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POPULATION ECOLOGY OF THE HARRIS' HAWK IN ARIZONA

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ABSTRACT - The Harris' Hawk (*Parabuteo unicinctus*) was studied in Arizona during 1976-1977. Where 2 separate populations once resided in Arizona, 1 now remains and occupies 3,880 km² of the Arizona Upland subdivision, Sonoran Desert. The former population along the Colorado River is extirpated.

Nests were built or old nests repaired from January to August and eggs were laid from mid-January to mid-August. Subsequent clutches were documented in 50 nesting ranges. Occasionally second clutches were laid before young of first broods were fledged. Fledging dates ranged from April to October. At 9 locations active nests were 0.8 km apart and at 2 locations nests were 0.5 km apart. Within 2 study areas nesting density was 2.5 km²/active nest. In 1977 Harris' Hawks reoccupied 91% of the nesting ranges used in 1976. More than 2 adults were observed at 46% of 227 nesting ranges.

Productivity for 396 nesting attempts averaged 3.16 eggs/clutch and 1.62 young fledged/nesting attempt. Seventy-four percent of the nesting attempts were successful.

Food consisted mainly of rabbits and ground squirrels. Mortality occurred mainly during the egg laying and incubation period. Early nest failures resulted in second broods, but successful pairs also had second broods. Habitat loss is the major cause of decline of the population followed by excessive human disturbance.

Research on raptors has become increasingly important as a result of the marked decline in several species over the past 3 decades (Arnold 1954; Cottam et al. 1961; Berger, Sindelar and Gamble 1969; Peterson 1969; Sprunt 1969; Henny and Wight 1972).

In the southwest, particularly in Arizona, the ranges of some species of raptors extend marginally into the United States, and here population studies are usually most informative. Most of these border species have received little investigation. For example, the Aplomado Falcon (*Falco femoralis*) showed signs of decline as early as 1890 (Phillips, Marshall and Monson 1964). Its range and status in Arizona was poorly documented (Phillips et al. 1964) until the study of Hector (1975). Where it was once thought to be locally fairly common, it is extinct (Hector 1975). Because of habitat destruction, Gray Hawk (*Buteo nitidus*) populations have declined during the last century (Richard Glinski pers. comm.).

The Harris' Hawk (*Parabuteo unicinctus superior*) is another relatively unstudied southwestern raptor. Studies by Hensley (1959) and Mader (1975a, 1975b, 1977) are the only major works on this species in Arizona. Because of sudden decline and apparent extinction in southern California (R. Guy McCaskie pers. comm.), and with the recent (late 1960) increased use for falconry, knowledge of the Harris' Hawk's status in Arizona is critical.

The primary purpose of this study was to establish base-line data on nesting distribution and abundance of the Harris' Hawk in Arizona and to compare these data with the historic record to determine nesting success of the present population.

STUDY AREA AND METHODS

Arizona falls into a southwestern bi-seasonal climatic pattern of winter precipitation, spring dry period, summer precipitation, and fall dry period. The spring dry period (May - June) has higher temp and the greatest influence on the plant and animal community (Lowe 1976).

Sellers (1960) divided the state into homogeneous sections with respect to climate, topography, and vegetation. From the southwest section (the area of importance in this study) to the plateau section there are extreme changes in climatic conditions. The plateau section has an average annual temp 20 to 25° F lower and annual precipitation 38 to 51 cm higher than the flat deserts of the southwest section. The southwest section contains the lowest, hottest and driest areas of the state (Sellers 1960).

Of the 6 life-zones in Arizona, only the Lower Sonoran, containing portions of the Sonoran, Mojave and Chihuahuan Desert (Fig. 1), was important to this study. The Sonoran Desert has 2 subdivisions in Arizona — the Lower Colorado and Arizona Upland subdivisions (Fig. 1). The Lower Colorado subdivision (ele-

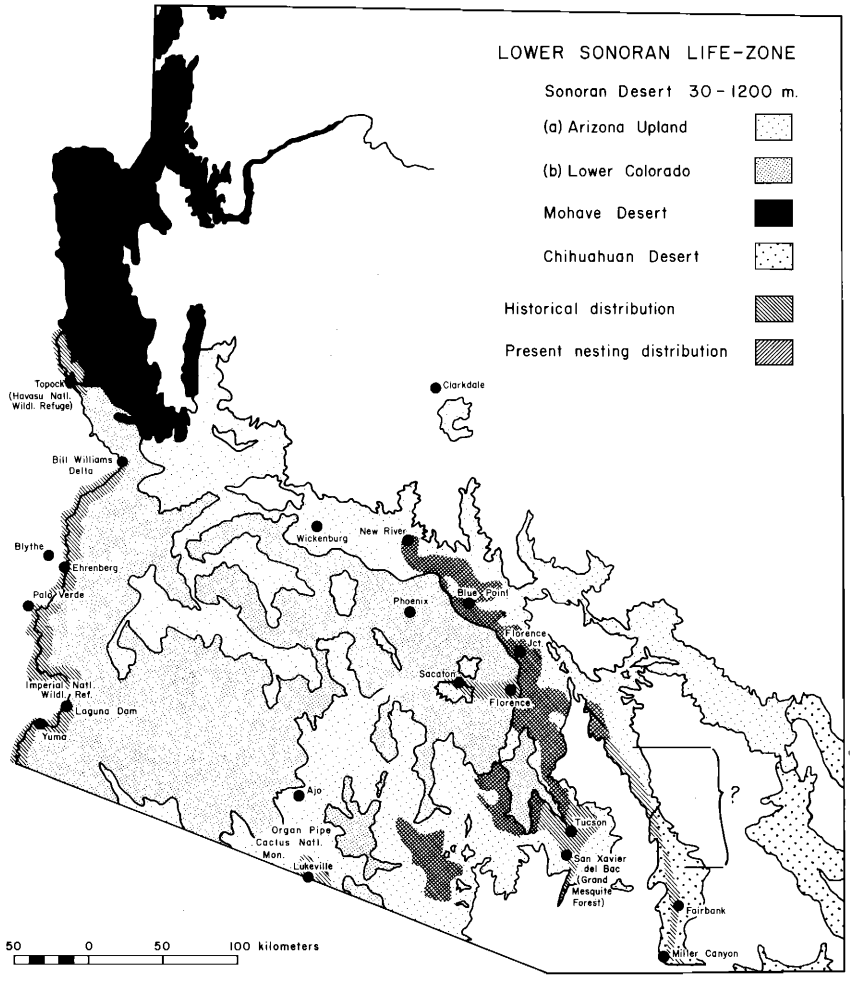

Figure 1. Map of the historical and present distribution of the Harris' Hawk in Arizona in relation to vegetational zones.

vation 30-90 m) is primarily a creosote bush-bursage (*Larrea-Franseria*) community and includes the hottest and most arid regions in Arizona. This subdivision is characterized by sandy and gravelly plains and mesas, sand dunes, lava flows, silty valleys, salt basins, rocky hills, and desert pavement. The Arizona Upland subdivision (elevation 150-1220 m) is typified by a paloverde-saguaro cactus (*Cericidium-Cereus)* association. It attains greatest development on the rocky soils of desert mountain slopes and on the coarse soils of upper bajadas that flank mountain ranges. The Arizona Upland subdivision has far greater numbers of plant species than the Lower Colorado subdivision.

The Mojave Desert (elevation 240-1580 m) scarcely reaches into northwestern Arizona. The higher aridity, lack of summer rains and longer periods of below freezing winter temp cause this desert to be poorer in plant and animal life than the Sonoran Desert (Lowe and Brown 1973).

The Chihuahuan Desert enters Arizona in a small southeastern section of the state, where it lies mostly above an elevation of 1070 m. This relatively complex desert is essentially shrubby with many grasses, several small species of cacti, and few desert trees.

Field work was conducted in 1976 and 1977 from January through October of each year. The Harris' Hawk in Arizona has never been observed nesting outside the Lower Sonoran Life-zone, so I eliminated the northern half of the state from the survey. After a broad general search of the Lower Colorado subdivision, I determined that the Arizona Upland subdivision was the most important area to nesting Harris' Hawks. Hills, windmill towers, and other elevated points were used to locate nests. In flat country I used an 8.5 m extension ladder mounted on the bed and cab of a pickup truck which allowed visual clearance above the vegetation.

All nest sites were plotted on USGS 1:250,000 topographic

quadrangles and series maps. Throughout the population continuum there were local concentration points and from 2 of these populous areas I attempted to find all active nests to determine total nesting density. The mean distance between nests was determined by measuring the distance from each nest and its nearest neighbor using the distance between any 2 nests only once. By halving the mean distance, a value r (radius) was obtained and used to determine average nesting range size by the formula $A = r^2$ under the assumption that nesting ranges were circular. I used only those nesting ranges that were active in a given year.

Each nest was visited a minimum of twice in order to determine number of eggs laid and number of young fledged (in 1976 nests were visited 3 to 5 times). When a clutch appeared small or incomplete, a later visit was scheduled in order to obtain data for full clutch size. Young were aged by comparison with color photographs of known age birds taken at 5 d intervals.

RESULTS

Distribution and Habitat Characteristics

Past Populations. — Historically, there were 2 localized populations of Harris' Hawk in Arizona. One population was resident in western Arizona in Lower Colorado habitat along the Colorado River from Yuma northward to Topock (Fig. 1). The Lower Colorado population was extirpated by 1969. A second population approximately 280 km eastward in Arizona Upland habitat (Fig. 1) remains today. The 2 localities are separated by a dry, barren expanse of the Lower Colorado Desert.

The earliest record for Harris' Hawk in Arizona was reported near Topock by Kennerly (1859). The Lower Colorado population likely originated from Baja California, extending its range into the United States along suitable segments of the Colorado River (Fig. 1). Along the river, nesting sites were near small lakes, lagoons and swamps in flooded mesquite and in willow and cottonwood trees (Wiley 1916, 1917; Bancroft 1920; Rowley 1936). Prey items included the Purple Gallinule (*Porphyrula martinica*), Sora (*Porzana carolina*), Common Teal (*Anas cyanoptera*), and Northern Flicker (*Colaptes auratus*) (Miller 1925, 1930). Gale Monson (pers. comm.; past manager of Havasu Natl. Wildl. Refuge) included the American Coot (*Fulica americanus*), Muskrats (*Andatra zibethicus*), Cotton Rats (*Sigmodon hispidus*), and Abert's Towhee (*Pipilo aberti*) as food found in nests. Harris' Hawks were frequently common at places along the river near Havasu National Wildlife Refuge with a resident average of 30 individual/y from 1947-59. As many as 50 individuals were often reported, and nests were sometimes less than 0.8 km apart (U.S.D.I. Fish and Wildlife Service 1952). Generally, 2 young/nest were reported with only 2 parent birds caring for them. Nests were often built on top of old Great Blue Heron (*Ardea herodias*) nests and were commonly only 3 to 5 m above water (Gale Monson pers. comm.). A population decline started in the late 1950's and by 1969 the Harris' Hawk disappeared from the refuge. A wild population has not since been observed along the Colorado River. A concurrent decline and extinction was noted at Imperial National Wildlife Refuge to the south. An extensive list of sources concerning Harris' Hawks along the Colorado River is included in Whaley (1979, Appendices A and B).

The Present Population (1976-1977). — The present Harris' Hawk population in Arizona occupies 3,880 km^2 in Arizona Upland habitat with elevations ranging from 396 to 1,036 meters ($\bar{x}$ = 701 m). Lowe and Brown (1973) delineate prime Arizona upland habitat as the region ". . . east then north of a line drawn from Ajo to Tucson to Florence Junction, then northwest to Wickenburg" and the Harris' Hawk followed this distribution closely (see Fig. 1). Nearly all nests were placed in paloverde-saguaro cactus habitat or in the more local narrow strips of blue paloverde-ironwood (*Circidium floridum-Olneya*) habitat of the large arroyos. Three exceptions were nests placed in large cottonwood trees in riparian communities that were juxtapose to the aforementioned habitat. No nests were found, nor birds seen, in riparian communities along rivers that were not associated with the Arizona Upland subdivision (Fig. 1).

Nest Site Characteristics

Saguaro cactus was the preferred plant species used for nest sites (Table 1). Five active nests and 42 old nests were placed on electrical transmission towers along a 13.7 km section of 110 kV powerline crossing paloverde-saguaro cactus habitat. Another nest was placed on a tower along a 345 kV electrical transmission line crossing excellent Harris' Hawk habitat.

Nest height ranged from 2.3 m [foothill paloverde (*C. microphyllum*) tree] to 21.3 m (electrical transmission tower). The average height for nests in saguaro cacti, blue paloverde trees, and foothill paloverde trees was 5.8 m, 6.3 m and 4.4 m, respectively. Seventy-two percent of all nests were placed in mature saguaro $\geq$ 4.9 m tall with substantial arms.

Table 1. Harris' Hawk nest sites in 1976 and 1977 in Arizona.

NEST SUPPORT	NUMBER OF NESTS	PERCENTAGE OF TOTAL
Saguaro Cactus	230	75.2
Foothill Paloverde	37	12.1
Blue Paloverde	23	7.5
Electrical Tower	6	2.0
Cottonwood	3	1.0
Ironwood	3	1.0
Mesquite	2	.6
Pine	1	.3
Palm	1	.3
Totals	306	100.0

Breeding Season Phenology

Courtship. — Courtship behavior of Harris' Hawks is typical of most raptors (Brown and Amadon 1968), but on 18 February 1977 I noted a very unusual "group courtship" display involving 8 adults. The adults flying at an altitude of 150-180 m, continually engaged in soaring, tail chasing, and stooping, accompanied by much vocalizing. The long vertical stoops, which often involved all 8 hawks, were followed by tail chasing and eventual return to their former altitude where the event was repeated. Similar behavior has been reported for Eleonora's Falcon *(Falco eleonorae)* when near the breeding cliffs (Brown and Amadon 1968) but is apparently rare in falconiforms. The observed behavior lasted approximately 45 min, when the adults departed in 3 directions. Later, an active nest was found in each of the 3 areas where the respective groups appeared to have flown. At 2 of these nests, 3 adults were present.

Copulations occurred over a 6-month period from 28 January to 26 July. Each copulation bout lasted from 15 to 40 sec. ($X = 24$ sec, $N = 23$). Courtship behavior did not always precede mating; on several occasions I witnessed copulations in which a male flew directly to a female and copulated without obvious display by either sex. More than 1 adult males were observed at many of the nest sites; 2 males were recorded at 41% and 3 at 5% of 227 active nesting ranges. On 11 February 1977, I observed 7 copulations in 2 h, involving a female and both males at a territory near Florence Junction. Polyandrous mating behavior has been previously reported for this species (Mader 1975a).

Nest Construction. — Harris' Hawks build or repair nests from January to August. Often one of several alternate nests is repaired or pairs may use the same nest several times in succession. Several nests may be repaired and 1 chosen for use. In 1 territory 8 nests were located, one of which had been repaired and was ready for eggs on 10 February 1977 (copulation observed on 28 January 1977). Materials are continually added to nests while eggs and nestlings are present.

Timing of Incubation, Hatching, Fledging. — Using a 35-d incubation period and a 45-d nestling period (Mader 1975b), I determined the time spans for beginning of incubation, for hatching and for fledging of young (Fig. 2). Eggs were laid from mid-January to mid-August. Fifty percent of all first clutches ($N = 284$) were laid between 20 February and 22 March (Fig. 2). A portion of clutches laid during and after April were second clutches for the given year (Fig. 2).

Double or triple clutches occurred 61 times involving 50 (21.6%) of the nests studied; 39 (63.9%) followed a successful first attempt, and 22 (36.1%) followed an unsuccessful first nesting attempt ($X^2 = P < .05$). Of those following a successful brood, the time interval between first and second clutches averaged 106 d. Within 8 nesting ranges the short interval between clutches ($\bar{x} = 75$ d) indicated that eggs were laid before the first young had fledged. This was confirmed within 2 nesting ranges. Within one, 2 eggs were laid in the same nest with a 23 to 25 d old chick. In Texas the time interval from fledging of the first attempt to completion of the next clutch was 28 d (range 7-59 d) for 6 second attempts (Brannon 1980).

January egg laying was documented only once during the study period (eggs laid mid-January 1976). On 12 February 1977 another nest containing 3 eggs was found which may have been started in January, but egg-laying or incubation date could not be determined since the eggs never hatched. Whenever pairs commenced laying of the first clutch early in the year, 3 clutches/breeding season were laid during both 1976 and 1977.

Hatching dates for 284 clutches spanned 8 months (mode = April) and fledging dates spanned

7 mo (mode = May) (Fig. 2). The latest fledging date was near 28 October. An extremely late fledging date of 8 November has been reported for Harris' Hawks in Texas (Brannon 1980).

Nesting Density and Territorial Fidelity

Nesting density of Harris' Hawks in Arizona was 1 nest/2.5 km^2 in 1977 for both Study Areas A and B (Fig. 3). The mean distance between nests in both study areas was 1.8 km. At 9 locations active nests were only 0.8 km apart, and at 2 locations active nests were just 0.5 km apart. As a result of the observed close nesting patterns, I expect that territories overlap.

Territorial attachment seems strongly developed. Eighty-four percent of 123 active territories occupied in 1976 were reoccupied and active in 1977. Another 9 territories occupied in 1976 had adults present in 1977 but active nests were not found. On this basis, Harris' Hawks reoccupied 91% of 123 nesting territories used in 1976. Mader (1982) found that the Savanna Hawk (*Buteogallus meridionalis*) also has strong territorial attachment from year to year.

Eight nests used by Harris' Hawks in 1976 were used by Great Horned Owl (*Bubo virginianus*) (N = 7) and Red-tailed Hawk (*Buteo jamaicensis*) in 1977 and appeared to have little influence on Harris' Hawks reoccupancy of old territory. The Red-tailed Hawk usurpation resulted in the Harris' Hawks locating a new nest 160 m from their 1976 site.

Productivity

I recorded a total of 396 nesting attempts (including second and third clutches) involving 306 nests within 231 active nesting ranges. In order to compare productivity with that from other studies (Mader 1975b; Griffin 1975; Griffin 1976; Brannon 1980), a successful nest was one in which a nestling reached the age of at least 28 d. Of 319 nesting attempts, 72% were successful. Seventy-seven nests had incomplete data. Seventy-five nests failed during the egg laying and incubation period. Fifteen nests failed during the nestling period (2 were man-caused, 2 were caused by inclement weather, and cause of failure could not be determined for 11).

Mean clutch size in 1976 was 3.04 (N = 67) and 3.22 (N = 95) in 1977 with a combined mean of 3.16 (N = 162) (clutch size/number of clutches: 1/4, 2/29, 3/73, 4/51, 5/5) for the study period. Number

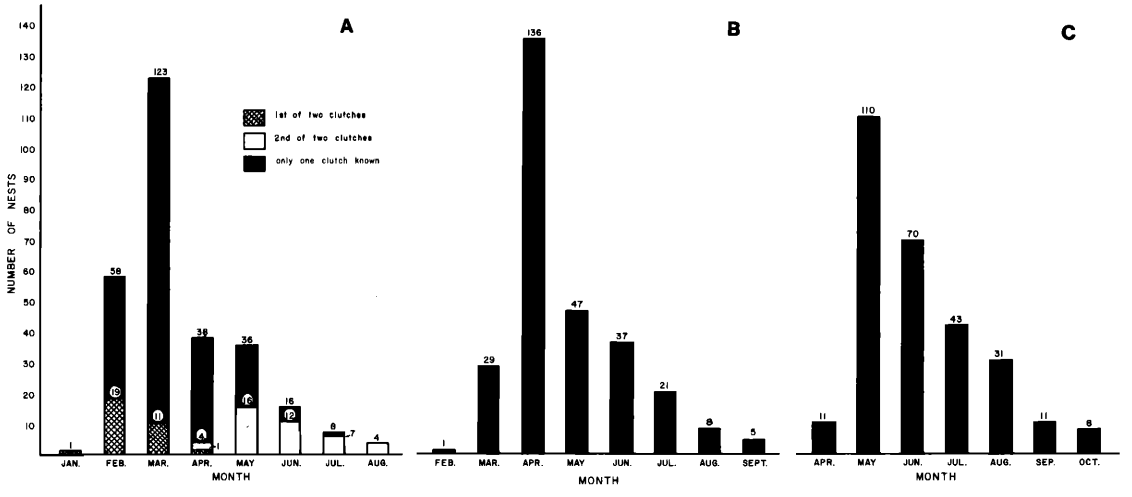

Figure 2. Number of nests in relation to (A) month when incubation begins, (B) month of hatching and (C) month of fledging for 284 Harris' Hawk nesting attempts in Arizona in 1976 and 1977.

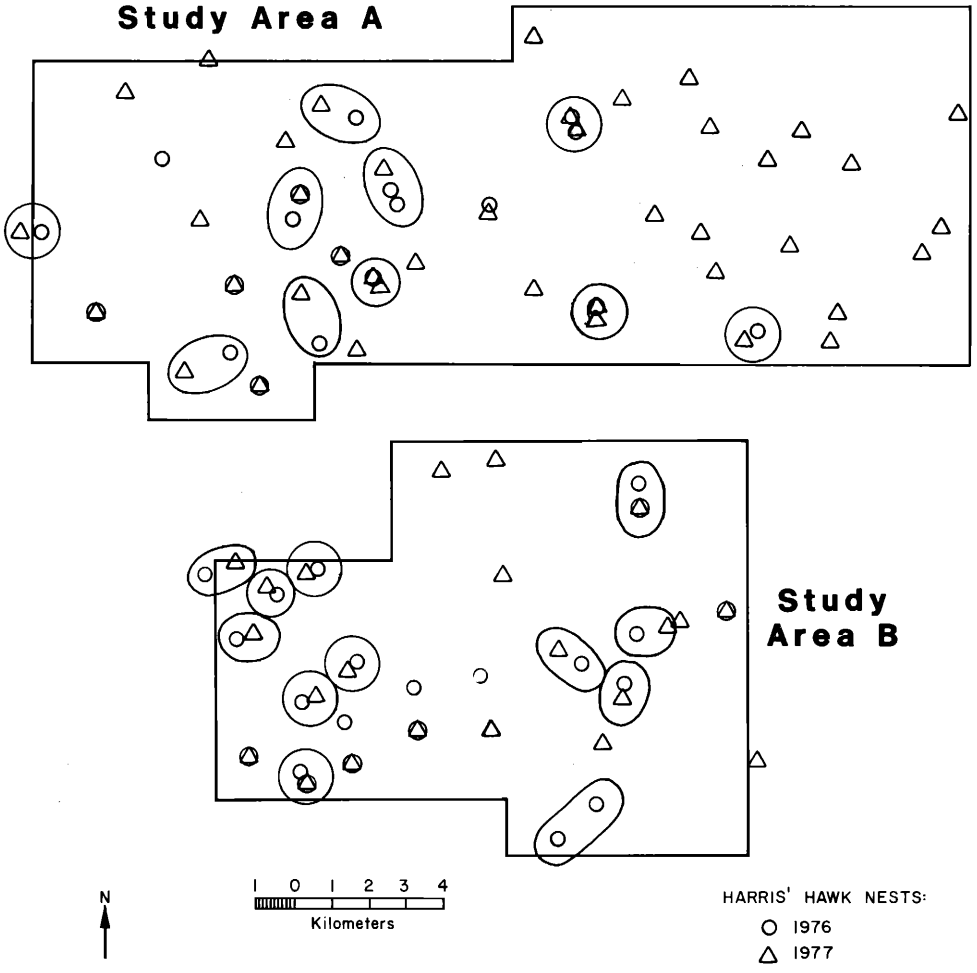

Figure 3. Proximity of Harris' Hawk nests in Study Area A (230 km²), containing 39 nesting ranges with 51 active nests, and in Study Area B (135 km²), containing 26 nesting ranges with 38 active nests. Large circles containing > 1 symbol indicate 1 nesting range and are not intended to delineate the size of a range.

of fledglings/nest ranged from 1 to 4 (number fledglings/number broods: 1/59, 2/75, 3/71, 4/24) and averaged 1.62 young/all attempts (Table 2).

I calculated productivity using the more complete data of 71 nesting attempts of 1976 and compared these values with productivity obtained when using the less complete, but larger sample size, of the foregoing. Using only the 1976 data, "hatching" and fledging success were calculated (Table 3). Values obtained for "mean clutch size" and "young fledged/all attempts" were similar to the corresponding values from the larger sample. There was a 51% loss in productivity between egg laying and fledging, most resulting from eggs failing to hatch (41%, Table 3). Egg loss was recorded for 89 nests, 42% due to nest failure (loss of complete clutches) and 58% due to partial hatching of clutches. A Texas population had a 41% productivity loss (Brannon 1980). At least 612 young fledged during the study period. Two hundred twelve nestlings were banded in 1977. Sex ratio of nestlings was 1.2 ♂♂: 1.0 ♀♀.

Harris' Hawks in sub-adult plumage were found to breed occasionally. Ten sub-adults within 6 ter-

Table 2. Harris' Hawk nesting success in Arizona, 1976 and 1977.

	TOTAL NUMBER OF NESTING ATTEMPTS	NUMBER OF SUCCESSFUL NESTS[1]	NUMBER OF YOUNG	YOUNG FLEDGED PER ALL ATTEMPTS	YOUNG FLEDGED PER SUCCESSFUL ATTEMPTS
1976	143	102 (71%)	229	1.60	2.25
1977	176	127 (72%)	289	1.64	2.28
Total nests and young	319	229 (72%)	518	1.62	2.26

[1]A nest was considered successful if a chick was raised to an age of at least 28 days. Only nests where adequate fledging data was obtained appear in the table.

ritories succeeded in raising 7 young. In each case the female was a sub-adult. In 3 territories all hawks were sub-adults.

Mortality Factors

Hatching success (59%, Table 3) indicates a high egg loss. Laying of infertile eggs, nest abandonment and destruction by predators contributed to reduced hatching success. Infertility appeared to be the most common cause (e.g., one pair laid 4 eggs in both 1976 and 1977; incubation times were 65 and 73 d, respectively, with no hatching and no embryo development in both years). Forty-seven young died or disappeared from nests during the 2-y period (7 young were taken by man, 5 were killed by man, 5 died of disease, 2 died when a cactus containing a nest fell, and 1 died when it fell from its nest). Cause of death of 27 young could not be determined. Other mortality factors for adults and fledglings were electrocutions (8 cases reported), and accidental trapping of Harris' Hawks by coyote trappers.

In 1976 a resident of Owl Head Ranch near Tucson stated that he found a dead Harris' Hawk and other birds floating in the metal livestock water tanks on his ranch. In July 1978 a dead juvenile female Harris' Hawk was found floating in a large livestock water tank (Larry Livingston pers. comm.) not far from where it was banded as a nestling in May 1977. Drowning deaths may be a significant cause of mortality, especially during the dry period (May-June) when livestock tanks are the only available source for drinking and bathing. Drownings in water tanks have been documented for the Prairie Falcon (*Falco mexicanus*) (Enderson 1964), American Kestrel (*Falco sparverius*) (Craig and Powers 1976) and Ferruginous Hawk (*Buteo regalis*) (Clayton White pers. comm.).

Cholla cactus (*Opuntia* sp.) may also cause mortality in Harris' Hawks. On 26 May 1976 I found a recently fledged Harris' Hawk partially immobilized (could not fly and could hardly walk) on the ground near its nest. Cholla cactus joints were stuck on its neck and between its legs. On another occasion I chased down and caught an older fledgling that was having difficulty flying and

Table 3. Summary of productivity data for 71 Harris' Hawk nesting attempts in Arizona in 1976.

	RESULTS	RANGE
Mean clutch size	3.07	1 - 5
Young fledged per all attempts	1.63	0 - 4
Young fledged per successful attempt	2.18	1 - 4
Percent hatching success	59	41% productivity loss (eggs failed to hatch)
Percent fledging success	90	10% productivity loss (young failed to fledge)
Percent successful nesting attempts	75	
Percent unsuccessful nesting attempts	25	

keeping its balance when landing. The bird was obviously weakened. I found 2 cholla cactus joints clasped in its feet such that it could not release its grip. Survival of a raptor in such condition is questionable since food would be difficult or impossible to obtain.

Table 4. Prey items observed at nests of Harris' Hawks in Arizona in 1976 and 1977.

SPECIES	NUMBER OF ITEMS	PERCENTAGE OF TOTAL
Mammals:		
Cottontail Rabbit *Sylvilagus audubonii*	144	22.4
Harris' Ground Squirrel *Citellus harrisii*	79	12.3
White-throated Woodrat *Neotoma albigula*	76	11.8
Black-tailed Jackrabbit *Lepus californicus*	9	1.4
Round-tailed Ground Squirrel *Citellus tereticaudus*	5	0.8
Pocket Gopher *Thomomys bottae*	2	0.3
Merriam's Kangaroo Rat *Dipodomys merriami*	1	0.2
Banner-tailed Kangaroo Rat *D. spectabilis*	1	0.2
Arizona Pocket Mouse *Perognathus amplus*	1	0.2
Unidentified Lagomorphs	65	10.1
Unidentified Kangaroo Rats	4	0.6
Unidentified Ground Squirrels	3	0.5
Unidentified Mice	2	0.3
Total Mammals	392	61.1
Birds:		
Gambel's Quail *Callipepla gambelii*	56	8.7
Cactus Wren *Campylorhynchus brunneicapillus*	42	6.5
Screech Owl *Otus kennicottii*	14	2.2
Northern Flicker *Colaptes auratus*	13	2.0

(Table 4 continued)

(Table 4 continued)

SPECIES	NUMBER OF ITEMS	PERCENTAGE OF TOTAL
Elf Owl *Micrathene whitneyi*	8	1.2
Mourning Dove *Zenaida macroura*	6	0.9
Curve-billed Thrasher *Toxostoma curvirostre*	4	0.6
Gila Woodpecker *Melanerpes uropygialis*	3	0.5
Road Runner *Geococcyx californianus*	2	0.3
American Kestrel *Falco sparverius*	1	0.2
Cooper's Hawk *Accipiter cooperii*	1	0.2
Unidentified Thrashers	12	1.9
Unidentified Doves	5	0.8
Unidentified Birds	12	1.9
Total Birds	179	27.9
Reptiles:		
Desert Spiny Lizard *Sceloporus magister*	63	9.8
Regal Horned Lizard *Phrynosoma solare*	2	0.3
Zebra-tailed Lizard *Callisaurus draconoides*	1	0.2
Western Whiptail Lizard *Cnemidophorous tigris*	1	0.2
Leopard Lizard *Crotaphytus wislizeni*	1	0.2
Unidentified Reptiles	2	0.3
Total Reptiles	70	11.0
Total Number of Prey Items	641	100.0

Food Habits

A quantitative analysis of food habits in Harris' Hawks was not possible during this study because of time restraints imposed by the large number of nests being observed. Often the only sign of occurrence of an avian prey species was the presence of feathers which denoted little or nothing of the number of individuals taken. Thus I could only indicate that a particular species was found. Since certain body parts of larger mammals (i.e., hind feet of Cottontail Rabbits [*Sylvilagus audubonii*] and tails of Harris' Ground Squirrels [*Citellus harrisii*]) were not eaten and remained in the nest for long periods of time, a more accurate figure for the number of these species taken could be obtained. The food data presented represents a qualitative study of the entire population, which may provide some idea of the total gamut of prey species taken throughout the Harris' Hawk population in Arizona.

Harris' Hawks are quite catholic in feeding habits. Twenty-five vertebrate species were recorded (Table 4), of which 61.1% were mammals. Brannon (1980) found 65.6% of Harris' Hawk prev in Texas to be mammals. Cottontail Rabbit appear to be important in the diet, carcasses at times covering the entire tops of nests. At one nest, pairs of hind feet indicated that at least 22 lagomorphs had been taken. Harris' Ground Squirrels, White-throated Woodrats (*Neotoma albigula*), Gambel's Quail (*Callipepla gambelii*), and Cactus Wrens (*Campylorhynchus brunneicapillus*) also appear to be important in Harris' Hawk diets in Arizona. Four raptors, Screech Owl (*Otis kennicottii*), Elf Owl (*Micrathene whitneyi*), Coopers' Hawk (*Accipiter cooperii*), and American Kestrel (*Falco sparverius*) were taken.

DISCUSSION

Phenology of the Breeding Season

Harris' Hawks in Arizona may lay eggs as early as January (Ellis and Whaley 1979) and sometimes fledge young as late as December (Radke and Klimosewski 1977) which gives them the distinction of having the longest known "breeding season" (as defined by Moreau 1950) of any temperate North American falconiform. In Sonora, Mexico (27 N°), eggs are even laid in November (Ellis and Whaley 1979), suggesting that there are continuous breeders in some southern parts of the Sonora Desert. The terminology "continuous breeder" follows Immelmann's (1971) definition that within a population eggs are laid during every month of the year. This is not the case (as currently known) in the Arizona population since no egg laying has been recorded for the period October-December.

Lack (1968) and Immelmann (1971) suggested that, since the reproductive period is the most rigorous and critical period of a bird's annual cycle, it is imperative that it be scheduled at a time when young can most profitably be raised with a minimum of energy expenditure on the part of the adults. A good example, Eleonora's Falcon of the Mediterranean region, delays breeding until August when it can feed its young on the numerous passerines in fall migration (Walter 1979). Eleonora's Falcons feed mainly on insects during the remainder of the year.

Harris' Hawks seem to follow a similar pattern, as they breed during periods of great prey abundance. Breeding starts quite early in Arizona. Incubation begins in February and March and hatching occurs primarily in April (Fig. 2). Prey species also exhibit long breeding seasons in Arizona. Harris' Ground Squirrel breeds from late February to May with its conception period running from 31 March to late May (Neal 1965). On this basis, Harris' Ground Squirrels are being born when the majority of Harris' Hawk eggs are hatching. Cottontail Rabbits breed year-round in Arizona with peaks for conception starting in April (peak hatch time for Harris' Hawks) and running through July (Hungerford, Lowe and Madsen 1973). The White-throated Woodrat has successive litters from January to August (Vorhies and Taylor 1940), which spans the time during which most Harris' Hawks are breeding. Thus, local abundance and long breeding seasons of prey species may be an important facilitatory factor for an extended breeding season of Harris' Hawks in southern Arizona.

Several other prey species that have long breeding seasons are Gambel's Quail (March to September, Bent 1932), Cactus Wrens (raise 3 broods from February to August, Anderson and Anderson 1960), Curve-billed Thrasher (*Toxostoma curvirostre*) (February to July, Smith 1971), and Mourning Dove (*Zenaida macroura*) (March to September, Brown 1967). The Harris' Hawk's catholic prey habits on species with long reproductive periods may have contributed to the development of an

extended breeding season and increased productivity through double brooding.

When the environment permits a species to raise > 1 brood/yr, breeding begins as early as possible even though the timing of the first attempt may be less favorable (Lack 1968). A species using this strategy would tend to produce the maximum number of offspring under the prevailing circumstances (Lack 1954). Harris' Hawks may follow this strategy, as second and third breeding attempts appear to be influenced by an early first attempt (Fig. 2). The outcome (i.e., success or failure) of the first breeding attempt appears to be less important than timing. Of females that laid double and triple clutches, 97% of the first breeding attempts were started before April, the majority beginning in February. The only January laying represented the first of 3 clutches produced in 1976 by a trio of adults which fledged 5 young from two of the three attempts. Without subsequent nesting, their productivity for 1976 would have been just 2 young. Within 6 other territories high productivity was attained through extra breeding attempts. Adults in 4 territories produced 6 and those in 2 territories produced 7 young/yr. Most of the clutches laid from June to August were second and third attempts (Fig. 2). An early laying pair of Harris' Hawks in Texas produced 7 young during 3 successful nesting attempts in one season (Brannon 1980). Triple clutches in 1 season have been reported 3 times previously for Harris' Hawks (Mader 1977; Whaley 1979), but in all cases only 2 of the 3 attempts were successful. Harris' Hawks begin egg laying earlier in Arizona than in Texas (*see* Brannon 1980), where clutches are started in March and April.

Productivity

Clutch Size. — Mean clutch size for Harris' Hawk populations in this study was 3.16 (N = 162) with 4 and 5 eggs/clutch regularly laid. Four eggs/clutch are not uncommon for Harris' Hawks in Texas (Griffin 1976) and Arizona (this study) whereas along the Colorado River 2 eggs/clutch are the rule (Bendire 1892). Mader (1975b) obtained an average of 2.96 eggs/clutch (N = 50) for Arizona, and Griffin (1976) calculated an average of 2.85 eggs/clutch (N = 20) for western Texas. South Texas populations appear to have a smaller clutch size of 2.33 eggs/clutch (N = 24) (Brannon 1980). Some females in my study were exceptional egg layers; 3 females each laid 16 eggs during the 2-yr period. One of these laid 4 clutches of 4 eggs, all but one of which was in the same nest.

Fledging Rate. — Productivity of Harris' Hawks in Texas is lower than for Arizona and New Mexico populations. Mader (1975) found that 1.60 young fledged/all attempts (N = 50) and 2.35 fledged/successful attempts (N = 34), which compares well with my results for Arizona (Table 2). Griffin (1975) reported similar results for New Mexico, with 1.59 (N = 17) and 2.45 (N = 11) young/attempt and young/successful attempt, respectively. Griffin (1976) reported values of 0.83 (N = 18) and 1.87 (N = 8) young/attempt and young/successful attempt, respectively, for western Texas. Brannon (1980) reported similar results of 1.37 (N = 24) and 2.06 (N = 16) for young/attempt and young/successful attempt for west Texas populations. Lower productivity in Texas populations is likely due to greater fluctuations in prey abundance (Griffin 1976) and less diversity in prey species. Texas populations are more nomadic, as year to year shifts in breeding distributions occur in accordance with rainfall patterns and prey abundance.

Dispersal of Young and Nest Helping

Harris' Hawks in Arizona are nonmigratory. Early reports of large migratory flocks (250 to 500) (Chambers 1921 and 1924; Allan Phillips pers. comm.) are unreliable, and likely the result of misidentification since Harris' Hawks in Arizona have a long breeding season which affords no time for migration.

Harris' Hawks occasionally wander during winter, but generally remain near or within their nesting ranges year round. Families often remained together. On 2 occasions I saw winter groups of 7 and 8 hawks comprised of adults and color-marked juveniles. Wilder (1916) also noted large winter groups of 10 to 20 hawks along the Colorado River in December.

Juveniles do not exhibit a strong tendency to disperse from the natal area. On 10 November 1977 two color-marked Harris' Hawks were trapped less than 0.4 km from where they fledged ca. 173 days earlier (Rich Glinski pers. comm.). On 9 occasions within those 1977 nesting ranges where nesting occurred twice in 1 year, color-marked juveniles of earlier nesting attempts were allowed within the immediate vicinity of, and often on the nest containing eggs or young of subsequent nest-

ing attempts. Those juveniles often seemed as concerned about my presence as the adults. On 22 occasions in 1976 unmarked juveniles which were likely still in natal ranges were sighted near active nests.

On 24 September 1977, while preparing to band 3 young from a second nesting (the first brood of 3 young fledged ca 120 d earlier), a color-marked female from the first brood brought prey to the nest. Also, on 3 occasions in 1979 Brannon (1980) observed prey deliveries by juveniles to the nests of their parents' second breeding attempts. On 12 May 1977 two juveniles that had fledged 2 or 3 weeks earlier were observed incubating 3 eggs of their parents' second clutch. Nest-helping by juveniles fledged earlier the same season has not been previously reported in raptors. The helper system of the Harris' Hawk may prove to be similar to that of the Florida Scrub Jay (*Aphelacoma coerulescens*) (Woolfenden 1975). Young of Galapagos Hawk (*Buteo galapagoensis*) also remain near the natal area for several months after fledging and occasionally retain close ties with their parents (de Vries 1973). On 1 occasion de Vries witnessed a 5-month-old juvenile still begging food from the male parent while the female was incubating eggs of a second nesting attempt.

Harris' Hawks do not appear to disperse great distances from their natal area over long periods of time. Based on 13 band returns, sightings and capture-releases, juveniles ($\geq$ 5 months fledged) traveled an average distance of 15 miles (range $<$ 5 miles for a male during 3 years and 30 miles for a female during 6 months). On 20 May 1977 I banded a male nestling near Florence Junction. The same male was trapped in its nesting territory nearly 8 yrs later on 12 January 1985 (Jim Dawson pers. comm.) 35 miles south of where it had fledged.

Past Populations of the Colorado River

The Harris' Hawk was a common resident along the Colorado River for at least 134 years. The population did not range far from the riparian community (U.S.D.I. Fish and Wildlife Service 1950); thus, events that may have affected this habitat may also have impacted the Harris' Hawk populations in that region. Extensive flooding along the Colorado River in the early 1900's evoked construction of several dams in the 1930's and 1940's. With flooding controlled, agricultural activities along the river increased. By the 1930's and 1940's, salt cedar (*Tamarix pentandra*) spread over large areas of the river and began to compete with the cottonwood community which was rejuvenating from past floods. Dredging operations began along the river during the 1940's and may have been a source of disturbance. Previously inaccessible areas of the swamp were now accessible by motor powered craft so subsequently there was increased use of the river for recreational activities during the 1950's (Gale Monson pers. comm.). At Havasu National Wildlife Refuge, where Harris' Hawks often nested low over the water in drowned out mesquite trees, increased recreational activities may have been a major factor during the nesting periods. Fishermen were seen destroying nests, probably under the mistaken impression of destroying Cormorant (*Phalacrocorax* sp.) nests (Gale Monson pers. comm.). Harris' Hawks were occasionally harassed by duck hunters who often referred to them as, "the big black hawk that catches ducks" (Miller 1925). Monson reported that Harris' Hawk numbers were sometimes slightly depleted by waterfowl hunters in the open areas above Topock (U.S.D.I. Fish and Wildlife Service 1949).

A combination of the above factors likely had an impact on Harris' Hawk populations along the Colorado River. Drastic habitat alteration and increased recreational activities perhaps yielded the greatest impact.

The Present Population

Qualitatively, the most obvious characteristic of Harris' Hawk habitat in Arizona is the presence of healthy stands of paloverde-saguaro desert scrub of the Arizona Upland subdivision. The present distribution of Harris' Hawks in Arizona strictly follows the Arizona Upland subdivision of the Sonoran Desert with no nests occurring outside this habitat. Thus, this hawk habituates the most structurally complex habitats within the Sonoran Desert, where prey density and diversity is the greatest.

The nesting distribution of the Harris' Hawk in Arizona has shrunk since the early 1900's due in part to the extirpation of populations along the Colorado, Gila, Santa Cruz, and San Pedro Rivers. Along the Gila and Santa Cruz habitat has been severely altered (Dawson 1921; Rea 1977). In order to determine susceptability of the present popula-

Table 5. Land ownership status for 306 nest sites and 396 nesting attempts for Harris' Hawk in Arizona in 1976 and 1977.

LAND OWNERSHIP	NUMBER OF ACTIVE NESTS	PERCENTAGE OF TOTAL	NUMBER OF NESTING ATTEMPTS	PERCENTAGE OF TOTAL
State Trust Land	140	45.8	184	46.5
Patented Land	73	23.9	84	21.2
BLM Land	40	13.0	57	14.4
Forest Service	18	5.9	24	6.0
Indian Reservation	18	5.9	23	5.8
Patented or State	7	2.3	10	2.5
BLM or State	5	1.6	8	2.0
Regional Park	3	.9	3	.8
U.S. Park	2	.7	3	.8
Totals	306	100.0	396	100.0

tion to possible habitat encroachment, I determined land ownership status for 306 active nest sites (Table 5). A large proportion of nests are on patented land, and therefore are more vulnerable to the effects of man's present and future activities. Since the Harris' Hawk appears to be habitat restricted in its nesting, the retention of both state and federal lands with healthy stands of paloverde-saguaro will be crucial for its future welfare in Arizona. Urban sprawl near several Harris' Hawk populations may result in continued loss of nesting range in Arizona. Harris' Hawk numbers near Tucson and Cave Creek have declined recently as a result of urban development. The Cave Creek population is currently threatened due to urban sprawl and may soon be decimated (Jim Dawson pers. comm.). Other habitats that are threatened by urban development are in areas near Rio Verde, Apache Junction, and Florence.

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