

A COMPARATIVE STUDY OF THE BREEDING ECOLOGY OF HARRIS' AND SWAINSON'S HAWKS IN SOUTHEASTERN NEW MEXICO¹

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Abstract. I compared productivity, habitat, and diet of breeding Harris' (*Parabuteo unicinctus*) and Swainson's hawks (*Buteo swainsoni*) to examine predictions that cooperatively breeding birds should produce fewer young and be more specialized in their use of habitat or food than closely related noncooperatively breeding species. Reproductive success of Harris' Hawk (1.73 young/year) and Swainson's Hawk (1.67) breeding units was similar. Harris' Hawks tended to exploit habitats with greater mean densities of large mesquites, less mean grass cover, and more exposed ground than Swainson's Hawks; but both species used a broad range of the habitats available. Swainson's Hawks were opportunistic generalists taking the most available prey, while Harris' Hawks were relative specialists on larger mammals and some birds. My data do not support habitat saturation or resource localization as important to the evolution of cooperative breeding in the Harris' Hawk.

Key words: Cooperative breeding; habitat saturation; resource localization; diets; nesting habitat; breeding biology; Harris' Hawk; Swainson's Hawk; New Mexico.

INTRODUCTION

Comparison of cooperatively breeding birds (where individuals other than the genetic parents assist in the rearing of young) with their noncooperative relatives (e.g., Brown 1974, 1978; Emlen 1978; Zack and Ligon 1985), suggests that the former tend to specialize on a particular resource (often a restricted habitat) or suite of resources, whereas the latter tend to be generalists. Furthermore, cooperative species seem to exist in a relatively competitive environment where survival may be more critical to fitness than high reproductive success (e.g., Woolfenden and Fitzpatrick 1984, Koenig and Mumme 1987). Noncooperative birds, on the other hand, are thought to exploit a broad range of conditions, and should be relatively fecund and possess good dispersal abilities (Brown 1974, 1987). In accordance with this view, Brown predicted that group-breeding species should have lower reproductive rates than their noncooperative relatives.

Koenig and Pitelka (1981) formalized some of these ideas and argued that habitat or resource limitation was an important factor in the evolution of avian cooperative breeding. They predicted that breeding territories should vary less

in quality in cooperative species when compared to closely related noncooperative species.

Here I compare the ecology of two species of large hawks that breed sympatrically in southeastern New Mexico to examine Brown's (1974) prediction that the sedentary, cooperative species, the Harris' Hawk (*Parabuteo unicinctus*), should have the lower reproductive rate; and Koenig and Pitelka's (1981) prediction that the noncooperative species, the Swainson's Hawk (*Buteo swainsoni*), should exploit a greater variety of habitats. In addition, I describe the food habits of these species to determine whether they differ in terms of diet specialization. Using the logic of Brown (1974) and Zack and Ligon (1985), I suggest that diet specialization might be an alternative constraint (Emlen 1982) that may favor cooperative breeding. Somewhat contrary to this argument, Brown (1987), on the basis of food-cost functions (effect of group size on food availability), proposed that food generalists are more likely to develop social groups than food specialists. No comparative study of cooperative and noncooperative birds has addressed potential differences or constraints related to diet.

In the study area, the Harris' Hawk is a year-round resident and often breeds cooperatively (Mader 1975, Bednarz 1987a). Nests of Swainson's Hawks were interspersed among the sites used by resident groups of Harris' Hawks. Swainson's Hawks breed only in pairs (pers. observ.)

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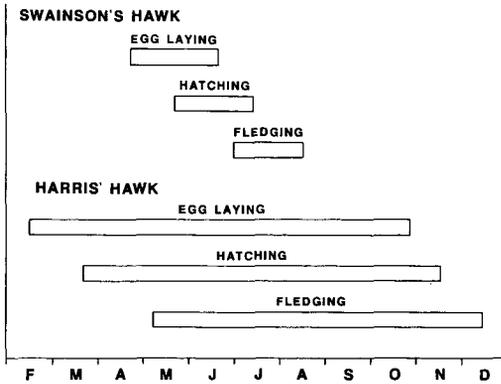


FIGURE 1. Nesting seasons of the Harris' and Swainson's hawks in southeastern New Mexico. Patterns depicted are based on estimated dates of egg laying, hatching, and fledging (see Methods).

and migrate to South America following nesting. Although these two species are not placed in the same genus, Harris' Hawks are more similar to *Buteo* hawks than to any other genus of hawks (Brown and Amadon 1968:22), and thus are thought to be relatively closely related to Swainson's Hawks.

METHODS

The study area is located in the shinnery-oak (*Quercus havardii*) shrublands of southeastern New Mexico and has been described previously (Bednarz 1987b). The habitat in the study area includes oak-mesquite (*Prosopis glandulosa*) associations on level to rolling sand substrates, sparse grasslands, and creosote (*Larrea tridentata*) shrub associations on level caliche soils. Both hawks nest in the small (4 to 7 m in height) mesquite or soapberry trees (*Sapindus drummondii*) scattered throughout the study area.

The prolonged breeding season of the Harris' Hawk (Bednarz 1987b; Fig. 1) led me to thoroughly search all known nesting areas of this species three times per year, once each in spring, summer, and autumn. (The nesting area is the general site where members of a specific Harris' Hawk group are usually observed and within which they locate their nests.) I attempted to make five visits to most Harris' Hawk nests in order to determine an estimate of group size (Bednarz 1987a). Reproductive success was determined during the last nest visit made at about the age of fledging (nestlings 40 to 46 days old; Bednarz 1987b).

Most Swainson's Hawk nests were found in May. I attempted to visit all Swainson's Hawk nests at least three times: one visit during the incubation period, one visit in the middle of the brood-rearing period (nestlings 10 to 30 days old), and one visit to each nest immediately before or at the age of fledging (nestlings 35 to 40 days old). Swainson's Hawks fledged at a mean age of 40.4 days (Bednarz and Hoffman, in press).

Nest success was calculated using the Mayfield (1961, 1975) method, with the standard error estimates proposed by Johnson (1979). This technique avoids overestimates of breeding success that result because some early nesting failures are probably undetected (Steenhof and Kochert 1982). The incubation and brood-rearing periods used for the Mayfield analysis for the Harris' Hawks were 34 and 46 days (Bednarz 1987b) and for the Swainson's Hawks were 34 and 40 days, respectively (Bednarz and Hoffman, in press). Hatching dates were estimated using the regression method described by Bednarz (1987b). The formula used to estimate nestling age, and thus hatching date, for Swainson's Hawks was: estimated age = $9.876 + (\text{length of seventh primary in mm} \times 0.141)$. Conventional measures of reproductive success (clutch size and fledgling success) also are reported.

Habitat data were collected following the standardized procedures suggested by B. R. Noon, M. R. Fuller, and J. A. Mosher (1980, unpubl.), using two concentric circles centered on a nest site. The inner plot had a radius of 25 m and the outer concentric sampling ring was located 25 to 75 m from the nest. Four line transects extending from the nest tree were laid out along the cardinal directions, each 75 m in distance. The transects were divided into 5-m intervals within 25 m of the nest (inner sampling circle) and into 10-m intervals between 25 and 75 m from the nest (outer sampling ring). Within each interval the percent cover of shrubs was estimated with the line-intercept method (Mueller-Dombois and Ellenberg 1974). One meter segments within each sample interval were selected randomly to estimate the percent cover of forbs, grass, litter, and exposed ground, also by use of the line-intercept method. These variables are presented as percent cover estimates. In addition, within each sample interval a random sampling point was located (Bednarz and Ligon, in press). At this sample point, quarters were established by centering 2-m

sticks on the point and orienting them along the cardinal directions. The following data were collected at each sampling point: (1) species, dbh (diameter breast height), size class, estimated distance, and estimated height of the nearest tree (dbh > 3 cm) in each quarter; (2) species, measured distance, and estimated height of the nearest shrub (>0.25 m in height and <3 cm dbh) in each quarter; (3) the number of vegetation contacts in each of four height intervals (level 1 = 0 to 0.3 m, level 2 = 0.3 to 1 m, level 3 = 1 to 2 m, and level 4 = 2 to 6 m) on a 1-cm diameter rod placed at the four ends of the meter sticks. This procedure yields 20 individual sample points and intervals in each of the two concentric sampling rings for each variable described above. Shrub and tree densities were determined by the point-quarter method (Mueller-Dombois and Ellenberg 1974). Importance values for the various shrub and tree species were estimated by multiplying the mean height and estimated density for each species at each site. Species importance values were retained in the analysis only if the frequency of a species was greater than 5% for the total sample (total $n = 6,720$ shrubs). At each sample site ($n = 42$) 1,840 vegetation measures were taken.

The variables used in the analysis were as follows: Shrub% = mean percentage of shrub cover, Forb% = mean percentage of forb cover, Grass% = mean percentage of grass cover, Litter% = mean percentage of litter cover, Ground% = mean percentage of exposed ground, Shrub density = the density of shrubs per 100 m², Shrub height = mean shrub height in meters, Sage importance = the importance (density \times height) of *Artemisia filifolia*, Snakeweed importance = the importance of *Gutierrezia sarothrae*, Mesquite importance = the importance of *Prosopis glandulosa*, Oak importance = the importance of *Quercus havardii*, Yucca importance = the importance of *Yucca campestris*, Shrub richness = the number of shrub species sampled at each nest site, Tree density = the density of trees per km², Tree trunk diameter = the dbh size class of trees (1 = 3 to 8 cm; 2 = 8 to 15 cm; and 3 = 15 to 23 cm), Tree height = mean tree height in meters, Mesquite tree importance = the importance of mesquite trees, Level1 vegetation = the total number of vegetation contacts recorded within four 0- to 0.3-m height intervals, Level2 vegetation = vegetation contacts at the 0.31- to

1.0-m height interval, Level3 vegetation = vegetation contacts at the 1.01- to 2.0-m height interval, and Level4 vegetation = estimated vegetation contacts at the 2- to 6-m height interval.

The habitat analysis was done at 23 Harris' and 19 Swainson's hawk nest sites. Because no differences were found between sites occupied by groups (>2 hawks) and pairs of Harris' Hawks by use of either univariate or multivariate statistical techniques (Bednarz and Ligon, in press), all sites used by this species were combined for interspecific comparisons.

The best estimates of the 21 variables describing the habitat at each nest site were assumed to be site means. Since no differences were found for 20 variable estimates between the inner and outer sampling rings using analysis of variance (ANOVA), the data were combined for all subsequent analyses. There was a slight trend in the variable Tree density: estimates for the inner sampling plot were greater than those of the outer sampling ring. This may have been due to the influence of the nest tree centered in the relatively small (diameter = 50 m) inner plot. For this reason, tree density estimates used in subsequent analyses were those calculated for the outer sampling ring. This should most accurately represent the habitat surrounding nest sites. Univariate analysis of the variable estimates were done by one- or two-way ANOVA if the assumptions of normality and homoscedasticity were met. If variable distributions deviated from statistical assumptions, data were square-root transformed before analysis (Grass%, Shrub height, Sage importance, Snakeweed importance, Mesquite importance, Oak importance, Yucca importance, Tree density, Tree trunk diameter, Mesquite tree importance, Level2 vegetation, Level3 vegetation, Level4 vegetation). This transformation resulted in closer adherence to statistical assumptions, but some variable distributions still deviated from normal (i.e., Shrub height, Sage importance, Snakeweed importance, Oak importance, Yucca importance, Tree trunk diameter, Mesquite tree importance, Level3 vegetation, and Level4 vegetation). Comparisons of the means of these variables also were made with Wilcoxon's nonparametric tests which produced results statistically identical to the ANOVAs. For consistency, results from the ANOVAs are reported for all variables.

Coefficients of variation (Sokal and Rohlf 1981)

were compared between species for all 21 habitat variables. Significant differences were examined with an *F*-test as described in Sokal and Rohlf (1981).

Stepwise discriminant function analysis was used to identify those most useful variables for separating the species by linear combination. The variables included in the stepwise analysis also were used in a multivariate analysis of variance to test for a significant difference between the species' centroids. Finally, variation of habitat variables was explored by principal component analysis, which represents the original variates as distinctive linear-combination subsets, each comprised of those variables most correlated with each other and less correlated with variables in other subsets (Harris 1985). The coefficients of variation of these linear-combination variables were also compared between the species. Such multivariate variables may or may not represent habitat dimensions perceived by the hawks. Variables transformed for the univariate analyses also were transformed in the same manner for the multivariate analyses.

Diets of nestling Harris' and Swainson's hawks were determined by identifying bones, bone fragments, feathers, and other prey parts found in and beneath nests, either singly or within pellets. For identification, I compared remains with known reference specimens at the University of New Mexico Museum of Southwestern Biology (UNMMSB). Mammal fur was not used in this analysis because guard hair characteristics seemed to be distorted and identification was not reliable. In addition, preliminary analysis of fur seemed to duplicate results obtained from skeletal remains. The minimum number of individuals of each prey species present at each nest was determined by the maximum number of a specific bone for each species represented in the remains. As I found no reliable character to distinguish immature cottontail (*Sylvilagus auduboni*) from immature black-tailed jackrabbit (*Lepus californicus*) limb bones, I recorded only bones larger than those of adult cottontails as jackrabbits. Biomass of the prey consumed was determined by multiplying numbers of prey taken by the average wet mass of prey types. Mean mass values for the three most important prey types: desert cottontail, woodrat (*Neotoma* spp.), and spotted ground squirrels (*Spermophilus spilosoma*) were based on samples collected at the study area (561 g, $n = 17$; 217 g,

$n = 288$; and 117 g, $n = 32$; respectively). The intermediate or overall mean mass values reported by Steenhof (1983) were used as biomass estimates for other prey types. Lagomorph femurs were measured from the notch between the greater trochanter and the head of the femur to the notch between the distal and lateral condyles.

Diet breadth was calculated by Levins' (1968) formula:

$$B = 1/\sum P_i^2$$

Where P_i is the proportion of the diet contributed by the *i*th prey type. Values calculated from this equation range from 1 to n . Overlap of the prey types included in the diet was estimated with Pianka's (1973) formula:

$$O = \frac{\sum P_{ij}P_{ik}^2}{(\sum P_{ij}^2 \sum P_{ik}^2)^{1/2}}$$

where P_{ij} and P_{ik} are proportions of the *i*th prey type in the diets of the *j*th and *k*th species. Values calculated from this index range from 0 (no overlap) to 1 (complete overlap). The most common prey types in the remains were assigned to prey categories by genus, but rarer items were grouped into size and ecological categories of prey types (e.g., medium-sized rodents included *Peromyscus* and *Onychomys*, small rodents included *Perognathus* and *Reithrodontomys*, and insects were divided into small (mostly coleopterans) and large (mostly orthopterans) categories.

All statistical analyses were done with SAS (Statistical Analysis System; Ray 1982). Except for habitat data, univariate data that deviated from normality were compared with Wilcoxon's tests. The level of statistical significance is $P < 0.05$ unless otherwise noted.

RESULTS

REPRODUCTIVE SUCCESS

The Harris' Hawks produced a larger mean clutch (3.01) than the Swainson's Hawks (2.42) over all years of the study (Wilcoxon's test, $z = -3.96$, $P < 0.001$; Table 1). No differences were found in the number of young fledged per successful nest (Harris' Hawks $\bar{x} = 1.96$, $n = 76$ and Swainson's Hawks $\bar{x} = 1.94$, $n = 31$). However, Swainson's Hawks averaged more fledged young per nest ($\bar{x} = 1.67$) than did Harris' Hawks ($\bar{x} = 1.25$) in each year (Table 1); when all years were combined this trend was marginally significant (Wilcoxon's test, $z = 2.0568$, $P = 0.04$). This pattern

TABLE 1. Reproductive success of Harris' and Swainson's hawks.

	Harris' Hawk			Swainson's Hawk			P ^a
	n	\bar{x}	SD	n	\bar{x}	SD	
Clutch size							
1981	27	3.03	0.81	7	2.71	0.49	0.17
1982	26	3.04	0.77	11	2.55	0.52	0.07
1983	25	2.96	0.54	13	2.15	0.69	<0.01
1981-1983	78	3.01	0.71	31	2.42	0.62	<0.01
Young fledged/nest							
1981	38	1.21	1.12	11	1.91	1.04	0.06
1982	37	1.38	1.14	11	1.91	0.83	0.18
1983	39	1.18	1.17	14	1.29	0.99	0.65
1981-1983	114	1.25	1.14	36	1.67	0.99	0.04
Young fledged/social unit							
1981	23	1.91	1.35	11	1.91	1.04	0.94
1982	27	1.82	1.47	11	1.91	0.83	0.76
1983	29	1.52	1.12	14	1.29	0.99	0.60
1981-1983	79	1.73	1.31	36	1.67	0.99	0.97
Per capita	59 ^b	0.76	0.52	36	0.83	0.49	0.35

^a Probabilities determined by Wilcoxon's tests.

^b Only includes breeding units in which number of nest attendants was estimated.

resulted because a greater proportion of Swainson's Hawk nests were successful (81%) than Harris' Hawk nests (68%; $P < 0.05$, Table 2).

The lower success of Harris' Hawks per nest was compensated for by the ability of this species to produce two broods in one year (Bednarz 1987b). On an annual basis Harris' Hawks pro-

duce slightly more fledglings ($\bar{x} = 1.73$) than Swainson's Hawks ($\bar{x} = 1.67$). On a per capita basis, Harris' Hawk groups had slightly lower reproductive success ($\bar{x} = 0.76$) than did Swainson's Hawk pairs ($\bar{x} = 0.83$), but this was not significant (Wilcoxon's test, $z = 0.93$, $P = 0.35$).

HABITAT

Five variables (Forb%, Litter%, Tree height, Oak importance, and Mesquite tree importance) differed significantly (two-way ANOVAs) among the years the habitat data were collected. Three of these variables were characteristics of perennial vegetation (Tree height, Oak importance, and Mesquite tree importance) and were only marginally significant ($P = 0.042$, 0.026 , and 0.043 , respectively). I suspect that these statistical differences were spurious. None of the five variables displaying slight temporal variation, except for possibly Tree height, was identified as potentially important in the interspecific comparison presented here. No significant interaction between species and years was found for any variable (two-way ANOVAs).

Most mean characteristics of the vegetation surrounding Harris' and Swainson's hawk nests were similar (Table 3). Harris' Hawk sites had greater densities of trees ($\bar{x} = 584/\text{km}^2$) and higher percentage of exposed ground ($\bar{x} = 67.3\%$) than did Swainson's Hawk sites ($\bar{x} = 221/\text{km}^2$, and 55.6% , respectively). Swainson's Hawk sites had

TABLE 2. Estimated proportion of breeding attempts initiated by Harris' and Swainson's hawks that was successful. Proportion was determined by the Mayfield method (see Methods).

	Harris' Hawk	Swainson's Hawk
1981		
Proportion	0.64	0.85
95% CI	0.84-0.85	0.61-1.00
n	34	10
1982		
Proportion	0.75	1.00
95% CI	0.59-0.95	- ^a
n	30	11
1983		
Proportion	0.66	0.67
95% CI	0.52-0.84	0.45-1.00
n	38	13
1981-1983		
Proportion	0.68	0.81
95% CI	0.58-0.78	0.67-0.98
n	102	34

^a Confidence intervals cannot be calculated if all sample nests were successful.

TABLE 3. Comparison of habitat characteristics estimated at nest sites of Harris' and Swainson's hawks. Sample size, *n*, is the number of nest sites sampled.

Variables	Harris' Hawk <i>n</i> = 23			Swainson's Hawk <i>n</i> = 19			<i>P</i>
	\bar{x}	SE	CV	\bar{x}	SE	CV	
Shrub%	26.4	1.9	35.3	25.9	1.5	25.8	0.863
Forb%	16.7	1.9	53.9	15.4	2.5	69.2	0.682
Grass%	10.3	1.5	53.5	16.6	2.1	55.8	0.009*
Litter%	17.9	1.8	48.5	21.9	2.1	41.0	0.151
Ground%	67.3	2.3	16.3	55.6	2.5	19.8	0.001*
Shrub density/100 km ²	33.9	5.4	76.6	31.3	3.5	49.0	0.709
Shrub height m	0.83	0.06	32.7	0.81	0.05	25.0	0.779
Sage importance	6.4	1.9	144.6	4.7	1.0	93.6	0.455
Mesquite importance	4.5	0.7	73.5	7.8	2.4	132.8	0.154
Snakeweed importance	1.7	0.7	206.2	1.9	1.0	238.4	0.883
Oak importance	4.9	1.4	140.6	4.9	1.4	120.5	0.995
Yucca importance	4.1	1.3	152.6	3.0	0.5	76.1	0.486
Shrub richness	6.0	0.4	29.7	5.2	0.5	40.5	0.229
Tree density/km ²	584	116	95.2	221	54	107.4	0.011*
Tree trunk diameter	1.20	0.04	16.7	1.14	0.03	11.5	0.273
Tree height	3.1	0.06	9.4	3.0	0.07	9.6	0.474
Mesquite tree importance	1,738	360	99.3	1,319	490	161.9	0.487
Level1 vegetation	14.2	1.0	34.2	14.5	0.9	26.7	0.833
Level2 vegetation	7.2	0.7	43.9	6.5	1.0	64.5	0.561
Level3 vegetation	2.7	0.6	107.5	1.7	0.5	141.1	0.213
Level4 vegetation	0.6	0.3	254.3	0.1	0.1	363.6	0.198

* Means significantly different at *P* ≤ 0.01, ANOVA.

a greater percentage of grass cover (\bar{x} = 16.6%) than did Harris' Hawk areas (\bar{x} = 10.3%).

Sites used by each species varied greatly in mean vegetation characteristics. Coefficients of variation of individual attributes ranged from 9 to 254% for the Harris' Hawks and 9 to 364% for the Swainson's Hawks (Table 3). None of the differences in the individual coefficients of variation for the individual variables approached significance (*F*-ratio test, *P* > 0.1). Swainson's Hawk

sites had greater coefficients of variation for 12 of the 21 variables measured (*P* > 0.1, sign test, Zar 1974). Coefficients of variation were similar for the three variables that showed significant differences between the two species (Grass%, 53.5 vs. 55.8; Ground%, 16.3 vs. 19.8; and Tree density, 95.2 vs. 107.4). These results suggest that variation in the habitats occupied by these two species was very similar.

The variables included in the stepwise discriminant function analysis in order of importance as determined by standardized canonical coefficients, were Ground% (1.12) and Level4 vegetation (0.68). A multivariate analysis of variance using these two variables indicates that a significant difference did exist between the habitat surrounding nest sites of the two species (*F* = 9.35, *df* = 2,39; *P* = 0.0005; Fig. 2). Harris' Hawk sites tend to have a greater density of vegetation above 2 m in height (Level4 vegetation) and more exposed ground than Swainson's Hawk sites (Table 3). The discriminant analysis correctly classified 78.3% of the Harris' Hawk sites and 63.2% of the Swainson's Hawk sites.

The first four principal components explained 54% of the variation in the habitat data (Table 4). The first principal component primarily rep-

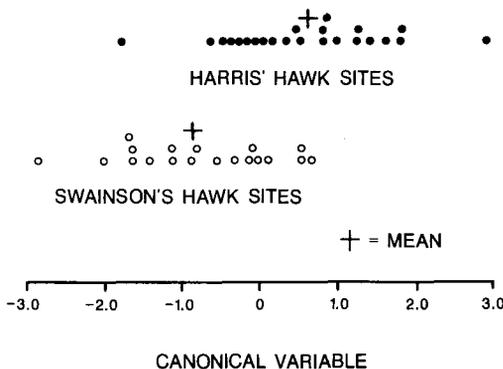


FIGURE 2. Discriminant analysis of 23 Harris' and 19 Swainson's hawk nest sites graphically represented by canonical scores.

TABLE 4. Correlations of habitat variables and the first four principal components of Harris' and Swainson's hawk nest sites.

Variable	PC1	PC2	PC3	PC4
Shrub%	0.63*	0.15	0.29	0.24
Forb%	-0.34	0.50*	-0.32	0.18
Grass%	-0.10	0.52*	0.17	-0.47*
Litter%	0.15	-0.04	0.68*	0.24
Ground%	0.04	-0.48*	-0.51*	0.59*
Shrub density	0.82*	0.28	0.17	0.19
Shrub height	-0.84*	0.31	0.15	0.16
Sage importance	0.54*	-0.05	0.02	0.43*
Snakeweed importance	0.47*	0.28	-0.15	0.32
Mesquite importance	-0.10	0.71*	0.13	0.02
Oak importance	0.63*	-0.36	0.32	-0.29
Yucca importance	0.56*	0.18	0.03	0.19
Shrub richness	0.13	-0.29	0.03	0.31
Tree density	0.05	-0.36	0.50*	0.46*
Tree trunk diameter	-0.30	-0.58*	-0.24	-0.18
Tree height	-0.16	-0.32	0.08	-0.32
Mesquite tree importance	-0.22	0.27	0.71*	0.71*
Level1 vegetation	-0.16	0.39	0.41*	0.24
Level2 vegetation	-0.31	0.19	-0.08	0.65*
Level3 vegetation	-0.61*	-0.11	0.30	0.40*
Level4 vegetation	-0.38	-0.14	0.43*	0.13
Percentage of variance accounted for by component	19.0%	12.6%	11.5%	11.0%

* Correlation coefficients $r > 0.39$, $P < 0.01$.

resents the overall variation in shrub vegetation. This component was positively related to shrub cover and density, and the importance of all shrub species except mesquite, but negatively correlated with Shrub height and Level3 vegetation (Table 4).

The second principal component corresponded with the variation in mesquite and ground cover (Grass% and Forb%; Table 4). It was negatively related to Ground% ($r = -0.48$) and Tree trunk diameter ($r = -0.58$). Variables positively corresponding to the third component were the importance of large mesquite (Mesquite tree importance and Tree density) and Litter%, while Ground% was negatively related. Component 4 was positively associated with larger mesquite (Mesquite tree importance and Tree density) and exposed ground (Table 4).

The variation of principal component scores for the first 14 components (accounting for 91% of the variation of the original variables) was similar between the two species. Figure 3 demonstrates a nearly homogeneous scattering of component scores for the two species for component axes 1 and 2. Similar spread of component scores between the two species was seen for

all 14 components evaluated. The coefficients of variation for 10 of these components were greater for the Harris' Hawk than the Swainson's Hawk sites. Like the univariate analysis, differences in the coefficients did not approach significance (F -ratio test, $P > 0.1$), suggesting that Harris' and Swainson's hawks exploit a similar range of habitat in southeastern New Mexico. Very similar patterns were obtained using factor analysis with a varimax rotation.

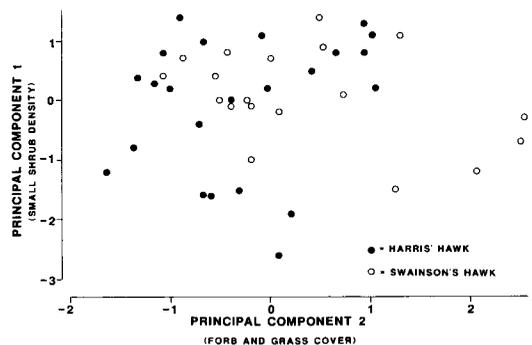


FIGURE 3. Plot of 23 Harris' and 19 Swainson's hawk nest-site principal component scores on component axes 1 and 2.

TABLE 5. Percentage of prey types represented in food remains found in and near Harris' and Swainson's hawk nests in southeastern New Mexico (1981 to 1983).

Prey type	Harris' Hawk <i>n</i> = 889		Swainson's Hawk <i>n</i> = 856	
	% frequency	% bio-mass	% frequency	% bio-mass
<i>Sylvilagus auduboni</i>	61.4	87.1	17.1	80.3
<i>Lepus californicus</i>	1.6	4.0	0.1	1.0
<i>Neotoma</i> spp.	5.4	3.0	3.4	6.2
<i>Spermophilus</i> spp.	4.4	1.3	1.8	1.7
<i>Dipodomys</i> spp.	2.8	0.4	6.2	2.8
<i>Geomys</i> spp.	0.4	0.2	1.1	1.8
<i>Sigmodon hispidus</i>	0.1	trace	0.1	trace
Medium-sized rodent ^a	0.1	trace	0.6	0.1
Small rodents ^b	0	0	0.2	trace
Quail ^c	5.6	2.5	1.2	1.7
Roadrunner	1.1	1.1	0.5	1.5
Other birds	2.6	0.2	0.8	0.3
<i>Phrynosoma texanus</i>	0.8	trace	7.2	1.1
<i>Eumeces</i> spp.	2.1	0.1	2.5	0.6
Other lizards	0.9	trace	1.8	0.2
Snakes	0	0	0.7	0.3
Large insects	3.1	trace	35.0	0.6
Small insects	7.4	trace	19.9	trace

^a *Peromyscus* spp. and *Onychomys leucogaster*.^b *Perognathus* spp. and *Reithrodontomys* spp.^c *Colinus virginianus* and *Callipepla squamata*.

COMPOSITION OF DIETS

Harris' and Swainson's hawks fed heavily on cottontails (Table 5), which made up 61.4% and 17.1%, respectively, of the prey types represented in the food remains. In biomass, lagomorphs made up 91.1% of the Harris' Hawk and 81.3% of the Swainson's Hawk prey remains. In addition, Swainson's Hawks took substantial numbers of kangaroo rats (*Dipodomys* spp.), 6.2%; horned lizards (*Phrynosoma texanus*), 7.2%; and insects, 54.9%. This last prey class, however, contributed little to the biomass consumed (0.6%). Other prey taken by Harris' Hawks in terms of biomass were the black-tailed jackrabbit (4.0%), woodrats (3.4%), quail (2.5%), and ground squirrels (1.3%). The proportion of rabbits and other mammals consumed at Harris' Hawk nests was similar in all 3 years of study ($P > 0.1$, χ^2 tests). The proportion of mammal remains at Swainson's Hawk nests varied significantly among years (Fig. 4; $\chi^2 = 67.0$, $P = 0.0001$, $df = 2$). In all years, Harris' Hawk remains contained significantly higher ($P < 0.0001$; χ^2 tests, Fig. 4) proportion of mammals, while, Swainson's Hawks consumed more insects and reptiles than did Harris' Hawks (Table 5).

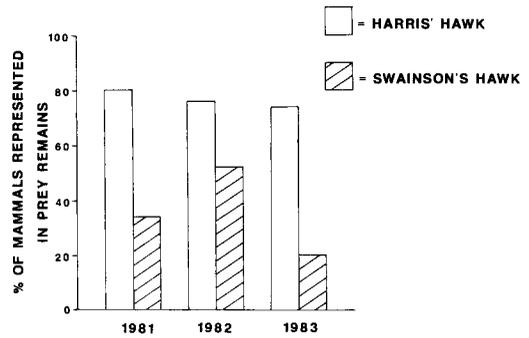


FIGURE 4. The percentage of mammals recorded in the prey remains found in and near Harris' and Swainson's hawk nests.

Overlap in diet between these species was relatively high (overlap estimates = 0.42 to 0.70). The greatest overlap occurred in 1982, when Swainson's Hawks took more rabbits (28.7%) and mammals (51.5%; Fig. 4) than recorded in other years. Diet breadth of Harris' Hawks was consistently less (2.2 to 2.8) than calculated for the Swainson's Hawks (3.7 to 5.0; Table 6). Harris' Hawks appear to specialize on desert cottontails. Although this prey type also was important to Swainson's Hawks, use of cottontails varied substantially among years (17.5%, 28.7%, and 12.0% in 1981, 1982, and 1983, respectively).

Both right and left femurs found in Harris' Hawk prey remains were consistently larger (Wilcoxon's tests; $P < 0.05$; for 1982 and 1983) than those in Swainson's Hawk remains (Table 7). In 1981 the pattern was consistent (Table 7) but not significant. These results suggest that Swainson's Hawks take more juvenile lagomorphs than Harris' Hawks. In addition, I found that the mean length of lagomorph femurs (right femur = 56.3, $n = 70$ and left femurs = 56.5, $n = 64$) in Swainson's Hawk prey remains were substantially smaller than femurs with ossified epiphyseal or growth disks (63.3 to 70.3 mm), as determined by examination of 30 complete cottontail skeletons at the UNMMSB. All femurs smaller than 63.3 mm in length had unossified epiphyseal disks whereas femurs larger than 67.5 mm were completely ossified. Therefore, New Mexico cottontails with femur lengths less than 63.3 mm may be classified as growing juvenile individuals. In Swainson's Hawk prey remains, 81.5% of the right femurs ($n = 70$) and 82.8% of the left femurs ($n = 64$) were smaller than 63.3 mm, supporting the suggestion that most lagoon

TABLE 6. Estimates of diet overlap and breadth for Harris' and Swainson's hawks in southeastern New Mexico (1981 to 1983).

Year	Diet overlap	Harris' Hawk diet breadth	Swainson's Hawk diet breadth
1981	0.444	2.786	3.672
1982	0.699	2.230	5.016
1983	0.417	2.554	4.248
1981-1983	0.485	2.539	4.920

morphs taken by this species are young animals. In contrast, only 50.5% of the right femurs ($n = 307$) and 55.4% of the left femurs ($n = 307$) in the Harris' Hawk remains were classified as juveniles. The difference in the proportion of juveniles taken by Harris' and Swainson's hawks was significantly different for both right and left femurs ($P < 0.0001$, χ^2 tests).

DISCUSSION

In this study, reproductive success of Harris' and Swainson's hawks does not appear to differ by any measure considered. Harris' Hawk nests have a higher probability of failing (0.32) than Swainson's Hawk nests (0.19), but this is compensated for by occasional double broods in one year (Bednarz 1987b). This finding does not support Brown's (1974) prediction that cooperative breeders should have lower reproductive rates than noncooperative species. Brown (1974, 1987) at least implied, however, that reproductive success differences between cooperative and non-cooperative breeders were in part due to delayed breeding in the former. Although there may be differences in the average age of first breeding between Harris' and Swainson's hawks, this is not obvious. Swainson's Hawks with immature plumage (approximately 1-year-old birds) have never bred on the study site, but I have observed nesting in two color-marked Harris' Hawks less than 2 years old. At this time, my limited observations suggest that most individuals of both species probably delay breeding until they are at least 2 years of age. The important difference seems to be the tactics used while waiting. Many Harris' Hawks stay with their parents, whereas Swainson's Hawks probably become floaters. More data, however, are needed to clarify this point.

Zack and Ligon (1985) recently have shown that the production of young in the cooperatively breeding Gray-backed Fiscal Shrike (*Lanius*

TABLE 7. Mean length of cottontail femurs found in the prey remains at Harris' and Swainson's hawk nests.^a

	Harris' Hawk		Swainson's Hawk	
	Right femur	Left femur	Right femur	Left femur
1981				
\bar{x} (mm)	60.67	60.75	58.23	58.25
SD	7.70	7.19	8.90	6.60
n	82	78	18	13
1982				
\bar{x} (mm)	61.09	59.60	55.15	55.46
SD	7.07	7.39	7.31	9.67
n	105	114	33	36
1983				
\bar{x} (mm)	61.99	62.12	56.50	57.32
SD	6.42	8.87	9.34	9.65
n	120	115	19	15
1981-1983				
\bar{x} (mm)	61.33	60.84	56.31	56.46
SD	7.00	7.98	8.29	9.07
n	307	307	70	64

^a Femur lengths were compared between species with Wilcoxon's tests (right femurs: $z = -1.46$, $P = 0.14$; $z = -4.07$, $P < 0.0001$; $z = -2.90$, $P = 0.004$; and left femurs: $z = -1.79$, $P = 0.09$; $z = -3.03$, $P = 0.003$; $z = 2.27$, $P = 0.02$; 1981, 1982, and 1983, respectively).

excubitorius) was similar to that of its noncooperative relative, the common Fiscal Shrike (*Lanius collaris*) and concluded their findings likewise did not support Brown's (1974) suggestion. Both the hawk and shrike results suggest that lower reproductive success per nest or per year is not necessarily a trait associated with cooperatively breeding birds.

A thorough analysis of vegetation characteristics surrounding nest sites of Harris' and Swainson's hawks revealed no obvious differences in the variation of habitats used. Both species were distributed almost equally along principal components representing variation in tree, shrub, and ground cover (Figs. 2 and 3). On my study site, the cooperatively breeding Harris' Hawk does not breed in a more restricted set of habitats than the Swainson's Hawk (cf. Koenig and Pitelka 1981).

Other comparative analyses have suggested that the noncooperative species does tend to inhabit a broader range of habitats than the cooperative breeder. Brown (1974) noted that the western Scrub Jay (*Aphelocoma coerulescens*) exploits a variety of habitat, whereas the cooperatively breeding Gray-breasted Jay (*Aphelocoma ultramarina*) is dependent on relatively mature woodland. Moreover, the Florida Scrub Jay, a well-

studied cooperative breeder, inhabits very restrictive oak-scrub patches. These jays avoid other vegetational associations immediately adjacent to the oak-scrub (Woolfenden and Fitzpatrick 1984). Recently, Zack and Ligon (1985) demonstrated that the cooperatively breeding Gray-backed Fiscal Shrike used primarily dense yellow-barked acacia (*Acacia xanthophloea*) woodlands with high density perennial shrub cover. The sympatric noncooperative Common Fiscal Shrike, exploits a broad range of situations varying from woodlands to open fields. Zack and Ligon (1985) showed that higher densities of edible insects were associated with the high density shrub cover during the dry season. In this case, the habitat used by the cooperative breeder appeared to be related to an important component of quality. The fact that my results do not show such a pattern provides further support for the suggestion that the suite of selective factors favoring the evolution of cooperative breeding probably differs among species (Fry 1972; Ricklefs 1975; Brown 1978, 1987; Emlen and Vehrencamp 1983; Koenig and Mumme 1987; Stacey and Ligon 1987).

Some differences were noted among mean characteristics of the habitat used by the two species. Harris' Hawks tend to use habitats with a greater density of larger mesquites as indicated by mean values for Tree density, Mesquite tree importance, and Level4 vegetation (Table 3), whereas Swainson's Hawks utilized habitat with more grass cover and less exposed ground. These patterns were underscored by the discriminant analysis which identified Level4 vegetation and Ground% as the variables that primarily discriminated between the species. I suggest that large mesquite are important to the Harris' Hawk because these provide suitable perch sites. Harris' Hawks primarily hunt from exposed perches, and in fact, spend more than 90% of their time on perches (Bednarz, unpubl. data). Conversely, Swainson's Hawks often hunt while in flight (pers. observ.) and thus probably require fewer perch sites than Harris' Hawks. The reason for the difference in ground cover at sites used by the two species is unknown; however, increased grass cover may maintain greater densities of the smaller prey (e.g., small rodents, lizards, arthropods) usually taken by Swainson's Hawks.

Diet information based on prey remains are probably biased towards larger prey items because smaller items are more likely to be dis-

torted or fragmented beyond recognition and are more difficult to find than larger bones. This bias, however, should be similar in my analyses of remains taken from both Harris' and Swainson's hawk nests and thus should have little bearing on the general patterns revealed in the comparative analysis. The most serious bias probably was an overestimate of lagomorph biomass in the Swainson's Hawk diet, because these hawks took significantly smaller rabbits than Harris' Hawks, and which probably are smaller than the average cottontail. The biomass expansion factor was based on the mean weight of a sample of 17 cottontails from the available population. Whether the proportion of adult-sized rabbits taken by Harris' Hawks (45 to 50%) approximates what is available during the nesting season is unknown.

Based on this analysis I suggest that Harris' Hawks typically take larger prey and exploit fewer prey types than Swainson's Hawks. My findings for the latter species agree with other food studies conducted on hawks that fed principally on mammals (e.g., Schmutz et al. 1980, Jaksic and Braker 1983, Steenhof and Kochert 1985; range of diet breadth reported = 1.1–6.5; range of diet overlap = 0.09–0.99). The Swainson's Hawk had a wide diet breadth (range = 3.7–5.0) and moderately high overlap (range = 0.42–0.70) with the sympatric Harris' Hawk. Swainson's Hawks seem to be opportunistic generalists and forage on the most available food types, as suggested by the broad range of prey types taken in each year (Table 5), as well as the variation among years in foods taken (Fig. 4). Presumably, this variation among years was related to the relative availability of the different prey types. For example, in 1982 when I saw very few orthopterans on the study area (no quantitative data were collected), a significantly higher proportion of mammals was found in the food remains of Swainson's Hawks (Fig. 4). Within its breeding range in North America, the Swainson's Hawk seems to fit Jaksic and Braker's (1983) contention that hawks are primarily opportunistic in their food habits.

Conversely, my data suggest that among raptors the Harris' Hawk may be a relative specialist. This species takes substantially larger prey than the Swainson's Hawk, as evidenced by significantly higher proportion of rabbits and significantly larger rabbits in the prey remains. The suggestion that Harris' Hawks may be relatively

specialized in their foraging opposes Mader's (1978) assertion that this species is a more versatile and generalized hunter than the Red-tailed Hawk (*Buteo jamaicensis*). However, Mader (1978) in fact listed more mammal and reptile prey types from Red-tailed Hawk nests than found at Harris' Hawk sites (Mader 1975), even though the sample of the former was substantially smaller ($n = 55$) than the latter ($n = 251$). The impression that Harris' Hawks may take a greater variety of prey is fostered because Mader found no identifiable bird parts in the prey remains from Red-tailed Hawk nests. I suggest that although it is not clear from Mader's (1975, 1978) data which species takes the greater variety of prey, his and Whaley's (1986) work in Arizona indicate that Harris' Hawks prey heavily on relatively large mammals (e.g., cottontails, woodrats, and ground squirrels) and some birds, especially quail (*Callipepla* spp.) and Cactus Wrens (*Campylorhynchus brunneicapillus*).

My evidence suggesting that Harris' Hawks tend to specialize, at first glance, seems to be at odds with Brown's (1987) argument that generalists are more likely to develop social breeding units than specialists. Brown deduced this correlation by comparing "food-cost functions" of nectarivores and omnivores (Brown 1987: 270–275). He reasoned that it would not be advantageous for nectarivores with a steep-cost function (e.g., food resources can be rapidly and severely depleted) to defend cooperatively relatively large patches. This is probably not the situation with Harris' Hawks. That is, although Harris' Hawks seem to be specialists, they cannot rapidly deplete their primary food resources, relatively elusive lagomorphs. Thus, Harris' Hawks may have a permissive food-cost function. My results clearly call for caution before linking the terms generalist and specialist to specific types of food-cost functions. Rather, the nature of the resource being exploited is probably most important when considering the utility of this intriguing hypothesis.

Two characteristics of Harris' Hawks may be related to the taking of large prey. First, toe-pad length, an index of talon size, is significantly larger (Wilcoxon's test, $z = -7.57$, $P < 0.0001$) for Harris' Hawks ($\bar{x} = 91.6$ mm, $n = 74$) than for Swainson's Hawks ($\bar{x} = 79.6$ mm, $n = 34$). Second, Harris' Hawks participate in group or cooperative hunts (Mader 1975; Bednarz, unpubl. data). Such group hunting may enhance the abil-

ity or the efficiency of the group to procure food: (1) because more eyes are available to detect prey; (2) groups may be able to subdue larger prey more efficiently (Caraco and Wolf 1975); (3) groups may have greater rates of foraging success (Mader 1979); or (4) groups may have greater success in capturing prey if peak time periods of prey vulnerability are limited (Bednarz and Ligon, in press). This could enhance the probability of survival for each group member and may be a key factor in the development of the social system of the Harris' Hawk. If group foraging does provide some advantage, this survival benefit conferred on group members could be more important in the maintenance of the group structure than any enhancement of reproductive success (Bednarz 1987a). The comparative analysis presented here suggests that foraging strategies may be critical to understanding the social structure of Harris' Hawks. Indeed, I have recently obtained preliminary results that suggest that benefits in terms of average energy available per individual in the nonbreeding season, increased up to a hunting party size of five hawks (Bednarz, unpubl. data).

This study provides some insight into factors potentially involved in the evolution of the life history traits of both hawks. The Swainson's Hawk seems to be an opportunistic predator on relatively small prey, and probably is capable of successfully inhabiting northern latitudes only when an abundance of small prey species or juveniles of larger prey species are available. In winter, such prey types become unavailable in North America, requiring that Swainson's Hawks migrate.

Recent work (Stacey and Ligon 1987; Bednarz and Ligon, in press; and this paper) suggests that neither habitat limitation nor resource localization (Selander 1964, Brown 1974, Stacey 1979, Koenig and Pitelka 1981, Emlen 1982, Koenig and Mumme 1987) is critical to the evolution of cooperative breeding in this hawk. The Harris' Hawk, primarily a tropical or subtropical species, probably tended toward taking larger prey, promoting the evolution of larger talons, perhaps enhancing the species' ability to reside year-round in the southwestern United States. A period of prolonged juvenile dependency probably is related to use of relatively large and elusive prey, and may be viewed as a form of extended parental care (see Ligon 1981). I suggest that retention of juveniles may have set the stage for

the development of both cooperative hunting and breeding. Since there seems to be no reproductive advantage to breeding in groups (Bednarz 1987a), I propose that some individual fitness advantage, probably enhanced foraging success via cooperative hunting that may translate into survival benefits, is the most important factor maintaining the group structure in the New Mexico population of the Harris' Hawk.

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