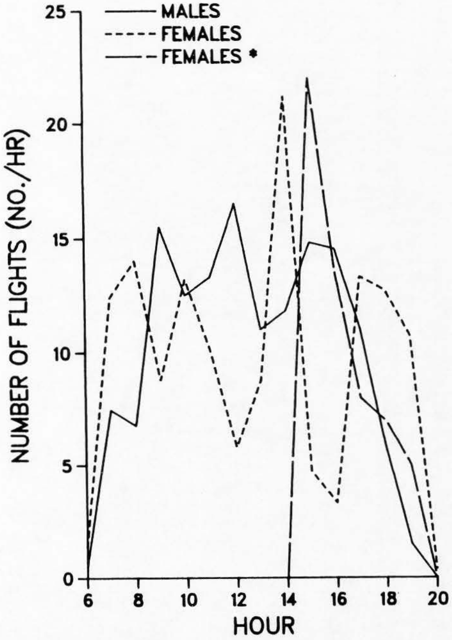

NONBREEDING
(JAN–FEB)
BREEDING
(MAR–APR)
POSTBREEDING
(AUG–SEPT)
MALES
FEMALES
TIME (MIN/HR)
0
2
4
6
8
6
8
10
12
14
16
18
20
HOUR

Fig. 3. Mean number of flights (no./hr, left graph) and mean hourly pattern (min/hr, right graph) of flight activities by kestrels during the postbreeding (Aug-Sept) season in northern Utah. Females * = flight activities of 2 females during thunderstorms.


MALES
FEMALES
FEMALES *
NUMBER OF FLIGHTS (NO./HR)
25
20
15
10
5
0
6
8
10
12
14
16
18
20
HOUR

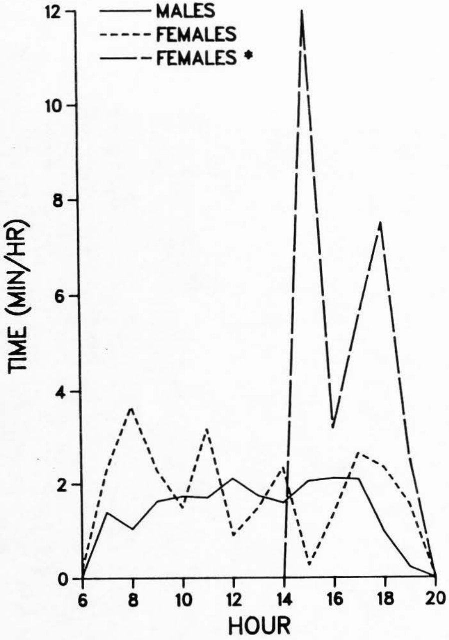

MALES
FEMALES
FEMALES *
TIME (MIN/HR)
12
10
8
6
4
2
0
6
8
10
12
14
16
18
20
HOUR

Fig. 4. Relationship between mean number of flights (no./hr) and mean time (min/hr) allocated to flight activities by kestrels during the postbreeding season (Aug-Sept) in northern Utah.

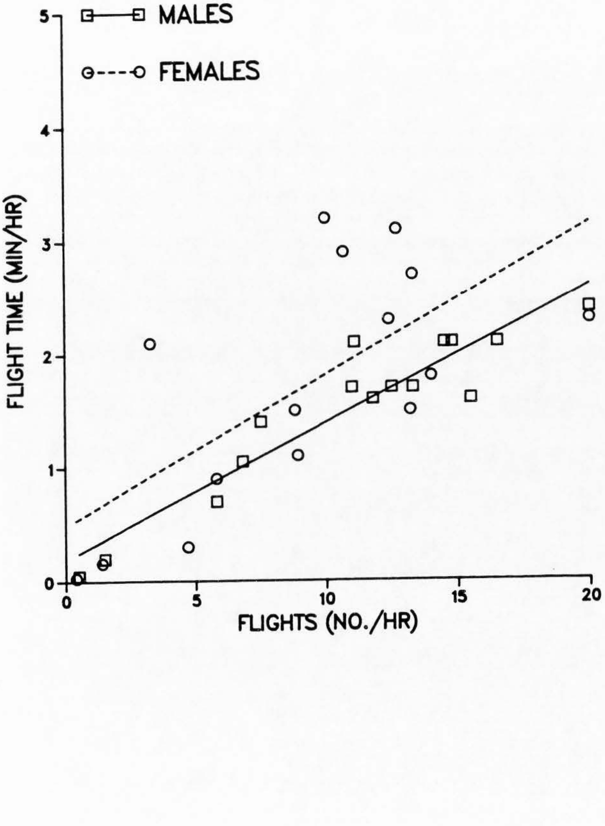

MALES
FEMALES
FLIGHT TIME (MIN/HR)
FLIGHTS (NO./HR)
0
1
2
3
4
5
0
5
10
15
20

Fig. 5. Mean hourly pattern (min/hr) of hovering by kestrels during the postbreeding (Aug-Sept) season in northern Utah. Females * = flight activities of 2 females during thunderstorms.

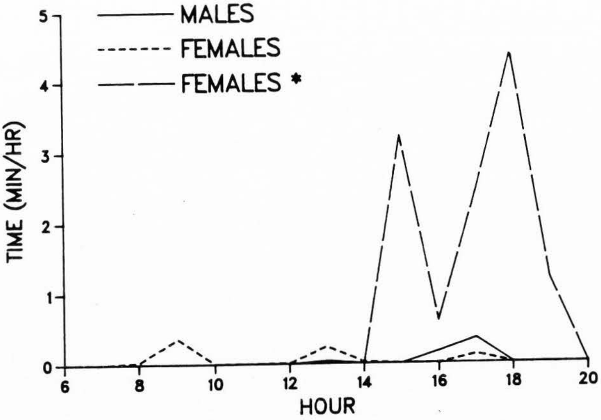

MALES
FEMALES
FEMALES *
TIME (MIN/HR)
0
1
2
3
4
5
HOUR
6
8
10
12
14
16
18
20

Fig. 6. Mean number (no./day) of kestrel interactions with conspecifics during the nonbreeding (Jan-Feb), breeding (Mar-Apr), and postbreeding (Aug-Sept) seasons in northern Utah.

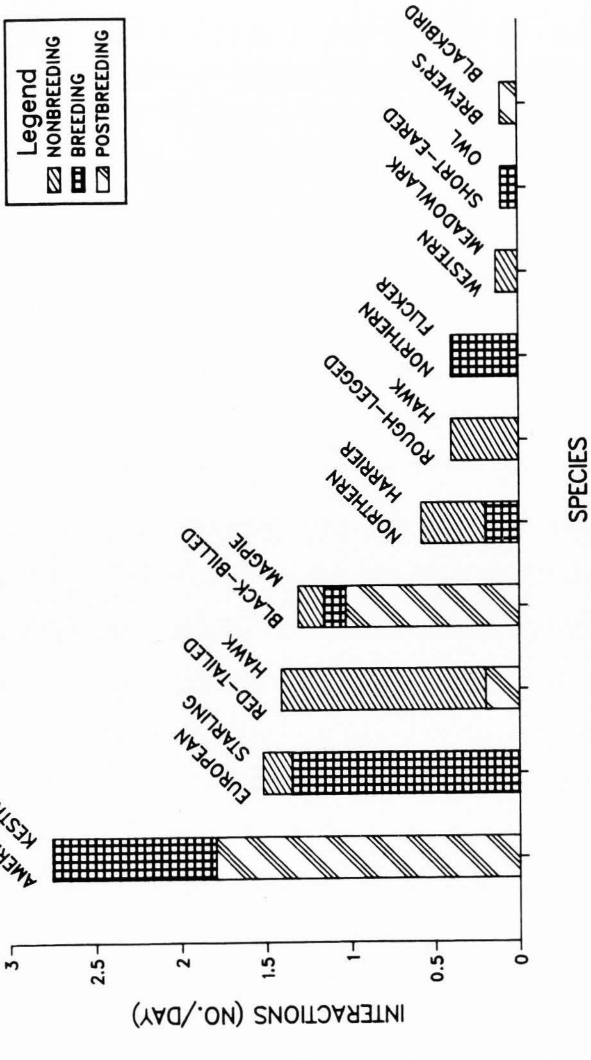
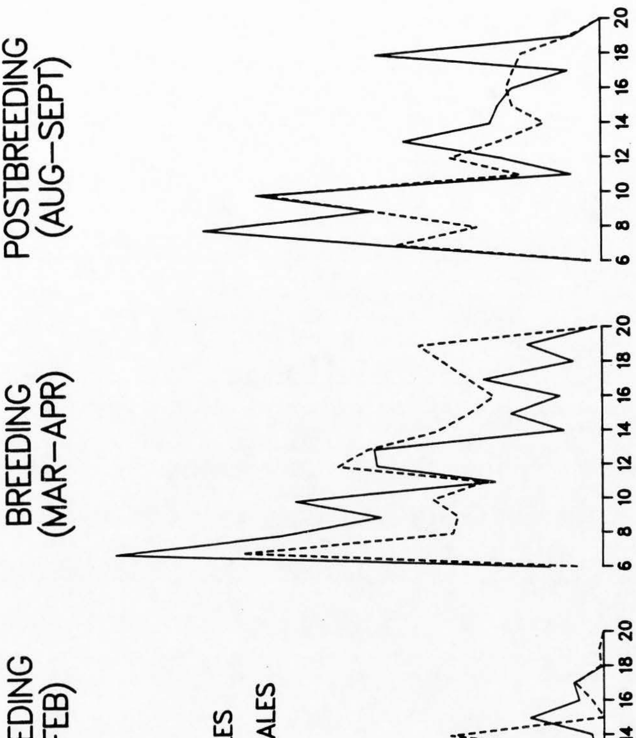

Legend
▨ NONBREEDING
▦ BREEDING
▧ POSTBREEDING
INTERACTIONS (NO./DAY)
0
0.5
1
1.5
2
2.5
3
SPECIES
AMERICAN KESTREL
EUROPEAN STARLING
RED-TAILED HAWK
BLACK-BILLED MAGPIE
NORTHERN HARRIER
ROUGH-LEGGED HAWK
NORTHERN FLICKER
WESTERN MEADOWLARK
SHORT-EARED OWL
BREWER'S BLACKBIRD

Fig. 7. Mean hourly pattern (min/hr) of preening by kestrels during the nonbreeding (Jan-Feb), breeding (Mar-Apr), and postbreeding (Aug-Sept) seasons in northern Utah.

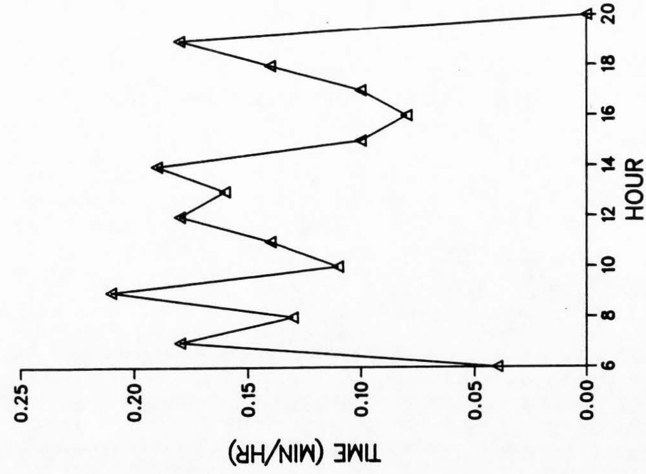


NONBREEDING (JAN–FEB)

BREEDING (MAR–APR)

POSTBREEDING (AUG–SEPT)

Fig. 8. Mean number of copulatory acts (no./hr, left graph) and mean hourly pattern (min/hr, right graph) of copulatory activities by kestrels during the breeding (Mar-Apr) season in northern Utah.


TIME (MIN/HR)
0.25
0.20
0.15
0.10
0.05
0.00
6
8
10
12
14
16
18
20
HOUR

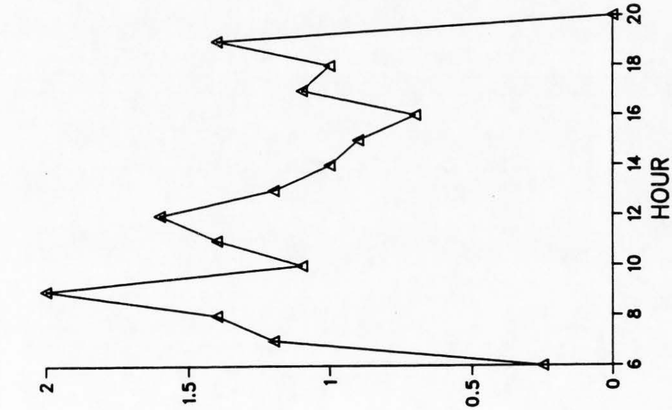

COPULATORY ACTS (NO./HR)
2
1.5
1
0.5
0
6
8
10
12
14
16
18
20
HOUR

Fig. 9. Total number of vertebrates captured by kestrels during the nonbreeding (Jan-Feb), breeding (Mar-Apr), and postbreeding (Aug-Sept) seasons in northern Utah.

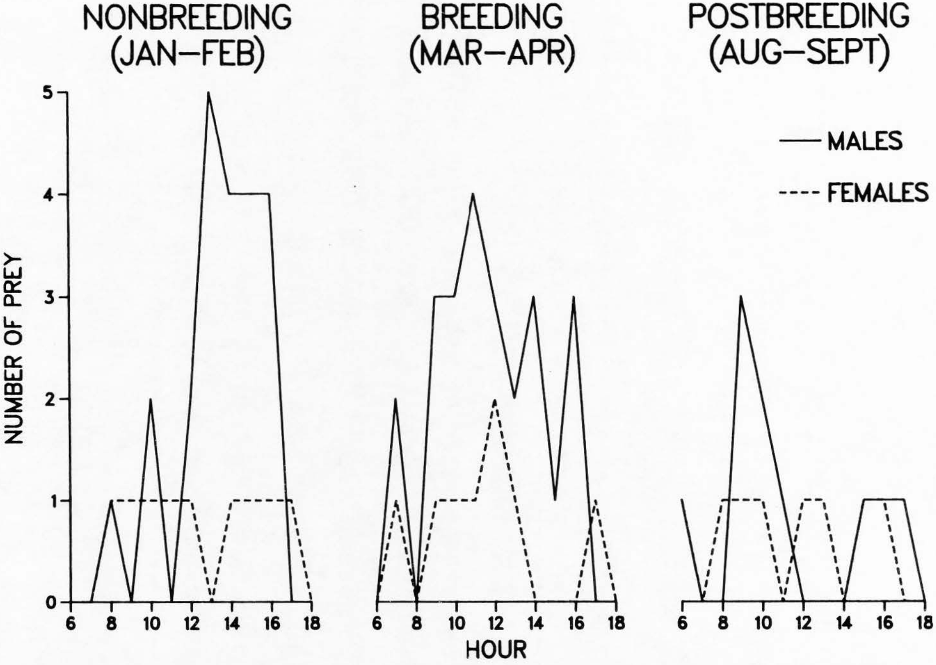

NONBREEDING
(JAN—FEB)
BREEDING
(MAR—APR)
POSTBREEDING
(AUG—SEPT)
MALES
FEMALES
NUMBER OF PREY
0
1
2
3
4
5
6
8
10
12
14
16
18
HOUR

Fig. 10. Mean number (no./hr) of invertebrates captured by kestrels utilizing 3 hunting methods during the postbreeding (Aug-Sept) season in northern Utah.

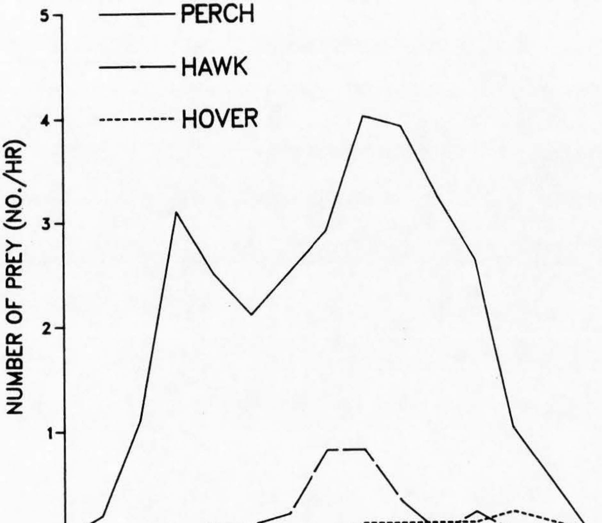

PERCH
HAWK
HOVER
NUMBER OF PREY (NO./HR)
0
1
2
3
4
5
6
8
10
12
14
16
18
20
HOUR

Fig. 11. Total number of vertebrates cached and retrieved by kestrels during the nonbreeding (Jan-Feb), breeding (Mar-Apr), and postbreeding (Aug-Sept) seasons in northern Utah.

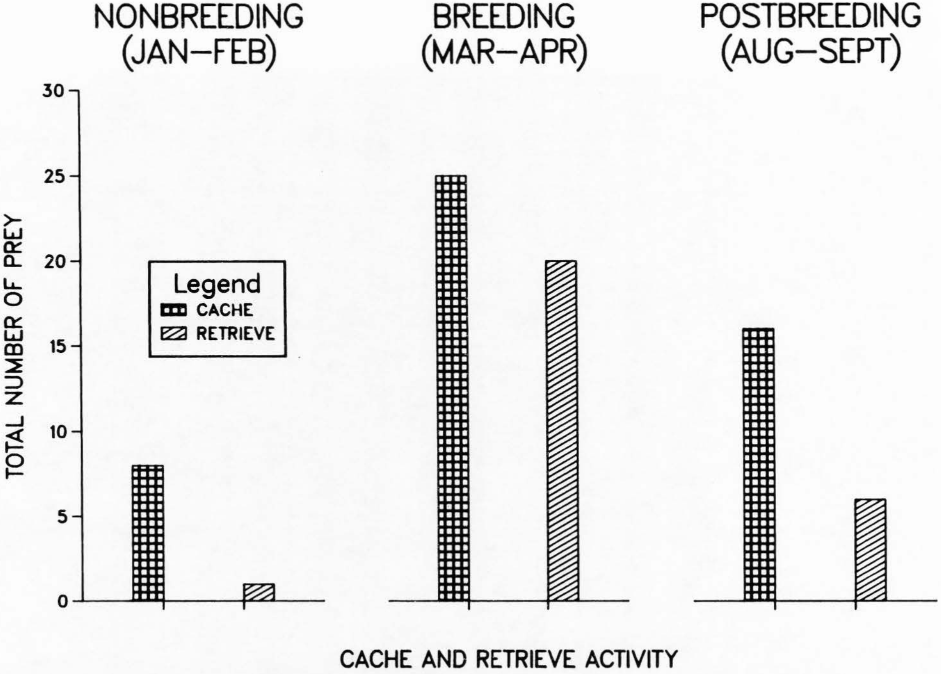
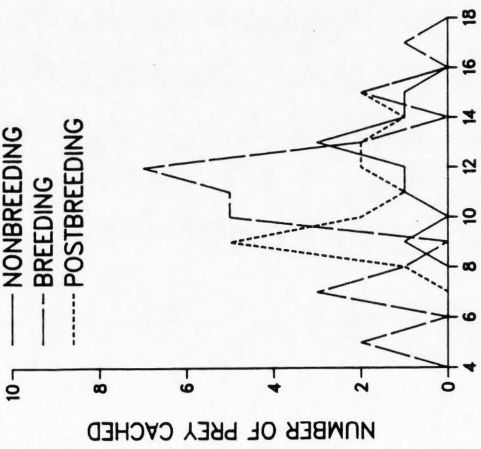

NONBREEDING
(JAN–FEB)
BREEDING
(MAR–APR)
POSTBREEDING
(AUG–SEPT)
30
25
20
15
10
5
0
TOTAL NUMBER OF PREY
Legend
▦ CACHE
▨ RETRIEVE
CACHE AND RETRIEVE ACTIVITY

Fig. 12. Hourly pattern of cached (left graph) and retrieved (right graph) vertebrates by kestrels during the nonbreeding (Jan-Feb), breeding (Mar-Apr), and postbreeding (Aug-Sept) seasons in northern Utah.


NUMBER OF PREY CACHED
10
8
6
4
2
0
4
6
8
10
12
14
16
18
HOUR
NONBREEDING
BREEDING
POSTBREEDING

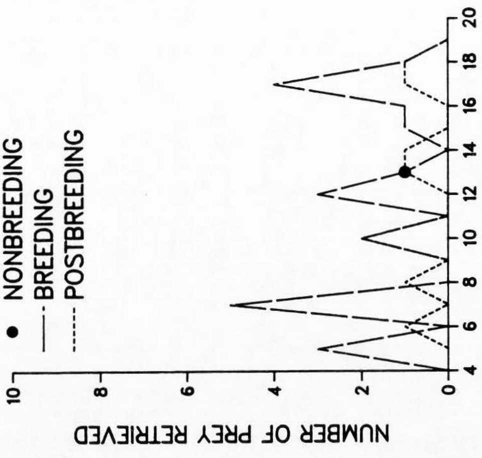
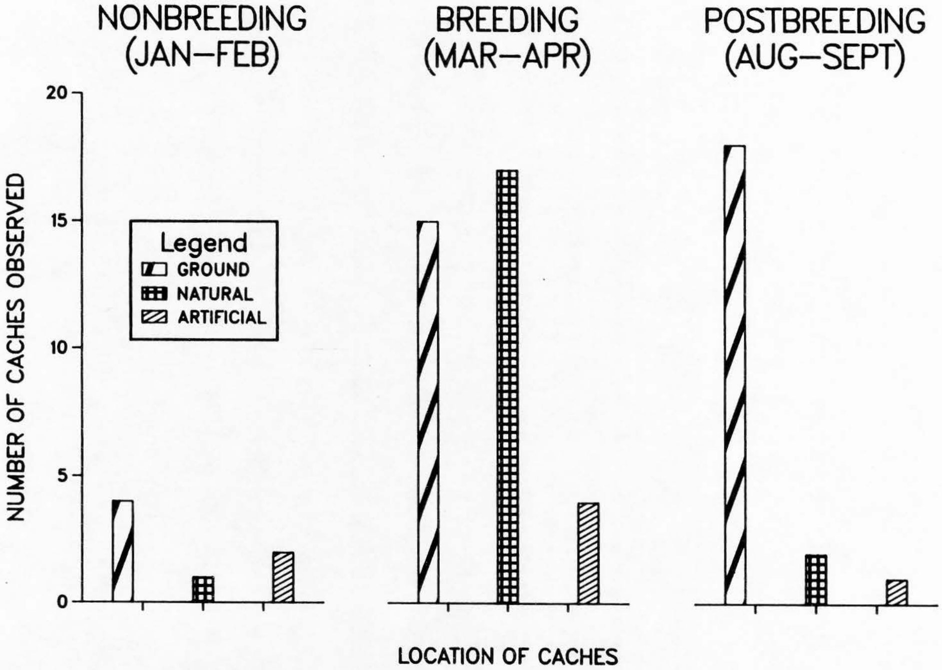

NUMBER OF PREY RETRIEVED
10
8
6
4
2
0
4
6
8
10
12
14
16
18
20
HOUR
● NONBREEDING
BREEDING
POSTBREEDING

Fig. 13. Location of caches selected by kestrels (see text for explanation) during the nonbreeding (Jan-Feb), breeding (Mar-Apr), and postbreeding (Aug-Sept) seasons in northern Utah.


NONBREEDING (JAN–FEB)
BREEDING (MAR–APR)
POSTBREEDING (AUG–SEPT)
NUMBER OF CACHES OBSERVED
20
15
10
5
0
Legend
GROUND
NATURAL
ARTIFICIAL
LOCATION OF CACHES