A COMPARATIVE NESTING STUDY OF RED-TAILED HAWKS AND HARRIS' HAWKS IN SOUTHERN ARIZONA

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ABSTRACT .-- I studied the nesting of Red-tailed Hawks in the Sonoran Desert of Arizona in 1969-1976, emphasizing its ecology relative to the Harris' Hawk, a species that I have found to be sometimes polyandrous and have nest helpers. Red-tails averaged 2.32 eggs per clutch (59 nests) and Harris' Hawks 2.96 (50 nests). The clutch size distributions of the two species were significantly different. Nest success was 81% for Red-tails and 68% for Harris' Hawks, but may actually be slightly lower because a nest was considered successful if a chick was raised to an age of at least 28 days but not always to fledging. For Red-tails, the average number of chicks produced was 1.55 per nest attempt (42 nests) and for Harris' Hawks 1.60 (50 nests). Red-tails nested exclusively in saguaro cacti, but the more agile Harris' Hawks used not only easily accessible saguaro sites but enclosed tree sites as well. Nest site availability seemed to have no significant role in population regulation. The nesting cycle of the Red-tailed Hawk, from egg laying to fledging, was from February to June; for Harris' Hawks it was from February to early December (because of second broods). Optimum habitat and greater hunting versatility in the Harris' Hawk may allow it a less restricted breeding season in saguaro-palo verde desert than the Red-tail by providing essential food resources. These two factors, and nest helping if it is common, probably contribute to maximizing the productivity of Harris' Hawks in an arid environment with variable food resources. Received 2 June 1976, accepted 5 October 1976.

THE Red-tailed Hawk (*Buteo jamaicensis*) has received little investigation in the southwestern deserts of the United States. This report presents information on the nesting ecology of this species in the Sonoran Desert of southern Arizona and compares it to that of the Harris' Hawk (*Parabuteo unicinctus*). Although both species are much the same size and occupy similar habitat in this desert, the Red-tailed Hawk is monogamous while the Harris' Hawk is at least in part polyandrous and has nest helpers. Recent evidence of pesticide contamination in the Red-tail (Seidensticker and Reynolds 1971) and Harris' Hawk (Mader 1977a) also lend importance to this investigation.

The Harris' Hawk is a species of primarily seasonally dry desert, savanna, or chaco and is here at the northern limit of its distribution; it is possible that winter conditions limit it to the north. The Red-tail, on the other hand, is here near the southern limits of its breeding distribution in arid lowlands, though it extends south into islands of the Caribbean and the highlands of western Panama (Brown and Amadon 1968).

STUDY AREA AND METHODS

I studied Red-tailed and Harris' Hawk populations from 1969 to 1976 in saguaro-palo verde (*Carnegiea gigantea-Cercidium* sp.) flatland in Pima and Pinal Counties, Arizona, where cliffs and riparian habitat are absent (Fig. 1). Details of Harris' Hawk breeding behavior and productivity, and a description of the study areas, are included in two earlier papers (Mader 1975a, 1975b) and will be referred to here only as needed for comparison with the Red-tail material.

I recorded clutch size in 59 Red-tail nests over the whole period. During the last 3 yr, when I concentrated on Red-tails rather than Harris' Hawks, I was able to determine nesting success and productivity of

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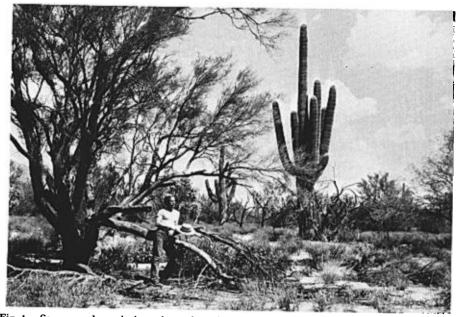


Fig. 1. Saguaro-palo verde desert in southern Arizona showing a palo verde tree on left and a saguaro on right. Triangle-bur sage (*Franseria deltoidea*) dominates the foreground.

young for 42 of these nests, and took additional notes on the ecology of the species including nest building and egg-laying dates, nest site selection, and prey remains found at nests. Red-tail and Harris' Hawk nests were located by car and on foot. Nest contents were checked periodically using an extension ladder and 1.5-m poles connected together with a mirror at the top. Nest and cactus heights were determined from these same breakdown poles to the nearest 15 cm. Approximate Harris' Hawk nest positions inside of tree canopies were measured to the nearest 5 cm from the top center of nest horizontally to nearest canopy edge and vertically to the top of the canopy. I estimated total saguaros potentially available to the hawks as nesting platforms within a nesting range (size previously determined to be about 5.0 km^2) by counting all suitable saguaros in a 0.65-km^2 area and then extrapolating these figures to 5.0 km^2 .

As in my earlier Harris' Hawk study (Mader 1975a), a nest was considered successful if a chick was raised to an age of at least 28 days. Although most chick mortality occurred before 28 days, actual nest success and fledglings produced for each species may be slightly lower than figures I report here. I used a 35-day incubation period (Hardy 1939, present study) for backdating some Red-tail nests from the known hatching dates to estimated laying dates. A 46-day fledging period (Fitch et al. 1946, Johnson 1975) was used to estimate fledging dates for nests not checked late in the nesting cycle.

Two 4.8-m tower blinds were erected at two Harris' Hawk nests attended by the same three adults in 1973 (164 h) and 1974 (87 h) to determine prey species caught. A $30 \times$ scope aided identifications. The two blinds were 18.6 m and 12.2 m from the nests, respectively; both afforded clear level views of the nests.

RESULTS AND DISCUSSION

Productivity.—Some Red-tails began building nests in late December, but most appeared to build in January and February. Red-tails laid eggs from 25 February to 2 April (N = 36 nests, includes estimated dates). Overall, laying centered around the first and second weeks of March (mean = 9 March). Hatching occurred from 25 March to 8 May and centered around the first and second weeks of April (mean = 12 April). Fledging centered around the last week of May and first week of June (computed mean = 27 May). The entire breeding season (egg-laying-fledging) spanned 118 days.

	Clutch size					E arga	
Years	1	2	3	4	No. eggs	No. nests	Eggs per nest
1969-1973	3	9	5	0	36	17	2.12
1974	0	7	6	1	36	14	2.57
1975	1	7	6	0	33	14	2.36
1976	1	8	5	0	32	14	2.29
Total	5	31	22	1	137	59	2.32

TABLE 1. Red-tailed Hawk clutch size in southern Arizona

Red-tail nests averaged 2.32 eggs per nest (N = 59, Table 1). Harris' Hawks averaged 2.96 eggs per clutch (range = 1-4; N = 50). The clutch size distributions of the two species differed to a highly significant degree (χ^2 = 23.7, 3 d.f., P < 0.001); 4-egg clutches were especially higher in Harris' Hawks (17, for 34%) than Red-tails (1, for 2%). Average clutch size for Red-tails in other studies has been: California, 2.00 (18 nests, Fitch et al. 1946) and 2.53 (53 nests, Wiley 1975); Utah, 2.89 (19 nests, Smith and Murphy 1973); Montana, 2.90 (22 nests, Seidensticker and Reynolds 1971); Alberta, 2.00 (98 nests, Luttich et al. 1971).

Most Red-tail nests found from 1969 to 1973 were not later checked to determine the number of young produced, hence I have such data only for the years 1974–1976 (Table 2). Of the 42 Red-tail nests, 34 (81%) were successful, producing 65 chicks (1.55 per nest attempt) of at least 28 days of age. The cause of Red-tail nesting failure was determined at only one nest. This nest, with two downy chicks, was apparently blown down by high winds. At another nest one of the adults, the female judging from size, was shot when the single chick in the nest was about 2 weeks old. The lone remaining adult raised the chick to at least 28 days of age. In Wisconsin, Orians and Kuhlman (1956) reported that 27 Red-tail nests averaged 1.80 fledglings per nest attempt in 1953, 33 nests 1.10 in 1954, and in 1955, 27 nests 1.40. Johnson (1975) estimated 1.57 fledglings per nest attempt for 121 nests in Montana, Gates (1972) 1.10 for 31 nests in Wisconsin, and Wiley (1975) 1.64 for 53 nests in California.

Henny and Wight (1972) estimated that 1.79–1.89 Red-tail young must be fledged per breeding age female in the southern United States to maintain a stable-age population. In my study 42 nests raised 1.55 chicks per nest attempt. The estimates of Henny and Wight may be slightly high for my desert study areas because nest success per year was stable and populations appeared widespread and evenly dispersed with no evidence of decline. Alternatively, it is possible that the breeding population is replenished by Red-tails coming from elsewhere.

Of the 50 Harris' Hawk nests, 34 (68%) were successful and averaged 1.60 chicks per nest attempt. Even though nest success of Harris' Hawks did not differ signifi-

Years	N (nests)	Successful nestsª	Chicks raised to at least 28 days	Chicks per nest
1974	14	10 (71.4%)	19	1.36
1975	14	11 (78.6%)	21	1.50
1976	14	13 (92.9%)	25	1.79
Total	42	34 (81.0%)	65	1.55

TABLE 2. Red-tailed Hawk nesting success in southern Arizona

^a A nest was considered successful if a chick was raised to an age of at least 28 days. Only nests that were initially found with eggs appear in the table. Figures in parentheses represent the number as a percentage of the total.

cantly from that of Red-tails (81%), part of the 12% difference may have been due to my investigation of the hawks in different years.

Habitat and nesting ranges.—Although I have occasionally seen Harris' Hawks in the winter in agricultural and mesquite (Prosopis sp.) areas, I have found them nesting only in saguaro-palo verde flatland with washes and ravines that slowly give way to low hills. When compared with adjacent steep mountains that rise abruptly out of the desert, this terrain appears relatively flat (local relief <100 m). Even though saguaros were sometimes locally uncommon and clearly not dominant, I still referred to the habitat as saguaro-palo verde. Red-tails, on the other hand, nested not only in flatland but in grassland, woodland, and mountainous desert outside of my study areas. On the whole, Harris' Hawks in my study areas occupied desert habitat where the vegetation was structurally complex and included saguaro, palo verde and ironwood (Olneya tesota) trees with assorted shrubs and cacti. Populations of small animals and birds in such areas were noticeably larger than in areas devoid of saguaros and large trees. Rabbit density in Sonoran Desert habitats is generally increased by plant species diversity through increased available edge (C. R. Hungerford pers. comm.). Also, Tomoff (1974) found that as the kinds and numbers of plants increased in the Sonoran Desert, so did the kinds and numbers of birds. In this kind of structurally complex habitat, Harris' Hawks were commonly more numerous than Red-tails and were occasionally the only large nesting hawk. In slightly less diverse desert, Harris' and Red-tailed hawks nested together. In more arid habitat, where creosotebush (Larrea divaricata) was the only large shrub, ironwood was absent, and saguaro and palo verde were uncommon and not of good condition and large size, Red-tails were often the only large nesting hawk encountered. On the other hand, in some seemingly good habitat, Harris' Hawks were inexplicably reduced in numbers. Harris' Hawks, then, generally appeared to occupy the most complex habitat, while Red-tails nested in simpler, more arid habitat, although some variation occurred.

Seven nesting ranges (the area and living requirements necessary for a nesting pair or trio, see Mader 1975a, Craighead and Craighead 1956: 247) of Harris' Hawks in structurally complex habitat averaged 5.0 km² in size. I do not have averages for Red-tail nesting ranges, but judging from the spacing at which I found Red-tail nests, I would anticipate that Red-tails occupy comparable nesting ranges in the same habitat, but much larger ones in poorer, more arid areas. Competition for nest sites seemed practically nonexistent, probably because saguaro nest sites are common. However, in one case a pair of Harris' Hawks occupied an old saguaro nest that 3 yr before had been used successfully by Red-tails. The Harris' nest was unsuccessful for unknown causes. Conversely, a pair of Red-tails occupied an old saguaro stick nest that 2 yr before was used successfully by Harris' Hawks. Outcome of the Red-tail nest was not known. I do not think that these were takeovers of nesting ranges, but a shift possibly caused when one species built a nest earlier than the other and farther away than usual from its previous site, thus allowing a neighboring species to take over the unoccupied nest.

Length of nesting cycle.—Harris' Hawks appear to have a much longer nesting season than Red-tails in saguaro-palo verde habitat. The period of egg-laying to fledging spans from February to June for Red-tails and from February to December for Harris' Hawks (Fig. 2). Time of egg-laying may vary each year. Radke and Klimosewski (1977) found a Harris' Hawk nest that fledged young from 2 to 4 December in 1975, and I have found nests with young in October. Nesting of Harris'

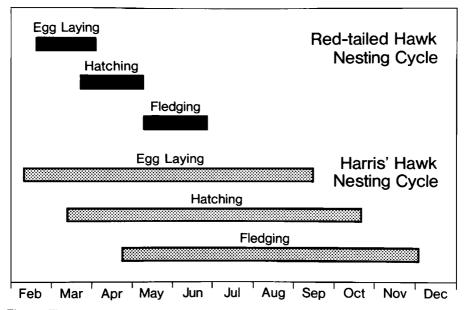


Fig. 2. The comparative duration of the nesting cycles of Red-tailed Hawks and Harris' Hawks in the Sonoran Desert of Arizona showing major events in the cycle. Second and third nesting attempts were recorded only for Harris' Hawks. Nest dates for Harris' Hawks, other than in this study, are by extrapolations of dates from Mader (1975a), and Radke and Klimosewski (1977). A 35-day incubation period was used to approximate egg-laying dates of Harris' Hawk clutches.

Hawks seemed to be centered on the period from March to June in my study years, but some pairs or trios will lay two or three clutches in one year, producing two broods (Mader 1975a, 1977b). Second nesting attempts after failure of the first appear not uncommon for Harris' Hawks in southern Arizona. However, late nesting from summer to winter may be of limited and local occurrence. To my knowledge, Red-tails have not been recorded nesting successfully twice in a year and I found no second nesting attempts. Unusually early egg-laying under optimum prey conditions or renesting by Red-tails after an initial clutch has failed may prolong the nesting season beyond that shown in Fig. 2, but apparently Red-tails do not nest in fall or winter, or if they do it is less frequent than in Harris' Hawks. Furthermore, it seems probable that Harris' Hawks may sometimes nest the year around, thereby extending the known nesting season into January, although I do not include January in Fig. 2.

Variable but sometimes extended food resources may explain why Harris' Hawks have a prolonged nesting season. Perrins (1970) indicated that food supply may limit the ability of birds to form eggs and Lack (1954, 1968) pointed out that many birds synchronize the nesting cycle to periods when food is plentiful. Thus, if eggs and young are to be produced, an adequate food supply must be on hand at the right season. My observations suggest that Harris' Hawks can sometimes breed longer and raise more broods than Red-tails for at least two reasons: (1) Habitat quality is generally better in Harris' Hawk nesting ranges, providing a longer and more continuous breeding period for important prey species and therefore a lengthened food supply, at least in certain years; and (2) Harris' Hawks are the more versatile and generalized hunter of the two and can exploit different prey types (mammals, birds, and reptiles) more effectively. The importance of each of these two factors will vary

	Nest one (observed 24 March4 May 1973)		Nest two (observed 26 July–20 August 1974	
Prey type	No. indiv.	% indiv.	No. indiv.	% indiv.
Mammals	30	51.7	22	66.7
Birds	24	41.4	8	24.2
Reptiles	4	6.9	3	9.1
Total	58	100.0	33	100.0

TABLE 3. Prey types observed brought to two Harris' Hawk nests and nearby area. Both nests were attended by the same three adults

because of habitat type (arid or complex), and yearly variation in climate and related changes in prey availability. For example, the reduced hunting versatility of Redtails may be a major factor that contributes to a restricted breeding season in complex habitat, which has high densities of mammals and birds. Conversely, the hunting versatility of Harris' Hawks may be an especially important factor in low prey years if prolonged breeding is to occur.

.In support of the first hypothesis, Hungerford (1964) found that Gambel's Quail (Lophortyx gambelii), an important prey species of Harris' Hawks in Arizona, had a longer and more continuous breeding period when habitat quality was high, and a reduction or complete lack of breeding in drought years when habitat was poor. Two more prey species, the Cactus Wren (Campylorhynchus brunneicapillus) and the Mourning Dove (Zenaida macroura) sometimes raise two or three broods of young in saguaro-palo verde habitat (Anderson and Anderson 1973, Irby and Blankenship 1966). This and the fact that late breeding by Harris' Hawks corresponds to a late rabbit breeding peak in July and August (see Hungerford et al. 1973), suggests that in some years high quality habitat can better support a prolonged breeding season by Harris' Hawks because the required food supply is present over the necessary period of time. This rabbit peak, although available to some Red-tails, may by itself not be enough to support breeding. All the late nestings of Harris' Hawks that I observed (N = 8) were in good quality (complex) habitat. This was also true of the late Harris' Hawk nest found by Radke and Klimosewski (1977).

In support of the second hypothesis, the number of prey species and types utilized is an important indicator of hunting versatility. Previously (Mader 1975a) I identified 17 prey species from remains and prey observed brought to Harris' Hawk nests (N = 251): 6 (35%) were mammals, 8 (47%) birds, and 3 (18%) reptiles. Harris' Hawks are versatile hunters in the desert, capable of shifting prey types when availability changes. For example, I tallied prey in successive years at two Harris' Hawk nests that were attended by the same three adults, but at different times of the year, one in spring and the second in mid-summer (Table 3). The proportion of mammal prey observed brought in changed from 51.7% at nest 1 to 66.7% at nest 2, while bird prey changed from 41.4% to 24.2%. Nest 2 was the second nesting by the three hawks for that particular year and both fledged young. This trio remained together from 1973 to 1975 and in this period nested at least 6 times, producing 14 fledglings for an exceptionally high average of 4.7 per year (Mader 1977b). If nest helping is common among Harris' Hawks in southern Arizona as suggested in earlier work (Mader 1975a, 1975b), an extra adult might be advantageous by providing more food for the nestlings in late summer and fall when some prey populations have declined. Trios were present at the earliest and the two latest nestings that I recorded, and also the one observed by Radke and Klimosewski (1977).

Species	No. indiv.	% indiv.
Mammals		
Cottontail rabbit (Sylvilagus audubonii)	3	5.4
Black-tailed jackrabbit (Lepus californicus)	1	1.8
Unidentified rabbit	16	29.2
Round-tailed ground squirrel (Citellus tereticaudus)	7	12.8
Harris ground squirrel (Ammospermophilus harrisii)	2	3.6
Bailey's pocket mouse (Perognathus baileyi)	2	3.6
Southern grasshopper mouse (Onychomys torridus)	1	1.8
Pocket gopher (Thomomys bottae)	1	1.8
Wood rat (Neotoma albigula) ^a	1	1.8
Total mammals	34	61.8
Reptiles		
Desert spiny lizard (Sceloporus magister)	4	7.4
Unidentified horned lizard (Phrynosoma sp.)	2	3.6
Gopher snake (Pituophis melanoleucus)	2	3.6
Unidentified rattlesnake (Crotalus sp.)	1	1.8
Unidentified snakes	12	21.8
Total reptiles	21	38.2
Total	55	100.0

TABLE 4. Prey remains found at Red-tailed Hawk nests in southern Arizona

^a In Mader (1975a, Tables 7 and 11) this species was misidentified as N. lepida.

At Red-tail nests, on the other hand, the 12 prey species from 55 prey remains included only mammals and reptiles (Table 4). The inherent bias of analyzing only prey remains data (see Snyder and Wiley 1976: 2, Mader 1975a: 70) and my modest sample size limit conclusions, but some speculation is in order. Small bird feathers at nests suggested that Red-tails preyed upon birds, but no substantial remains were found to warrant their inclusion in Table 4. At a Red-tail nest studied by Hensley (1959) in saguaro-palo verde desert, prey consisted mostly of rodents with the roundtailed ground squirrel (Citellus tereticaudus) most common. The desert spiny lizard (Sceloporus magister) and Clark's spiny lizard (S. clarki) were also found in this nest and an adult Red-tail was seen flying overhead carrying a snake. Snyder and Wiley (1976) showed that Red-tails preyed most heavily on mammals (50.5%) and invertebrates (36.8%) (N = 189 items from stomach analyses and prey observed caught or brought to nests). Also, prey remains found at Red-tail nests in other western states suggest that mammals are heavily preved upon: California, 89.4% mammals (625 items, Fitch et al. 1956); Wyoming, at least 89.9% mammals (189 items, Craighead and Craighead 1956); Utah, 89.1% (330 items, Smith and Murphy 1973). In Wisconsin, however prey remains suggest that there birds are heavily preyed upon (Orians and Kuhlman 1956, Gates 1972).

Harris' Hawks are swifter and more agile in flight than Red-tails and probably better able to pursue different prey types. Harris' Hawks successfully hunted birds, mammals, and reptiles (lizards) in a variety of ways when I watched from blinds at nests (see Mader 1975a: 74). This included cooperative hunting by two or three adults. It is likely that Harris' Hawks are morphologically more adept than Red-tails at hunting in some of the close cover present in saguaro-palo verde desert, where their comparatively longer tail and slightly shorter wings are an advantage. Therefore, it seems reasonable that Red-tails in my desert areas may be more restricted feeders and less versatile hunters than Harris' Hawks, and prey primarily on mammals and to an extent reptiles.

Migratory status, duration of fledgling dependency, and behavior of the two hawk species also affect the length of the nesting season. Harris' Hawks seem largely

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TABLE 5. Height of Red-tailed Hawk nests and saguaro cacti used as nesting sit	TABLE 5.	Height of Red-tailed	Hawk nests and saguaro	cacti used as nesting site
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	Nest height	Saguaro height
Number nests	35	35
Mean height (m)	6.6	8.4
Range (m)	2.9-9.4	5.0-11.0

resident. Twenty-one banded Harris' Hawks (some with color bands), 13 of which were banded as chicks, were last sighted or retrapped an average of 278 days (range = 44-1,349) after their first capture at an average distance of 1,300 m (range = 400-6,800); one immature was later recovered 70 km north of its second sighting. The migratory status of Red-tails in Arizona is poorly understood. Although I banded 40 Red-tails as chicks and adults, I received only one banding return, this in the same county where I had originally captured the hawk. Young Harris' Hawks generally have an extended fledgling dependency period of at least 2-3 months, although variation occurs. I have no data on fledgling dependency of Red-tails in my study, but Johnson (1973) reports that in Montana immature birds are associated with their parents from 30 to 70 days after fledging. The long nesting period of Harris' Hawks can be attributed largely to renesting and to second broods that occur from late summer to winter. When two broods were raised in one year, the first appeared to reduce its dependency on the adults before the second clutch hatched. Even so, long dependency of fledglings on adults can occur, but this apparently does not always discourage a second brood the same year. On three occasions I saw an adult male of a trio pass prey to an immature hawk with a broken wing that was from this group's first brood of the year, even though there were chicks in a nearby nest from the second brood (see Mader 1975a: 78). This seems to be a result of the unusual social organization and behavior of this falconiform. Even if Red-tails do or could get adequate food to promote multiple clutching and brooding, the less socialized breeding structure of this species would possibly limit it.

Optimum habitat, in the form of structurally complex desert, and hunting versatility, then, may be two factors that render Harris' Hawks in saguaro-palo verde flatland less sensitive to fluctuating bird or mammal populations that might delay or prevent the food intake essential to egg-laying and a prolonged breeding season.

Snakes as possible prey.—It is not clear why Harris' Hawks do not usually prey on snakes in saguaro-palo verde desert while Red-tails regularly do so. Even though snakes, including venomous rattlesnakes (Crotalus sp.), were common near the Harris' Hawk nests that I studied from blinds, the hawks did not attempt to catch them, seeming to prefer comparatively lively and conspicuous mammals and birds. It is possible that Harris' Hawks react more to active prey as opposed to slower moving, less conspicuous animals such as snakes. The fact that Harris' Hawks capture fastmoving lizards with long tails that resemble snakes supports this idea. Snyder (1975) and Snyder et al. (1976) showed in laboratory settings that Red-tailed and Ferruginous (*Buteo regalis*) hawks selectively captured the more active of two prey animals. Prey activity alone does not satisfactorily explain why Harris' Hawks do not catch snakes. It may also be physically safer for Harris' Hawks to pass up snakes, if they are morphologically better adapted to capturing mammals and birds. The toes of Harris' Hawks are comparatively long and powerful for the body size (Grossman and Hamlet 1964: 280), while snake eagles typically have short, thick toes that are more suitable for gripping and killing snakes (Brown 1970: 49). As regards physical safety,



Fig. 3. An adult Harris' Hawk with young at a nest in a palo verde tree, showing type of foliage and enclosed position of nest in tree canopy. Branches immediately in front of nest have been removed.

a Red-tail was reported killed by a rattlesnake in Bent (1937). Prey activity levels and morphologic adaptation to other prey types may thus partially account for the low frequencies of Harris' Hawk predation on snakes in my study areas.

Nesting sites.—All the Red-tail nests in my study were in saguaro cacti. Nest heights of 35 nests averaged 6.6 m while heights of the saguaros used averaged 8.4 m (Table 5). Fitch et al. (1946) recorded an average height of 15.6 m for 10 nests in California, while Orians and Kuhlman (1956) observed an average height of 17.4 m for 49 nests in Wisconsin. Red-tail nests in saguaro-palo verde flatland are lower than in the above studies because saguaros are the tallest sites available.

In some saguaro-palo verde flatland, Harris' and Red-tailed hawks occupy seemingly identical habitat. In this type of habitat, where cliffs and large tree sites along riparian stream courses are absent, I found Red-tails nesting exclusively in saguaros. In comparison, Harris' Hawks nested commonly in both saguaros and trees, primarily palo verde and ironwood. Saguaro nests of both species are usually not distinguishable from one another. Harris' Hawk nests in saguaros averaged 5.9 m in height (N = 27) while total saguaro height averaged 8.2 m. These figures are about the same as Red-tail nests, and saguaro heights of 6.6 m and 8.4 m, respectively. Harris' Hawk nests in trees (palo verde and ironwood) averaged 5.7 m in height (N = 31) while total tree height averaged 7.0 m. Harris' Hawks, then, build nests at roughly the same height and utilize sites of the same height as do Red-tails, except that Red-tails use only (or at least primarily) saguaros as nesting sites while Harris' Hawks use both saguaros and trees. I hypothesize that Red-tails do not often utilize palo verde and ironwood trees in saguaro-palo verde flatland because the canopies in most of these trees are difficult to penetrate and construct nests in. Palo verde and ironwood trees are spinescent and limber. Physical injury in entering such sites may also be a factor. Twenty Harris' Hawk tree nests (12 palo verdes, 8 ironwoods)

averaged 1.25 m (range = 0.50-2.85 m) horizontally from the edge of the tree canopy and 1.65 m (range = 1.10-2.35 m) vertically, indicating that large hawks, such as Harris' and Red-tails, must build nests well inside the canopy if they are to be supported (Fig. 3). Red-tails are soaring birds of usually open spaces and are not adept at regularly flying through cover. Red-tail nests in saguaros have easy access and departure routes for flight with less chance of injury. For this reason, it may not only be easier for Red-tails to utilize saguaro sites but also safer. Harris' Hawks, on the other hand, are more agile in flight and can enter saguaro and tree sites with ease.

The Great Horned Owl (*Bubo virginianus*) is somewhat agile and capable of penetrating dense cover; in saguaro-palo verde flatland it utilizes both saguaros and trees as nesting sites (Mader 1973), using old nests of course. This lends support to my idea that Red-tails nest primarily in saguaros because these sites are the most accessible platforms available and insure easy access and departure routes.

Using recorded heights of Red-tail nests as a guide and the fact that at least two saguaro limbs of sufficient size are ordinarily needed to support a nest, I estimated how many suitable nesting sites of saguaro were available for nesting Red-tailed and Harris' hawks within one nesting range (5.0 km²). I chose a nesting range that both Red-tailed and Harris' hawks had used in the last 5 yr in "typical" saguaro-palo verde habitat. I estimated that approximately 490 saguaros were available to Red-tailed and Harris' hawks as potential nest platforms. Since Red-tails nest almost exclusively in saguaros, and but once a year, they are utilizing about 0.2% of the total platforms available for nesting in a given year. In habitat with more saguaros, the percentage is probably less, while the converse relationship may occur in habitat where saguaros are fewer. For Harris' Hawks, the percentage is probably much lower than 0.2 because so many tree sites are also available. On the other hand, if a Harris' Hawk pair or trio nests two or three times in a year, the percentage will be higher. It seems unlikely that nest site availability has any significant role in population regulation in this habitat; instead, prey densities may be an important factor.

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LITERATURE CITED

ANDERSON, A. H., & A. ANDERSON. 1973. The Cactus Wren. Tucson, Univ. Arizona Press. BENT, A. C. 1937. Life histories of North American birds of prey. U.S. Natl. Mus. Bull. 167.

BROWN, L. 1970. Eagles. New York, Arco Publ. Co. Inc.

CRAIGHEAD, J. J., & F. C. CRAIGHEAD, JR. 1956. Hawks, owls and wildlife. Harrisburg, Pa., Stackpole Co.

FITCH, H. S., F. SWENSON, & D. F. TILLOTSON. 1946. Behavior and food habits of the Red-tailed Hawk. Condor 48: 205-237.

GATES, J. M. 1972. Red-tailed Hawk populations and ecology in east-central Wisconsin. Wilson Bull. 84: 421-433.

GROSSMAN, M. L., & J. HAMLET. 1964. Birds of prey of the world. New York, Clarkson N. Potter, Inc. HARDY, R. 1939. Nesting habits of the western Red-tailed Hawk. Condor 41: 79–80.

HENNY, C. J., & H. M. WIGHT. 1972. Population ecology and environmental pollution: Red-tailed and Cooper's Hawks. Pp. 229–250 in Population Ecology of Migratory Birds: A Symposium. U.S. Dept. Interior Wildl. Res. Rept. No. 2.

- HENSLEY, M. M. 1959. Notes on the nesting of selected species of birds of the Sonoran Desert. Wilson Bull. 71: 86-91.
- HUNGERFORD, C. R. 1964. Vitamin A and productivity in Gambel's Quail. J. Wild. Mgmt. 28: 141-147.
 , C. H. LOWE, & R. L. MADSEN. 1973. Population studies of the Desert Cottontail (Sylvilagus auduboni) and Black-tailed Jackrabbit (Lepus californicus) in the Sonoran Desert. Desert Biome, U.S. Intern. Biol. Program, Res. Mem. 73-20. 15 pp.
- IRBV, H. D., & L. H. BLANKENSHIP. 1966. Breeding behavior of immature Mourning Doves. J. Wild. Mgmt. 30: 598-604.
- JOHNSON, S. J. 1973. Post-fledging activity of the Red-tailed Hawk. Raptor Res. 7: 43-48.
- -----. 1975. Productivity of the Red-tailed Hawk in southwestern Montana. Auk 92: 732-736.
- LACK, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.
- ------. 1968. Ecological adaptations for breeding in birds. London, Methuen.
- LUTTICH, S. N., L. B. KEITH, & J. D. STEPHENSON. 1971. Population dynamics of the Red-tailed Hawk (Buteo jamaicensis) at Rochester, Alberta. Auk 88: 75-87.
- MADER, W. J. 1973. Notes on Nesting Great Horned Owls in southern Arizona. Raptor Res. 7: 109-111.
- -----. 1975a. Biology of the Harris' Hawk in southern Arizona. Living Bird 14: 59-85.
- -----. 1975b. Extra adults at Harris' Hawk nests. Condor 77: 482-485.
- ——. 1977a. Chemical residues in Arizona Harris' Hawk eggs. Auk. 94: 587–588.
- -----. 1977b. Harris' Hawks lay three clutches of eggs in one year. Auk. 94: 370-371.
- ORIANS, G., & G. KUHLMAN. 1956. Red-tailed Hawk and Horned Owl populations in Wisconsin. Condor 58: 371–385.
- PERRINS, C. M. 1970. The timing of bird's breeding seasons. Ibis 112: 242-255.
- RADKE, E. L., & J. KLIMOSEWSKI. 1977. Late fledging date for Harris' Hawks. Wilson Bull. in press.
- SEIDENSTICKER, J. C., & H. V. REYNOLDS. 1971. The nesting, reproductive performance and chlorinated hydrocarbon residues in the Red-tailed Hawk and Great Horned Owl in south-central Montana. Wilson Bull. 83: 408-418.
- SMITH, D. G., & J. R. MURPHY. 1973. Breeding ecology of raptors in the eastern great basin of Utah. Brigham Young Univ. Sci. Bull., Biol. Ser. 18 (3). 76 pp.
- SNYDER, N. F. R., & J. W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithol. Monogr. 20: 1–96.
- SNYDER, R. L. 1975. Some prey preference factors for a Red-tailed Hawk. Auk 92: 547-552.
- ------, W. JENSON, & C. D. CHENEY. 1976. Environmental familiarity and activity: Aspects of prey selection for a Ferruginous Hawk. Condor 78: 138–139.
- TOMOFF, C. S. 1974. Avian species diversity in desert scrub. Ecology 55: 396-403.
- WILEY, J. W. 1975. The nesting and reproductive success of Red-tailed Hawks and Red-shouldered Hawks in Orange County, California, 1973. Condor 77: 133-139.