

SUCCESSIVE NESTING AND AUTUMNAL BREEDING IN HARRIS' HAWKS

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ABSTRACT.—I monitored 24–29 breeding groups of Harris' Hawks (*Parabuteo unicinctus*) in southeastern New Mexico during a 40-month period. Each year 29–70% of these groups made a second breeding attempt in either late summer or autumn, often following successful spring breeding. The interbrood period was positively correlated with the size of the first brood. Clutches were initiated between 17 February and 1 November. The mean number of hawks fledged from autumn nests was less (0.94) than that produced from spring (1.30) and summer (1.36) nests. The composition of prey remains found at nests in different seasons was similar. The number of second nests initiated was correlated with the number of lagomorphs but not with precipitation. Harris' Hawks did not time nesting to coincide with peak population levels of their principal prey; rather, this species has a flexible and prolonged breeding season that may have evolved in part to minimize the impact of stochastic climatic conditions that increase the probability of nest failure. *Received 21 February 1986, accepted 27 August 1986.*

AVIAN breeding seasons typically coincide with circumstances such as abundant food, decreased competition, minimal predation, or benign climatic conditions (ultimate factors) that result in the successful recruitment of young into the population (Immelmann 1971). Birds breed in different months in different regions of the world, but each species usually lays its eggs at about the same date each year. The initiation of reproduction is triggered by the proximate cues that most reliably predict the onset of key ultimate factors (Perrins 1970, Immelmann 1971).

For most temperate-region birds, photoperiod is the most important proximate cue used to time the breeding seasons (Murton and Westwood 1977). In the tropics, where photoperiod varies little, or in unpredictable desert environments, precipitation is regarded as an important cue in the initiation of reproduction (see Brown and Britton 1980). In both temperate and tropical regions, food supply is probably the most important ultimate factor in the determination of avian breeding seasons (Lack 1968, Perrins 1970, Immelmann 1971). At northern latitudes, therefore, breeding seasons typically coincide with the annual spring and summer pulse of productivity. A few species such as the Red Crossbill (*Loxia curvirostra*; Tordoff and Dawson 1965), Tricolored Blackbird (*Agelaius tricolor*; Orians 1960, Payne 1969), and Pinyon Jay (*Gymnorhinus cyanocephalus*; Ligon 1971) also breed in the autumn.

Birds of prey normally raise only one brood in a year (Newton 1977, 1979), although some of the smaller raptors, such as the American Kestrel (*Falco sparverius*) and the Black-shouldered Kite (*Elanus caeruleus*), occasionally rear two broods in one year (Pickwell 1930, Stahlecker and Griese 1977, Toland 1985). Of the larger species, the Common Barn-Owl (*Tyto alba*) breeds almost year-round, primarily in tropical environments (Otteni et al. 1972, Bunn et al. 1982, Lenton 1984). De Vries (1975) recorded three successful second-brood attempts by the equatorial Galapagos Hawk (*Buteo galapagoensis*). Harris' Hawks (*Parabuteo unicinctus*) in temperate North America are known to nest in the autumn in Texas (LeSassier and Williams 1959, Brannon 1980), Arizona (Radke and Klimosewski 1977, Ellis and Whaley 1979), and New Mexico (Pache 1974). Mader (1975) and Whaley (1986) documented that Harris' Hawks laid eggs as early as January and fledged young as late as October. In addition, Mader (1975) observed five cases in which breeding groups with one or more banded adults re-nested after successfully rearing a first brood. Harris' Hawks, therefore, are unusual among large Temperate Zone raptors in having a prolonged breeding season and in rearing successive broods in one year.

Here I report year-round observations on the reproductive efforts of breeding groups of Harris' Hawks in a New Mexico population over a 40-month period, and describe the temporal

patterns of breeding and successive nesting attempts. I then relate these patterns to fluctuations in available prey and precipitation to identify potential proximate and ultimate factors.

STUDY AREA AND METHODS

The study area was approximately 150 km² and was located in Eddy and Lea counties in southeastern New Mexico. The habitat is mesquite-oak shrubland with rolling sandy soils. The dominant shrubs include mesquite (*Prosopis glandulosa*), Havard's oak (*Quercus havardii*), sand sage (*Artemisia filifolia*), snakeweed (*Gutierrezia sarothrae*), yucca (*Yucca compestris*), and creosotebush (*Larrea tridentata*). Harris' Hawks nested primarily in larger mesquite and soapberry trees (*Sapindus drummondii*) dispersed throughout the study area. This region of New Mexico is dry with a normal annual total precipitation of 30.25 cm (30-yr average; NOAA 1973). Typically, there is a daily temperature fluctuation of 15°C or more. Summer temperatures can exceed 40°C during the day and may drop below 20°C at night. In winter, night temperatures below -10°C are recorded regularly. Snow or ice storms can occur in the study area from mid-October through April, and violent summer rainstorms are common.

Data were collected between August 1980 and November 1983. I made at least one visit to the study area in each month except December and February. Each year (1981-1983) all known nesting ranges were searched thoroughly at least three times (in spring, summer, and autumn) for the presence of active nests. If no nests were found during any of these searches, I reexamined ranges without active nests until I was reasonably sure that no nesting attempt had been missed. If a nest failed early in the incubation stage, this often could be determined by the presence of broken eggshells either in the nest or on the ground. Given the intensity and frequency of my search efforts, conspicuousness of nests, and scarcity of suitable nest trees, I believe I missed very few breeding attempts that failed during early incubation. Fledging was recorded as successful only after volant young were seen away from the nest. The nesting area of Harris' Hawks in New Mexico does not seem to be defended actively (Bednarz 1986) and thus should not be referred to as a territory. Therefore, I use the term "nesting range," defined as the area habitually occupied by a breeding group of hawks and within which they placed their nests.

Adults and nestlings were banded with unique color combinations of vinyl tarsal bands. Bands were made with Norcross virgin vinyl (Norcross Industries, West Palm Beach, Florida) strips (7 cm in length for males and 7.5 cm for females; width = 1.6 cm) riveted together, leaving a trailing tab approximately 2.5 cm in length. Adults were trapped with bal-chatri

(Berger and Mueller 1959) and padded steel leg traps. During the study, I color-marked 163 hawks. By November 1983 about half of the approximately 75 adult-plumaged hawks in the population were banded.

Age of nestling hawks was estimated by use of the regression equation: estimated age = 8.73991 + (length of seventh primary in mm × 0.19797), determined from 200 measurements of 24 known-age nestlings of both sexes ($F = 4.135$, $P < 0.0001$, $r^2 = 0.95$). Males and females exhibited no significant differences in the growth of this primary feather during the measurement period. The relationship of seventh-primary length and age is linear after the feather begins emerging at about 8 days of age (Fig. 1).

All nestlings were measured and weighed during each nest visit, and hatch dates were estimated with the above equation. Because most nests contained multiple nestlings that were measured several times, I was able to calculate an average estimated date of hatching. I estimated dates for clutch initiation and fledging for 78 nests by using standard incubation (34 days, $n = 4$ clutches) and brood-rearing periods (46 days, $n = 12$ nestlings). Males tended to fledge earlier than females (mean = 43.5 days, $SD = 1.76$, $n = 6$ vs. mean = 48.6 days, $SD = 3.14$, $n = 6$; $P > 0.1$).

For nests that failed before the eggs hatched ($n = 33$ nests), the date of nest initiation was estimated based on the length of time the nest was known to be active and when the adults abandoned the nest. For these nests the estimated date of nest initiation could be in error by as much as 14 days. Clutch initiation for 4 nests that were found just after the young fledged was determined by using the estimated date of fledging and subtracting 80 days (34-day incubation + 46-day brood-rearing periods).

Food consumed by nestling Harris' Hawks was 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. Mammal fur was not used in this analysis because it was difficult to identify conclusively, and preliminary analysis of fur paralleled the results obtained from skeletal remains. The minimum number of individuals of each prey taxa present at each nest was the maximum number of a specific bone for each species represented in the remains. As I found no reliable character to distinguish cottontail rabbit (*Sylvilagus audubonii*) 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 estimated by multiplying numbers of prey taken by the average wet mass of prey types, assuming no waste. Mean mass values for three dominant prey types, desert cottontail, woodrat (*Neotoma* spp.), and spotted ground squirrel (*Spermophilus spilosoma*), were

based on samples collected at the study area (561 g, SD = 197, $n = 17$; 217 g, SD = 29, $n = 288$; and 117 g, SD = 73, $n = 32$, respectively). The intermediate or overall mean mass values reported by Steenhof (1983) were used as biomass estimates for rarer prey.

Road counts of cottontails and black-tailed jackrabbits were conducted twice each month from May 1981 to October 1983, except February and December. The census was run in alternating directions over the same 16-km route beginning 15-25 min before sunset and ending at sunset. The transect route dissected almost the entire study area (ca. 150 km²), and I feel that the mean values for each month were representative of relative numbers of lagomorphs available to the hawks.

For several analyses, nests were classified as spring, summer, or autumn nests: spring nests = young hatched before 1 June, summer nests = young hatched between 1 June and 31 August, and autumn nests = young hatched 1 September or after. Standard parametric analyses were used where suitable; however, most data were analyzed with Kruskal-Wallis or Spearman's correlation statistics because distributions deviated from normal (Sokal and Rohlf 1981).

RESULTS

Temporal breeding patterns.—In autumn 1980, I found 7 active Harris' Hawk nests, 2 initiated in August and 5 initiated in September, in an area about one-third the size of the study area. Based on findings in subsequent years, I believe I thoroughly searched 10 Harris' Hawk nesting ranges at that time. If all of these ranges were occupied in 1980, then 70% of this sample of hawk ranges were used for autumn breeding in that year. Of the 7 nests, 5 failed during rain (1) or snowstorms (4) and 2 were successful.

In 1981, I thoroughly searched 22 nesting ranges throughout the year. Range 21 was not checked adequately for breeding in the autumn, and range 25 was discovered in late August and thus was not examined during the previous spring (Fig. 2). The earliest clutch in 1981 was initiated on about 17 February. By May, 20 groups (91% of those monitored year-round) were tending active nests in stages varying from egg laying to fledging (Fig. 2). Of the 16 groups that successfully fledged young during their spring breeding attempt, 8 (50%) nested a second time and 6 of these (37.5%) successfully produced a second brood. Breeding pair 7 initiated its second clutch only 9 days after its first young fledged, and then laid a third clutch of eggs in October after successfully fledging 2 broods of one young (Fig. 2).

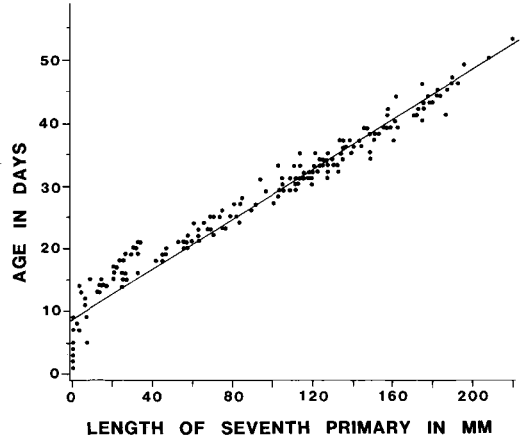


Fig. 1. Regression of nestling age on seventh primary length.

Three of the 5 breeding units that were unsuccessful in their first attempt successfully reared young from a second nest. Group 9 made four nesting attempts, and the female laid a minimum of 14 eggs in 4 clutches in 1981 (Fig. 2). Group 4 initiated its first and, as far as known, only breeding attempt in September. The latest clutch of eggs was laid between 16 October and 1 November by group 9, but failed before the eggs hatched. Had it been successful, young would have fledged in January. The latest successful breeding effort recorded (group 4) was initiated on 16 September, and one young left the nest about 5 December and was seen alive in January. Group 19 was caring for nestlings until at least the second week in December, when the nest was destroyed by an unknown predator. These observations suggest that under ideal conditions Harris' Hawks in southern New Mexico can fledge young well into December. In 1981, active hawk nests were present on the study area for more than 300 days of the year.

In 1982 initial breeding attempts were much more synchronous than in 1981 (Fig. 3). Of the 28 breeding groups followed year-round, 93% were nesting by early April. Seven (33%) of the 21 groups that were successful during their first attempt bred a second time, and 5 of these fledged two broods. Three of the 6 groups whose first nests failed tried a second time; all of these were unsuccessful. Group 9 initiated its first and probably only breeding effort of the year in September. The earliest 1982 clutch (group 17) was laid on 3 March, and the last

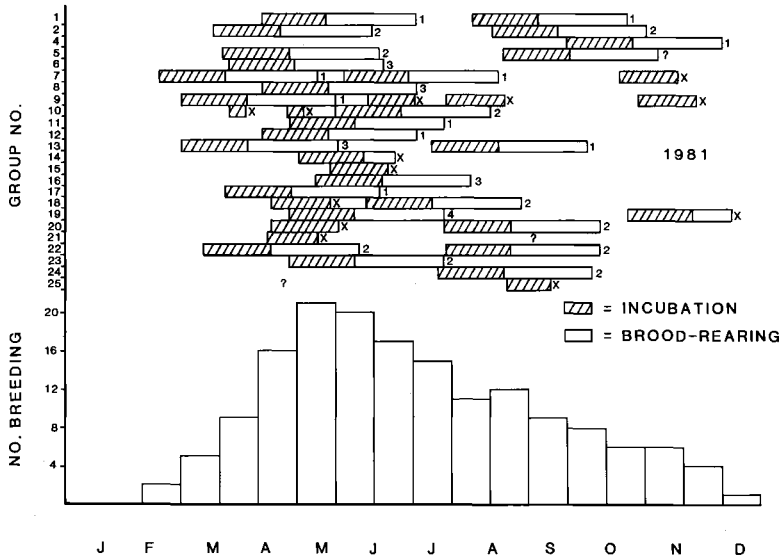


Fig. 2. Temporal pattern of Harris' Hawk breeding in 1981. Histogram shows the number of groups actively tending nests within 20-day intervals. The numbers to the right of the horizontal bars indicate the number of young fledged, and X's indicate nest failure.

young were fledged on about 17 November (group 7).

The frequency of groups breeding throughout the year exhibited a distinctly bimodal pattern. This probably was due to the interbrood

period (days from fledging of the first brood to the initiation of the second clutch), which was significantly greater ($P = 0.006$) in 1982 (mean = 81.0 days, $SD = 27.1$, $n = 7$) than in 1981 (mean = 40.8 days, $SD = 20.6$, $n = 8$), when some

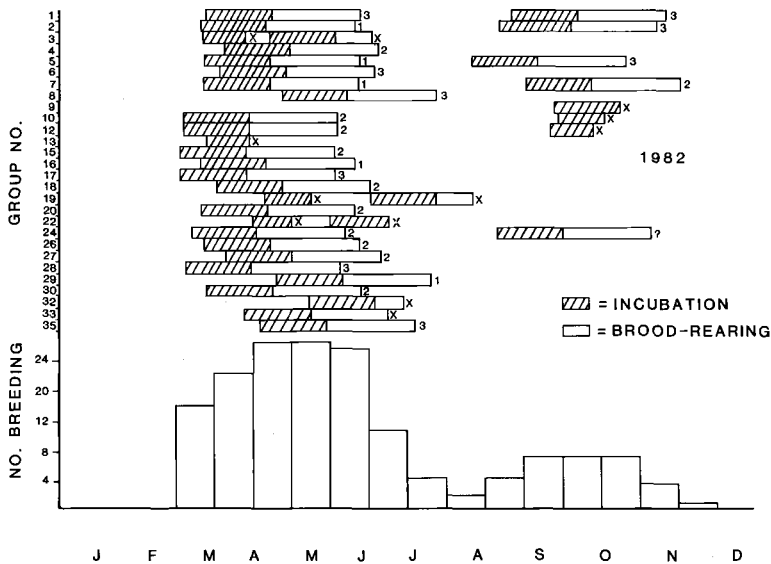


Fig. 3. Temporal pattern of Harris' Hawk breeding in 1982. See Fig. 2 for further details.

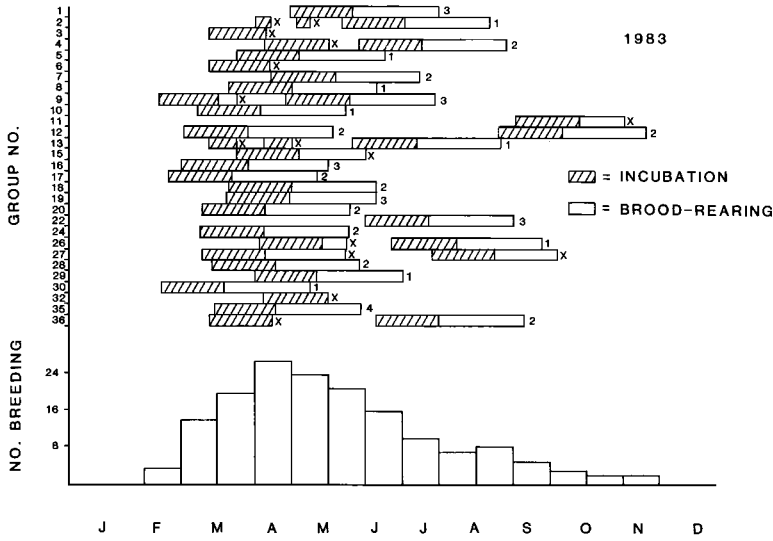


Fig. 4. Temporal pattern of Harris' Hawk breeding in 1983. See Fig. 2 for further details.

successful groups renested almost immediately (e.g. group 7).

First breeding attempts in 1983 were relatively asynchronous and autumnal nests were few (Fig. 4). The greatest frequency (93%) of active nesting by the 29 monitored groups occurred during the second week of April. Of the 17 groups successful in the spring, only 1 (5.9%) nested a second time. Seven (63%) of the 11 groups that were initially unsuccessful attempted a second nest; 6 of these groups eventually were successful. The female of pair 11 laid eggs for the first time in 1983 on 30 August. The latest fledging date recorded in 1983 was 8 November (group 12).

Nest success by season.—There were no significant trends (Kruskal-Wallis tests, $P > 0.1$) in either clutch size or number of young fledged among the three seasons during the study period (Tables 1 and 2). The number of young

fledged per nest in autumn tended to be low in all years except 1982. The percentage success of autumn nests for 1981–1983 (44.4%, 62.5%, and 50.0%, respectively) was consistently below that of spring nests (78.6%, 76.9%, and 55.6%, respectively). Likewise, nest success in autumn 1980 was very low (28.6%). The percentage success ($\chi^2 = 4.3$, $P = 0.12$, $df = 2$) and the number of young fledged per successful nest (Kruskal-Wallis test, $P > 0.1$) were not significantly different among seasons (Table 2).

Interbrood period.—In 1981 there was a significant linear relationship between the number of young fledged and the length of the interbrood period ($F = 13.2$, $P = 0.01$, $r^2 = 0.69$; Fig. 5). The trend in 1982 was similar, but did not approach significance ($F = 0.7$, $P = 0.45$, $r^2 = 0.12$; Fig. 5). In 1983 only one group renested after successfully rearing a brood.

Diet.—Harris' Hawks relied heavily on cot-

TABLE 1. Mean clutch size for Harris' Hawks in different seasons.

	Spring			Summer			Autumn		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
1980		No data			No data		2.50	0.71	(2)
1981	3.50	0.55	(6)	2.80	0.94	(15)	3.17	0.41	(6)
1982	3.05	0.81	(21)	2.67	0.58	(3)	3.50	0.71	(2)
1983	2.90	0.54	(21)	3.25	0.50	(4)		No data	
1981–1983	3.04	0.68	(48)	2.86	0.83	(22)	3.25	0.46	(8)

TABLE 2. The mean number of Harris' Hawk young fledged per nest attempt and successful nest in different seasons.

	Spring			Summer			Autumn		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
1980		No data			No data		0.71	1.25	(7)
1981	1.43	1.09	(14)	1.38	1.20	(16)	0.50	0.76	(8)
1982	1.46	1.03	(26)	0.75	1.50	(4)	1.43	1.40	(7)
1983	1.07	1.17	(27)	1.60	1.17	(10)	1.00	1.41	(2)
All nest attempts									
1981-1983	1.30	1.10	(67)	1.36	1.22	(30)	0.94	1.14	(17)
Successful nests									
1981-1983	1.89	0.80	(46)	2.05	0.89	(20)	2.10	0.74	(10)

tontails for food throughout the year (Table 3). Cottontails (or young jackrabbits no larger than adult cottontails) comprised over 80% of the total prey biomass in each year and in each season. Larger jackrabbits were most important in late spring, although they were taken occasionally throughout the year. Jackrabbits are undoubtedly more important in the Harris' Hawk's diet than Table 3 indicates, because I could not distinguish bones of juvenile *Lepus* from those of juvenile *Sylvilagus*. Woodrats (*Neotoma* spp.) also were an important prey, especially during spring. Quail and a variety of other birds were relatively common in the diet during summer and autumn (Table 3). Insects were eaten by nestlings in the summer, but these contributed little to the diet (Table 3). Most of these insects (68.6%) were small coleopterans.

Diets in spring and autumn were similar in that lagomorphs and other mammalian prey predominated (Table 3). There were no differences between years ($P > 0.1$); however, a significant trend was found when comparing the number of mammal vs. other prey types taken among seasons ($\chi^2 = 51.3$, $P < 0.0001$, $df = 2$). This was due primarily to an increase in consumption of insects and reptiles in the summer (Table 3). Nevertheless, mammals made up 94.5% of the biomass of the food consumed by nestlings during the summer because of the great size of lagomorphs as compared with other prey types. Some bias in the prey analysis undoubtedly exists, in that smaller items are more easily distorted or fragmented beyond recognition and also are more difficult to find than larger bones. However, I believe this bias was not great because (1) complete limb bones and skulls of medium-size rodents and reptiles

were common in the remains, (2) data from Swainson's Hawk (*Buteo swainsoni*) nests in the same area reveal that smaller types of prey were found in significantly ($P < 0.0001$) greater proportions (Bednarz 1986), and (3) some extremely small and rare animals on the study site were found among the prey remains (e.g. *Reithrodontomys* sp.) (Gennaro 1982).

Lagomorph numbers, precipitation, and nest initiation.—To examine the role of potential proximate factors involved in the timing of Harris' Hawk breeding, I used Spearman's correlation analysis (Sokal and Rohlf 1981) to identify patterns among 2-month precipitation (total precipitation during month of nest initiation and previous month), mean monthly cottontail numbers, mean total lagomorph numbers (cottontails and jackrabbits), the number of nests initiated in each month, and the number of second nesting attempts initiated each month. The observation period extended from May through October in 1981 (no lagomorph data were collected during March and April), and March through October in 1982 and in 1983. For this analysis, I included second nesting efforts after both successful and unsuccessful first-breeding attempts. I believe that the propensity for a particular group to renest may be best measured in this manner, given that in some years certain groups do not renest if the first brood is lost. In addition, second nesting attempts after nest failure cannot be equated with the clutch replacement observed in other large raptors, because Harris' Hawks may initiate second nests if broods about to fledge are lost and may lay second clutches up to 6 months after failure of the first clutch of the year.

No patterns were detected between the number of Harris' Hawk nests initiated and cotton-

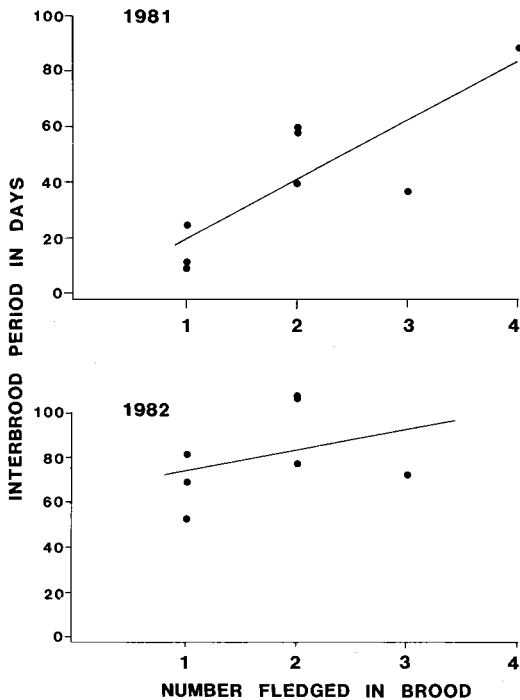


Fig. 5. Relationship of the number of Harris' Hawk young fledged in the first brood to interbrood period in days for 1981 and 1982.

tails observed ($r = 0.1$, $P = 0.67$, $n = 22$ months), total lagomorphs ($r = 0.1$, $P = 0.67$, $n = 22$), or 2-month precipitation ($r = -0.35$, $P = 0.11$, $n = 22$) when data for all years were combined. However, number of second nests initiated correlated significantly with the numbers of cottontails ($r = 0.53$, $P = 0.01$, $n = 22$) and of total lagomorphs ($r = 0.52$, $P = 0.01$, $n = 22$). The relationships between lagomorph numbers and

renewing were consistent for analyses done within years, but were not statistically significant. In 1982, the number of second nesting attempts was almost significantly correlated with cottontail numbers and total lagomorphs ($r = 0.63$, $P = 0.09$, $n = 8$, and $r = 0.63$, $P = 0.07$, $n = 8$, respectively). Correlations of other variables changed signs between years and, except for one case, did not approach significance. The exception is that 2-month precipitation was negatively correlated with the number of all nests initiated in 1983 ($r = -0.78$, $P = 0.02$, $n = 8$). This trend was not seen in 1981 and 1982, suggesting that the 1983 pattern may be spurious.

Analyses including only nests initiated after the first brood fledged successfully likewise revealed that the number of second nests initiated was significantly correlated with the number of cottontails ($r = 0.78$, $P < 0.01$, $n = 12$) and total lagomorphs ($r = 0.73$, $P < 0.01$, $n = 12$). Only the months May through October, when the initiation of such nesting attempts was observed, were included in this analysis. I omitted 1983 because only one second nesting occurred. Again, 2-month precipitation was not correlated with the number of second nests initiated ($P > 0.2$).

A final analysis was done to examine the suggestion that hawks may time breeding so that fledging coincides with the peak period of prey availability (see Immelmann 1971, Snyder and Wiley 1976). No relationship was found between the number of nests that fledged young and cottontail numbers ($r = 0.2$, $P = 0.4$, $n = 20$ months) or total lagomorphs ($r = 0.31$, $P = 0.2$, $n = 20$). The months May through November were included in this analysis because lagoon

TABLE 3. Percentage of prey types represented in food remains found in and near nests of Harris' Hawks breeding in different seasons.

Prey type	Spring ($n = 422$)		Summer ($n = 237$)		Autumn ($n = 230$)	
	Frequency	Biomass	Frequency	Biomass	Frequency	Biomass
<i>Sylvilagus auduboni</i>	65.4	84.8	46.0	88.2	70.0	90.6
<i>Lepus californicus</i>	2.8	6.6	0.4	1.4	0.4	1.0
<i>Neotoma</i> spp.	8.3	4.2	1.7	1.3	3.9	2.0
<i>Spermophilus</i> spp.	5.0	1.3	5.9	2.4	1.7	0.5
Other rodents	2.1	0.3	5.5	1.2	3.9	0.6
Quail ^a	3.8	1.6	5.1	3.1	9.6	3.9
Other birds	2.6	0.9	5.1	2.1	4.3	1.4
Reptiles	4.7	0.2	5.1	0.4	0.9	Trace
Insects	5.2	Trace	25.3	Trace	5.2	Trace

^a *Colinus virginianus* and *Callipepla squamata* occur on the study site.

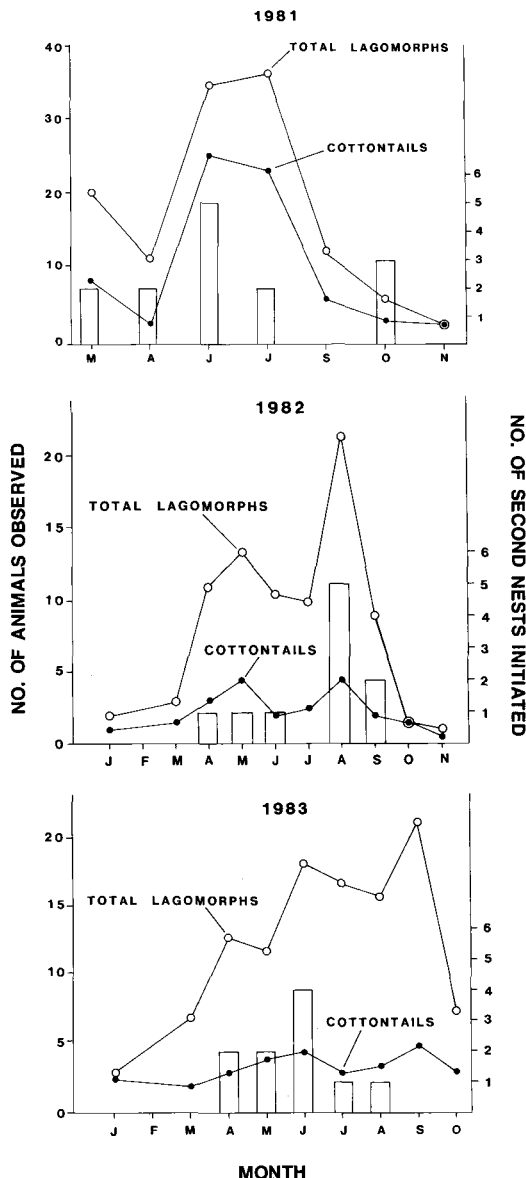


Fig. 6. Mean numbers of cottontails and total lagomorphs counted on census route and numbers of second nests initiated (histograms) each month in 1981-1983.

morph data were available and 98.7% of the successful fledgings occurred in this period.

Lagomorph numbers peaked primarily in mid- to late summer, which corresponded with the period during which most second nests were initiated. Although lagomorph numbers were high throughout 1981, 50% of the renestings were initiated in July and August when prey

populations peaked (Fig. 6). The relationship was similar in 1982, when 70% of the second nests were initiated during the July-August lagomorph population peak (Fig. 6). Reproductive success was low in 1983, and all but one second breeding attempt were initiated after nest failures. These nest starts corresponded with the late spring increase in lagomorph populations (Fig. 6).

The cottontail population was high in 1981 and apparently crashed during the winter of 1981-1982 (Table 4). Jackrabbit numbers, on the other hand, showed no significant trends during the three years. The greatest tendency to renest occurred in 1981, when cottontails were most numerous. In that year, 55% of the 20 spring or summer breeding attempts were followed by a second effort (Fig. 2). In addition, the interbrood period was significantly shorter in 1981 (mean = 40.8 days) compared with 1982 (mean = 81.0 days). In contrast, in 1982 and 1983, both relatively poor cottontail years, the percentages of spring and summer breeding attempts followed by a second nesting were 37.1% and 28.6%, respectively (Figs. 3 and 4).

The incidence of groups nesting in autumn 1980 was high (7 of 10 known breeding ranges contained active nests). This corresponded to a peak in rabbit populations, as deduced from lagomorph counts conducted by Gennaro (1982) on the study area in 1977-1979 and 1981. During the 4 yr I monitored the Harris' Hawk population, the frequency of autumn nesting and second breeding attempts was greatest during the 1980-1981 period of cottontail abundance. In 1982 and 1983 the decrease of late nesting apparently paralleled a decline in lagomorph populations (Table 4).

DISCUSSION

Harris' Hawks in southeastern New Mexico commonly breed in the spring, summer, and autumn when environmental conditions are suitable. The breeding season normally commences about mid-February and may continue into November or early December. Most breeding attempts in late summer and autumn are undertaken by groups that bred in the previous spring. During a good prey year (1981) the percentage of groups nesting in the fall was more than 50% and in 1980 it might have been as high as 70%. In Texas, Brannon (1980) found Harris' Hawks nesting from February through

November. Mader (1978) and Whaley (1986) reported that the breeding season of Harris' Hawks in Arizona ended in late October, although Whaley (1979) noted one exception. These studies, as well as more recent work (J. Dawson pers. comm.), suggest that the frequency of autumnal nesting in Arizona is much lower than I recorded in New Mexico.

In species that breed successively (mostly passerines), it has been predicted that if food conditions are poor or if broods are large, one should expect longer intervals between broods, as energy and protein reserves will be depleted by the care of early broods (Ricklefs 1974, Jones and Ward 1976). In 1981 I found a significant positive relationship between the size of the first brood and the interbrood period, supporting this suggestion (also see Murphy 1978, Smith and Roff 1980, McGillivray 1983). This trend also was present in 1982, but was not statistically significant. Moreover, the interbrood period was significantly shorter in 1981, the best prey year, than in 1982, a relatively poor prey year. These results support the view that available food resources are an important factor in an individual's ability to initiate a second clutch. Second nesting attempts by Harris' Hawks did not result in smaller clutches or broods of young (Table 1), as McGillivray (1983) found for the House Sparrow (*Passer domesticus*). These results do not support Perrins's (1970) suggestion that late clutches should be small so that incubation can start earlier and so that each young will be better nourished.

Commencement of breeding in late winter and early spring was not correlated with either precipitation or lagomorph abundance. Both the numbers of cottontails and precipitation were low in March, making it highly unlikely that these were proximate cues that triggered the onset of spring breeding. Variation in day length is well substantiated as a proximate timing factor for many species, whereas there is little evidence to suggest that increasing temperatures trigger breeding (Lofts and Murton 1968). Thus, Harris' Hawks in New Mexico probably are similar to Temperate Zone species in that they use photoperiod to "predict" the impending increase in prey numbers.

Harris' Hawk is primarily neotropical in distribution (Brown and Amadon 1968), and may have only recently extended its range into the southwestern United States. If this is the case, I suggest that the "ancestral" tropical and sub-

TABLE 4. Mean numbers of cottontails and jackrabbits recorded on all road counts done between May and September in different years. Different letters indicate a significant difference between years at the $P < 0.05$ level (analysis of variance).

	1981 (n = 9)		1982 (n = 10)		1983 (n = 10)	
	Mean	SD	Mean	SD	Mean	SD
Cottontails	14.3	10.9	3.0	2.3	3.6	1.8
Significance group	A		B		B	
Jackrabbits	10.3	2.9	10.4	5.7	13.0	4.6
Significance group	A		A		A	

tropical Harris' Hawks bred in response to resource availability, as many tropical species do today. Whether tropical Harris' Hawks have or had a defined breeding season or were continuous breeders probably depended on local fluctuations in prey populations. As the hawk moved into more seasonal temperate climates and was subjected to a more or less reliable burst of prey in spring, they may have become more sensitive to increasing day lengths to take maximal advantage of the spring increase in lagomorphs. Following the development of a sensitivity to photoperiod, the actual time an individual female hawk laid eggs would depend on the availability of sufficient resources to compensate for the energy and protein demands of egg formation (Newton 1979). This proposed sequence is similar to that suggested by Lofts and Murton (1968) for the evolution of a photoperiodically controlled cycle in Temperate Zone species derived from equatorial birds not dependent on photostimulation. Because Harris' Hawks in New Mexico can breed throughout most of the year, it is unlikely that they have the well-developed refractory period found in many Temperate Zone species (Murton and Westwood 1977). Comparisons of breeding season and ecological data between temperate and tropical populations of Harris' Hawks would be useful in evaluating these ideas, but data on tropical populations do not exist.

The abundance of cottontails in late summer probably is the most critical factor responsible for autumnal breeding attempts in Harris' Hawks. Correlations between the number of second nests initiated and the numbers of available lagomorphs, as well as the decreased

interbrood period in the resource-abundant year of 1981, support this contention. The importance of suitable food resources as a proximate cue for other autumnal breeders has been shown for the Tricolored Blackbird (Payne 1969) and the Pinyon Jay (Ligon 1974). De Vries (1975) noted that heavy rainfall preceded peak egg laying in the Galapagos Hawk by 3 months and speculated that responses of prey to precipitation were probably the most important factor triggering nesting.

The ultimate value of successive nesting and autumn breeding must be that some late nests produce birds with some probability of establishing themselves in the breeding population. Late nests fail more often than earlier nests, but this trend was not significant statistically. The late summer and autumn nests were initiated when available food resources were most abundant, but the peak food demands of large nestlings occurred in November when cottontail populations were declining. Obviously, autumnal breeding attempts are not timed so that young will fledge during optimal conditions (see Immelmann 1971). Rather, Harris' Hawk's strategy apparently is to prolong the breeding season when adequate food is available.

After fledging, Harris' Hawk young remain on their natal range and share prey with their parents for at least 3-6 months (Bednarz 1986). Thus, parents presumably can assist offspring from a late breeding attempt with food procurement during the lean winter period. I suspect that the extended parental care strategy initially evolved in response to other factors (e.g. those favoring the development of cooperative breeding; Bednarz 1986), rather than to the late breeding habit.

Other factors of possible importance to Harris' Hawk are unpredictable climatic events and possibly predation that result in nest failure. Although stochastic processes leading to nest failure operate during all seasons, violent, unpredictable summer storms could be particularly important to Harris' Hawk breeding. These storms may lessen the advantage of summer breeding by increasing the probability of nest failure at the time when available food resources are at their yearly maxima. On the other hand, autumn, which often is climatically mild, in some years might provide favorable conditions for the production of young despite the decreased density of cottontails. Two patterns observed during this study are consistent

with this suggestion. First, precipitation in summer occurs primarily in the form of violent convective thunderstorms that typically are accompanied by strong gusting winds (Houghton 1959), whereas precipitation in other seasons generally does not involve destructive winds. Second, the hawk population exhibits a slight depression in breeding activity in mid-summer (Figs. 2-4) even though the lagomorph population is at its yearly peak (Fig. 6). Whether this is the result of a recovery period after the first nesting attempt of the year, the need to provide parental care for the first brood, or a postponement until arrival of the milder conditions of autumn is unknown.

I suggest that the relatively high probability of stochastic events (e.g. violent storms and possibly predation) that result in nest failure throughout the year, in combination with the extended availability of an adequate food supply, has resulted in the prolonged and flexible breeding season of Harris' Hawk. In addition, the frequent violent summer storms may tend to negate any advantage of breeding in this season even though prey populations are at a peak. These factors may have instead favored the bimodal breeding pattern described here.

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