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HUNTING METHODS AND FACTORS AFFECTING THEIR USE BY FERRUGINOUS HAWKS

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Recent theory suggests that a predator's food-searching behavior should be predictable, given that the energetic costs and benefits of its foraging options are known (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Rapport 1971, Pulliam 1974). Efficient foraging patterns should bestow a selective advantage upon the individual and, if heritable, eventually should become widespread within the population. Thus an animal should hunt in profitable areas and select an optimal diet.

Similar predictions can be derived from learning theory which was extant in the psychological literature prior to the development by ecologists of optimal foraging theory. Drawing on earlier studies, Estes (1962) concluded that when confronted with two alternative tasks which offer different rates of reward, laboratory rats divide their time between them in proportion to the reward. Herrnstein (1961) obtained similar results with pigeons. Later, Bitterman (1965) showed that laboratory birds and mammals, when given enough time, learn to concentrate their efforts on the more rewarding task out of proportion to the probability of reinforcement, although they never completely abandon the less rewarding alternative. Other investigators have tended to support Bitterman's conclusions (Sutherland and Mackintosh 1971: 405–409). Probability learning should be viewed as an important proximate influence on foraging patterns of vertebrates, whereas the underlying morphological and physiological adaptations, and the necessary behavioral flexibility, are the products of natural selection.

Recent studies of captive and free-living birds have documented that the spatial distribution of their food-searching efforts is related to the amount of food they can collect per unit of foraging time or energy expended (Heatwole 1965, Goss-Custard 1970, Smith and Dawkins 1971, Smith and Sweatman 1974). It has rarely been noted, however, that many predators hunt with several techniques that vary both in rate of energy expenditure and in rate of return. Most papers equate foraging time with energy expenditure, a simplifying assumption that is valid only for predators who use one foraging method.

This paper describes the hunting methods used by free-living Ferruginous Hawks (*Buteo regalis*), and attempts to analyze the birds' use of those methods in relation to the amount of time and energy expended per prey item captured.

STUDY AREA AND METHODS

The study area was located in Curlew Valley, Idaho, 8 km N of Snowville, Utah (for description, see Wakeley 1978), and consisted of the home ranges of two adult male Ferruginous Hawks. I watched Male 1 in 1974 and Male 2 in 1975. The study area was a patchwork of cultivated fields (alfalfa, wheat, and barley), old fields, and grazing land.

The hawks' hunting activities were observed in 4-week periods during the nestling stage of the nesting season. During those intervals, the males did all of the hunting for their mates and their two (1975) or three (1974) young. Observations were made through a spotting scope from a blind located about 300 m from the nest. The study began on 19 May in 1974 and on 26 May in 1975, when the hawks' nestlings were slightly less than 1 and 2 weeks old, respectively.

During a hawk's foraging bouts, its hunting method was recorded at 2-min intervals until the bird either captured a prey item, returned to the nest site without prey, or was lost to view. Each time an attempt at prey capture was observed, the hawk's hunting method and success were noted. Four hunting methods were recognized, depending on the bird's location when starting a strike: (1) from a perch, (2) from the ground, (3) from low-altitude (active) flight, and (4) from high-altitude (soaring) flight. Low-altitude (usually below 30 m) flights involved nearly constant wing beating with brief periods of gliding. Soaring flights usually took place at altitudes well above 30 m.

RESULTS

HUNTING METHODS

In two years, I saw the hawks make a total of 808 attempts to capture prey. These strikes have been grouped under the four hunting methods.

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 a capture, a hawk would

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

Bird and year	Hunting method	Number of strikes				Success ratio (%)
		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% level, 'a' and 'c' are different at the 5% level, 'b' and 'c' are different at the 10% level. Categories that were not different at the 10% level 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.

leave its perch with one or more shallow wing beats, glide at 1 m or less above the ground, 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. Successful strikes were marked by an abrupt stop, which occasionally sent the hawk sprawling in the dirt with the prey grasped in its talons.

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, as indicated by the short strike distance (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 initiated in two ways: from normal, forward flight and from stationary, hovering flight. Male 1 infrequently hovered at low altitude, but Male 2 often did so, 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°, and a short, low 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 more than 30 m above the ground; 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. 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 end of the descent was usually near vertical, but occasionally the hawk glided a few meters at low level before impact.

SUCCESS RATIO

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

The hawks' use of hunting methods did not seem to be related to the success ratio they attained by them. This finding is true whether the use of a hunting method is measured in

TABLE 2. Rates of striking and rates of prey capture by Ferruginous Hawks using four hunting methods ($n = 63.9$ h of hunting time in 1974 and 54.6 h in 1975). Means and standard deviations were calculated from weekly values.

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

terms of number of strikes (Table 1) or amount of time devoted to it (Table 2). Apparently some factor other than success ratio had a stronger influence upon the birds' choice of hunting methods.

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 apparently was 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 rate of success probably was 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, both in terms of hours spent and strikes made. This possibility will be examined later.

Because strikes from high altitude probably were attempted only on the most vulnerable prey, one might expect the frequency 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 ratios for high and low flight tended to support this hypothesis, but the differences were not significant (Table 1).

CAPTURE RATE

One possible influence upon a hawk's use of hunting methods was its rate of prey capture: that is, the number of prey individuals caught per unit of hunting time. Because prey items could not be identified at the time they were caught, I had to assume that prey animals were of a constant average size that was not related to method of capture, and that all prey were equally palatable and nutritious to the birds. Prey animals ranged in size from the Townsend's ground squirrel (*Spermophilus townsendi*; mean weight 204.5 g) to the deer mouse (*Peromyscus maniculatus*; mean weight 20.2 g) (Wakeley, in press), but I found no indication that hunting methods were selective for particular sizes of prey.

Both hawks were remarkably similar in their striking rates and capture rates using each hunting method (Table 2). 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 2) 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, I observed high-altitude flight 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 by each technique.

TABLE 3. 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			
Calypte anna		5.5	Pearson (1950)
Selasphorus sasin		6	Pearson (1950)
Calypte costae	12	7	Lasiewski (1963)
Eulampis jugularis	13.2		Hainsworth & Wolf (1969)
Amazilia fimbriata	14		Berger & Hart (1972)
Budgerigar			
Melopsittacus undulatus	12.8		Tucker (1968)
Melopsittacus undulatus		6	Tucker (1966)
Pigeon			
Columba livia	13.4	8	LeFebvre (1964)
Laughing Gull			
Larus atricilla	11–14		Tucker (1969)
American Kestrel			
Falco sparverius	12.5		J. A. Gessaman*

* Pers. comm., Utah State University, July 1975.

ENERGY EFFICIENCY

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 3). 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) lasting no more than a few seconds, 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 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. Lacking a better value, 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 capture/cost ratios were then compared with the amount of time each hawk spent hunting by each hunting method (Fig. 1). In both years, the hawks' average uses of sit-and-wait hunting and of hunting from low flight were roughly proportional to the capture/cost ratios for those methods. Thus the birds tended to spend more time hunting by their more efficient method. In that way, each hawk may have maintained a higher benefit/cost relationship than it could by using those hunting methods at random.

The hawks varied greatly in their foraging behavior, which complicated the analysis and resulted in statistically inconclusive 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 proportional to the benefit it derived; and each hawk spent more than twice as much time soaring as expected from that method's benefit/cost value. Second, results were consistent with the predictions of previously cited 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 probably occurred in the observed use of mid-day soaring flights, as 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 capture/cost ratios and levels of use of those methods using only data gathered between the hours of 06:00 and 09:00, when foraging undoubtedly was the hawks' chief 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. 1), except that the use of high-altitude flight, and the capture/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.

These results demonstrate the need for caution in projecting simple behavioral principles onto a field situation. The overall trend of the hawks' behavior conformed 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.

Both hawks' use of hunting methods was proportional to their capture/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 eaten enough to alleviate their hunger; 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, I observed 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 value 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 3). In 1975, the estimated cost of sit-

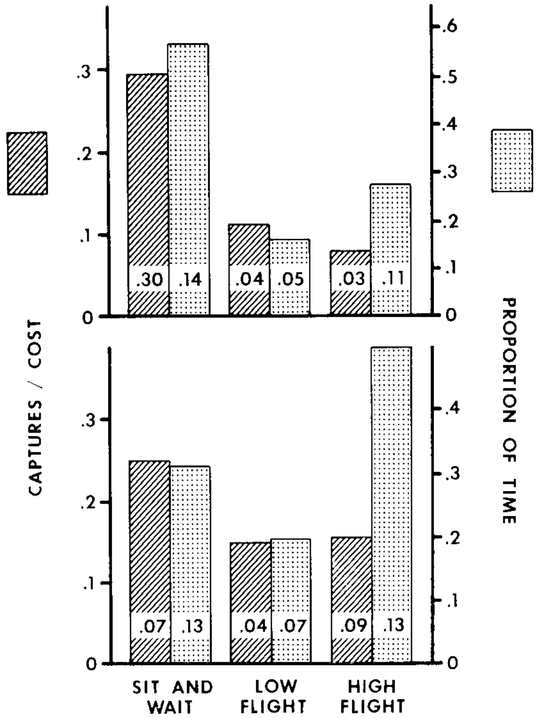

FIGURE 1. Comparison between the estimated capture/cost ratio for each hunting method and the proportion of a hawk's hunting time devoted to each method. Due to their similar costs, hunting from a perch and from the ground were combined into the sit-and-wait technique. Means ± SD were calculated from weekly samples (figure within column is SD).

and-wait hunting could be as high as 5.5 × SMR and the cost of high-altitude flight as low as 5.8 × SMR without altering the conclusions. The 1974 results are even less sensitive to changes in the cost indices.

DISCUSSION

SUCCESS RATIOS

Success ratios, 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% of attempted strikes, but their success varied significantly with hunting method. Lambert (1943) and Ueoka and Koplin (1973) calculated an average success of 89 and 82%, respectively, for Ospreys (*Pandion haliaetus*). An average rate of 7.6% was determined by Rudebeck (1951) for four European raptors (*Accipiter nisus*, *Falco columbarius*, *F. peregrinus*, and *Haliaeetus albicilla*). Collopy (1973) recorded a 51% success ratio 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% of their strikes. Apparently, species which feed largely on small birds and mammals have relatively low success ratios, whereas those which feed mainly on insects (e.g., the kestrel) have relatively high success. The fish-eating Osprey has the highest known success ratio of any raptor.

USE OF HUNTING METHODS

The amount of time the hawks devoted to each hunting method was related neither to to their success ratios (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 ratios and low capture rates. In contrast, hunting from low-altitude flight was relatively uncommon despite high capture rates and moderate success ratios.

With the exception of the high-altitude technique, the hawks' use of hunting methods apparently was related 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, 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.

Male 1 had a home range 26% larger than that of Male 2 (Wakeley 1978), and had a larger brood to feed, circumstances that may have affected its foraging behavior. Male 1 spent nearly one-third of its foraging time on its most efficient technique, whereas Male 2 devoted less than one-quarter to its best hunting method. One might conclude that Male 1, having to cope with a greater energy demand, was compelled to adopt a more efficient mode of foraging. However, both birds spent more than one-third of the average 15-h day perched near their nests where I never saw them hunt (Wakeley, in press). Apparently there was ample time in a day to gather the prey they required and neither bird needed to optimize its foraging efforts.

This study indicates that considerations of energy efficiency were important in the hawks' use of hunting methods, but the evidence is inconclusive. A critical assumption is that hunting methods were not selective for prey of a certain size. If one technique consistently provided larger-than-average prey individuals, the energy calculations could be biased. Unfortunately, that assumption could not be evaluated. Furthermore, the conclusions are weakened by the lack of measurements of the energetic cost of various activities by free-living birds.

Both hawks spent far more time in high-altitude (soaring) flight than expected on the basis of their capture/cost ratios for that hunting method. Soaring probably was not exclusively a method of hunting but had some additional function. 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. In any case, if soaring had a function in addition to foraging, its use by 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 capture/cost ratio. Although some early works describe soaring as the typical hunting technique for a *Buteo* (e.g., Bent 1937:291), my study suggests that a soaring hawk is more likely to be engaged in some activity other than foraging.

SUMMARY

Hunting methods used by two adult male Ferruginous Hawks in southern Idaho were studied during the nesting seasons of 1974 and 1975. The birds hunted (1) from a perch, (2) from the ground, (3) from low-altitude (active) flight, and (4) from high-altitude (soaring) flight. The hawks captured prey on 16.6% of their strikes, but their success ratios varied significantly with hunting method. Each bird struck about seven times per hour of hunting time and caught about one prey item per hour. The hawks' use of hunting methods seemed to be related to the number of captures they made per unit of energy expended.

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