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FOOD-SEARCHING BEHAVIOR OF FREE-LIVING FERRUGINOUS HAWKS:

FACTORS AFFECTING THE USE OF HUNTING

METHODS AND HUNTING SITES

by

James Stuart Wakeley

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

of

DOCTOR OF PHILOSOPHY

in

Wildlife Ecology

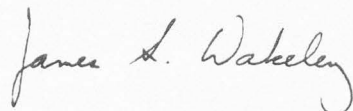
Approved:

UTAH STATE UNIVERSITY  
Logan, Utah

1976

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James Stuart Wakeley

## TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS . . . . .	ii
LIST OF TABLES . . . . .	v
LIST OF FIGURES . . . . .	vi
ABSTRACT . . . . .	vii
INTRODUCTION . . . . .	1
STUDY AREA . . . . .	4
METHODS . . . . .	9
RESULTS . . . . .	12
Timing of Foraging Activity . . . . .	12
Hunting Methods . . . . .	15
Hunting from a perch . . . . .	15
Hunting from the ground . . . . .	15
Hunting from low flight . . . . .	16
Hunting from high flight . . . . .	16
Success Rates . . . . .	17
Foraging Patterns . . . . .	19
Distribution of searching time . . . . .	19
Distribution of observed strikes . . . . .	22
Tests of randomness in foraging patterns . . . . .	22
Factors Affecting Foraging Patterns . . . . .	25
Effect of vegetation type . . . . .	25
Effect of prey distribution . . . . .	26
Effect of cover density . . . . .	31
Effect of previous experience . . . . .	33
Effect of Previous Experience Upon Use of Hunting Methods . . . . .	37
Switching of Major Hunting Areas . . . . .	39
Effect of Time and Energy Budgets Upon Choice of Hunting Method . . . . .	41
Time budgets . . . . .	41
Energy budgets . . . . .	43

## TABLE OF CONTENTS (Continued)

	Page
Effect of Energy Budgets Upon Choice of Hunting Sites . . .	51
DISCUSSION . . . . .	52
Success Rates . . . . .	52
Use of Hunting Methods . . . . .	52
Use of Hunting Sites . . . . .	54
Short-term and Long-term Foraging Efficiency . . . . .	58
Importance of Flexibility of Foraging Behavior . . . . .	59
LITERATURE CITED . . . . .	61

## LIST OF TABLES

Table	Page
1. Outcome of all observed strikes grouped by hunting method . . . . .	18
2. Mean number of pocket gopher mounds in 0.1-ha circular plots . . . . .	30
3. Density of vegetative cover in measured fields . . . . .	32
4. Frequency of return on the next hunting foray to the grid square in which the hawk made its last prey capture . . . . .	35
5. Location of consecutive prey captures by Ferruginous Hawks . . . . .	36
6. Comparison between the hunting method used by each hawk at the beginning of a new hunting foray and the method by which the bird's last prey item was captured . . . . .	38
7. Rates of striking and rates of prey capture by Ferruginous Hawks using four hunting methods . . . . .	44
8. Ratio of metabolic rate in flight to either the standard or resting metabolic rate in non-passerine birds . . . . .	46

## LIST OF FIGURES

Figure	Page
1. Location of the study area in Curlew Valley, Idaho . . . . .	5
2. Vegetation map of the study area . . . . .	6
3. Activity periods of Males 1 and 2 expressed as the percentage of each hourly interval spent away from the vicinity of the nest . . . . .	13
4. Average number of prey captured by Males 1 and 2 throughout the day . . . . .	14
5. Percentage of searching time spent by Male 1 (1974) in each grid square . . . . .	20
6. Percentage of searching time spent by Male 2 (1975) in each grid square . . . . .	21
7. Distribution of observed strikes (n = 430) by Male 1 (1974) . . . . .	23
8. Distribution of observed strikes (n = 378) by Male 2 (1975) . . . . .	24
9. Deviation from expected use of vegetation types . . . . .	27
10. Relationship between rodent biomass index and vegetation type . . . . .	29
11. Deviation from expected use of cover-density classes . . . . .	34
12. Strikes by Male 2 (1975) in each grid square expressed as a percentage of total strikes seen each week . . . . .	40
13. Comparison between the percentage of foraging time (solid circles) spent by Male 2 in grid square E-6 and its capture rate (hollow circles) in that square . . . . .	42
14. Comparison between the estimated captures/cost ratio for each hunting method and the proportion of a hawk's hunting time devoted to each method . . . . .	48

## ABSTRACT

Food-Searching Behavior of Free-Living Ferruginous Hawks:  
Factors Affecting the Use of Hunting  
Methods and Hunting Sites

by

James Stuart Wakeley, Doctor of Philosophy

Utah State University, 1976

Major Professor: Dr. David F. Balph  
Department: Wildlife Science

Food-searching behavior of two adult male Ferruginous Hawks (Buteo regalis) was studied by direct observation in Curlew Valley, Utah-Idaho, during the nesting seasons of 1974 and 1975. This paper analyzes the effects of vegetation type, prey distribution, cover density, previous experience, and time and energy budgets upon the predators' choice of hunting methods and hunting sites.

Both hawks hunted actively throughout the day (0600 to 2100 hours MDT). Male 1 (1974) and Male 2 (1975) captured an average of  $8.7 \pm 2.0$  and  $9.0 \pm 1.5$  prey items per day, respectively, during the 4-wk observation period in each year. The hawks hunted by four distinguishable methods: (1) from a perch, (2) from the ground, (3) from low-altitude (active) flight, and (4) from high-altitude (soaring) flight. The birds made a total of 808 observed strikes and were successful in securing prey in 129 (16.6 percent) of those strikes. Success rate (successful strikes/total attempted strikes) varied significantly with hunting method.



The hawks were selective in their use of vegetation types for hunting. Both birds used the "bare ground" and "pasture" types more than expected by chance. Male 2 also over-used the "alfalfa" type. Both hawks significantly under-used the "grass-shrub," "grass or grain," "old field," "juniper," and "rush-grass" cover types. The differences in use of vegetation types could not be related to differences in prey biomass. The birds were selective in their use of areas which differed in density of vegetative cover. Areas with no cover were used by both hawks more than expected by chance; all other areas were under-used with the single exception of "dense" cover in 1975.

Previous experience was important to the birds' choice of hunting sites and hunting methods. Each hawk returned directly to the site of its last prey capture on more than half of its hunting forays. Similarly, each hawk tended to initiate a new hunting effort by using the hunting method that had been successful on its previous hunt.

In 1975, Male 2 switched its emphasis to a new major hunting area during the fourth week of observation. The apparent reason for the switch was a decline in success at the first hunting area due to the growth of vegetation which concealed prey.

Males 1 and 2 averaged  $0.94 \pm 0.43$  and  $1.27 \pm 0.55$  prey captures per hour of hunting time, respectively. Capture rates (captures/time) varied with hunting method. The amount of time a hawk spent hunting by each method was not related to its capture rate by that method. However, each bird's total use of sit-and-wait hunting (from a perch or from the ground) and of hunting from low-altitude flight was proportional to estimates of the number of captures per unit of

energetic cost for those methods. Both hawks hunted from high-altitude flight more than expected on the basis of their catch/cost ratios for that technique. This suggests that soaring was not exclusively a hunting technique, but that it had some additional purpose unrelated to food gathering. There was some evidence that the hawks used major hunting sites which provided high benefit/cost ratios relative to the rest of their foraging ranges.

Both hawks foraged efficiently by concentrating more of their foraging time on the hunting method and in the hunting sites which yielded the highest number of prey captures per unit of energy expended. The birds' use of secondary hunting areas may have contributed to their long-term foraging efficiency by informing them of changes in the foraging potential of different portions of their home ranges. Such flexible foraging patterns may be critical to the survival of predators which rely on highly variable small-mammal populations.

(73 pages)

## INTRODUCTION

Laboratory studies have established that many predators and parasites modify their food-searching activity to increase the chance of finding prey. It has been shown that insect predators and parasites seek out environments likely to contain their prey, independent of the actual presence of prey (Laing 1937, Fleschner 1950, Banks 1957, Dixon 1959). After finding its first prey item, the insect usually concentrates its subsequent searching effort in the same area by adopting a more twisted and localized search path (Laing 1937, Varley 1941, Fleschner 1950, Banks 1957, Kaddou 1959, Chandler 1969). Similar behavior has been observed in the searching patterns of some birds (Smith 1974, Baker 1974). Several studies have shown that invertebrate predators can learn to associate novel cues, such as color and odor, with the presence of prey (Monteith 1963, Arthur 1966, Landenberger 1966, Taylor 1974). Vertebrate predators in experimentally controlled situations tend to return to sites of previous success in food gathering (Beukema 1968, Croze 1970, Alcock 1973, Smith and Dawkins 1971, Smith and Sweatman 1974). They also learn to search in the same type of hunting site where they previously found food (Krebs et al. 1972). When confronted with two alternative tasks which offer different rates of reward, laboratory animals learn to concentrate on the task with the higher rate of reinforcement, yet they never completely abandon the less-rewarding alternative (Herrnstein 1961, Bitterman 1965, Sutherland and Mackintosh 1971:405-409, Fischer 1972). Similarly,

birds in an aviary learn to concentrate their food-searching efforts in profitable areas while continuing to use less-profitable areas at lower frequency (Smith and Dawkins 1971, Smith and Sweatman 1974). These observations suggest that, to some extent, a predator is able to assess the benefit/cost relationships of its food-searching activities and to modify its behavior accordingly. Several theoretical papers have attempted to predict a predator's feeding behavior from the caloric benefit it obtains per unit of foraging time (e.g., Emlen 1966, MacArthur and Pianka 1966, Schoener 1971).

It is difficult to determine the extent to which laboratory findings and foraging theory can be extrapolated to the wild. The elusiveness of predators and the complexity of natural environments often make benefit/cost analyses of food searching impractical. Furthermore, many wild predators exhibit multiple hunting techniques which differ both in energy expenditure and in rate of return. This phenomenon precludes the equating of foraging time with energetic cost, a practice which has become standard in most laboratory studies and theoretical papers.

This study of the food-searching behavior of free-living Ferruginous Hawks (Buteo regalis) was designed to determine the extent to which elementary behavioral principles could be applied to a field situation. This paper examines the searching patterns of hawks in relation to spatial variations in vegetation type, cover density, and prey distribution within the birds' foraging ranges. It also examines the influence of previous experience on the hawks' searching patterns, and the effects of time and energy budgets on the birds' choice of

hunting methods as well as hunting sites. The purpose of the study was to test the hypothesis that a wild predator devotes most of its foraging time to the hunting method and the hunting site which provide it with the most prey per unit of energetic cost.

## STUDY AREA

The study area was located in Curlew Valley, Idaho, about 8 km north of Snowville, Utah (Fig. 1). It consisted of the home ranges of two adult male Ferruginous Hawks, Male 1 in 1974 and Male 2 in 1975. Both birds had mates, and observations were made during the nestling stage of the nesting season. Male 1 had three young and Male 2 had two. Range boundaries were determined by drawing a line around the outermost sightings of each bird. Nearly all of the birds' diurnal movements were thought to have occurred within those boundaries. The two hawks occupied ranges of similar size and shape and nested at sites less than 1 km apart (Fig. 2). Each nest was located about 3 m above the ground in the crown of a Utah juniper (Juniperus osteosperma) tree. Males 1 and 2 occupied ranges of 21.7 and 17.2 km<sup>2</sup>, respectively.

Most cultivated fields in the study area were laid out in 16-ha squares which formed a convenient grid system for recording the location of the hawks' activities (Fig. 2). Each grid square was designated by its row and column headings (e.g., E-5) and had the same designation in both years.

The study area was divided into eight vegetation types (Fig. 2). Most plant names were determined from Holmgren and Andersen (1971).

Bare ground--Usually plowed fields without vegetation. Included some hard-packed dirt areas.

Pasture--Areas of grass or forbs cropped closely by continual livestock grazing. Common species were Agropyron cristatum, Bromus tectorum, B. mollis, Taraxacum officinale,

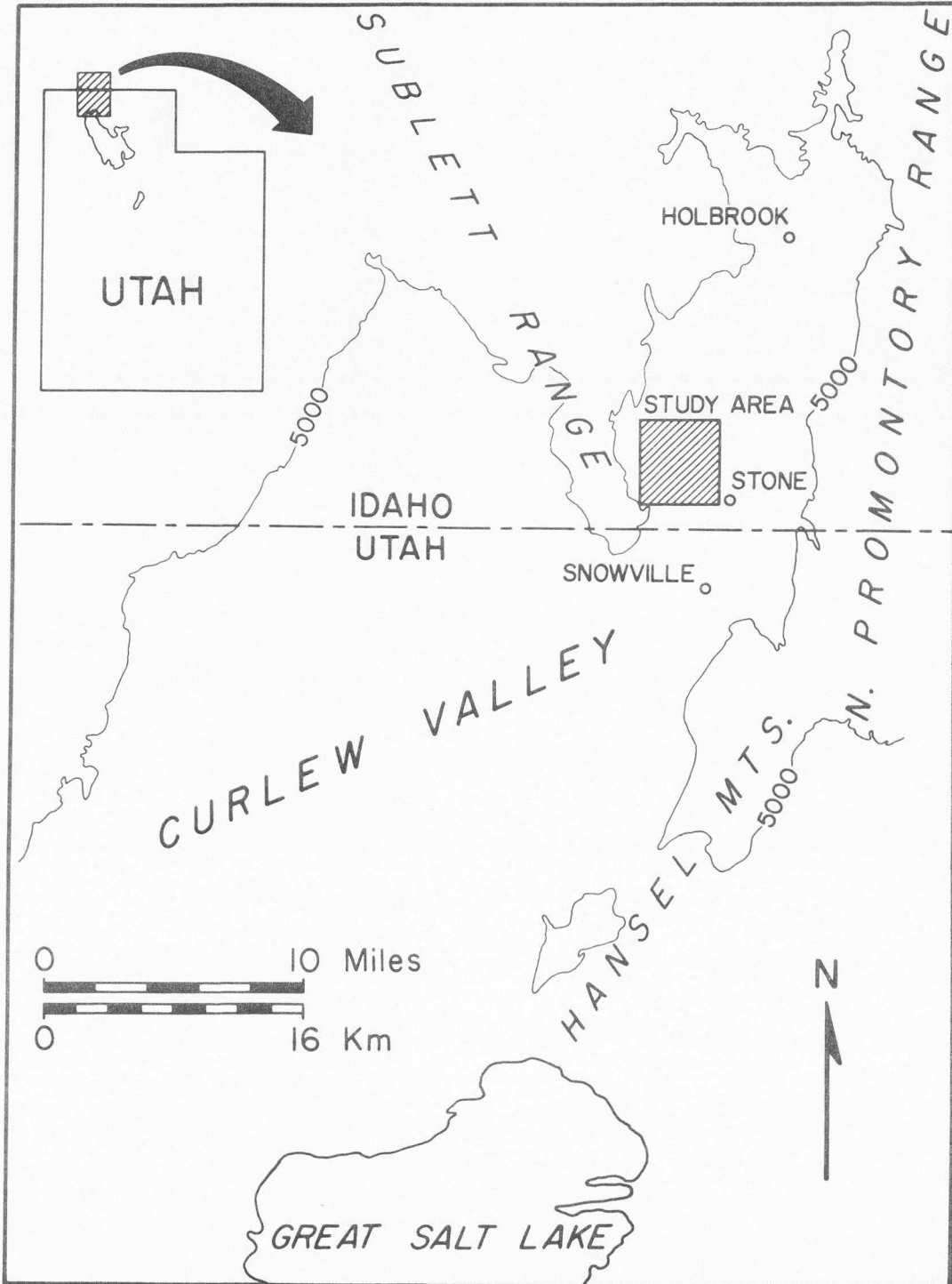


Fig. 1. Location of the study area in Curlew Valley, Idaho. The valley is outlined by the 5000 ft (1524 m) contour line.

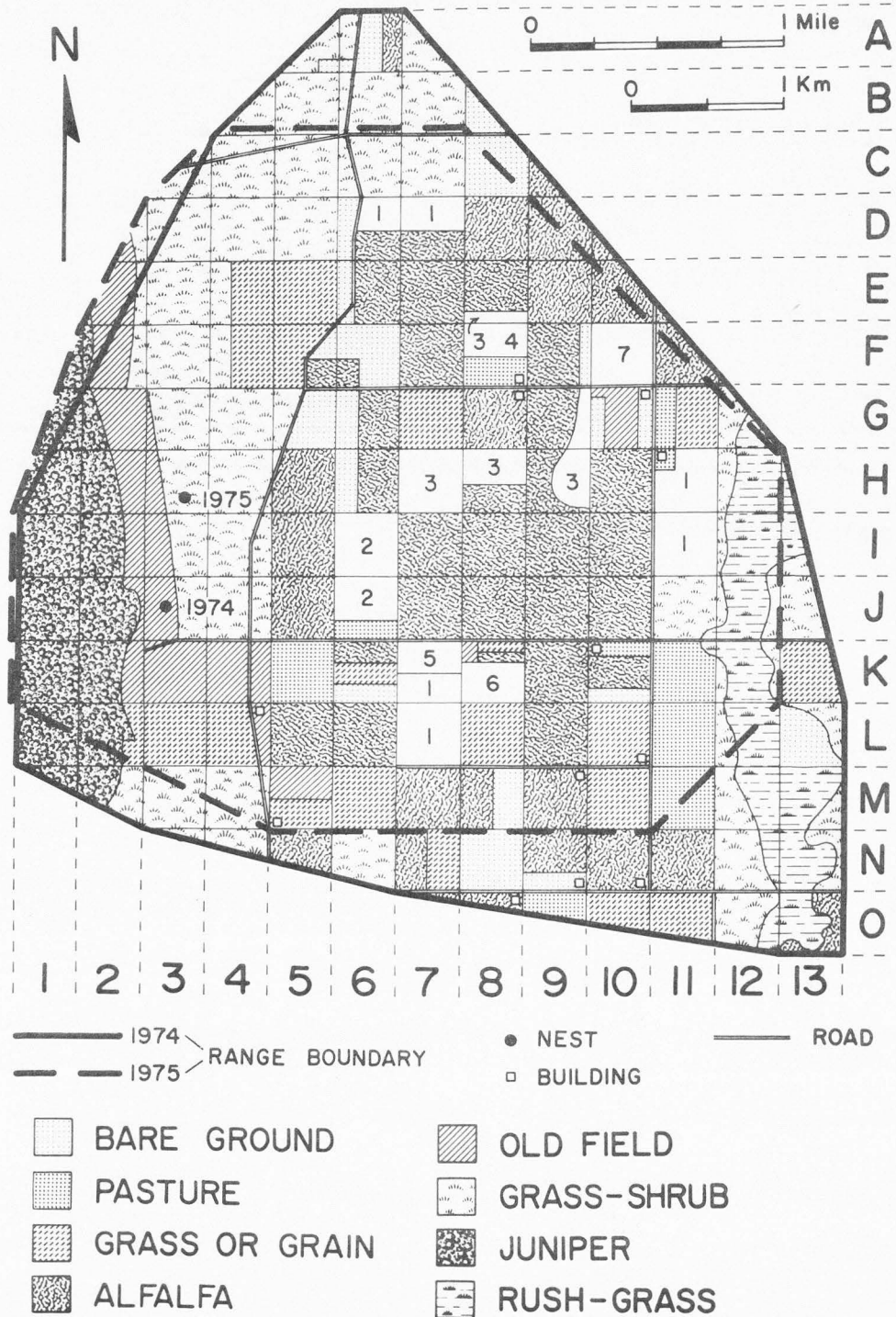


Fig. 2. Vegetation map of the study area. Numbered fields changed vegetation between 1974 and 1975, respectively, as follows: (1) grass or grain to bare ground, (2) bare ground to grass or grain, (3) alfalfa to grass or grain, (4) alfalfa to pasture, (5) grass or grain to pasture, (6) old field to grass or grain, (7) old field to bare ground.



Eragrostis hypnoides, Salsola kali, Descurainia sophia,  
Kochia scoparia, Grindelia squarrosa, Lepidium perfoliatum,  
and Hordeum jubatum.

Grass or grain--Cultivated grain (barley, wheat) or ungrazed  
crested wheatgrass (Agropyron cristatum) fields; combined  
into a single vegetation type due to their similar structure.

Alfalfa--First-growth alfalfa (Medicago sativa) fields. None  
was harvested during the observation periods.

Old field--Previously cleared or cultivated land which had  
reverted to weedy vegetation. Common species in some or all  
of these fields were Bromus tectorum, B. mollis, Ranunculus  
testiculatus, Lepidium perfoliatum, Tragopogon dubius,  
Salsola kali, Lappula redowski, Medicago sativa, Camelina  
microcarpa, and Agropyron cristatum.

Grass-shrub--Open shrubland with grass understory. Shrubs were  
mainly Artemisia tridentata in the west and A. tridentata  
and Chrysothamnus nauseosus in the east. Major grasses were  
Agropyron cristatum in the west and Bromus tectorum in the  
east. All areas contained Ranunculus testiculatus and  
Lepidium perfoliatum.

Juniper--Juniperus osteosperma forest with some Artemisia  
tridentata and a sparse Bromus tectorum understory.

Rush-grass--Wet-meadow area surrounding Deep Creek. Dominant  
plants were Juncus balticus, J. torreyi, Agropyron smithii,  
and Hordeum jubatum.

The study area was essentially flat but sloped gently from the foothills of the Sublett Range in the west to Deep Creek in the east.

In climate, Curlew Valley is typical of the "cold desert" region of the Great Basin. During the observation periods in May and June, daily maximum temperatures ranged from 10.0 to 37.8°C and daily minimum temperatures ranged from -6.1 to 11.1°C (U. S. Weather Bureau data for Snowville, Utah). There were periods of rain in May and occasional afternoon and evening thundershowers in June.

## METHODS

To minimize the risk of nest abandonment, the observation period started after the young had hatched. Observations began on 19 May in 1974 and on 26 May in 1975, when the hawks' nestlings were about 1 and 2 wks old, respectively. In each year, the observation period lasted 4 wks, although some additional data were collected during a fifth week in 1975. During each week of observation, all hours of the day were sampled, from 0600 to 2100 hours MDT. Sunrise and sunset occurred at about 0615 and 2030 hours, respectively. An average of about 10 hrs per day was spent watching the hawks, 5 days per week. Observations were made from a blind in 1974 and from the cab of a pickup truck in 1975. In each year, the observation post was about 300m from the nest. Viewing was aided with binoculars and a spotting scope.

Three types of information were collected:

Activity data--At 5-min intervals during sample periods of

1 hr, the hawks' ongoing activities were noted. From these data, the proportion of each hour spent away from the nest site was calculated. Sample hours were scattered throughout each day and each week to sample all time periods with about equal intensity.

Search data--During a hawk's foraging bouts, its position relative to the grid and its hunting method were recorded at 2-min intervals. Data were taken until the bird either captured a prey item, returned to the nest site without prey, or was

lost to view. Four hunting methods were recognized: hunting (1) from a perch, (2) from the ground, (3) from low-altitude (active) flight, and (4) from high-altitude (soaring) flight. Low-altitude flights involved almost constant wing beating with brief periods of gliding and usually occurred below 30 m altitude. Soaring flights usually took place at altitudes well above 30 m. Hunting methods are described in Results.

Strike data--Each time an attempt at prey capture was observed, the time, grid location, vegetation type, hunting method, and success were recorded. The bird's subsequent activity (prey eaten at point of capture, prey returned to nest, or continued search) was also noted.

All data were numerically coded and recorded in a form compatible with machine processing. Additional observations, such as weather conditions and unusual activities, were logged in a field notebook.

After the observation period, rodent populations were surveyed to determine their species composition and relative size throughout the study area. Rodents were sampled with snap-trap lines of 10 traps each and an intertrap distance of 10 m. Traps were baited with rolled oats and peanut butter and were checked morning and evening for 3 days. The trapping period was divided into "trap-nights" and "trap-days." Traplines which did not accumulate at least 20 trap-nights and 20 trap-days in 3 days (due to sprung traps or missing bait) were run an additional 24 hrs. After that time, the data were discarded if 20 trap-nights and -days had not been accumulated. Traplines were

placed throughout the study area in all vegetation types. Fifty-eight lines were set in 1974 and 15 were set in 1975.

Traplines were effective in sampling all rodents except pocket gophers and ground squirrels. On 31 May 1975, gopher populations were surveyed by counting mounds which had accumulated since snowmelt. Mounds were counted on 0.1-ha circular plots, four of which were located at random within each of 11 sampled fields. Ground squirrels were sparsely and unevenly distributed in the range and were difficult to survey. Their presence was recorded whenever they were observed. Lagomorphs were essentially absent from the study area. Only one, a mountain cottontail (Sylvilagus nuttalli), was sighted in the juniper forest. No lagomorph remains were found in or near the hawks' nests.

Estimates of the density of vegetative cover were made in selected fields throughout the study area. The method was a simplified point-quadrat technique (Greig-Smith 1964, Kershaw 1964). A 1-m<sup>2</sup> wooden frame was laced with string, forming a 5x5 grid of sample points with an interpoint distance of 20 cm. At each sampling station in a field, the grid was held above the vegetation and the number of points whose vertical projection intercepted vegetation before reaching the ground was visually determined. Twenty sampling stations were located at random within each of 14 fields. The percentage of sample points which intercepted vegetation provided an estimate of cover density. An estimate of variance was calculated by comparing the results obtained at each of the 20 sampling stations per field.

## RESULTS

During the 4-wk observation periods in both years, only the adult male hawks hunted. Their mates and young fed exclusively on prey brought to the nest areas by the males. These observations contradict those of Cameron (1914) and Angell (1969) who witnessed hunting behavior by both sexes of nesting Ferruginous Hawks. During the fifth week of observations in 1975, when the young were less than 1 wk from fledging age, the adult female captured her own prey for the first time. However, the female apparently restricted its hunting activities to the immediate vicinity of the nest and did not forage with the male.

### Timing of Foraging Activity

Both males spent the majority of each day away from the nest sites, although they differed in the timing of this activity (Fig. 3). During this time, the birds foraged, interacted with other birds, transported prey items from the hunting areas to the nests, and explored their ranges. Foraging activity occurred throughout the day, as indicated by the frequencies of prey capture by both hawks (Fig. 4). Males 1 and 2 differed somewhat in the timing of their catches. However, they were remarkably similar in their average daily capture rates:  $8.7 \pm 2.0$  and  $9.0 \pm 1.5$  prey items per day for Males 1 and 2, respectively.

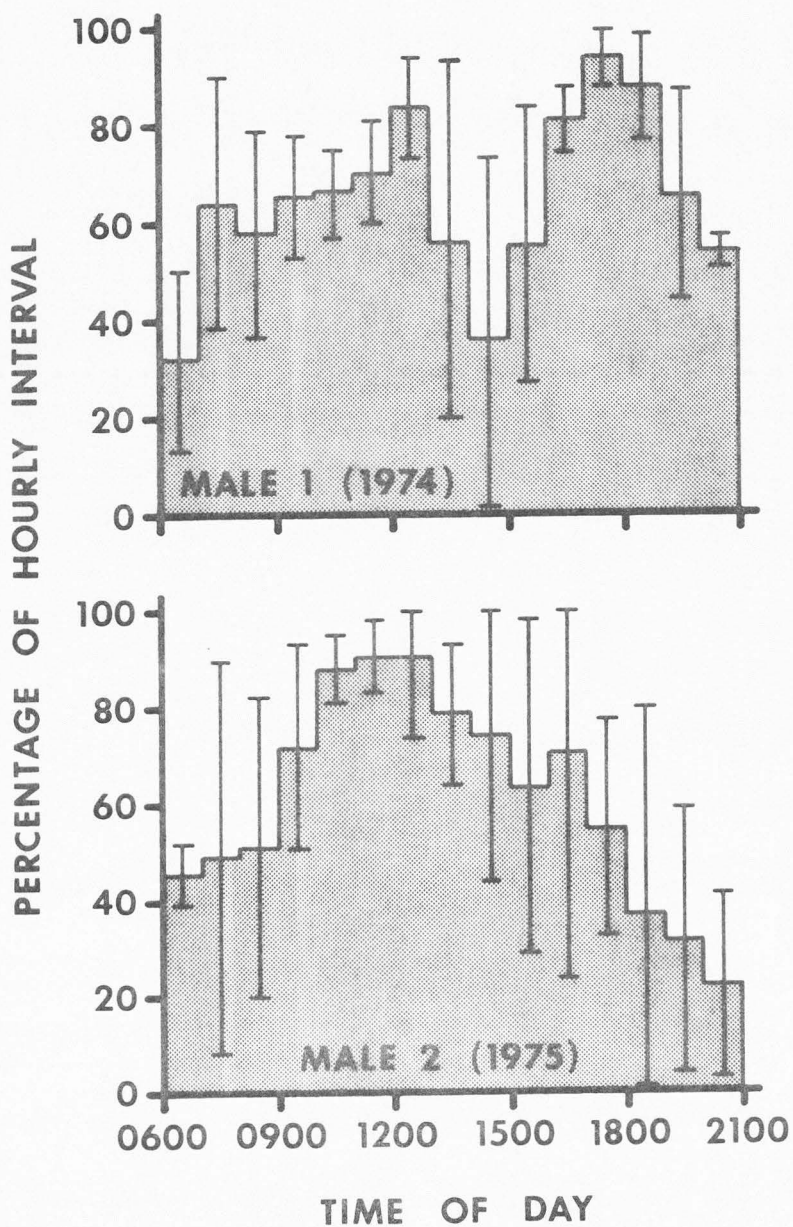


Fig. 3. Activity periods of Males 1 and 2 expressed as the percentage of each hourly interval spent away from the vicinity of the nest. Means  $\pm$  SD were calculated from weekly samples.

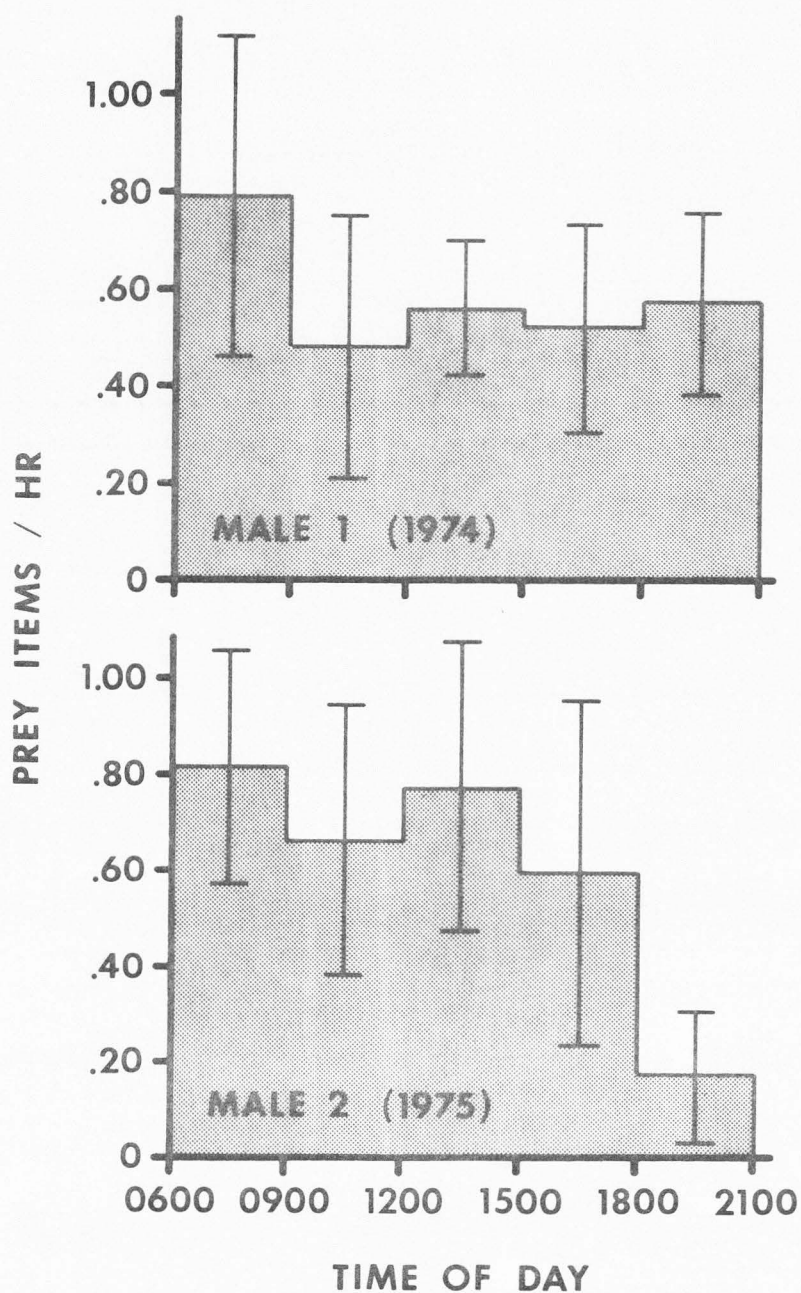


Fig. 4. Average number of prey captured by Males 1 and 2 throughout the day. Includes captures that were directly observed as well as those inferred when additional prey were brought to the nests. Data have been averaged over 3-hr intervals. Means  $\pm$  SD were calculated from weekly samples.



### Hunting Methods

In two years, the hawks made a total of 808 observed attempts to capture prey. These strikes have been grouped under four hunting methods, which were distinguished by the position of the bird at the initiation of the strike.

#### Hunting from a perch

Both males almost always used wooden fence posts as hunting perches. Male 2 occasionally hunted from telephone poles. Other potential perches (abandoned buildings and farm machinery, scattered trees and shrubs) were largely ignored. Both birds regularly perched on juniper trees near their nests but were rarely seen to hunt there, despite the presence of prey as revealed by trapping.

When attempting to capture a detected prey item, a hawk would leave its perch with one or more shallow wing beats, glide for a distance at altitudes often less than 1 m, and strike with the feet, usually raising a cloud of dust upon impact. The distance between perch and prey varied from less than 10 m to more than 100 m. If the strike was unsuccessful, the bird often flew directly to another perch after the brief impact. Successful strikes were marked by an abrupt stop, which occasionally sent the hawk sprawling in the dirt.

#### Hunting from the ground

The hawks probably hunted from the ground only in places where they previously had detected a rodent at the entrance to its burrow. The strike distance was often less than 1 m.

When hunting from the ground, a hawk either sat with its belly in contact with the dirt or stood, usually with its body in a near-horizontal posture. The bird seldom moved. Its attention seemed to be focused upon the entrance to a particular burrow. The hawk struck by suddenly lunging at the prey with its feet.

#### Hunting from low flight

Strikes from low-altitude flight were of two types: those initiated from normal, forward flight and those initiated from stationary, hovering flight. Male 1 infrequently hovered at low altitude, but Male 2 often used this technique, hovering for several seconds before vertically dropping upon its prey.

Strikes from forward flight were more common than were those from a hover. Prey animals directly beneath the flying hawk evoked a near-vertical dive and an apparent hard impact. Usually, however, the descent toward prey was at less than  $45^\circ$ , and a short, low-level glide often preceded the actual strike. After unsuccessful strikes, the hawk usually continued its flight without landing. A prey capture always brought the bird to an immediate halt.

#### Hunting from high flight

High-altitude flights were those greater than 30 m above the ground. However, most such flights were at altitudes greater than 100 m. High-altitude strikes differed from other strikes in that more time elapsed between detection and attempted capture of the prey item. At high altitudes, a hawk may strike only at the most vulnerable prey.

Most high-altitude strikes were initiated from stationary, hovering flight. The vertical descent was usually slow, as the hawk drifted on partially-folded wings. The bird often hovered briefly at intermediate levels in its descent, perhaps reacting to movements of its prey, and occasionally abandoned the attempt while still at high altitude. The final phase of the descent was usually near vertical, but occasionally the hawk glided a few meters at low level before impact.

#### Success Rates

In two seasons, I witnessed 808 strikes, of which 16.6 percent were successful (Table 1). Males 1 and 2 were 14.8 and 18.7 percent successful, respectively, a difference which was not very significant (chi-square test;  $P = 0.15$ ). In some cases, success rate varied significantly with the hunting method used (Table 1).

In 1974, hunting from the ground was the most successful technique. Two likely reasons for this were the very short striking distance involved and the fact that the bird's attention was apparently focused upon a particular prey individual. In 1975, ground hunting was also relatively successful, but the sample size was too small to be meaningful.

In both years, hunting from a perch was the least successful technique. The low success was probably due to the longer striking range and to the need for rapid acceleration from a stationary position. The technique requires relatively little energy expenditure, however, which may explain its frequent use. This possibility will be examined in greater detail later.

Table 1. Outcome of all observed strikes grouped by hunting method. In calculating success rate, strikes of unknown success were omitted from the total.

Bird and Year	Hunting Method	Number of Strikes				Success Rate (%)
		Total	Successful	Unsuccessful	Unknown	
Male 1 (1974)	Ground	81	21	59	1	26.2 a*
	Perch	178	16	157	5	9.2 b
	Low Flight	120	14	96	10	12.7 c
	High Flight	51	10	38	3	20.8 c
	Subtotal	430	61	350	19	14.8
Male 2 (1975)	Ground	14	3	11	0	21.4 a
	Perch	106	11	93	2	10.6 a
	Low Flight	108	18	84	6	17.6 c
	High Flight	150	36	108	6	25.0 c
	Subtotal	378	68	296	14	18.7
TOTAL		808	129	646	33	16.6

\*Letters denote results of comparisons made by chi-square test: 'a' and 'b' are significantly different at the 1 percent level, 'a' and 'c' are different at the 5 percent level, 'b' and 'c' are different at the 10 percent level. Categories that were not different at the 10 percent level share the same letter and were combined in further comparisons (e.g., in 1975, the combined perch and ground sample was tested against the combined flight sample). No comparisons were made between years.

Because strikes from high altitude probably were attempted only on the most vulnerable prey, one might expect the rate of success from high altitude to be greater than that from low altitude, where strikes may have been immediate responses to the prey stimulus. In both years, the relative success rates for high and low flight tended to support this hypothesis, but the differences were not significant (Table 1).

### Foraging Patterns

#### Distribution of searching time

In each year, the distribution of searching time over a bird's range was determined by tabulating all position records (taken at 2-min intervals) from the time the hawk left the vicinity of its nest until the bird either captured a prey item, returned without prey, or was lost to view. If the bird captured one prey item, ate it, and continued to hunt without returning to the nest, the next search effort was recorded as beginning at the place of capture of the first prey, after that item had been consumed.

In 1974 and 1975, 1,916 and 1,637 position records, respectively, were classified as searching. The distribution of searching time by each hawk is shown in Figs. 5 and 6. In each year, one grid square received a disproportionate amount of the bird's total searching time. In 1974, Male 1 spent 48.6 percent of its time in square J-6 and spent no more than 5.7 percent of its time in any other square (Fig. 5). In 1975, Male 2 spent 36.0 percent of its searching time in E-6 and 8.3 percent or less in other squares (Fig. 6).

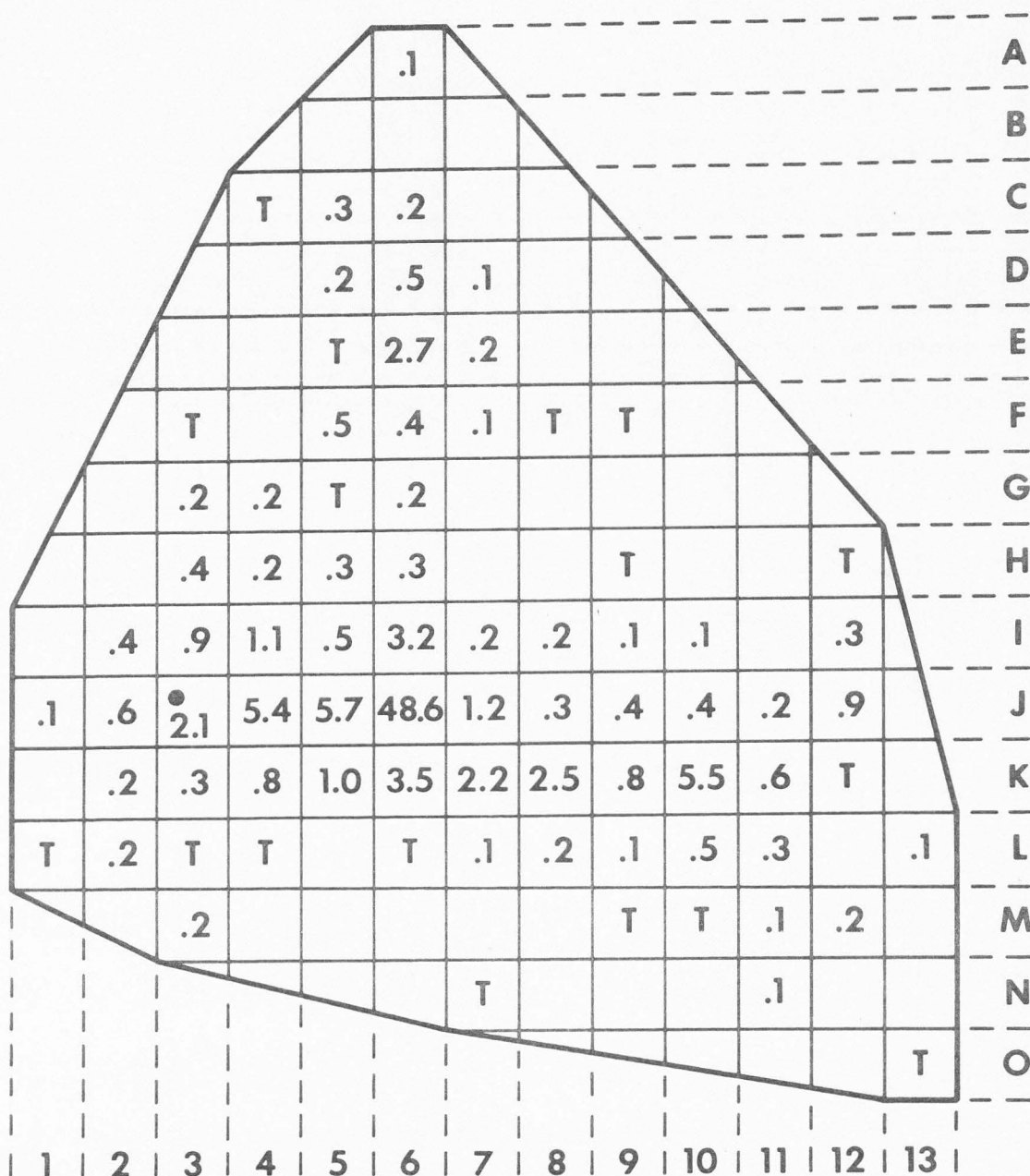


Fig. 5. Percentage of searching time spent by Male 1 (1974) in each grid square ( $n = 1,916$  position records or 64 hrs of observation time). T denotes  $<0.1$  percent. Solid circle marks nest site.

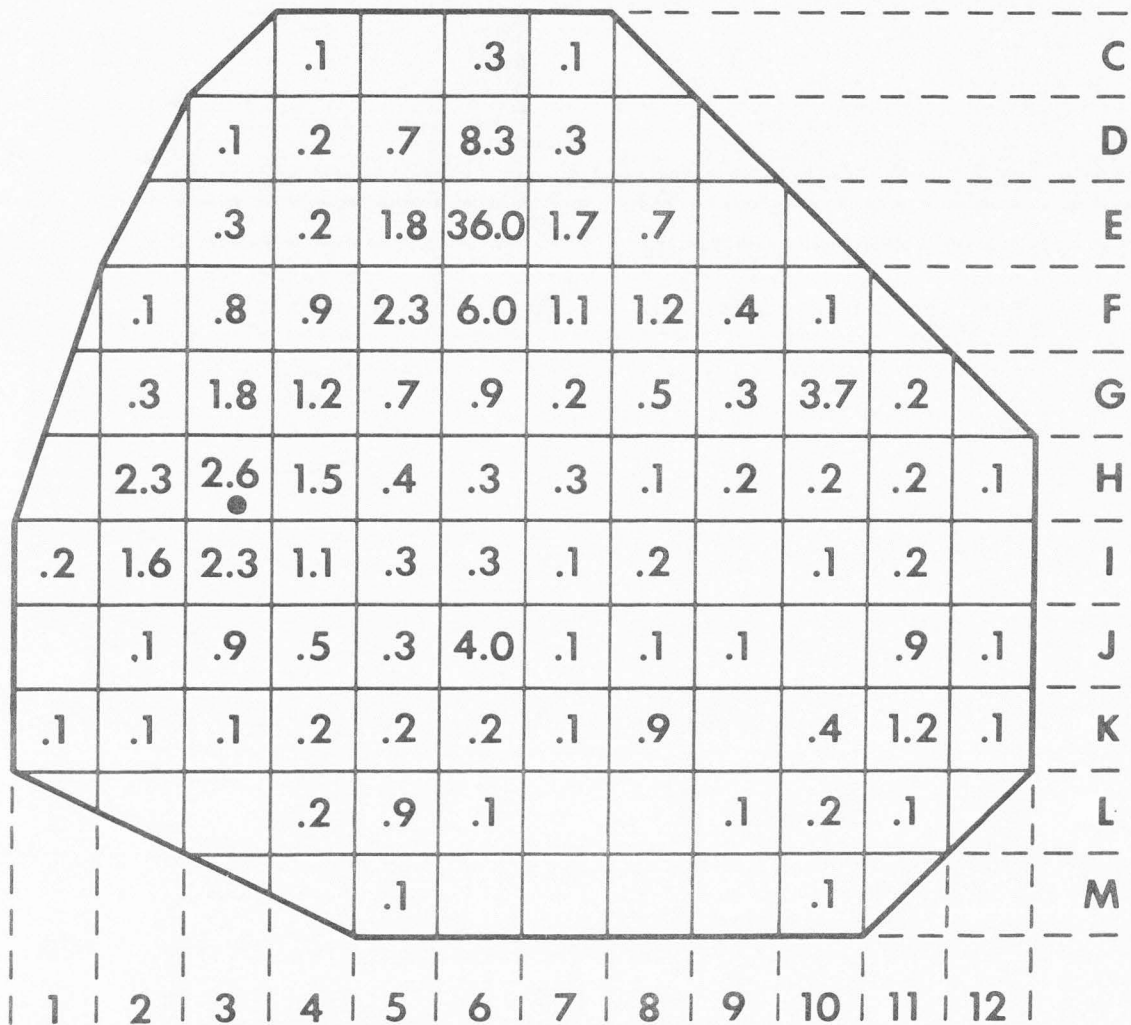


Fig. 6. Percentage of searching time spent by Male 2 (1975) in each grid square ( $n = 1,637$  position records or 55 hrs of observation time). Solid circle marks nest site.

### Distribution of observed strikes

In 1974 and 1975, I observed 430 and 378 attempts at prey capture, respectively. More than half of the strikes in each year were concentrated in one grid square, J-6 in 1974 and E-6 in 1975 (Figs. 7 and 8).

The search distributions (Figs. 5 and 6) and their respective strike distributions (Figs. 7 and 8) were highly correlated. The linear correlation coefficients ( $r$ ) for 1974 and 1975 were 0.99 and 0.98, respectively. By eliminating the data from the most influential square in each year (J-6 in 1974 and E-6 in 1975), the correlation coefficients were reduced to 0.81 and 0.83, respectively, which were still highly significant ( $P < 0.001$ ). Because the search and strike distributions were so highly correlated, I have used them interchangeably as indicators of the hawks' foraging patterns.

### Tests of randomness in foraging patterns

Before I examine factors influencing the foraging patterns of the hawks, the assumption that the birds did not forage at random over their ranges must be tested. I shall use the 1974 data as an example.

If searching time were randomly distributed over the entire range, one would expect the recorded frequency of sighting the hawk in each grid square to approximate a Poisson distribution around the overall mean number of sightings per square. If one uses only those squares in which Male 1 was recorded (Fig. 5), the mean number of sightings per square was 24.6 (i.e., 1,916/78). The expected (Poisson) and observed frequency distributions were significantly different



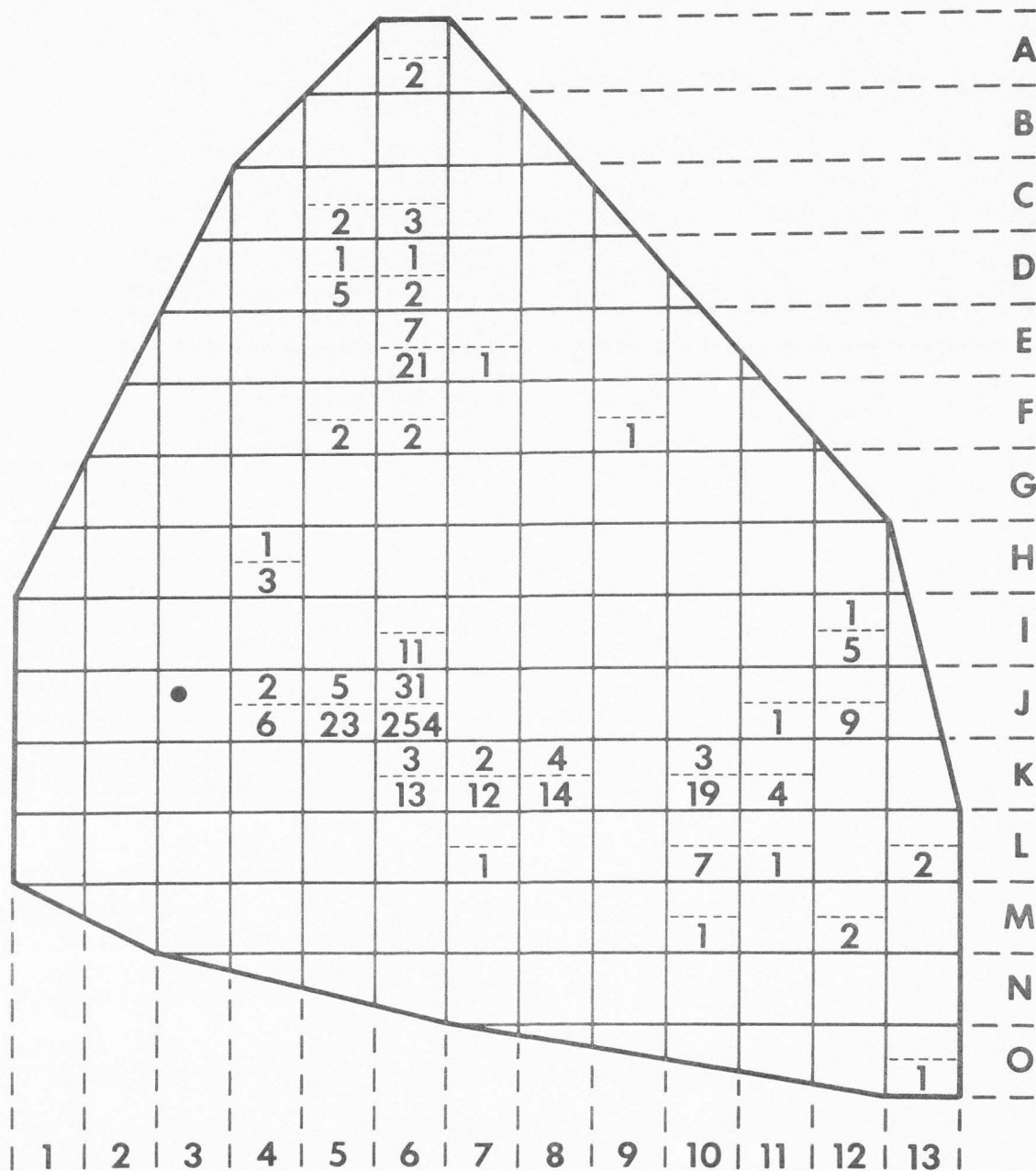


Fig. 7. Distribution of observed strikes ( $n = 430$ ) by Male 1 (1974). In each square, upper figure denotes number of successful strikes and lower figure denotes total number of strikes. Solid circle marks nest site.



(Goodness-of-fit test;  $P < 0.001$ ). Only 10 grid squares were used more than the mean, whereas 68 were used less.

Because the bird had a center of activities at the nest site, a random distribution of range use might result in a bivariate normal distribution of recorded positions centered at the nest. Rather than calculating the whole expected distribution (the observed pattern of use was obviously skewed to the east), I computed the expected univariate normal distribution of all records within a belt, three squares wide, extending from the nest to the eastern boundary of the range (rows I, J, and K; columns 3 through 12). When the expected and observed distributions were compared, the difference was highly significant (Goodness-of-fit test;  $P < 0.001$ ).

An analysis of Male 2's foraging pattern yielded similar results. Thus, the hawks' foraging efforts were neither randomly distributed throughout their ranges nor normally distributed around their nests. The birds must have been highly selective in their choice of hunting sites and in the amount of searching time expended in each.

### Factors Affecting Foraging Patterns

#### Effect of vegetation type

To determine whether or not each hawk was selective in the types of vegetation in which it hunted, I compared the number of strikes in each vegetation type with the number of strikes expected on the basis of the area of each type in the bird's range. In both years, the differences were highly significant (chi-square test;  $P < 0.001$ ). The method of Neu et al. (1974) was then used to find out which specific

cover types were significantly over- or under-used. Availability and use of vegetation types were significantly different in every case ( $P < 0.05$ ).

Males 1 and 2 were very similar in their use of vegetation types (Fig. 9). Both birds hunted in bare ground and pasture areas significantly more than expected and hunted in grass-shrub, grass or grain, old field, juniper, and rush-grass areas significantly less than expected. The two birds differed only in their use of alfalfa fields. Male 1 showed a significant under-use of such areas, whereas Male 2 showed the opposite. This contradictory result was due almost entirely to Male 2's heavy use of the alfalfa field in grid square E-6. Probable reasons for this behavior by Male 2 are discussed later.

#### Effect of prey distribution

Ferruginous Hawks are diurnal foragers. Because of this, I had originally intended to use a trap-day index to rodent populations and to ignore trap-night captures. But most traplines (80 percent) caught nothing during the day. In addition, prey remains collected during the observation periods showed that the hawks caught rodent species during the day which the traplines captured only at night. Apparently, all rodents in the study area were at least occasionally active diurnally, although some were not vulnerable to trapping at that time, perhaps because they were not feeding.

All snap-trapped rodents were weighed and identified as to species. The numbers, species, and weights in grams (mean  $\pm$  SD) of

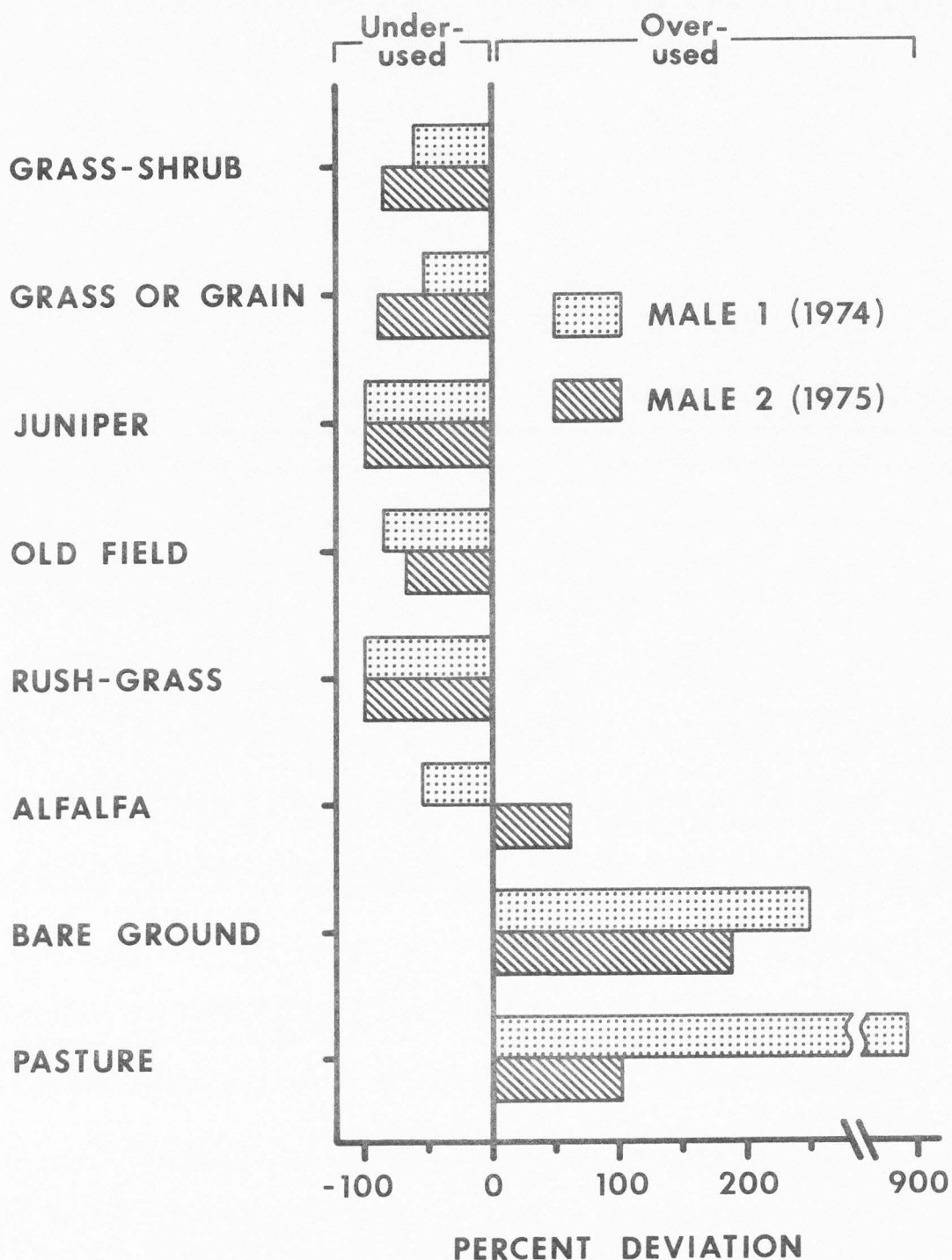


Fig. 9. Deviation from expected use of vegetation types. Expected use, based on area of each type, is represented by the vertical line. Observed use is based on number of strikes. Deviations are expressed as a percentage of the expected level of use. All deviations are significant at the 5 percent level.

rodents captured in traplines were: 314 Peromyscus maniculatus ( $20.23 \pm 4.68$ ), 26 Eutamias minimus ( $32.65 \pm 3.61$ ), 4 Perognathus parvus ( $18.00 \pm 2.16$ ), 4 Microtus montanus ( $41.00 \pm 10.23$ ), 3 Dipodomys ordi ( $49.67 \pm 11.68$ ), 2 Eutamias dorsalis ( $52.50 \pm 2.12$ ), and 1 Spermophilus townsendi (146.0). A trap index was calculated for each trapline by summing the weight of animals caught per trap-night with that caught per trap-day, which produced an index based on biomass per 24-hr trapping period. Traplines run in 1974 and 1975 were combined because differences within years were greater than those between years.

Within each vegetation type, and even within individual fields, trap indices were extremely variable (Fig. 10). Only the rush-grass and juniper vegetation types differed significantly in their trap indices ( $P < 0.05$ ). Thus the significant differences in use of vegetation types by the hawks could not be explained on the basis of trap indices alone.

In May 1975, mounds made by northern pocket gophers (Thomomys talpoides) were counted on 0.1-ha plots placed at random within selected fields (Table 2). Only alfalfa fields contained appreciable gopher populations.

Townsend's ground squirrels (Spermophilus townsendi) could not be counted directly but were noted wherever they were observed. Ground squirrels were apparently present only in areas which were relatively free from disturbance, especially from plowing. Squirrels seemed to be most abundant in the grass-shrub vegetation type but were also observed in old fields, pastures, and crested wheatgrass fields.

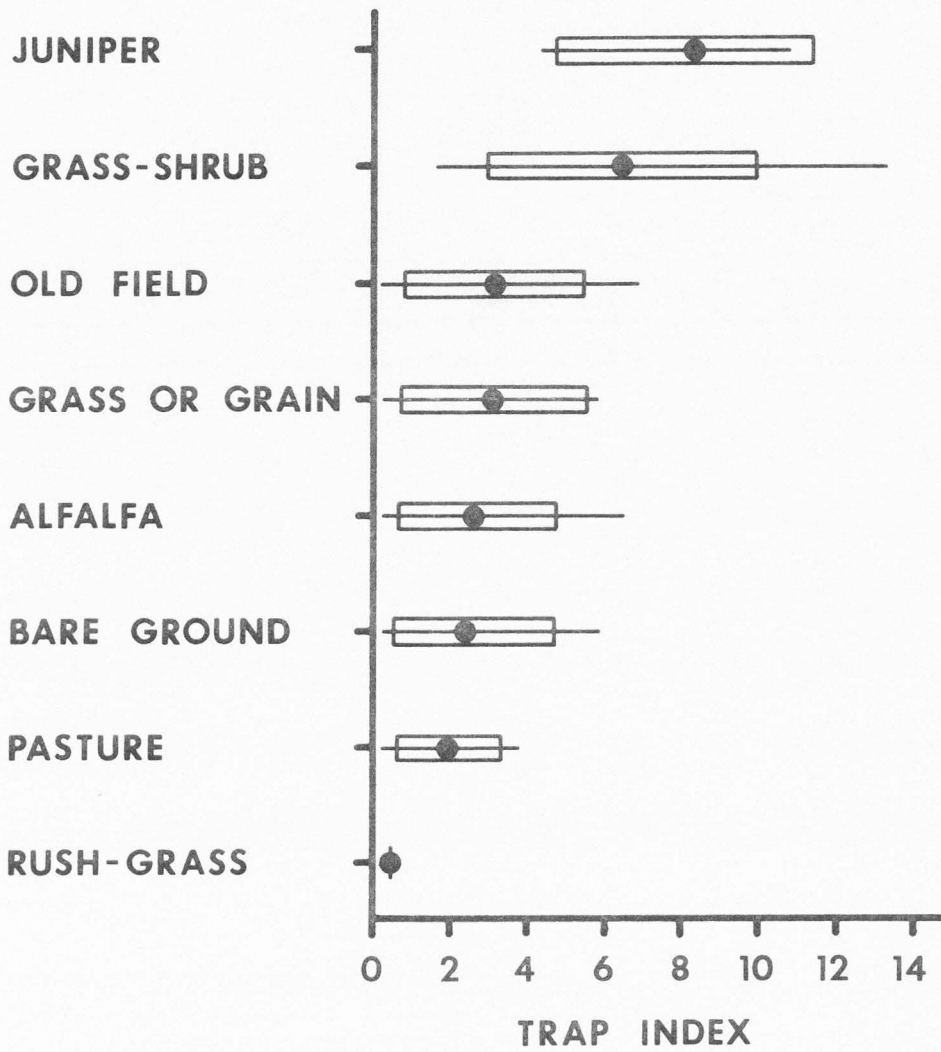


Fig. 10. Relationship between rodent biomass index and vegetation type. Solid circles, lines, and boxes denote means, ranges, and standard deviations of trap indices, respectively.

Table 2. Mean number of pocket gopher mounds in 0.1-ha circular plots. Four plots were located at random within each field.

Grid Location	Vegetation Type	Number of Mounds per Plot (Mean $\pm$ SD)
E-6	Alfalfa	80.0 $\pm$ 29.2
F-5	Alfalfa	44.8 $\pm$ 43.5
J-8	Alfalfa	8.3 $\pm$ 10.7
K-7	Pasture	1.0 $\pm$ 2.0
G-5	Bare ground	0 $\pm$ 0
D-6, E-6	Bare ground	0 $\pm$ 0
F-5	Grass	0 $\pm$ 0
H-4	Grass-shrub	0 $\pm$ 0
K-11	Pasture	0 $\pm$ 0
J-2	Juniper	0 $\pm$ 0
K-4	Old field	0 $\pm$ 0



My sampling procedures were generally inadequate to show significant differences in rodent biomass among vegetation types. In spite of this, the data suggest that the juniper, grass-shrub, and alfalfa cover types were highest in prey biomass. However, all three of these cover types were significantly under-used by Male 1, and the first two types were significantly under-used by Male 2 (Fig. 9). The lack of a direct relationship between rodent biomass and use by foraging hawks suggests that some factor other than prey density was critical to the birds' choice of hunting sites.

#### Effect of cover density

The density of vegetative cover in 14 sampled fields was measured by a simplified point-quadrat method. In the remainder of the study area, the density of vegetation was estimated visually. Fields were grouped into four cover-density classes which generally coincided with groupings of the eight vegetation types. The four density classes were: dense (>75 percent covered), moderate (20 to 75 percent covered), sparse (5 to 20 percent covered), and absent (<5 percent covered). Table 3 gives the results of measurements in the 14 fields, grouped into their respective cover-density classes. A low coefficient of variation (SD/mean) indicates homogeneous cover, whereas a high coefficient of variation indicates patchy cover.

In each year, a chi-square test of the relative availability (based on area) versus use (based on number of strikes) of cover-density classes gave highly significant results ( $P < 0.001$ ). Further testing by the method of Neu et al. (1974) showed that, in both years,

Table 3. Density of vegetative cover in measured fields.

Cover-density Class	Grid Location	Vegetation Type	Cover Density (%) (Mean $\pm$ SD)	SD/Mean
Dense	J-9	Alfalfa	94.6 $\pm$ 11.7	0.124
	K-9	Alfalfa	94.6 $\pm$ 8.3	0.088
Moderate	K-10*	Alfalfa	71.2 $\pm$ 33.1	0.465
	K-6*	Alfalfa	49.4 $\pm$ 16.9	0.342
	K-8	Old field	23.2 $\pm$ 18.1	0.780
Sparse	F-5	Grass	15.2 $\pm$ 9.1	0.598
	D-5	Grass-shrub	13.6 $\pm$ 15.4	1.132
	K-5*	Pasture	12.8 $\pm$ 9.5	0.742
	D-5	Grass-shrub	10.8 $\pm$ 18.2	1.685
	J-4	Grass-shrub	9.8 $\pm$ 12.3	1.256
Absent	J-6	Pasture	4.2 $\pm$ 3.6	0.857
	K-11	Pasture	0.0 $\pm$ 0.0	---
	J-6	Bare ground	0.0 $\pm$ 0.0	---
	D-6, E-6	Bare ground	0.0 $\pm$ 0.0	---

\*Fields measured particularly because the density of their vegetation appeared appreciably different from the average density for that vegetation type.

the "absent" cover class was used by the hawks significantly more than expected by chance ( $P < 0.05$ ). All other density classes were used less than expected ( $P < 0.05$ ), except for the "dense" class in 1975 which was significantly over-used ( $P < 0.05$ ) (Fig. 11).

#### Effect of previous experience

If previous experience had an important influence on a predator's foraging patterns, and if prey items were clumped in their distribution, one would expect to see the predator return directly to sites of previous captures. This behavior was exhibited by both Ferruginous Hawks.

On 40 occasions in 1974 and on 55 occasions in 1975, I observed enough of the next hunting effort after a prey capture to determine whether or not a hawk returned to the site of its last success (Table 4). In all, 52 percent of captures were followed by a direct return to the same grid square on the next hunting effort and 14 percent were followed by a direct return to one of the eight grid squares immediately adjacent to the first. Twelve percent of captures were followed by an indirect return (i.e., return to the site of capture following an unsuccessful hunt in another grid square). In only 23 percent of subsequent hunts was the previous capture site ignored.

Often I was able to observe where the hawks caught prey on consecutive hunting forays and thus I was able to compare the sites of capture of one prey and the next. In 1974 and 1975, I witnessed a total of 64 such pairs of prey captures (Table 5). In 38 of these, the second prey item was caught in the same grid square as the first. In 14, the second prey was taken in a square adjacent to the first.

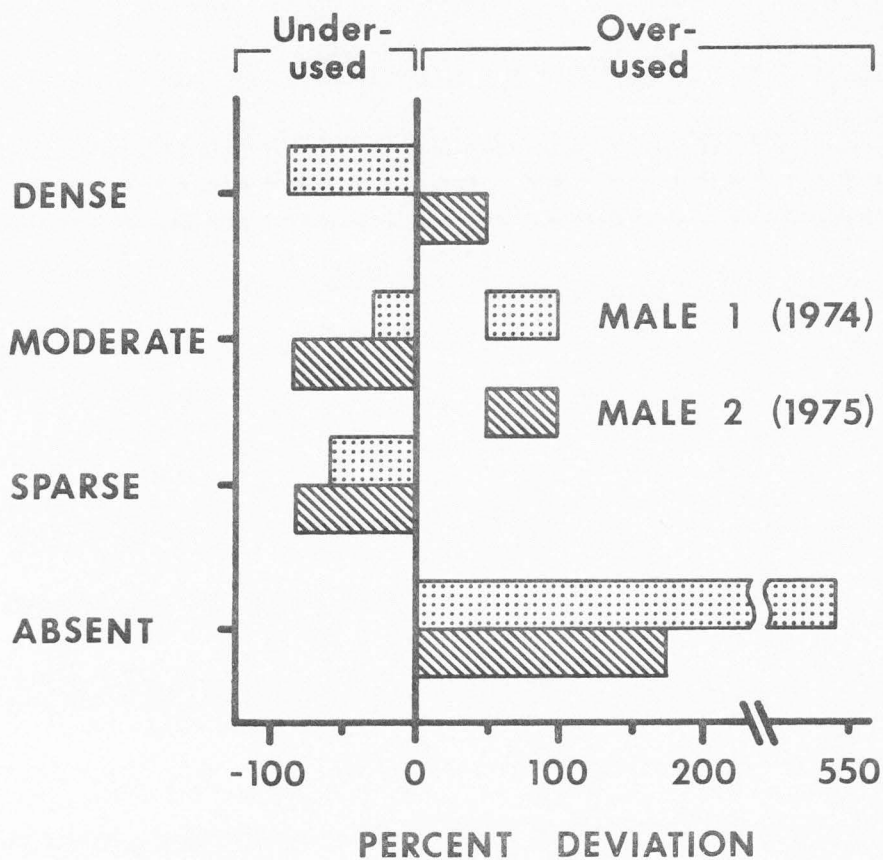


Fig. 11. Deviation from expected use of cover-density classes. Expected use, based on area of each class, is represented by the vertical line. Observed use is based on number of strikes. Deviations are expressed as a percentage of the expected level of use. All deviations are significant at the 5 percent level.

Table 4. Frequency of return on the next hunting foray to the grid square in which the hawk made its last prey capture (percentages in parentheses).

Bird and Year	Sample Size	Direct Return to Same Square	Direct Return to Adjacent Square	Indirect Return to Same Square	No Return
Male 1 (1974)	40	20 (50)	6 (15)	4 (10)	10 (25)
Male 2 (1975)	55	29 (53)	7 (13)	7 (13)	12 (22)
TOTAL	95	49 (52)	13 (14)	11 (12)	22 (23)

Table 5. Location of consecutive prey captures by Ferruginous Hawks (percentages in parentheses).

Bird and Year	Number of Consecutive Captures Observed	Grid Square in Which Second Capture Was Made		
		Same	Adjacent	Other
Male 1 (1974)	32	20 (62)	6 (19)	6 (19)
Male 2 (1975)	32	18 (56)	8 (25)	6 (19)
TOTAL	64	38 (59)	14 (22)	12 (19)

In only 12 was the second prey captured in a grid square more than one square removed from the first. Thus, there was a 59 percent chance that a prey capture observed at random would be followed by a capture in the same field on the hawk's next hunting foray.

As expected, the frequency of direct return to the site of the last capture was highest for the birds' major hunting sites (i.e., grid squares J-6 in 1974 and E-6 in 1975). These frequencies were 80 (16/20) and 65 (22/34) percent, respectively. However, the frequencies of direct return to all other grid squares (19 percent in 1974 and 33 percent in 1975) were significantly higher than would be expected by chance, given that each grid square occupied less than 1 percent of a bird's total range (chi-square test;  $P < 0.001$ ).

These data show that there was a high probability that a hawk would return to the site of a previous capture, suggesting that immediate prior experience influenced the birds' choice of hunting sites.

#### Effect of Previous Experience Upon Use of Hunting Methods

To determine whether or not a hawk's use of hunting methods was influenced by its immediate prior experience, I compared the hunting method used by a bird at the initiation of a hunting foray with that used to capture its previous prey item (Table 6). The hawks always started to hunt by flying from their nest sites toward the hunting areas. Therefore every hunting effort started from flight, although the hawks may not have been attentive to prey until a particular hunting site was reached. For that reason, I used a hawk's first

Table 6. Comparison between the hunting method used by each hawk at the beginning of a new hunting foray and the method by which the bird's last prey item was captured.

Bird and Year	Previous Capture Made From:	Next Strike Made From:				Total
		Ground	Perch	Low Flight	High Flight	
Male 1 (1974)	Ground	4	5	0	0	9
	Perch	2	5	3	1	11
	Low Flight	2	3	6	1	12
	High Flight	1	0	2	3	6
	Total	9	13	11	5	38
Male 2 (1975)	Ground	0	0	1	1	2
	Perch	0	6	2	0	8
	Low Flight	0	2	3	2	7
	High Flight	0	1	2	16	19
	Total	0	9	8	19	36



attempted strike as an indication of its initial hunting method. Some errors probably were made when a bird hunted for some time, by more than one method, without striking. However, I believe that this bias was small.

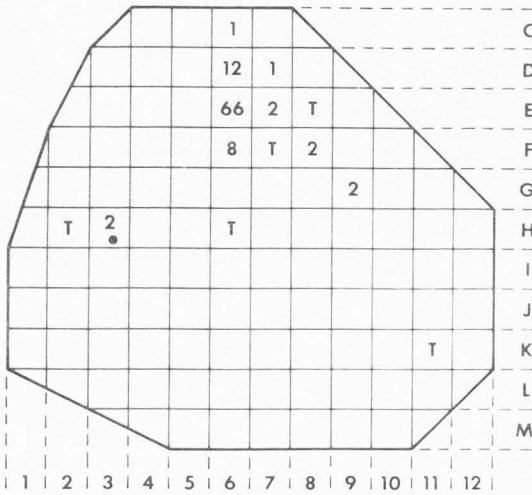
Males 1 and 2 initiated 47.4 percent (18/38) and 69.5 percent (25/36) of their hunting forays, respectively, with the same method that had been successful on their previous hunts. Under the null hypothesis that the use of each hunting method was equally likely, each hawk's preference for the method that was successful previously was highly significant (chi-square tests;  $P < 0.005$ ).

#### Switching of Major Hunting Areas

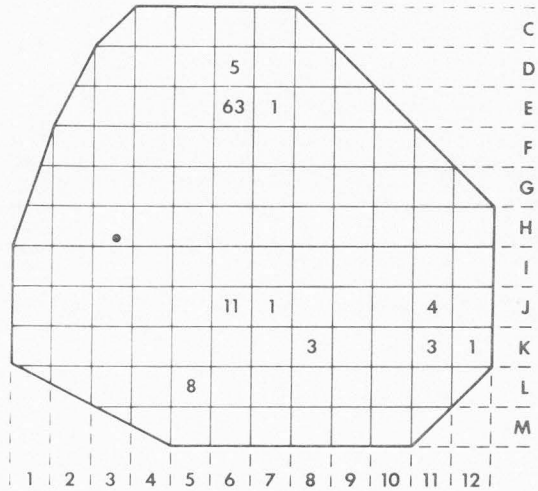
The time Male 1 spent foraging in various parts of its home range did not change appreciably during the 4-wk observation period in 1974. Grid square J-6 was consistently its most important hunting area. Male 2, however, showed a definite shift in its foraging pattern, which is why observations continued for a fifth week in 1975.

Figure 12 shows, by weeks, the spatial distribution of observed strikes by Male 2, expressed as a percentage of total strikes seen each week. The shift in emphasis from grid square E-6 to square J-6 is unmistakable. Data from weeks 1 and 2 were combined because in both weeks square E-6 was most important and square J-6 was not used. In week 5, one strike occurred in square F-12, outside the range boundary which had been determined from the hawk's movements during weeks 1 through 4.

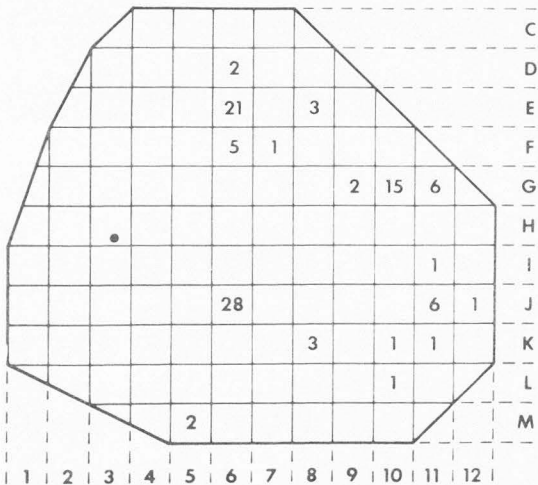
WEEKS 1 AND 2 (N=213)



WEEK 3 (N=76)



WEEK 4 (N=89)



WEEK 5 (N=43)

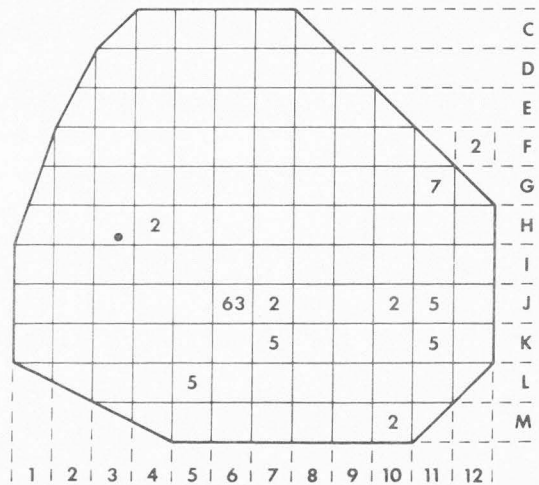


Fig. 12. Strikes by Male 2 (1975) in each grid square expressed as a percentage of total strikes seen each week. T denotes <0.5 percent. Solid circle marks nest site.

During weeks 1 through 3, square E-6 was the hawk's most important hunting site, receiving more than half of all strikes seen each week. By week 5, however, square J-6 was receiving 63 percent of observed strikes. Week 4 was a period of transition. That week the hawk hunted more widely, concentrating no more than 28 percent of its strikes in any one square. This was evidently a time of active investigation and testing of new hunting sites.

Although grid square E-6 received a large part of the hawk's hunting time through week 4, the bird's rate of prey capture in that square fell off after week 3 (Fig. 13). The hawk was apparently forced to switch hunting areas due to declining success in its old hunting site. Possible reasons for the decline will be discussed later.

#### Effect of Time and Energy Budgets

##### Upon Choice of Hunting Method

This section examines the extent to which each hunting method was used by the hawks and possible reasons for the differences in use that were observed. I have assumed that prey animals caught by the hawks were of a constant average size which was not related to method of capture, and that all prey were equally palatable and nutritious to the birds.

##### Time budgets

During a hawk's foraging efforts, its method of hunting was recorded at 2-min intervals. Strikes and prey captures were logged according to the bird's hunting technique. From these data, the

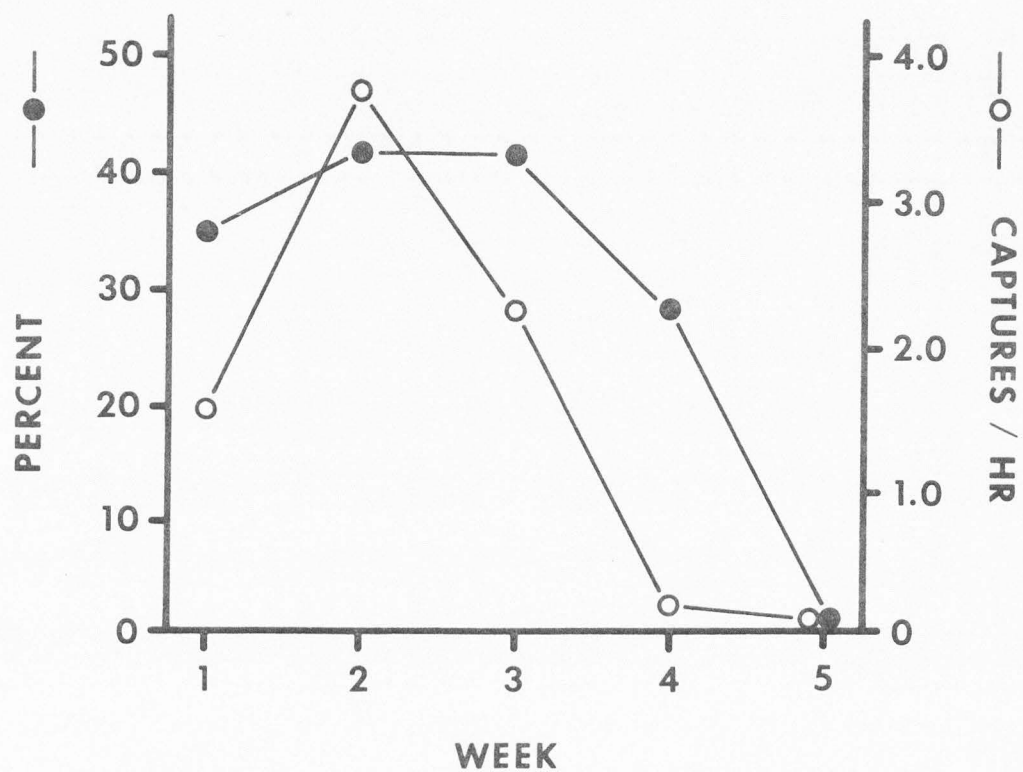


Fig. 13. Comparison between the percentage of foraging time (solid circles) spent by Male 2 in grid square E-6 and its capture rate (hollow circles) in that square.

proportion of the time that a bird used each hunting method was calculated, along with its striking rate and capture rate using each method (Table 7). Both hawks were remarkably similar in their striking rates and capture rates. Both averaged nearly seven strikes per hour and captured about one prey item per hour.

The amount of time a hawk was observed hunting by each method is believed to be an unbiased sample of the bird's total use of each method, with the single exception of the high-altitude technique. Hunting efforts from the ground, from a perch, and from low-altitude flight were easily observed. High-altitude flights, however, were often difficult to follow. Therefore, the amount of time each hawk was observed in high flight (Table 7) probably underestimates its actual use of that technique relative to the other hunting methods.

In each year, hunting from low flight produced the highest capture rate, yet it was one of the methods used least often. In contrast, hunting from a perch in each year produced one of the lowest capture rates but was a commonly used technique. In each year, high-altitude flight was observed far more than expected on the basis of the capture rates it produced, despite the fact that time spent soaring was already underestimated relative to the other techniques. Thus, the birds' use of hunting methods was not directly related to their capture rates using each technique.

#### Energy budgets

Logically, the next step in this analysis is the conversion of the birds' capture rates by each hunting method (Table 7) to estimates

Table 7. Rates of striking and rates of prey capture by Ferruginous Hawks using four hunting methods. Means and standard deviations were calculated from weekly values.

Bird and Year	Hunting Method	Proportion of Time Spent (Mean $\pm$ SD)	Total No. of Strikes	No. of Strikes per Hour (Mean $\pm$ SD)	Total No. of Captures	No. of Captures per Hour (Mean $\pm$ SD)
Male 1 (1974)	Ground	0.27 $\pm$ 0.07	81	4.82 $\pm$ 1.38	21	1.34 $\pm$ 1.09
	Perch	0.31 $\pm$ 0.13	178	9.61 $\pm$ 5.50	16	0.84 $\pm$ 1.11
	Low flight	0.16 $\pm$ 0.05	120	12.29 $\pm$ 2.25	14	1.43 $\pm$ 0.51
	High flight	0.27 $\pm$ 0.11	51	3.19 $\pm$ 1.90	10	0.65 $\pm$ 0.27
	Total	1.00 $\pm$ 0.00	430	6.86 $\pm$ 1.88	61	0.94 $\pm$ 0.43
Male 2 (1975)	Ground	0.04 $\pm$ 0.01	14	5.93 $\pm$ 2.84	3	1.30 $\pm$ 0.99
	Perch	0.27 $\pm$ 0.13	106	7.12 $\pm$ 0.44	11	0.82 $\pm$ 0.30
	Low flight	0.19 $\pm$ 0.07	108	10.95 $\pm$ 1.14	18	1.87 $\pm$ 0.51
	High flight	0.50 $\pm$ 0.13	150	5.28 $\pm$ 2.06	36	1.26 $\pm$ 0.72
	Total	1.00 $\pm$ 0.00	378	6.99 $\pm$ 0.77	68	1.27 $\pm$ 0.55

of the catch per unit of energy expended by the hawks. To make the conversion, estimates of the rate of energy expenditure by each hunting method are needed. Measurements of metabolic rate in flight and at rest have been made for several birds, but data on the energetic cost of other activities are lacking (King 1974:55). Therefore, an analysis of energy budgets of foraging hawks is necessarily speculative.

Existing data suggest that metabolic rate in flight averages 12 to 13 times the standard (basal) metabolic rate and 6 to 7 times the resting metabolic rate in non-passerine birds, independent of body size or flight behavior (Table 8). Standard metabolic rate (SMR) is the minimal level of heat production. It is usually measured with the animal at rest, in thermoneutral surroundings, and in a post-absorptive state (Gessaman 1973:3). In contrast, the resting metabolic rate (RMR) is more loosely defined as the metabolic rate of an animal which is at rest but which is not post-absorptive. Thus the RMR includes the SMR as well as heat liberated in digestion of food and in thermoregulation (Gessaman 1973:3).

The Ferruginous Hawks in low (active) flight probably expended energy at a rate about 12.5 times the SMR. Therefore, I shall use 12.5 as an index to the energetic cost of hunting from low-altitude flight. Sit-and-wait hunting, either from a perch or from the ground, required occasional bursts of activity (strikes) together with longer periods of waiting. Each hawk averaged less than seven strikes per hour using this method. The rate of energy expenditure probably was only slightly greater than the resting metabolic rate. Because the RMR is about twice the standard level, the cost of sit-and-wait

Table 8. Ratio of metabolic rate in flight to either the standard or resting metabolic rate in non-passerine birds.

Species	Flight/ Standard	Flight/ Resting	Authority
Hummingbirds			
<u>Calypte anna</u>		5.5	Pearson (1950)
<u>Selasphorus sasin</u>		6	"
<u>Calypte costae</u>	12	7	Lasiewski (1963)
<u>Eulampis jugularis</u>	13.2		Hainsworth & Wolf (1969)
<u>Amazilia fimbriata</u>	14		Berger & Hart (1972)
Budgerigar			
<u>Melopsittacus undulatus</u>	12.8		Tucker (1968)
"		6	Tucker (1966)
Pigeon			
<u>Columba livia</u>	13.4	8	LeFebvre (1964)
Laughing Gull			
<u>Larus atricilla</u>	11-14		Tucker (1969)
American Kestrel			
<u>Falco sparverius</u>	12.5		J. A. Gessaman*

\*Personal communication, Utah State University, July 1975.



hunting was probably 3 to 4 times the SMR. I shall use 3.5 as an index to the cost of hunting from perch or ground. Finally, hunting from soaring (passive) flight required less energy than did hunting from low flight but more energy than did sit-and-wait hunting. I have assumed a cost index of 8.0, midway between those of low flight and of sit-and-wait hunting.

Capture rates were converted to estimates of the number of captures per unit cost by dividing each rate by its respective energy-cost index. These captures/cost ratios were then compared with the amount of time each hawk spent hunting by each hunting method (Fig. 14). In both years, the hawks' average use of sit-and-wait hunting and of hunting from low flight was roughly proportional to the captures/cost ratios for those methods. Thus the birds tended to spend more time hunting by their more efficient technique. In that way, each hawk probably maintained a higher benefit/cost relationship than it could by using those hunting methods at random. The amount of time each hawk spent hunting from high-altitude flight was about twice that expected on the basis of the catch/cost ratio for that technique. This suggests that soaring was not exclusively a hunting technique but that it had an additional purpose unrelated to food gathering.

The hawks were highly variable in their foraging behavior. This variability complicated the analysis and resulted in a lack of statistical confidence in the results. However, the validity of the conclusions is strongly supported by three separate lines of evidence. First, results were identical for the two hawks. Each bird's average use of sit-and-wait hunting and of hunting from low-altitude flight was

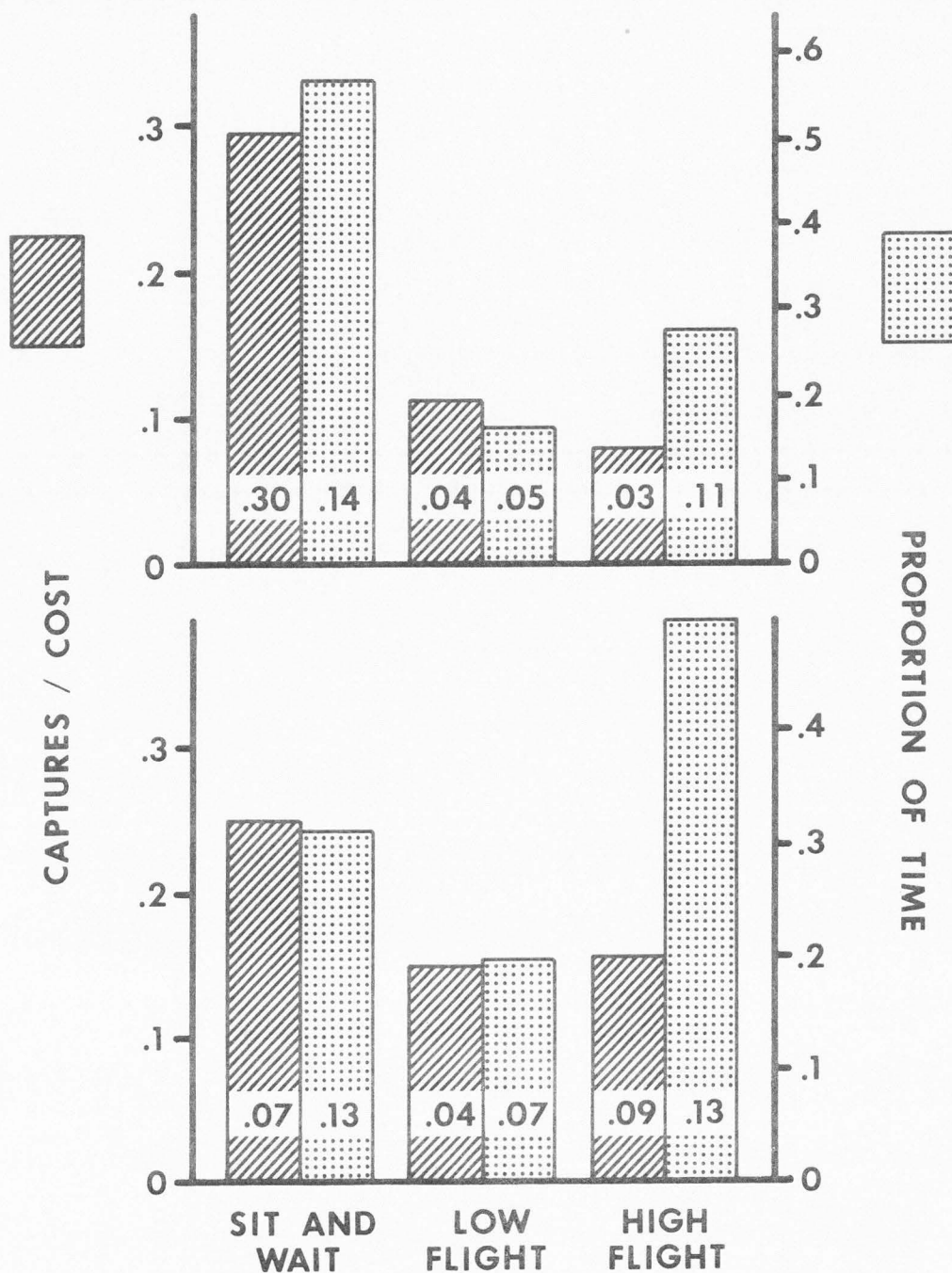


Fig. 14. Comparison between the estimated captures/cost ratio for each hunting method and the proportion of a hawk's hunting time devoted to each method. Due to their similar costs, hunting from a perch and from the ground were combined into the sit-and-wait technique. Means  $\pm$  SD were calculated from weekly samples.

proportional to the benefit it derived; and each hawk spent more than twice as much time soaring than expected from that method's benefit/cost value. Second, results were consistent with the predictions of simple laboratory studies and theoretical papers. Finally, results did not change when potentially biased data were excluded from the calculations. For example, search records for some hours of the day could have been biased by the inclusion of time spent in non-foraging activities that could not be distinguished from foraging. This likely occurred in the observed use of mid-day soaring flights, as I mentioned previously. To check for inconsistencies in the results concerning the use of sit-and-wait hunting and of hunting from low-altitude flight, I calculated captures/cost ratios and levels of use of those methods using only data gathered between the hours of 0600 and 0900, when foraging undoubtedly was the hawks' highest-priority activity and when the biases caused by the inclusion of non-foraging time were minimal. The results were nearly identical to those shown earlier (Fig. 14), except that the use of high-altitude flight, and the captures/cost ratio for that hunting method, were both zero at that time of day. Therefore, the observed use of sit-and-wait hunting and of hunting from low-altitude flight was not the result of biases in the classification of the hawks' activities.

This study clearly demonstrates the need for caution in projecting simple behavioral principles onto a field situation. The overall average of the hawks' behavior conformed very well to that expected from laboratory studies. However, a knowledge of general principles

alone would not have been useful in predicting the birds' foraging behavior during any particular hour or even during any particular day.

It was an interesting result that both hawks' use of hunting methods was proportional to their captures/cost ratios for those methods even in the morning when the birds' hunger was probably greatest. At that time of day, one might expect that the birds would hunt exclusively by their most efficient technique until they had captured enough prey to alleviate their hunger; but that was not the case. For the same reason, one would expect the hunter to eat the first prey item it captured in the morning, rather than to take that food to the nest. However, observations showed that the first prey item of the morning, or at least part of that item, was usually carried to the nest.

The results of this analysis are fairly insensitive to variations in the assumed cost indices for each hunting method. The figure for the cost of low-altitude flight (12.5 times the standard metabolic rate) is the best available estimate from studies of avian energetics (Table 8). In 1975, the estimated cost of sit-and-wait hunting could be as high as 5.5 x SMR and the cost of high-altitude flight as low as 5.8 x SMR without altering the conclusions. The 1974 results are even less sensitive to changes in the cost indices.

Effect of Energy Budgets Upon Choice  
of Hunting Sites

In the previous section, I showed that the hunting method which the hawks used most frequently was energetically their most efficient technique. One could hypothesize that the birds' choice of major hunting sites also should depend upon benefit/cost relationships.

Using the cost indices derived in the last section, in addition to the number of hours the hawks devoted to each hunting method and the number of recorded captures, I calculated a catch/cost figure for each bird's major hunting site (i.e., grid square J-6 in 1974 and E-6 in 1975) and for the rest of each hawk's range exclusive of the main hunting area. For 1974 and 1975, respectively, the captures/cost estimate at each major hunting area was  $0.24 \pm 0.19$  and  $0.27 \pm 0.18$ , whereas ratios for the remainder of each range were  $0.12 \pm 0.04$  and  $0.10 \pm 0.05$ . The latter figures may be biased by the inclusion of costly travel between hunting sites. Thus, there is support for the idea that both hawks spent the majority of their foraging time in the hunting areas which gave them high catch/cost ratios relative to the rest of their ranges, but the evidence is not strong. Furthermore, the data were insufficient to derive a benefit/cost ranking of secondary hunting sites.

## DISCUSSION

### Success Rates

Success rates, often called predatory efficiencies, have been determined for only a few raptors and the results have varied widely. On the average, the Ferruginous Hawks were successful in securing prey in 16.6 percent of attempted strikes, but their success rates varied significantly with hunting method. Lambert (1943) and Ueoka and Koplín (1973) calculated an average success of 89 and 82 percent, respectively, for American Ospreys (Pandion haliaetus). An average rate of 7.6 percent was determined by Rudebeck (1951) for four European raptors (Accipiter nisus, Falco columbarius, F. peregrinus, and Haliaeetus albicilla). Collopy (1973) recorded a 51 percent success rate for American Kestrels (Falco sparverius). He also showed that Kestrels were more successful when hunting from a perch than from a hover. Clark (1975:35-36) found that Short-eared Owls (Asio flammeus) were successful in about 20 percent of their strikes. Apparently, species which feed largely on small birds and mammals have relatively low success rates, whereas those which feed mainly on insects (e.g., the Kestrel) have relatively high success. The fish-eating Osprey has the highest known success rate of any raptor.

### Use of Hunting Methods

The amount of time the hawks devoted to each hunting method was related neither to their success rates (successful strikes/total

strikes) nor to their capture rates (captures/time) by those methods. In each year, for example, hunting from a perch was one of the most common techniques despite low success rates and low capture rates. In contrast, hunting from low-altitude flight was relatively uncommon despite high capture rates and moderate success rates.

Most empirical and theoretical studies of foraging behavior have concentrated on species which use only one foraging technique (e.g., Royama 1970, Smith and Dawkins 1971, Baker 1974, MacArthur and Pianka 1966, Schoener 1971). In those studies, foraging time budgets could be assumed to be equivalent to energy budgets, and the number of captures per unit time could be used as an indicator of the benefit to the predator per unit of energetic cost. In the present study, however, the hawks used several hunting methods which differed in the rate of energy expenditure. For that reason, capture rates could not be used as an estimate of benefit per unit cost and a captures/cost index was devised.

With the exception of the high-altitude technique, the hawks' use of hunting methods was proportional to the number of captures they made per unit of energy they expended. Both birds spent more time hunting by the sit-and-wait technique, either from a perch or from the ground, than by the low-flight method. Their benefit/cost ratios were also higher by the former method. The hawks therefore achieved greater foraging efficiency than they could by using each hunting technique at random.

Both hawks spent far more time in high-altitude (soaring) flight than expected on the basis of their captures/cost ratios for that

hunting method. A likely reason is that soaring was not exclusively a hunting technique but had some additional function unrelated to food gathering. For example, mid-day soaring flights by desert raptors could have a thermoregulatory function (Madsen 1930: cited by Dawson and Schmidt-Nielsen 1964). The flights could also function as territorial displays. Alternatively, soaring may be a form of exploratory behavior. According to Barnett (1963:15-33), an animal explores in order to alter the intensity or variety of the stimuli it receives. The specific function of exploration by a hawk may be to familiarize the bird with its surroundings and to enable it to monitor changes within its home range. In any case, if soaring had a function in addition to foraging, its use by the hawks should have been greater than that expected from prey captures alone. In each year, less than half of the hawks' use of high-altitude flight could be predicted from the captures/cost ratio. Although some early works describe soaring as the typical hunting technique for a Buteo (e.g., Bent 1937:291), this study suggests that the soaring hawk is more likely to be engaged in some activity other than foraging.

#### Use of Hunting Sites

Both hawks hunted in the "pasture" and "bare ground" vegetation types far more than expected by chance. The birds under-used all other vegetation types with the exception of the "alfalfa" type in 1975. Their use of vegetation types for hunting apparently was not related to prey density. However, both hawks showed a strong selection for areas that were free of vegetative cover, although Male 2 also



hunted in "dense" cover more than expected by chance. The birds' previous experience with specific hunting sites was also an important influence upon their food-searching patterns, in that each hawk returned directly to the site of its last prey capture on more than half of its searching efforts.

The hawks' use of hunting sites was apparently related to the benefit/cost ratio resulting from that use. In each year, for example, the grid square which was the hawk's major hunting area provided a higher number of captures per unit cost than the average value for the remainder of the bird's foraging range. Other studies have shown similar results. Great Tits (Parus major) in an aviary learned to concentrate their food-searching efforts in profitable areas (Smith and Dawkins 1971, Smith and Sweatman 1974). In a maze-like experimental tank, Three-spined Sticklebacks (Gasterosteus aculeatus) gradually increased their searching efficiency by reducing visits to areas already scanned and by avoiding parts of the tank which never contained prey (Beukema 1968:109-110). Goss-Custard (1970) showed that Redshanks (Tringa totanus) tended to gather in areas where prey density was highest and where the amount of energy expended per unit of prey biomass collected was least. A similar study by Heatwole (1965) showed that Cattle Egrets (Bubulcus ibis) obtained more food per unit effort when associated with cattle than when foraging alone.

The hawks' strong selection for hunting areas which were free of vegetative cover probably resulted from the birds' frequent use of their most profitable hunting technique, that of sit-and-wait hunting from a perch or from the ground. The hawks may have preferred to hunt

by that method in bare areas because the low viewing angle from the ground or from a low perch would have magnified the concealing effect of any vegetation present. Only the "pasture" and "bare ground" vegetation types were free of concealing cover, which is consistent with the higher-than-expected use of those types by both hawks. Furthermore, the lack of a clear relationship between rodent index and use of areas by the hawks suggests that cover density was a more critical factor in their foraging patterns than was prey density.

In addition to the selection for areas of "absent" cover, Male 2 showed a small but significant selection for the "dense" cover class. This was due almost entirely to the bird's concentration on the alfalfa field in grid square E-6. A likely reason for this intensive use was the large pocket gopher population which the field contained. More gopher mounds were counted there than in any other field measured. Despite the relatively high cover density, gopher mounds were exposed when upthrown soil parted or flattened the surrounding vegetation, making gophers vulnerable to attack from the air. Late in the observation period, however, the diggings were concealed by overhanging vegetation. At that time, the hawk switched its emphasis to other hunting areas with less concealing vegetation. The bird's second major hunting area was the pasture in square J-6 which was used intensively by Male 1 the previous year.

The role of immediate prior experience in the hawks' feeding behavior probably was to reduce the amount of time and energy spent in searching for profitable hunting areas. Other studies have shown that a predator often will return to the site of its last prey capture.

Morris (1954), studying the snail-eating behavior of the Song Thrush (Turdus ericetorum), noticed that after a thrush had broken open and eaten a snail on a nearby "anvil," it usually returned to the area of its last capture and continued its search. Croze (1970) saw a similar pattern in free-living Carrion Crows (Corvus corone). In his observations of wild Great Tits, Tinbergen (1960) noted that a bird, after bringing a prey item to the nest, often flew off in the general direction of its last prey capture. It usually made several flights in a row in the same direction before switching to a new area. Royama (1970) found that prey species brought to the nest were not in random order but in runs of a single prey type. He speculated that the tits paid successive visits to profitable hunting sites. Smith and Sweatman (1974) found that tits were spatially selective in their foraging bouts over short time intervals but that the birds tended to range more widely during longer periods.

Another way in which a predator could reduce the energetic cost of food searching is to use the nearest suitable hunting areas, thereby cutting costly travel time. Both hawks intensively hunted in the patch of pasture vegetation which was closest to their nests (i.e., grid square J-6), with the exception of the pasture in square K-5 which probably was ignored because of its higher-than-average cover density for that vegetation type (Table 3). The birds' use of other vegetation types was more scattered, however, and did not seem to be related to distance from the nests.

In the laboratory, Great Tits learned to search in the same type of feeding site where they previously were successful in securing food

(Krebs et al. 1972). The birds were able to generalize among similar hunting areas without having to acquire first-hand experience with every hunting site available to them. In 1975, the hawk hunted in nearly every patch of pasture available to it but tended to limit its use of the other cover types to specific areas. The bird's favorable experience with certain patches of pasture may have led it to generalize among all similar pieces of habitat as "good" hunting sites.

#### Short-term and Long-term Foraging Efficiency

Each Ferruginous Hawk concentrated more of its foraging time on the hunting method and in the hunting sites which yielded the highest number of prey captures per unit of energy expended. Thus each bird achieved a foraging efficiency appreciably greater than it could attain by using each technique and each area at random. However, neither hawk spent all of its foraging time hunting by its most profitable hunting method nor in its most profitable hunting site. Therefore, neither bird approached its highest potential benefit/cost ratio.

The hawks apparently were under no pressure to optimize their foraging efficiency. The birds were capable of capturing more than enough prey to satisfy their needs in the time that they allotted to foraging. In fact, both hawks spent more than one-third of the average day perched near their nests. Had prey density been lower, the birds may have had to "fine tune" their foraging behavior so as to attain a higher benefit/cost relationship.

The hawks' sacrifice of time and energy in unprofitable areas could have served to increase their long-term foraging efficiency without seriously affecting the satisfaction of their immediate food needs. By continually monitoring the foraging potential of secondary areas, the birds buffered themselves against sudden declines in success at their major hunting sites, such as that experienced by Male 2. The hawks' tendency to explore less-profitable hunting sites probably was reinforced by the occasional prey captures they made in those areas. In the same way, animals that are trained to choose the more rewarding of two alternative stimuli in simple laboratory tests never choose correctly all the time (Sutherland and Mackintosh 1971:409-412). They continue to respond to the less-profitable stimulus at low frequency, probably because they occasionally are rewarded for that response. The maintenance of the tendency to explore in a wild predator may be critical to its survival in a changing environment. By expending energy in secondary areas, the hawks probably achieved greater long-term foraging efficiency, although they may have sacrificed some short-term benefit.

#### Importance of Flexibility of Foraging Behavior

Both hawks exhibited considerable flexibility in their food-searching behavior. They apparently were able to adjust their use of hunting methods and hunting sites to maintain higher benefit/cost ratios than they could attain by chance. Their use of secondary hunting areas also may have contributed to their foraging efficiency by keeping them abreast of changes in the foraging potential of

different portions of their home ranges. The development of such flexible foraging patterns may be critical to the success of predators which must rely for their survival on highly variable small-mammal populations. The behavioral flexibility shown by the hawks indicates that they are well adapted to changeable prey resources.

As man's agricultural practices extend farther into the desert regions where Ferruginous Hawks breed, this flexibility of behavior will become increasingly important to the birds' survival. At least in their foraging behavior, the hawks seem well adapted to cope with changes in their habitat brought about by changes in land-use practices, as long as those practices do not result in the elimination of prey populations. The maintenance of a diversified agriculture may be important to breeding hawks in that it produces a diverse prey resource and insures that prey are available in some part of a bird's range throughout the nesting season. Monoculture could result either in low prey numbers or in low prey availability at the time when plant cover is densest. A simple change in species composition of prey populations, from that of natural habitat, probably would not be detrimental to Ferruginous Hawk populations. The preservation of nesting sites and the protection of the birds themselves probably are more critical to the species' well-being than is the preservation of large tracts of native vegetation.

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