EFFECT OF VEGETATIVE COVER ON FORAGING SITE SELECTION BY SWAINSON'S HAWK

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ABSTRACT.—Foraging bouts of male Swainson's Hawks (*Buteo swainsoni*) were observed using radio-telemetry to determine the effect of plant cover on the selection of foraging sites. Home ranges consisted of varying amounts of cultivated and uncultivated habitats. Cultivated fields were the most abundant and they supported large amounts of prey, but were not hunted until crop harvest reduced the density of their plant canopy. A negative correlation between estimates of plant cover and foraging suggested that habitat differences such as vegetative cover were of greater importance than prey density in the selection of hunting sites. A correlation between foraging and prey biomass after it had been adjusted for vegetative concealment indicated that models relating prey abundance with raptor foraging should consider the effect of such a habitat difference on the availability of a hunting site's food supply.

The efficient selection of hunting sites is critical for foraging birds. Because physical features vary among habitats, it is logical to assume that these differences would influence the availability of food and a bird's hunting success. Discussions of avian foraging have begun to emphasize the importance of such factors as plant cover, distance of travel, and weather in the selection process (Goss-Custard 1970, Royama 1970, Hassell 1971, Smith and Dawkins 1971, Zach and Falls 1976a, b, Kushlan 1979, Eiserer 1980, Fitzpatrick 1980). Although descriptions of habitat use by foraging raptors are limited, they indicate that, for species such as hawks and owls, plant cover and weather may have a greater effect than prey abundance on the suitability of their foraging habitats (Southern and Lowe 1968, Wakeley 1978, Stinson 1980). If this is true, predator-prey models that assume a direct relationship between hunting and prey density (MacArthur and Pianka 1966, Emlen 1968, Simons and Alcock 1971, Alcock 1973, Poole 1974) would need to be reconsidered when applied to raptors.

I report here the results of a study I conducted to determine the effect of plant cover on the availability of Swainson's Hawk (*Buteo swainsoni*) prey. I predicted that, if plant cover limited the productivity of potential hunting sites, a reduction in a habitat's cover would increase its use by foraging hawks. Birds nesting in farmland of southeastern Washington were ideal to study because crop harvest reduced plant cover in large portions of their nesting habitat. Using estimates of plant cover together with estimates of prey density, I compared the distribution of foraging efforts before and after harvest for a possible correlation between a habitat's use and its vegetative cover.

STUDY AREA

The study was conducted in two areas within Whitman County, Washington. Area 1 was located about 5 km southwest of Pullman and included most of the Washington State University Experimental Dairy Farm. It contained the home ranges of three nesting male Swainson's Hawks, designated Males 1, 2, and 3. Male 1 was followed in 1978 and Males 2 and 3 were followed in 1979. Area 2 was located approximately 11 km southwest of Pullman and included the home range of one nesting male Swainson's Hawk, designated Male 4. This bird was followed in both 1978 and 1979.

I observed foraging during the nestling stage of the nesting season when males provided most of the food for brooding females and developing young. In addition to their mates, Males 1, 2, 3, 4 (1978), and 4 (1979) supported broods at hatching of 4, 3, 2, 2, and 2 young, respectively. Nests of Males 1 and 4 were constructed 10.2 and 9.7 m above the ground in black locust (*Robinia pseudoacacia*) trees and those of Males 2 and 3 were located 8.8 and 4.8 m up in cherry (*Prunus* sp.) and hawthorn (*Crataegus douglasii*) trees, respectively.

This area of Washington has been classified as a shrub-steppe region (Daubenmire 1970) and has open, rolling terrain, currently being used for wheat and pea cultivation. I selected the two areas so that the presumed ranges of males contained different amounts of land being cultivated and planted in either of these crops. Harvesting of pea fields began after 20 July and was completed by the first week of

TABLE 1. Average cover and frequency of plant species occurring within the six vegetation types observed in the home ranges of male Swainson's Hawks nesting in southeastern Washington.

Vegetation type	Plant species	Frequency (percent)	Coverage (percent)
Fallow field	—	—	—
Wheat field	wheat (*Triticum* sp.)	100	93.5
Pea field	pea (*Pisum* sp.)	100	86.6
Mustard field	mustard (*Brassica* sp.)	100	83.7
Pastureland	*Medicago sativa*	100	28.3
	Bromus inermis	100	24.4
	Lithophragma parviflora	4	0.1
	Capsella bursa-pastorus	3	1.2
	Thalaspi sp.	5	0.8
	Lomatium triternatum	10	0.2
	Bromus tectorum	24	0.6
	Phleum pratense	12	4.6
	Crepis sp.	24	0.6
	Erodium cicutarium	20	0.5
Eyebrow	*Poa pratensis*	82	21.1
	Symphoricarpos albus	42	3.6
	Tragapogon sp.	36	1.1
	Bromus inermis	72	6.4
	Bromus tectorum	10	0.2
	Achillea millifolium	10	1.7
	Rosa woodsii	10	0.7
	Verbascum thapsis	14	1.3

August. Wheat harvest began in August and continued through the rest of the nesting season.

METHODS

I used radio-telemetry to locate foraging males. Birds were trapped using a mist-net (18 × 3 m, mesh size 10 cm) and a stuffed Great Horned Owl (*Bubo virginianus*). I placed the net within 50 m of the nest tree with the owl approximately 1 m from the net and 1 m above ground. Trapped males were fitted with tail-mounted radio-transmitters developed by Cedar Creek Bioelectronics Laboratory. Transmitting frequencies ranged from 151.000 to 151.990 mHz. A Wildlife Materials, Inc. multiple-channel receiver and a four-element Yagi antenna were used to locate birds. I attached radios to the inner two rectrices with silk thread and model-airplane glue.

Males were observed to determine home range areas and the distribution of food searches. For each foraging bout, I recorded the location and type of habitat hunted at 5-min intervals. Each male was monitored for a 4-h period, either from 08:00 to 12:00 or from 13:00 to 17:00. Observation periods were alternated so that each week I obtained a complete 8-h foraging schedule for each bird. Each male was observed a total of 48 h over a six-week period from about 25 June to 15 August.

I recorded locations on U.S.G.S. 7.5-min topographic maps and determined home range area from sightings farthest from the nest site. I divided home ranges into six possible habitat types, which were described using the canopy-coverage method of Daubenmire (1959) (Table 1). I drew the areas covered by each vegetation type on the same topographic maps using visual estimates made in the field and calculated the areas of home ranges and habitat types on a weight basis by cutting out the ranges and weighing the pieces on an analytical balance. All vegetation types, except pasture and "eyebrows," had been plowed before the start of the study and either planted with their crops, or left fallow. "Eyebrow" is a local term for narrow patches of unplowed land on steep, usually north-facing, hillsides. Pastures and "eyebrows" were not plowed; these areas I referred to as uncultivated land. Both were either mowed in June and July for hay and/or grazed by livestock throughout the summer.

I determined prey items by examining food in nests and from castings. Bones and feathers in castings were identified by comparison with specimens in Washington State University's Conner Museum. Hairs were identified by microscopic examination and compared to reference specimens collected from prey species in the area and to illustrations in Moore et al. (1974) and Adorjan and Kolenosky (1969). Prey were tabulated and summed to provide estimates of relative percent frequency for each prey taxon on the basis of the total number identified (Curtis and McIntosh 1950).

Prey density and plant cover were estimated for the habitat types within each male's home range. I obtained density estimates for deer mice (*Peromyscus maniculatus*) and voles (*Microtus montanus*) using 280 × 20 m (0.56 ha) grids of 30 Sherman live traps placed at 20-m intervals. In "eyebrows," fallow fields, and pasture of the range of Male 4, 140 × 20 m (0.28 ha) grids of only 15 similarly spaced traps were used due to the small areas involved. I used six grids in the range of Male 1, and seven in the range of Male 4 in 1978. During 1979, six, seven, and seven grids were used in the ranges of Males 2, 3, and 4, respectively. I placed grids randomly in each habitat and ran them bimonthly for three consecutive days. Traps were baited with rolled oats and sunflower seeds and checked daily in the morning. I individually marked rodents by toe clipping and estimated the density of each species using the Jolly-Seber mark-and-recapture method (Seber 1973). To estimate density, I determined the effective trapping radius of traps and found it to be 10 m. My density indices for northern pocket gophers (*Thomo-*
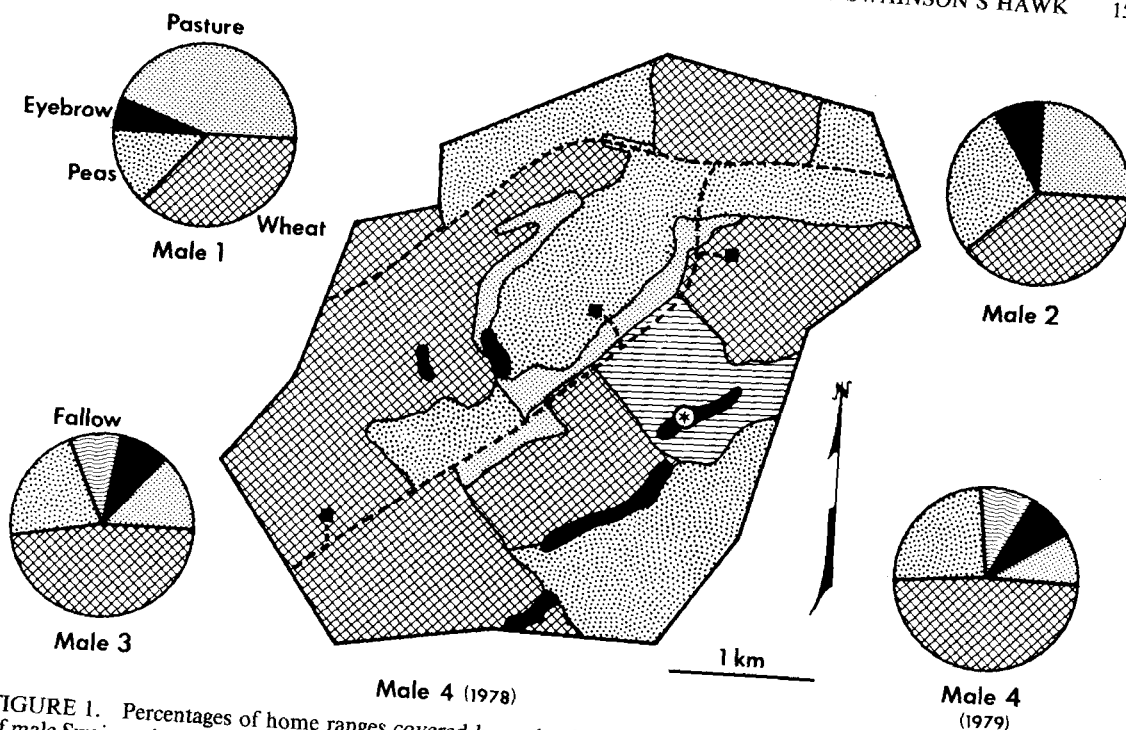
FIGURE 1. Percentages of home ranges covered by each of the four vegetation types occurring in nesting habitats of male Swainson's Hawks. Circle graphs show percentages in the home ranges of Males 1, 2, 3, and 4 (1979). The map gives percentages in the home range of Male 4 (1978). The star indicates the location of the nest, squares indicate buildings, and dashed lines indicate roads.

mys talpoides) were also obtained twice monthly by counting the number of fresh gopher mounds occurring within 1.0 m of either side of 500-m line transects (Hansen and Ward 1966). Again, because of the small areas involved, transects in "eyebrows," fallow fields, and pasture of Male 4 were 250 m in length. My counts were based on averages for three lines randomly placed in each habitat. The number of gopher mounds was converted to gopher density estimates using the technique of Reid et al. (1966). I estimated plant cover by measuring the percent of visible incident radiation that penetrated the plant canopy to ground level. I took light readings twice monthly as close to noon as possible using a Weston foot-candle meter with a quartz filter held at breast height and at ground level. Light readings were taken at 10-m intervals using line transects similar to those used to estimate northern pocket gopher densities.

RESULTS

Home range size averaged 886 ha (Table 2). This mean was similar to the mean of 980 ha obtained for other Swainson's Hawks nesting in Washington (Fitzner 1977). Most of the land within each range had been cultivated and was either planted in wheat, peas, or mustard, or left fallow (Fig. 1). The remainder consisted of uncultivated land, most of which was pas-

ture. The home range of Male 4 contained the largest amount of cropland and ranges of Males 3, 2, and 1 contained decreasing amounts, respectively. I obtained a significant ($P \leq 0.01$) product-moment correlation (Sokal and Rohlf 1969) between the total home range area and the amount of cultivated land it contained ($r = 0.97$, df = 3). A negative correlation was also found between the amount of cultivation and the number of young fledged from nests ($r = -0.90$, df = 3, $P < 0.01$). Male 4 used the range with the largest amount of farming and fledged only 2 and 1 young in 1978 and 1979. Males 3, 2, and 1, using decreasing amounts of cropland, however, fledged 2, 3, and 3 young, respectively.

TABLE 2. Comparisons between Swainson's Hawk home range size, fledging success, and the amount of range being cultivated.

Male	Number of observations	Home range area (ha) (a)*	Area being cultivated (ha) (b)**	Fledging success (young/nest) (c)
1	459	602	319	3
2	494	723	494	3
3	538	788	670	2
4 (1978)	502	1,282	1,134	1
4 (1979)	525	1,036	963	2

* a vs. b significant, $r = 0.97$, $P \leq 0.01$.
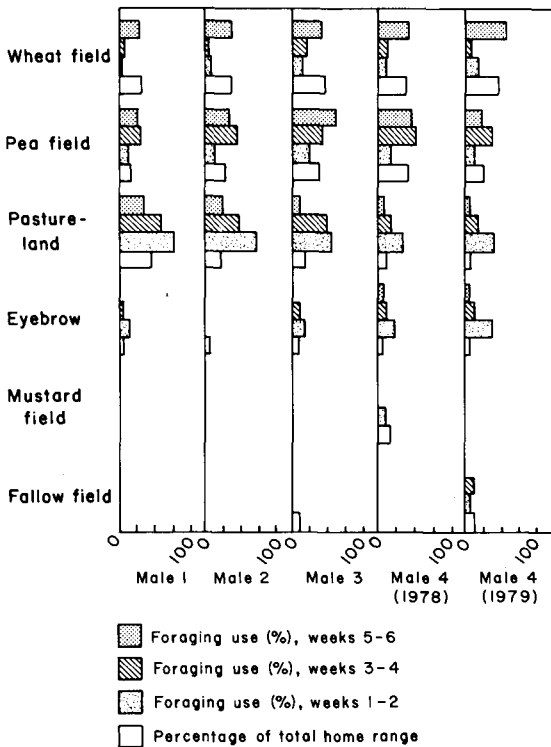** b vs. c significant, $r = 0.90$, $P \leq 0.01$.

FIGURE 2. Comparison of the percentage of the home range covered by habitat types and the percentage of time male Swainson's Hawks spent foraging in each (n = 198, 278, 236, 349, and 247 position records for Males 1, 2, 3, 4 [1978], and 4 [1979], respectively).

I recorded a total of 2,518 bird locations. Of these, 198, 278, 236, 349, and 247 records were classified as food searches for Males 1, 2, 3, 4 (1978), and 4 (1979), respectively. Males hunted mostly in wheat fields, pea fields, pastureland, and "eyebrows." I compared the distribution of each male's food searches with the area of each cover type but did not obtain a significant correlation (P > 0.05) for wheat fields (r = 0.28, df = 13), pea fields (r = 0.31, df = 13), pastureland (r = 0.30, df = 13), or "eyebrows" (r = 0.42, df = 13) (Fig. 2). Males

spent disproportionate amounts of time hunting in pastures and "eyebrows" during the first two weeks after nestlings hatched (late June and early July). Because of its limited availability, heavy use of uncultivated habitat concentrated food searches in small portions of each range. Foraging became more widespread late in July and August. In late July, pea harvest began and males shifted foraging sallies to harvested pea fields. Use of these fields increased until early August when pea harvest was completed. Subsequently, wheat harvest began and males once again shifted their food searches, this time to harvested wheat fields. After switching habitats, Males 1, 2, 3, 4 (1978), and 4 (1979) spent 63, 83, 92, 76, and 90% of their respective foraging times hunting harvested cropland.

Males preyed mostly on rodents (Table 3). Deer mice and northern pocket gophers were the most common prey species. While captures of deer mice remained consistently high all summer, those of northern pocket gophers reached a maximum in early July and declined thereafter. Voles, Columbian ground squirrels (*Citellus columbianus*), and birds were also taken, ground squirrels most frequently in June and voles and Ring-necked Pheasants (*Phasianus colchicus*) after mid-July. Reptiles were not of dietary importance; I found the remains of only a single gopher snake (*Pituophis melanoleucus*) in one nest.

Populations of deer mice and voles were similar in all ranges. Densities of both species varied between habitats of the same range but these variations were not significant (P > 0.05) for deer mice (Anova, F = 1.2, df = 3,40) or for voles (F = 0.6, df = 3,40). Estimates of 126.7 ± 43.6 (±1 SE), 92.8 ± 31.5, 90.8 ± 55.0, 35.6 ± 22.8, and 81.0 ± 11.0 deer mice/ha and 6.7 ± 5.8, 3.2 ± 2.5, 13.8 ± 11.0, 3.5 ± 2.8, and 2.5 ± 1.9 voles/ha that I obtained in wheat fields, pea fields, pasture, "eyebrows," and mustard fields, respectively, were

TABLE 3. Prey of four male Swainson's Hawks nesting in southeastern Washington. Prey species were determined from nestling diets. Prey of Male 4 are given for both 1978 and 1979.

Prey species	Number of individuals					Percent frequency[a]				
	Male 1	Male 2	Male 3	Male 4 (1978)	Male 4 (1979)	Male 1	Male 2	Male 3	Male 4 (1978)	Male 4 (1979)
Small mammals	21	22	16	23	21	90	91	88	96	84
Northern pocket gopher	13	11	8	15	13	56	46	44	62	52
Vole	3	4	5	4	2	13	17	29	17	8
Deer mouse	4	7	2	4	4	17	28	11	17	16
Columbian ground squirrel	1	—	1	—	2	4	—	5	—	8
Birds	2	2	1	1	4	10	9	6	4	16
Ring-necked Pheasant	1	2	1	—	4	5	9	6	—	16
Gray Partridge (*Perdix perdix*)	—	—	—	1	—	—	—	—	4	—
House Sparrow (*Passer domesticus*)	1	—	—	—	—	5	—	—	—	—

[a] Percent frequency based on the total number of individuals identified.

TABLE 4. Estimates of total prey biomass and foraging use of vegetation types occurring within the home ranges of male Swainson's Hawks nesting in southeastern Washington. Prey biomass estimates obtained by summing deer mouse, vole, and northern pocket gopher biomasses contained in each vegetation type. Biomass expressed in kg per hectare ±1 SE.

Weeks	Vegetation type	Male 1		Male 2		Male 3		Male 4 (1978)		Male 4 (1979)	
		Percent use	Prey biomass	Percent use	Prey biomass	Percent use	Prey biomass	Percent use	Prey biomass	Percent use	Prey biomass
1–2	Wheat field	3	5.8 ± 3.4	3	2.5 ± 1.4	7	3.6 ± 1.4	7	4.7 ± 2.7	9	2.0 ± 0.7
	Pea field	6	2.6 ± 1.9	14	1.7 ± 0.9	17	1.4 ± 0.9	20	3.0 ± 1.4	4	2.9 ± 1.7
	Pastureland	77	5.6 ± 1.5	83	4.1 ± 1.2	64	3.7 ± 0.8	35	2.8 ± 1.2	39	2.3 ± 1.0
	Eyebrow	14	1.0 ± 0.7	0	0.4 ± 0.3	12	0.6 ± 0.4	31	2.3 ± 1.3	45	2.2 ± 0.9
	Mustard field							7	2.4 ± 0.1		
	Fallow field					0	0			3	0.1 ± 0.5
3–4	Wheat field	6	5.0 ± 3.8	2	2.0 ± 1.1	9	3.0 ± 0.9	7	4.4 ± 2.7	7	1.9 ± 1.3
	Pea field	12	2.3 ± 1.8	48	2.4 ± 1.3	37	2.0 ± 0.7	55	3.3 ± 1.4	46	3.1 ± 0.7
	Pastureland	82	8.8 ± 2.9	50	5.5 ± 1.8	48	5.0 ± 1.3	18	1.7 ± 0.9	22	1.9 ± 0.8
	Eyebrow	0	1.4 ± 0.9	0	0.4 ± 0.2	6	0.9 ± 0.3	20	2.4 ± 0.8	17	1.9 ± 1.1
	Mustard field							0	2.3 ± 0.6		
	Fallow field					0	0.3 ± 0.1			6	0.4 ± 0.2
5–6	Wheat field	32	3.9 ± 1.6	48	2.6 ± 1.4	31	2.0 ± 1.5	39	4.1 ± 1.1	22	3.0 ± 1.9
	Pea field	29	2.5 ± 1.2	21	1.6 ± 0.1	63	2.1 ± 0.9	52	4.0 ± 1.2	25	2.9 ± 1.7
	Pastureland	39	9.2 ± 1.8	31	3.8 ± 1.0	6	3.8 ± 1.1	6	3.1 ± 0.8	8	2.4 ± 1.1
	Eyebrow	0	1.5 ± 0.9	0	1.5 ± 0.6	0	0.7 ± 0.3	3	2.7 ± 1.0	7	2.0 ± 0.7
	Mustard field							0	2.1 ± 1.2		
	Fallow field					0	0			1	0.2 ± 0.1

similar to averages of 68 deer mice/ha and 4 to 9 voles/ha obtained by Francik (1979), Farris (1971), and Wright (1971) in uncultivated and cultivated habitats of southeastern Washington. My estimates of gopher density were similar to those found in Colorado (Hansen and Ward 1966, Turner et al. 1973). Gopher densities did vary significantly ($P \le 0.01$) both between ranges (F = 59.8, df = 4,40) and between habitats of the same range (F = 239.0, df = 3,40). Gophers were most dense in pastures averaging 25.0 ± 4.6, 71.4 ± 3.4, 26.7 ± 5.8, 7.9 ± 2.3, 9.3 ± 3.1 individuals/ha in the ranges of Males 1, 2, 3, 4 (1978), and 4 (1979), respectively. Populations were smaller and similar in the other cover types. There, they averaged 2.9 ± 1.0, 3.7 ± 1.6, 5.8 ± 1.9, 2.6 ± 1.1, and 2.1 ± 1.3 gophers/ha in wheat fields, pea fields, "eyebrows," mustard fields, and fallow fields, respectively.

I converted the prey density estimates for each cover type to estimates of total prey biomass (Table 4), which I obtained by multiplying each species population density by its average weight. Average weights for deer mice (23.5 ± 1.8 g, n = 987) and voles (34.8 ± 2.6 g, n = 108) were obtained by weighing trapped animals. I did not trap gophers but calculated an average weight of 84.6 ± 2.6 (n = 69) from records in Washington State University's Conner Museum. Total prey biomass estimates varied significantly ($P \le 0.01$) between ranges (Kruskal-Wallis One-Way Analysis of Variance, Siegel 1956; H = 15.4, df = 4). The range of Male 1 contained the largest amount of prey

biomass and that of Male 4, the least. Within ranges, biomass varied significantly between the four major cover types (H = 59.3, df = 3, $P \le 0.001$). In the range of Male 4, prey biomass was most dense in wheat fields, but in the ranges of Males 1, 2, and 3, it was most dense in pastureland. Prey biomass consisted primarily of deer mice in all cover types, except pastureland. There, northern pocket gopher biomass was greater, significantly so in the pastures hunted by Males 1, 2, and 3 (H = 28.2, df = 4, $P \le 0.001$).

The percent of time spent foraging in each habitat type (arcsin transformation) was not correlated with total biomass estimates. Spearman Rank correlation coefficients (Siegel 1956) of 0.14 (df = 13), 0.28 (df = 13), 0.38 (df = 13), and 0.41 (df = 13) were not statistically significant ($P > 0.05$) for wheat fields, pea fields, pastureland, and "eyebrows," respectively. By avoiding cropland until late in the breeding season, Male 4 failed to use the apparent large prey biomass in wheat fields. Males 1, 2, and 3 did forage in areas with greatest prey biomass early in the season but by switching later to harvested cropland selected habitats with less food.

Plant cover was greatest (the fraction of incident visible light at ground level least) in wheat fields and pea fields during Weeks 1 through 4 (Fig. 3). Wheat fields were most densely covered with cover decreasing progressively in pea fields, pastureland, and "eyebrows." Cover remained low in uncultivated fields throughout the study, but decreased
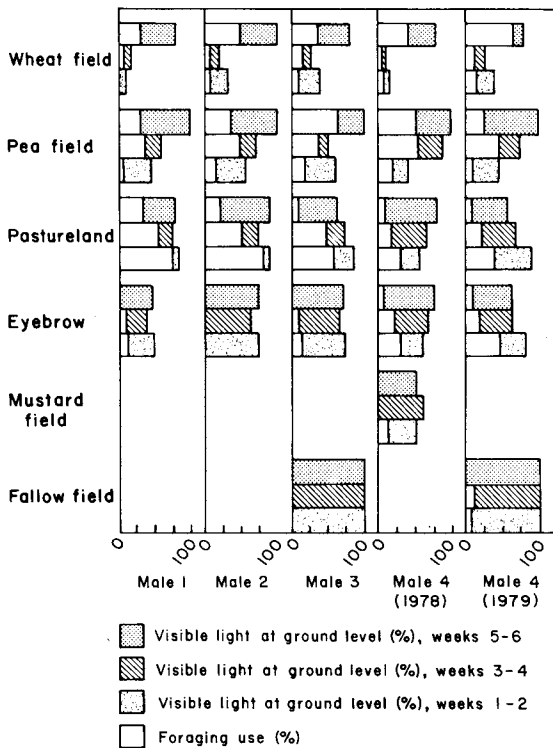
FIGURE 3. Comparison between estimates of the vegetative cover in the habitat types available to male Swainson's Hawks and the percentage of foraging time spent in each (n = 198, 278, 236, 349, and 247 position records for Males 1, 2, 3, 4 [1978], and 4 [1979], respectively).
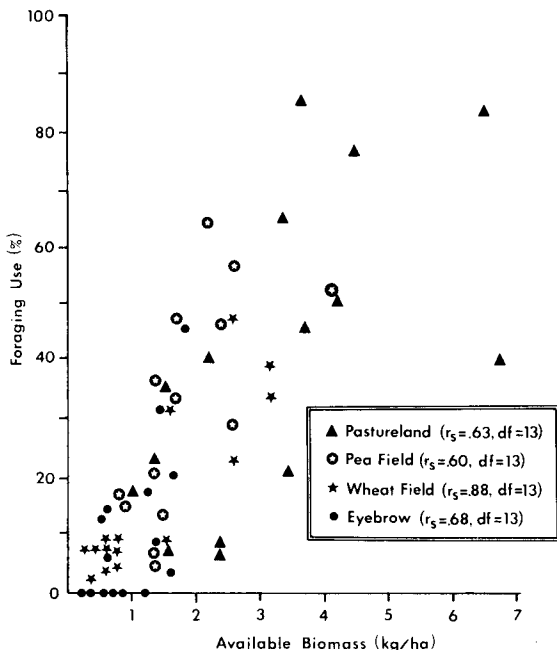

FIGURE 4. Relationship between foraging use of habitat types in male Swainson's Hawk home ranges and the available biomass. All r_s values are statistically significant at the 5% level.

sharply in cultivated habitats after harvest (Weeks 5 and 6).

Foraging in cropland was cover-dependent. Cultivated fields were avoided before harvest, but after harvest reduced their cover, these fields were hunted heavily. Comparison of the percent of time spent foraging in cropland (arcsin transformed) with the fraction of incident light at ground level gave statistically significant ($P \leq 0.05$) negative Spearman Rank correlations of -0.85 (df = 13) and -0.65 (df = 13) for wheat and pea fields, respectively. In view of the relationship between a habitat's vegetative cover and its foraging use, I estimated the total prey biomass actually available for capture using the equation: estimated available biomass = estimated prey biomass × fraction of incident light at ground level. After this conversion, a comparison of habitat use with its "available" prey biomass gave significant ($P \leq 0.05$) Spearman Rank correlation coefficients of 0.88 (df = 13), 0.60 (df = 13), 0.63 (df = 13), and 0.86 (df = 13) for wheat fields, pea fields, pastureland, and "eyebrows," respectively (Fig. 4).

DISCUSSION

My foraging data indicate that vegetative cover is more important than prey abundance in the selection of hunting sites by Swainson's Hawks. The birds I studied preyed mostly on gophers and deer mice, yet did not hunt in habitats where the biomass of these rodents was greatest. In fact, by avoiding cropland for much of the time, they avoided using a considerable portion of their potential rodent prey. A negative correlation between a habitat's use and its vegetative cover indicated that vegetative cover limited the accessibility of prey. I concluded that increased rodent availability in sparsely covered habitats made these areas more profitable hunting sites even though they supported fewer prey.

Many models of predator-prey relationships presuppose a direct relationship between prey capture and prey density (Poole 1974). Studies of habitat selection by Ferruginous Hawks (*Buteo regalis*; Wakeley 1978) and Tawny Owls (*Strix aluco*; Southern and Lowe 1968) indicate that the response of raptors to prey may be more complex than this hypothesis suggests. A correlation between my index of available rodent biomass and Swainson's Hawk foraging indicated that these birds probably use a combination of habitat features as cues to select suitable hunting sites. In order to improve their accuracy, models of raptor foraging should consider the effects of habitat differences (such as vegetative cover) on the availability of a hunting site's food supply. A method similar to the one that I used to show

prey availability might be used to demonstrate this relationship.

The effect of plant cover on the suitability of raptor foraging sites may explain the apparent declines of hawks and owls in agricultural areas. Better concealment of prey in densely covered cropland would reduce prey availability, limit foraging efficiency, and decrease the reproductive success of these populations. I have reported (Bechard 1980) that Swainson's Hawks nesting in farmland of southeastern Washington experienced considerable brood reduction because of an apparent lack of food. A correlation between the amount of land undergoing cultivation and fledging success implied that, by forcing males to rely heavily on small amounts of unplowed land, crop cultivation seriously limited the amount of food available for Swainson's Hawk reproduction and was probably a critical factor in the local decline of this species.

ACKNOWLEDGMENTS

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