COMPETITION AND PATTERNS OF RESOURCE USE BY TWO SYMPATRIC RAPTORS[1]

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Abstract. We examined the diets of two sympatric raptors, Swainson's Hawks (*Buteo Swainsoni*) and Harris' Hawks (*Parabuteo unicinctus*), during a prey decline that resulted in lowered reproductive success for both species. Contrary to the predictions of competition theory, diets of the two species did not become more specialized. However, we observed interspecific aggression by Swainson's Hawks, which evidently defended a large territory against Harris' Hawks. We conclude that direct competition for food did not take place between these two hawks because such competition was mediated by competition for territories and the subsequent partitioning of space.

Key words: Buteo swainsoni, competition, Harris' Hawks, Parabuteo unicinctus, resource partitioning, Swainson's Hawks, territoriality.

INTRODUCTION

Top predators generally, and raptors specifically, are not subject to predation or other interference that would hold population sizes below the limits imposed by food supply. Consequently, co-occurring species of raptors are considered likely competitors for food when these resources decline (Lack 1946, Hairston et al. 1960, Schoener 1982). However, Jaksic and Braker (1983), reviewing literature on raptor food habits, suggested that competition for food was not a structuring force in raptor communities. Jaksic (1985) proposed that behavioral factors such as agonistic behavior, specifically "aggressive exclusion," might be more important in community structure. Aggressive exclusion during the breeding season would correspond with the idea that species coexistence can result from spatial and/or temporal partitioning of resources (Levin 1992).

We evaluated these opposing ideas by studying the food habits of two sympatric raptors, Harris' (*Parabuteo unicinctus*) and Swainson's (*Buteo swainsoni*) Hawks, during a prey decline. These two species were essentially the only diurnal raptors nesting on our study site, and showed high dietary overlap (Bednarz 1988a) with overlapping breeding periods. Potential nest sites are abundant in our study area (Bed-

narz et al. 1990), which should result in breeding density, as well as overall numbers, being limited by food supply (Newton 1991).

Our data indicate that food supply limited breeding numbers during the five years of our study. A severe decline in lagomorph prey, which composed the greatest portion of prey biomass for both species, was significantly correlated with reproductive success of both species of hawks (Bednarz 1995, Bednarz and Hayden, unpubl. data).

Competition theory predicts that as food resource levels decrease, diets should become more specialized, reducing the overlap in resource use between competitors (MacArthur and Levins 1967, May 1973). We analyzed the prey taken by the two raptors before and during the prey decline to determine whether the diet shifts predicted by competition theory occurred. We also observed the territorial and aggressive behaviors of the two species to evaluate the likelihood that these would reduce or eliminate competition for food (Jaksic 1985).

METHODS

STUDY AREA

Our study area is approximately 48 km east of Carlsbad, New Mexico, in the area known as Los Medaños, and includes approximately 200 km² centered on the Waste Isolation Pilot Project (WIPP) site. Dominant vegetation is mesquite (*Prosopis glandulosa*) shrubland and grassland (Bednarz et al. 1990). All work was done between 1981 and 1989, with the most intensive

work completed between 1981–1983 and 1986–1987.

LAGOMORPH ABUNDANCES

We counted lagomorphs during road surveys starting approximately 15 min before sunset, driving the transects at approximately 25 km hr^{-1} and counting all jackrabbits (*Lepus californicus*) and cottontails (*Sylvilagus auduboni*) seen. Ground vegetation generally obscures rabbits beyond the edge of roads, so we only counted animals in the road or immediately next to it. From 1981 to 1983, the survey route covered 16 km of shinnery oak (*Quercus havardii*) grasslands. Road modification for the WIPP plant forced a route change from 1985 to 1987; 8 km of the original route were maintained and another 8 km was added 1.3 km to the west of the original route. This new section ran through creosote (*Larrea tridentata*) grassland, and we believe was comparable, in terms of lagomorph use, to the original road transect. We have included only censuses run between 15 April and 15 August, corresponding to the time when breeding hawks were present on the study area.

Roadside counts have been an accepted method used to monitor annual population fluctuations in cottontail rabbits (Wight 1959, Kline 1965, Fafarman and Whyte 1979) and correlate well with other indices of cottontail population abundance (Drew et al. 1988). Significant correlations have been shown in our study area between lagomorph road-counts and reproductive success for both Harris' Hawks (Bednarz 1987, 1995) and Swainson's Hawks ($r_s > 0.7$, $P < 0.05$ for correlations between total lagomorphs counted and clutch size and number of young fledged; Bednarz and Hayden, unpubl. data). On the basis of these significant findings, we argue that road count indexes provide a useful relative measure of the cottontail prey available to both Swainson's and Harris' Hawks.

We used counts of fecal pellets to assess the number of lagomorphs in the vicinity of nest trees, sampling 10 1-m^2 quadrats placed at random intervals along a line extending 1,000 m on a random compass bearing from the nest tree. Pellets of diameter greater than approximately 8 mm were assigned to jackrabbits, whereas those of smaller diameter were assumed to be cottontails (Bednarz and Ligon 1988).

PREY SIZE AND DIET COMPOSITION

As an index of prey size, we measured lagomorph femur lengths from the notch between the greater trochanter and head to the notch between the distal and lateral condyles. We also categorized prey as adult or juvenile if the epiphyseal discs were fused or unfused, respectively.

We measured a total of 1,083 femurs ranging in length from 35.3 to 100.1 mm. The length of femurs with fused epiphyseal disks was generally between 60 and 70 mm, with only 3 of 378 measurements (59.8, 59.9, and 70.4 mm) falling outside that range. Consequently, we divided femurs into three classes. Because the femurs with fused disks were found only in the mid-range of measurements, we considered them to be from adult cottontails. Femurs with unfused disks and length greater than 70 mm we classified as juvenile jackrabbits, and those with unfused disks and length less than 70 mm were classified as juvenile lagomorphs (species undetermined).

We analyzed diet from prey remains and pellets gathered under nests or nearby perches during and immediately following the nesting period. Remains were identified by comparison with specimens in the Museum of Southwestern Biology, University of New Mexico. The prey categories used in analyzing diet trends were juvenile *Lepus*, adult *Sylvilagus*, juvenile lagomorphs, small mammals, reptiles, and birds. Insect remains were not included in the diet proportions because they account for an extremely low percent of prey biomass (Bednarz 1988a) and their numerical abundance is difficult to determine.

Prey remains were collected from all Swainson's Hawk nests and from Harris' Hawk nests that hatched between 1 March and 31 August. This period coincides with the shorter nesting period of the Swainson's Hawks, roughly 15 April to 15 August. Harris' Hawks generally nested earlier than Swainson's Hawks in our area (Bednarz 1987, 1988a), but actively foraged throughout the summer with their young and continued to hunt in the same areas year-round. We observed that after the Harris' Hawks fledged, the color-marked young often returned and fed at the nest site. Therefore, we collected their prey remains from nests and adjacent branches both during the nestling period and for one to three weeks after fledging.

To assess the accuracy of prey percentages

calculated from remains, we visually observed prey deliveries to nests, starting at first light and ending around 11:00. We placed blinds from 35 to 150 m from the nests, allowing us to identify most of the prey to the species level. We observed four Swainson's Hawk nests for a total of 70 hr in 1986, and two nests for a total of 45 hr in 1987. Between 1985 and 1987, we observed 51 different Harris' Hawk nests for a total of 338 hr.

HOME RANGE

During 1986 and 1987, we radio-tracked 13 Harris' Hawks and 1 adult male Swainson's Hawk. Tracking often allowed incidental observations of interactions between the two species; during the nesting season these interactions were presumably of birds from adjacent or nearby nests.

The nearly flat terrain and shrubby vegetation in the study area allowed good visibility and almost continuous monitoring of hawk positions. While tracking the one Swainson's Hawk, we also noted the activities of its mate. We recorded positions for both the radiotagged male and its mate when the birds were perched or flying just above the ground (ca. 4 m or less), allowing positions to be plotted with good accuracy, probably within 10 m in most cases. Swainson's Hawks generally hunt from a perch or from low flight (Palmer 1988, pers. observ.), so this method gives a good estimate of the bird's territory. We began tracking in the morning after visibility was adequate to avoid accidentally flushing the hawks, and terminated observations when the male began soaring about mid-day. High soaring raptors often move outside their territory (Newton 1979), and soaring Swainson's Hawks in our study area did not appear to be foraging. The morning observation periods corresponded to the times we saw prey delivered to the nest. We also tracked in late afternoon and evening when the birds were not soaring but were actively hunting away from the nest.

When radio-tracking Harris' Hawks, we plotted the bird's location on topographic maps every 10 min, excluding birds that were soaring. Monitored Harris' Hawks included six adult and seven immature-plumaged birds, and sampling was done year-round. Locational data collected outside the breeding season were used in this study because the areas exploited by Harris' Hawks do not normally change from season to season (Bednarz 1995). Analysis of a larger sample of Harris' Hawk radio-location data indicated that there were no significant differences in sizes of home ranges used by the different sexes and age classes (Bednarz and Hayden, unpubl. data). Immature Harris' Hawks often associate closely with adult breeders (Bednarz 1988b, Faaborg and Bednarz 1990) and their range is typically identical to that of their parents, except when they begin dispersal.

Our estimates of Harris' Hawk home range size were based on 10 radio-tagged hawks. Two adult females were excluded from this analysis because they were closely attending nests and thus had extremely small ranges (under 0.5 km^2, less than 15% of the mean area used by other radio-tagged hawks) that distinctly under-represented the foraging area used by the breeding group as a whole. We also omitted one immature-plumaged bird with an unusually large range (9.9 km^2, an obvious outlier), that we suspected was in the process of dispersal.

DATA ANALYSES

Home range areas were estimated using version 1.2 of McPaal, a public domain home range analysis program developed at the Conservation Research Center, National Zoological Park, Smithsonian Institution, Washington, D.C.

Other data were analyzed using main-frame SAS version 5.16 (SAS Institute 1986). Significance was determined at the $P < 0.05$ level except where noted. No data met the criteria for normality; consequently, we used nonparametric or other suitable forms of analysis. Distribution of femur length measurements was largely normal except for a few outliers; pairwise comparisons of these measurements were computed using the method of trimmed and windsorized means (Koopmans 1987). Right femurs were plotted in Figure 2 because the sample size was slightly larger than for left femurs. Values reported below are means ± SD.

RESULTS

LAGOMORPH CENSUSES

Counts of lagomorphs decreased from 1981 to 1987 (Fig. 1); the difference is significant for both cottontails (Kruskal-Wallis test, $\chi^2_4 = 17.4$, $P < 0.001$) and jackrabbits ($\chi^2_4 = 28.4$, $P < 0.001$). Mean cottontail numbers were very high in 1981 (16.8 ± 11.1), but decreased between 1982 and 1986, and were extremely low in 1987 (1.3 ± 1.3). Mean jackrabbit numbers were high
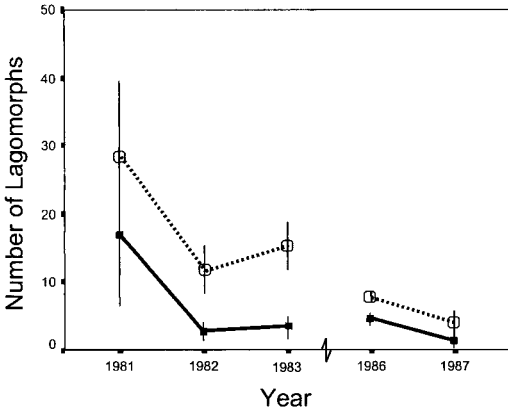
FIGURE 1. Lagomorph counts along road transects, 15 April to 15 August, 1981–1983 and 1986–1987. Both cottontails (solid line) and the total of cottontails and jackrabbits (broken line) are shown. Vertical lines show the 95% confidence intervals.
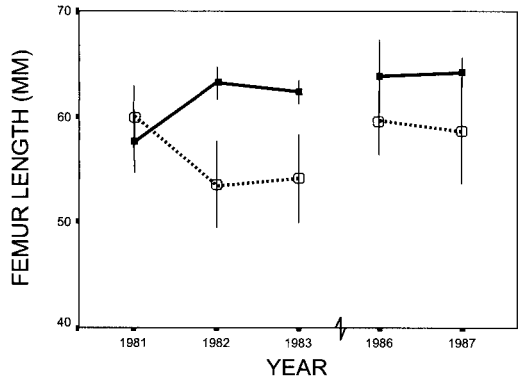

FIGURE 2. Femur lengths of lagomorphs in prey remains of Harris' Hawks (solid line) and Swainson's Hawks (broken line). Vertical lines show 95% confidence intervals determined by the method of trimmed and windsorized means (see text).

in 1981 (11.4 ± 2.1), remained relatively high through 1983, then were much lower in 1986–1987 (2.7 ± 1.6 for 1987). Counts before and after 1984 are not directly comparable because the route was altered to accommodate road modifications in 1985. However, the counts on the portion of the route which remained the same show the same pattern of decline as the counts over the entire route, and we believe that counts on both routes provide a reliable index of the change in available lagomorph populations.

Data collected from a 10-year period (1981–1990, excluding 1984) showed raptor reproductive success to be significantly correlated with the lagomorph counts used in this analysis (Bednarz and Hayden, unpubl. data). Cottontail counts were significantly correlated ($r_s > 0.75$, $P < 0.02$, $n = 9$ years) with Harris' Hawk clutch size, number of young fledged per nest, and the percentage of successful nests (Bednarz 1987, 1995). For Swainson's Hawks, cottontail counts were significantly related to clutch size and number of young fledged ($r_s > 0.70$, $P < 0.05$, $n = 9$ years), and jackrabbit counts were related to the number of young fledged and the percentage of successful nests ($r_s > 0.68$, $P < 0.05$, $n = 9$ years) (Bednarz and Hayden, unpubl. data).

PREY SIZE

The size of right femurs found at both Swainson's Hawk (Kruskal-Wallis test, $\chi^2_4 = 10.5$, $P = 0.03$) and Harris' Hawk nests ($\chi^2_4 = 17.2$, P

< 0.002) varied between years (Fig. 2). This pattern also was present for left femurs, and differences also were significant ($\chi^2_4 = 13.5$, $P < 0.001$ for Swainson's Hawks; $\chi^2_4 = 19.4$, $P < 0.001$ for Harris' Hawks).

Pairwise comparisons between prey femur lengths show the right femurs in Harris' Hawk prey to be significantly larger than Swainson's Hawk prey in 1982 and 1983 (method of trimmed and windsorized means, $P < 0.001$ for both years), but there was no significant difference in the other years ($P > 0.50$ for 1981, 1986, and 1987). Results were the same for left femurs. Because multiple comparisons were made for the five years, the significance level used for this comparison was $P < 0.05/5$, or $P < 0.01$ (Koopmans 1987).

There was no significant correlation of cottontail abundances with the difference in mean femur lengths between hawk species (Kendall rank correlation, $r = -0.40$, $P = 0.33$ for right femurs; $r = -0.60$, $P = 0.14$ for left femurs).

DIET COMPOSITION

In the Los Medaños area, Harris' and Swainson's Hawks had similar diets. However, Harris' Hawks tended to take a higher percentage of lagomorphs generally, and more adult *Sylvilagus* specifically, than Swainson's Hawks (Table 1). Swainson's Hawk diets show a high percentage of juvenile lagomorphs, and consistently included a wider variety of reptiles and insects than Harris' Hawks (Tables 1, 2; Bednarz 1988a). For both species, analysis of prey remains and of

TABLE 1. Percentages of prey types found in prey remains at Swainson's and Harris' Hawk nests.

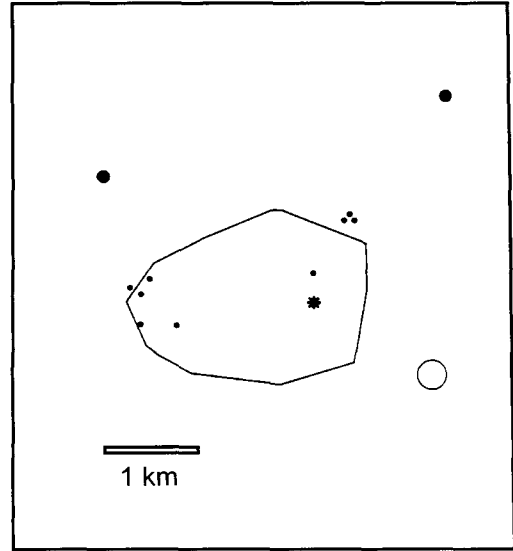|	Swainson's Hawk	Harris' Hawk
1981		
Lagomorphs	38.5	58.0
Juvenile *Lepus*	4.5	1.5
Adult *Sylvilagus*	2.3	14.1
Juvenile lagomorph	31.7	42.4
Other vertebrates	61.5	42.0
1982		
Lagomorphs	46.8	79.5
Juvenile *Lepus*	0.0	2.3
Adult *Sylvilagus*	2.0	46.8
Juvenile lagomorph	44.8	30.4
Other vertebrates	53.3	20.4
1983		
Lagomorphs	35.8	74.4
Juvenile *Lepus*	4.7	3.4
Adult *Sylvilagus*	3.1	34.2
Juvenile lagomorph	28.0	36.8
Other vertebrates	64.3	25.7
1986		
Lagomorphs	43.6	72.5
Juvenile *Lepus*	6.1	17.3
Adult *Sylvilagus*	6.1	20.7
Juvenile lagomorph	31.4	34.5
Other vertebrates	56.4	27.6
1987		
Lagomorphs	28.9	64.5
Juvenile *Lepus*	3.8	12.0
Adult *Sylvilagus*	1.3	20.8
Juvenile lagomorph	23.9	31.7
Other vertebrates	71.1	35.5

FIGURE 3. Minimum convex polygon representation of home range of a nesting Swainson's Hawk pair (solid line). Asterisk shows the Swainson's Hawk nest site. Large black circles are Harris' Hawk nests, the white circle is the location of a non-nesting group, and the small black circles show sightings of Harris' Hawks made while tracking the Swainson's Hawk.

observed prey deliveries showed the importance of cottontails in their diet. Lagomorph percentages from the prey remains may be somewhat higher than what was actually taken because these larger bones are easier to find and survive weathering better than the bones of smaller prey.

HOME RANGE

A minimum convex polygon representation of home range, based on 87 points plotted for both the radio-tagged male Swainson's Hawk and his mate, shows a generally oval shaped area of 4.0 km² (Fig. 3). Observed Harris' Hawk locations are shown, and generally cluster around the bor-

TABLE 2. Observed prey deliveries to hawk nests.

Prey	Swainson's Hawk 1986–1987		Harris' Hawk 1985–1987	
	No.	Percent	No.	Percent
Lagomorphs				
Desert cottontail (*Sylvilagus auduboni*)	11	21.2	15	17.9
Black-tailed jackrabbit (*Lepus californicus*)	0	0.0	2	2.4
Unidentified lagomorphs	0	0.0	6	7.1
Total lagomorphs	11	21.2	23	27.4
Other mammals	13	25.0	36	42.9
Reptiles	17	32.7	19	22.6
Birds	0	0.0	2	2.4
Insects	11	21.2	0	0.0
Unidentified	0	0.0	4	4.8

der of the Swainson's Hawk home range. In addition, we observed a Harris' Hawk perched on the Swainson's Hawk old nest tree on 16 September, after Swainson's Hawks migrated from the area.

We recorded between 85 and 150 locations for each Harris' Hawk included in the analysis. These 10 hawks used home ranges varying from 2.1 to 5.9 km², with a mean of 3.9 ± 1.5 km².

DISCUSSION

Demonstration of resource limitation is a necessary precondition for the evaluation of possible competition, because by definition (Pianka 1994) competition involves the use of resources in short supply. The correlation between the decline in lagomorph prey on our study site and the decline in both Swainson's and Harris' Hawk productivity (Bednarz 1987, 1995, Bednarz and Hayden, unpubl. data) indicates that the assumption of resource limitation is warranted for our study.

Potential foraging areas of the two hawk species overlapped substantially in our study area. Between 1985 and 1987, one 77.7 km² portion of our study area contained a mean of 16 (range 14–18) Harris' Hawk nests and a mean of 10 (range 7–13) Swainson's Hawk nests. If the observed foraging territory sizes of approximately 4 km² were typical for both Swainson's and Harris' Hawks, then 26 nests of both species would require a total of 104 km² of foraging area. Thus, as much as 34% of the foraging area may have been shared in our intensive study area (104.0 km² − 77.7 km² = 26.3 km² of estimated common use foraging area). This overlap in foraging area, along with the overlap in nesting periods, indicates the potential for competition for food. Our home-range estimates are probably indicative of foraging areas, because we excluded all observations of soaring hawks, and the hawks appeared to be constantly searching for prey when perched or flying low over the ground.

LAGOMORPHS AS PREY

Based on analysis of prey remains, Bednarz (1988a) found that cottontails provided the greatest proportion of prey biomass for the two hawks (91% for Harris' Hawks and 81% for Swainson's). Our results (Tables 1, 2) support that conclusion. Few lagomorphs were taken with femurs longer than 70 mm, strongly suggesting that relatively few jackrabbits were tak-

en as prey by either species of hawk, at least during the breeding season. Of the three categories of lagomorphs, adult *Sylvilagus* and juvenile lagomorphs constitute a much higher percentage of prey than juvenile jackrabbits. A high percentage of the juvenile lagomorphs were probably cottontails, because our nest observations show that most of the lagomorphs taken as prey were *Sylvilagus* (Table 2). Therefore, we consider the cottontail data as the best single indicator of prey abundance available to hawks for all the years of the study.

PREY LEVELS AND DIET COMPOSITION

Competition theory predicts that when food resource levels fall, diets should become more specialized, reducing overlap in resource use between consumer species and minimizing the competition between them (May 1973). A variety of factors, including harsh or nonequilibrial environmental conditions, could reduce the intensity or frequency of competition, although these will not ultimately reduce the selective value of resource partitioning, and niche differences are still necessary for species coexistence (Chesson and Huntly 1997). These differences can be spatial or temporal or both (Levin 1992).

In our study, the co-occurrence of high cottontail counts and a high overlap in resource use in 1981, the great drop in cottontail counts in subsequent years, and the correlation between cottontail numbers and reproductive success for both hawks, are all consistent with the classical view (Lack 1946) of high overlap as an indicator of relaxed competition due to high resource abundance. Consequently, comparison of resource use in periods of relatively abundant and relatively scarce resources should reveal the presence of competition (Lack 1946, Steenhof and Kochert 1985).

Two observations indicate that Harris' Hawks may be better adapted to taking larger prey than Swainson's Hawks, and should therefore specialize on larger prey when prey populations fall. First, Harris' Hawks have significantly larger feet than Swainson's Hawks by a ratio of 1.15:1 (Bednarz 1986), and they may therefore be anatomically better adapted for taking larger prey. In addition, Swainson's Hawks generally hunt individually in open areas (Palmer 1988, pers. observ.). In contrast, Harris' Hawks are agile in pursuing prey around ground-level obstacles (Mader 1988), and hunt cooperatively, uti-

lizing terrain where numerous perches are available, and a group of hawks can move from perch to perch while following and attacking prey (Bednarz 1988b, Mader 1988). These tactics presumably enhance the ability of Harris' Hawks to take jackrabbits and adult cottontails, as reflected in the consistently higher percentages of these prey in prey remains from Harris' Hawk nests (Table 1).

An increased difference in prey size in the low prey years after 1981 would indicate dietary specialization. However, there was no statistical correlation between cottontail abundance and the difference between femur lengths of lagomorphs taken by the two hawks. Although femur lengths of prey taken by Harris Hawks were larger after 1981, the overall pattern was inconsistent (Fig. 2). The two hawks utilized lagomorphs of equal size when prey was abundant in 1981, then different-sized lagomorphs in 1982 and 1983, after the prey population declined. However, in 1986 and 1987, lagomorph femur lengths of Swainson's Hawk prey increased sufficiently that the two hawks again utilized the same size prey (Fig. 2). Our data suggest that available prey may have been at the lowest point during these two years, as indices of both cottontail and jackrabbit abundance dropped severely during this period (Fig. 1).

Similarly, greater segregation of prey types by the two hawk species did not occur during the prey decline (Table 1). This result again fails to support the predictions of competition theory. In all years, regardless of prey levels, Harris' Hawks consistently took more lagomorphs and less of the other prey categories than Swainson's Hawks. Harris' Hawks did show some evidence for dietary specialization on larger prey at the beginning of the prey decline, as the percentage of adult cottontails in their diet rose from 15% in 1981 to 45% in 1982. However, in 1986 and 1987, while the prey population remained low, the percentage of adult cottontails taken by Harris' Hawks declined to almost its original level (Table 1). The percentage of adult cottontails in the Swainson's Hawk diet was consistently low, with the highest utilization in 1986, when cottontail numbers were low.

These patterns could be the result of simple foraging opportunism. Local variation in timing of lagomorph reproduction could change the abundance, age, and size of available prey during the nesting season. This would be especially true for hawks preying on dispersing, juvenile lagomorphs. Overall prey age-distribution might also change. In 1982, when cottontails crashed, juvenile cottontails might have been relatively scarce, with their numbers slowly increasing in later years. Thus, during 1986 and 1987, Harris' Hawks might have opportunistically taken more juveniles as their numbers rose relative to the number of adults.

Steenhof and Kochert (1985) suggested opportunism as a likely explanation for diet changes in hawks during a prey decline, although the presumption of resource limitation is weakened in their study by the inconsistent response of the two raptors studied to the decline in prey: neither species showed a decline in nesting numbers, and only one a decline in nest productivity. Opportunism provides an equally valid explanation of results in our area, where the interspecific territoriality displayed by Swainson's Hawks evidently results in separation of hunting areas of the two species. Within these territories, each species could forage independently and opportunistically.

SEPARATION OF HOME RANGE BY TERRITORIALITY

Where raptors are interspecifically territorial, the size of the territory varies from the immediate nest area to large hunting territories (Newton 1979). Harris' Hawks show some territorial behavior (Dawson and Mannan 1991), but this is only weakly displayed in our New Mexico study area (Bednarz 1987, 1995). In contrast, Swainson's Hawk aggressiveness towards other raptors is well documented, and this aggressiveness appears related to interspecific territoriality (Porton 1977, Rothfels and Lien 1983).

Schmutz et al. (1980) experimentally found Swainson's Hawks to be both qualitatively and quantitatively more aggressive than Ferruginous Hawks (*Buteo regalis*) when near the nest, and Swainson's Hawks were the aggressors in natural interactions with Ferruginous and Red-tailed Hawks (*Buteo jamaicensis*). The authors suggested that the aggressiveness of Swainson's Hawks explained their ability to nest near, and even displace, Ferruginous Hawks. Janes (1984) found that late arriving Swainson's Hawks could displace Red-tailed Hawks from portions of their established territories, describing the aerial combat involved as "impressive."

The ability of Swainson's Hawks to aggres-

sively displace hawks with established territories would be an obvious advantage in the Carlsbad area, where Harris' Hawks are present year-round and begin nesting before Swainson's Hawks arrive (Bednarz 1988a). From 1985 through 1989, Bednarz and T. Hayden (unpubl. data) observed 15 aggressive interactions between Swainson's and Harris' Hawks in our study area. The earliest was on 22 April and the latest on 2 September. In 14 interactions, the Swainson's Hawk was the aggressor, stooping or diving on the Harris' Hawks from above on 12 occasions. In one interaction, a single Swainson's stooped on a group of four Harris' Hawks after they had made a kill. An especially prolonged, violent encounter occurred in an area where pairs of both species nested within 175 m of each other, with the Swainson's Hawk repeatedly driving the Harris' Hawks from the area. Both these pairs successfully fledged young, even though they nested relatively late in the season and a pellet-count transect showed that the nest area supported only an average number of lagomorphs.

The home range of our radio-tagged Swainson's Hawk was between two nesting groups of Harris Hawks, and there was a non-nesting group in the vicinity (Fig. 3). We observed only nine Harris' Hawk positions while tracking the nesting Swainson's Hawks, even though most tracking was done from a ridge which allowed good visibility over the entire home range. Seven of these nine positions were located on the perimeter of the Swainson's Hawk home range (Fig. 3), supporting the premise that Swainson's Hawks are interspecifically territorial and exclude Harris' Hawks from a large territory. Of the two plotted locations inside the perimeter, one (north of the nest) was observed three days after the Swainson's nestling had fledged. The other (to the west), even though inside the perimeter, was still approximately 1.5 km from the nest. Although we did not observe any conspicuously antagonistic behavior between the two species while radio-tracking, we did observe them circling close together at the edge of the Swainson's Hawk territory.

Because we did not capture and radio-tag the male until the nest was well established, the Swainson's Hawks may have established their home range and excluded Harris' Hawks from their territory before we started radio-tracking at this site, accounting for the lack of observed in-teractions. Harris' Hawk incursions into the territory three days after the chick fledged, and later in the fall after Swainson's Hawks migrated from the area, indicate the potential for intrusion into the territory if it were not defended. Because these tracking observations are limited to one territory, we could not directly observe the effect of territoriality on competition for food. However, the tracking observations are consistent with our other observations of Swainson's Hawk aggressiveness, and support the broader idea that competitive territorial exclusion repressed direct competition for food during our study.

CONCLUSIONS

Even though food supply limited Swainson's Hawk population size during the years of our study, we did not find the prey specialization expected from competition theory. We conclude either that the predictions of the theory do not apply to our situation, or that direct competition for food did not occur between the two raptor species. We believe that the latter was correct, and that competition for food was mediated by aggressive behavior, as Jaksic (1985) suggested. In our study, aggressiveness was primarily on the part of Swainson's Hawks, which evidently excluded Harris' Hawks from a large territory around the nest.

Raptors (and "top predators" as a general class) are capable of quite complex behavior, and these behaviors may allow coexistence without the resource shifts theoretically expected. It is impossible to state that these behaviors are evolutionary responses to the pressures of interspecific competition, and behaviors such as territoriality may have a completely unrelated evolutionary origin. The apparent proximate effect of territoriality on foraging in our study was to replace direct competition for food with interference competition for foraging areas, resulting in prey selection patterns that presumably reflected foraging opportunism rather than competition.

helped with much of the logistics of Swainson's Hawk work as well. B. Dennis and M. Engbring provided figures. Stuart Janes helped relocate some original field notes. We appreciate constructive criticism of earlier drafts from S. Mills, K. Steenhof, and two anonymous reviewers. Field work in 1986 and 1987 was partially supported by the U.S. Department of Energy (Waste Isolation Pilot Plant studies).

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