AMERICAN KESTREL FORAGING BEHAVIOR IN THE CALIFORNIA WHITE MOUNTAINS

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Abstract. Observations of American Kestrel (*Falco sparverius*) hunting behavior were made in the White Mountains of California at elevations from 3200 meters to 3700 meters during the summer of 1984. Four hunting methods were observed: (1) perch hunting, (2) hover hunting, (3) hawking, and (4) ground foraging. However, hawking was rare and therefore not included in the analysis of this study. Ground foraging, an atypical hunting method, was the second most common hunting behavior observed. It was correlated with time of season, grasshopper density, and vegetative cover of hunted areas. Perch hunting was also correlated with season, grasshopper density, and vegetative cover. Hovering was correlated with season and windspeed. The common use of ground foraging indicates that it is a foraging method particularly well adapted to an alpine environment.

Introduction

American Kestrels (*Falco sparverius*) are small falcons widely distributed throughout North America. They are easily visible and exhibit several hunting methods. These characteristics make the kestrel an ideal subject to study the adaptive significance of foraging strategy to different habitats. Kestrels commonly use three hunting methods: (1) hunting from a perch, (2) hovering or stationary flight, and (3) hawking or aerial insect capture. These methods have been described by Balgooyen (1976), Evans (1976), Norberg (1977), Rudolph (1982), Bildstein and Collopy (1983), and Collopy and Koplin (1983). In general perch hunting appears to be the prevalent hunting method, accounting for over 70% of total hunting effort (Balgooyen 1976, Cruz 1976, Collopy and Koplin 1983).

A fourth hunting method kestrels use is ground foraging in which hunting attempts are initiated from the ground (Berdan 1976). Ground foraging appears to be rare, occurring when prey densities are low early in the season (Balgooyen 1976). However, in northwestern California kestrels ground forage after heavy rainstorms for earthworms (Berdan 1976, Koplin pers. comm.). Because of the apparently infrequent use of ground foraging, its significance compared to the other hunting methods has not been assessed.

Several significant predictor variables of kestrel foraging strategy have been described: food availability (Evans 1976, Norberg 1977), prey type (Roest 1957, Rudolph 1982, Collopy and Koplin 1983), number of young supported by breeding kestrels (Rudolph 1982), windspeed and perch site availability (Balgooyen 1976). These predictor variables have been correlated with hovering and perch hunting in the following ways: (1) kestrels appear to be more successful in capturing invertebrate prey when perch hunting than when hovering (Roest 1957, Collopy and Koplin 1983) and (2) as windspeed increases (Balgooyen 1976) and number of young supported increases (Rudolph 1982) kestrels tend to increase their use of hover hunting.

The present study describes the hunting methods kestrels use in three alpine areas and attempts to correlate the hunting methods used with 7 predictor variables. The 7 predictor variables are: (1) season, (2) time, (3) sex, (4) windspeed, (5) density of grasshoppers (order: Orthoptera, a primary food source of kestrels, McAtee 1932, Knowlton and Telford 1947, Roest 1957, Heintzelman 1964, Balgooyen 1976, Cruz 1976), (6) height and density of vegetative cover, and (7) temperature.

Methods and Study Area

This study was conducted from July to September 1984 in the Alpine Zone of the California White Mountains. Three study areas were selected for observing kestrel hunting behavior. According to a vegetation reconnaissance of the White Mountain Scientific Area (Taylor 1975), I classified Area 1 as Alpine Steppe Grassland, Area 2 as a mix of Alpine Steppe and Sedge Meadow, and Area 3 as Sagebrush Scrub. Each area I further characterized by percent and height of vegetative cover.

Foraging behavior was recorded for a five-minute interval whenever a kestrel was observed hunting in one of the study areas. Time spent in each of the hunting modes was quantified with a stopwatch. After each five-minute period, each of the 7 predictor variables was determined. Season, indicated by the date of the observation, was categorized as July 16 - July 31, August 1 - August 15, and August 16 - August 31. Sex, determined by plumage coloration, was categorized as male, female, and unknown. Windspeed was measured with a handheld anemometer and categorized as 0-8 kmph, 9-16 kmph, and 17-24 kmph. Grasshopper density was estimated using five nearest-neighbor measurements (Blackith 1958) and a formula derived by Craig (1953). Density (x) was then categorized as $0.00 < x < 0.99$, $1.00 < x < 1.99$, $2.00 < x < 2.99$, and $3.00 < x < 3.99$. X is the estimate of the number of grasshoppers per meter squared. Temperature was recorded on a thermograph at the Barcroft Weather Station. I categorized it in 3°C intervals. The non-parametric Kruskal - Wallis test (Neter, et al. 1985) was used to analyze each predictor variable against each hunting method. The predictor variables were coded into the discrete intervals just described and each hunting method was quantified by the percentage of the five-minute interval it made up. The Kruskal-Wallis test was also used to analyze the predictor variables for multicolinearity.

Results and Discussion

A total of 72 five-minute observations were recorded. Perch hunting accounted for 62%, ground foraging for 23%, and hover hunting for 15% of the total observed hunting time. Hawking was rare and never observed during an observation period. It was difficult to determine whether a perching kestrel was actually hunting or simply resting on a perch. Therefore, time spent resting may have been interpreted as perch hunting and the estimated percentage of perch hunting is probably an overestimate.

Previous studies on two of the hunting methods studied here have related foraging method to energy cost. Hovering has been shown to be more productive than perch hunting but also costing 6-8 times the energy (Rudolph 1982). Thus, hovering is classified as a high-cost hunting method and perch hunting as a low-cost hunting method. To my knowledge, ground foraging has not been related to perch hunting or hover hunting in energetic terms.

If a bird using hunting method A spent roughly the same relative amounts of time in similar activities as when using hunting method B, then the energetic cost per unit time of the two methods A and B should be similar. In this study, I separated hunting time into two types of activities. The first type was time spent searching for prey which included all stationary activities such as perching, sitting on the ground, and hovering. It should be noted that perching and sitting on the ground are similar energetically but hovering is more costly. The second type was time spent pursuing prey (Table 1). The percentages in each activity were similar between perch hunting and ground foraging. Because ground foraging is essentially perch hunting from the ground and the activity states between the two are similar, the energetic cost between the two methods should be similar. Therefore, ground foraging relative to hover hunting is also a low-cost hunting method.

Table 1. Separation of each hunting method into percent time searching for prey and into percent time pursuing prey.

	perch hunting	ground foraging	hover hunting
% time searching	89	90	46
% time pursuing	11	10	54

Each hunting method was analyzed separately against each predictor variable with a computer aided Kruskal-Wallis test. This analysis revealed several significant correlations (Table 2). Season was correlated differently with each hunting method. Ground foraging occurred proportionately more in early August (August 1 - August 15) than in late July (July 16 - July 31) or in late August (August 16 - August 31). It was least prominant in late July. Perch hunting, on the other hand, occurred proportionately more in late July than in early or late August. Hovering occurred proportionately more in late August and was least prominant in late July. Of the three methods only hovering showed a linear relationship with season in that the amount of hovering increased as time of the season progressed.

Hovering was positively correlated with windspeed. It has been suggested that increased windspeed decreases the energetic cost of hovering, i.e. hovering becomes 'cheaper' as windspeed increases (Balgooyen 1976, Rudolph 1982). If hover hunting yields a preferred food source (a food source with a relatively large energetic value) then its use is expected to increase as its cost decreases. The expected correlation between hovering and windspeed was observed in this study.

Perch hunting and ground foraging were correlated to grasshopper density in a non-linear fashion. Ground foraging was most prominant at moderate densities and least prominant at low densities. On the other hand, perch hunting was most prominant at the low densities.

From the transect analysis, the amount of tall vegetation (over 5 cm.) in Areas 1,2, and 3, was 20%, 61%, and 48%, respectively. The amount of tall

Table 2. P-values from a Kruskal-Wallis analysis between each predictor variable and each hunting method.

	perch hunting	ground foraging	hover hunting
time of season	$0.01 > p > 0.025$	$0.005 < p < 0.01$	$0.05 > p > 0.01$
time of day	$p > 0.1$	$p > 0.1$	$p > 0.9$
sex	$p > 0.1$	$p > 0.1$	$p > 0.1$
temperature	$p > 0.1$	$p > 0.1$	$p > 0.1$
windspeed	$0.05 < p < 0.1$	$p > 0.1$	$p < 0.005$
grasshopper density	$0.025 < p < 0.05$	$0.025 < p < 0.05$	$p > 0.1$
vegetative* cover	$p < 0.005$	$0.01 < p < 0.025$	$p > 0.1$

*Each area was characterized by the estimated percentage of vegetative cover over 5 cm. tall.

vegetative cover was negatively correlated to the amount of ground foraging. Because ground foraging requires maneuverability on or near the ground, this result is not surprising. Perch hunting was also correlated to amount of tall vegetation but nonlinearly. Perch hunting was most prominant in the area with 48% tall vegetation and least prominant in the area with 20% tall vegetation.

The reader should be aware of the dependence between the hunting methods. As can be seen from the results of the Kruskal-Wallis test if one type of hunting method is related to a particular predictor variable then the other hunting methods are also likely to be related. Thus, the results are somewhat redundant except for the type of relation, whether linear or not, between the different hunting methods and the predictor variables.

Within the predictor variables, season showed colinearity with grasshopper density and area hunted ($p < 0.005$). During early August, the period from August 1 - August 15, the density of grasshoppers was highest and kestrels mostly hunted the area with the greatest amount of open ground or least amount of tall vegetation. High grasshopper densities or efficient hunting methods are necessary for a kestrel whose diet is primarily orthopteran since it takes 30 - 40 grasshoppers to equal the food energy of an average mammal (such as a mouse) and 8 - 12 grasshoppers to equal the food energy of an average lizard by weight (Balgooyen 1976).

Several reasons may account for the common use of ground foraging in this study. First, the Alpine Steppe Grasslands that make up much of the White Mountain Alpine Zone are characterized by low vegetation and open ground (Taylor 1975). High grasshopper densities in these areas with low vegetative cover may attract the use of ground foraging. Second, vulnerability to terrestrial predators while on the ground is probably insignificant because there is little cover and good visibility. Finally, ground foraging may be a more efficient method than perch hunting or hover hunting for grasshoppers. Its increased use may be a response to the greater energetic requirements of an alpine existence (Welty 1982) and to the abundance of grasshoppers in these areas during this season. However, the energetic relation of ground foraging to perch hunting and hover hunting requires further research to substantiate this hypothesis.

Conclusion

The most important result of this study was the frequent occurrence of ground foraging, a hunting method that has generally been described as rare. Ground foraging probably has an energetic cost per unit time close to that of perch hunting because similar percentages of time are spent in the same activities. Ground foraging was correlated to 3 of the 7 predictor variables: season, vegetative cover, and grasshopper density. The multicolinearity present within these 3 variables gave rise to some inference on why ground foraging was so frequently used. During the mid part of the season grasshopper densities were highest, and the area mostly hunted was the one with the most open ground or least tall vegetation. Therefore, ground foraging seems to be a hunting method particularly well adapted to the concomitant conditions of low vegetation and high grasshopper densities found in these alpine regions in the White Mountains during specific times of the summer season.

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