

# THE ROLE OF TERRITORIALITY IN THE SOCIAL ORGANIZATION OF HARRIS' HAWKS

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**ABSTRACT.**—We studied territoriality and sociality in a population of Harris' Hawks (*Parabuteo unicinctus*) in Arizona during breeding and nonbreeding periods from 1984 to 1986. Our study area contained 22 to 26 breeding groups and density of nests averaged 1/2.0 km<sup>2</sup>. The number of hawks in breeding groups ranged from 2 to 7 and averaged 3.8. Hawks in breeding groups rarely ranged beyond 0.8 km from active nests, except to visit sources of water, and we did not observe overlap of hunting ranges in any groups. Hawks from different groups formed social aggregations in zones between nesting areas. Aggregations formed only during nonbreeding periods (autumn and winter) and the frequency of aggregations peaked approximately 3 weeks before egg laying. Aggregations averaged 5.9 hawks (range = 4–11), and were composed of members of 2 or 3 adjoining groups and transient hawks. Aggregations may allow potential immigrants to assess and be assessed by group members, and may provide benefits to participants via cooperative hunting. All aggressive behaviors observed during the study, except supplanting (i.e. one hawk replacing another at a perch), were more common between individuals in aggregations than in groups. The most intense aggressive behaviors (e.g. chasing and foot grabbing) were never observed between group members. Resident hawks chased trespassing conspecifics out of the nest area in all incursions observed during breeding and nonbreeding periods. Residents also showed aggression toward a trained conspecific released at 13 of 14 active nests. Our evidence that Harris' Hawks are territorial contradicts part of the information that has been used to reject the habitat saturation model for the development of cooperative breeding in this species. We propose that water, an important resource during the summer, may represent an ecological constraint that favors group living in Harris' Hawks in the Sonoran Desert. *Received 29 May 1990, accepted 15 January 1991.*

THE RELATIONSHIPS between territoriality, sociality, and breeding biology have been described in detail for several species of birds that breed cooperatively (e.g. Craig 1979, Emlen and Vehrencamp 1983, Ligon 1981, Woolfenden and Fitzpatrick 1984, Hunter 1987, Koenig and Mumme 1987). Harris' Hawks (*Parabuteo unicinctus*) commonly breed cooperatively in the southwestern United States (Mader 1975, Griffin 1976, Whaley 1979, Brannon 1980, Bednarz 1987, Dawson and Mannan 1989). Territorial behavior has not been studied intensively in Harris' Hawks, and existing information about the level and nature of territorial behavior in this species is contradictory. Nesting groups have been reported to maintain discrete territories (Griffin 1976), to have overlapping territories (Whaley 1986), and most recently to be nonterritorial (Bednarz 1987, Bednarz and Ligon 1988).

Use of foraging areas by Harris' Hawks also has not been reported in detail. Bednarz (1986) felt that Harris' Hawks could move freely through the ranges of neighboring groups dur-

ing breeding. He implied that foraging areas may be shared by >1 breeding group. During nonbreeding periods, Harris' Hawks have been reported to remain on their breeding ranges (Mader 1975), to wander widely in large groups (Chambers 1921, 1924), and to form social aggregations composed of >1 breeding group (Mader 1975, Bednarz et al. 1988).

We studied territoriality and sociality in Harris' Hawks during their breeding and nonbreeding periods. Here we describe the size and composition of social aggregations, intra- and intergroup interactions, and temporal and spatial relationships of territories and aggregation zones.

## STUDY AREA AND METHODS

We studied Harris' Hawks in a 46.5 km<sup>2</sup> area located in Pinal County, Arizona, ca. 50 km north of Tucson. The topography of the area was characterized by gently sloping plains with scattered low hills. Elevation ranged from 709 to 956 m and annual precipitation averaged 28 cm. Vegetation in the area was representative of the palo verde-cacti-mixed scrub series found

in the Arizona Upland Subdivision of the Sonoran Desert (Turner and Brown 1982). Common overstory plants were saguaro cacti (*Carnegiea gigantea*), palo verde trees (*Cercidium microphyllum*), and mesquite trees (*Prosopis juliflora*). Common understory plants included triangle leaf bursage (*Ambrosia deltoidea*) and species of *Opuntia* cacti. The study area contained 12 man-made water sources for cattle, 5 man-made water sources for wildlife, and 1 natural spring.

In this paper, we refer to the social unit present at one or more nesting attempts as a *group*. We use the term *nest* to describe the physical site of a breeding attempt that contained eggs or young. During nonbreeding periods, *nest* refers to the site used in the previous breeding attempt. An *aggregation* refers to a congregation of hawks from >1 group. A *member* is a hawk observed at least once to participate in nesting or group behaviors at an active nest (e.g. group hunting or group defense against predators). The term *helper* describes members that were additional to the dominant male and female at a nest and is not a strict assessment of breeding status in this polygamous species (see Dawson and Mannan 1991). A *transient* is a hawk that was observed or trapped in the study area, but was not confirmed as a member of any group during previous nesting attempts. A *trespasser* is a hawk observed in the territory of a group to which it did not belong.

We marked 362 Harris' Hawks, each with 3 colored leg bands and a metal numbered band in a unique combination. We trapped hawks with Bal-chatri traps (Berger and Mueller 1959). Nestlings were color-marked between the ages of 35 and 48 days.

We measured 9 morphological characteristics to aid in determination of sex. Hamerstrom and Hamerstrom (1978) reported that the weights of male and female Harris' Hawks in Texas did not overlap. We also found that body weight was the most useful measurement for determining sex in Harris' Hawks in Arizona (confirmed males, based on observations of copulations:  $n = 59$ , mean weight = 703.8 g, range = 610–803 g; confirmed females, based on observations of copulations and egg laying:  $n = 64$ , mean weight = 1,063.7 g, range = 923–1,633 g). All other measurements overlapped between males and females. Hawks were categorized as adults or immatures, based on plumage differences (Brown and Amadon 1968).

We searched for nests from February through August, 1984–1986, in areas frequented by groups. Areas in which groups were not observed, but which were large enough to support a group, were searched at least once during the peak breeding period. We also searched known breeding areas in October and November, 1984–1986, to locate nests initiated in autumn. We arbitrarily named each group after a distinct characteristic of the territory or group (e.g. Cholla Group). Nests were visited at least 6 times to record number of eggs or nestlings.

We observed groups during the breeding period

(i.e. from 2 weeks before egg laying to fledging of young) from elevated, fully enclosed blinds placed within 10 m of nests (Dawson and Mannan 1989). We observed the behavior of groups at active nests for a total of 2,013 hours. We used all-occurrences sampling (Altmann 1974) to record affiliative and aggressive behaviors. We also placed blinds near sources of open water and monitored use of water by Harris' Hawks during late spring and summer (73 h).

During the nonbreeding period, we observed the behavior of hawks in groups (305 h) and aggregations (186 h). Most of these observations were made between late December and March, when weekly surveys of each territory were made. We usually were able to approach in a vehicle to within 75 m of groups and aggregations, and to observe behavior with spotting scopes and binoculars. Individual hawks were generally easy to identify by their bands because they commonly perched on the tops of saguaro cacti.

We estimated territory boundaries and aggregation zones by plotting locations of color-banded hawks on topographic maps. Although some territory boundaries may be biased toward roads and vantage points, we believe that this bias is small because Harris' Hawks are highly visible in the Sonoran Desert and because the study area contained a thorough network of roads.

Trepassers rarely approached nests during the breeding period. We simulated trespassing by releasing a captive Harris' Hawk near nests. We used 2 Harris' Hawks (an immature female and an adult male) trained by falconry techniques (McElroy 1977). The trained hawks were free-flying and were not wearing leg-jesses, bells, or radio transmitters when released. We released 1 of the 2 hawks from an observation blind near an active nest after 1 to 4 h of observation of the resident group, and we continued to observe group behavior for 1 h after the release.

## RESULTS

*Size and composition of groups and aggregations.*—The study area contained 22–26 groups from 1984 to 1986, and nesting density averaged 1 nest per 2.0 km<sup>2</sup>. Groups occupied their breeding territories year-round, but nesting was restricted to January through August. Most nests (69.3%,  $n = 105$ ; this sample includes nests from areas adjacent to the main study area) contained eggs by April, and young fledged in June. We found nests in palo verde trees (63%), mesquite trees (8%), and saguaro cacti (29%).

The number of hawks in breeding units at 64 nests ranged from 2 to 7 ( $\bar{x} = 3.8$ ; Dawson and Mannan 1991). Groups of 3 were most common, but groups of 4–7 accounted for 50.9% of our sample. Adult males were most common as members of groups (Fig. 1), and the sex ratio of

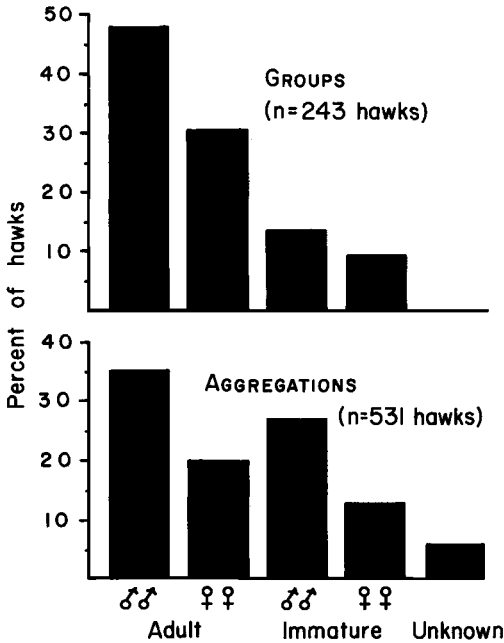


Fig. 1. Sex and age compositions of Harris' Hawks in groups at 64 nests and in 90 social aggregations.

males to females within groups was 1.54:1 (61% males, 39% females). Sex ratios within age classes were 1.64:1 (adult) and 1.17:1 (immature). Helpers represented 47% of total members ( $n = 243$ ). Adult males were most common (45.2%) as helpers, and adult females were least common (9%) as helpers. A typical group of 4 included 1 adult female breeder, 1 adult male breeder, 1 adult male helper, and 1 immature male or female helper (see Dawson and Mannan 1991).

Dispersal of offspring from natal groups occurs by age 3 yr, and adult and immature helpers can be related or unrelated to dominant pairs in groups (Dawson and Mannan 1991). We observed 3 instances of dispersal by color-banded immature hawks that joined other groups in the study area.

Social aggregations of Harris' Hawks averaged 5.9 birds (range 4-11) and were independent of breeding group sizes ( $n = 90$ ; Chi-square contingency test for independence:  $\chi^2 = 30.98$ ,  $df = 3$ ,  $P < 0.0001$ ). Harris' Hawks associated in aggregations only during autumn and winter when groups were not breeding. Group participation in aggregations was frequent during January and February (32.6% of 610 group locations in 1984). The number of aggregations

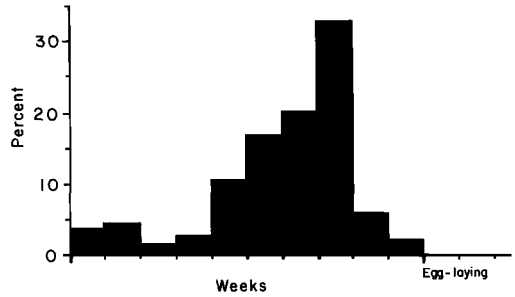


Fig. 2. Frequency of occurrence of Harris' Hawk aggregations during 10-week period before egg laying.

observed peaked ca. 3 weeks before egg laying and decreased abruptly to zero shortly thereafter (Fig. 2).

Transient hawks ( $n = 25$ ) were common in the study area only during the autumn and winter, and accounted for 7.1% of hawks in aggregations. Transients did not associate harmoniously with groups outside aggregations and usually moved through the study area alone; often they associated with several different aggregations before leaving the area. Some hawks ( $n = 13$ ) that were trapped in the winter and had not been a member of a study group during previous nesting attempts remained in or near the study area (within 23.7 km of the trap site) and either established a new territory or joined an existing group.

We observed the recruitment of transients (4 adult males) into established groups in the study area in 4 instances (1 pair, 2 groups of 3, 1 group of 4). We first observed aggregations comprising a transient and the group it later joined from 7 to 4 weeks ( $\bar{x} = 5.6$  weeks) before egg laying, and we first observed transients associating with groups near the nest 4 to 1 week before egg laying ( $\bar{x} = 3.0$  weeks). None of the groups changed in membership since last breeding; however, all groups lacked offspring helpers from the previous brood. Immature hawks banded as nestlings in the study area joined other groups in the study area in 3 instances (group sizes = 3, 3, 5). In 2 of these instances, immature hawks (2 females) joined groups with nest sites that were 3.7 km and 6.4 km (1 territory and 3 territories, respectively, between natal and nonnatal groups) from natal nest sites. The third immature hawk (a male) joined a neighboring group whose territory was adjacent to the natal territory. We detected no

TABLE 1. Affiliative and aggressive behaviors observed in breeding groups and social aggregations of Harris' Hawks in Arizona, 1984-1986.

Behavior	Description
<b>Affiliative behaviors</b>	
Communal perching	Hawks (2-7) crowd together on the same perch site (e.g. the horizontal arm of a saguaro cactus).
Backstanding	A hawk stands upon the back of another hawk and neither hawk engages in copulatory behavior (see Mader 1975).
<b>Aggressive behaviors*</b>	
Threat posturing	A hawk holds its body in a near-horizontal position with neck arched, head facing down, wings drooping slightly, and feathers raised on neck and back. A threat posturing hawk often positions itself sideways to a second hawk and walks slowly and stiffly.
Supplanting	A hawk flies toward a second hawk and the second hawk leaves its perch site as the first hawk approaches to $\leq 2$ m. The first hawk then perches on the site vacated by the second hawk.
Direct attacking	A hawk flies directly toward and strikes a second hawk.
Chasing	A hawk closely pursues ( $\leq 2$ m) a second hawk in flight for $\geq 30$ m.
Foot grabbing	Two hawks stand side by side on the ground ( $< 1$ m apart) and adopt threat postures. The hawks maintain these positions until one moves toward the other. As they make contact, each turns onto its side and grabs the feet of the other. The hawks stay locked together on the ground until one leaves the area (up to 6.5 min). Foot grabbing is interspersed with brief bouts of fighting in which hawks strike one another with their wings and feet.

\* Aggressive behaviors are listed in order of occurrence during interactions that escalated into intense conflicts.

changes in membership preceding the recruitment of these immature hawks but only the group of 5 contained an immature helper (a male offspring from the previous brood).

*Social behaviors.*—Harris' Hawks used 7 distinct behaviors during social interactions (Table 1). Two of these—communal perching and backstanding (Mader 1975)—appeared to serve affiliative functions among group members. Communal perching was distinctive and hawks often perched so close together that they touched one another. Physical contact during communal perching was probably deliberate because many unoccupied perch sites were available nearby.

*Backstanding*, in which one hawk perched on the back of another hawk without exhibiting sexual behavior, occurred only between members of the same group and took place on the tops of large saguaros. Most (91%) incidents of backstanding ( $n = 78$ ) involved 2 hawks, but some (9.0%) involved 3 hawks that were "stacked-up" 3 birds high. Of 44 incidents of backstanding by 2 hawks in which we identified all participants, 31 (71%) involved a subordinate male perched on a dominant male, 5 (11%) involved a subordinate female perched on a dominant male, 8 (18%) involved a dominant female perched on a subordinate male (see Dawson and Mannan 1991 for methods used to

evaluate dominance). We identified participants in 3 instances of backstanding by 3 hawks; subordinates perched on the backs of dominants in 2 instances and, in the third observation, the second-ranking hawk (male) perched on the back of the most dominant hawk (female), who perched on the back of a lower ranking male. Durations of backstanding by 2 hawks ranged from 0.6 to 19.8 min ( $\bar{x} = 8.4$  min) and by 3 hawks ranged from 0.3 to 5.2 min ( $\bar{x} = 3.8$  min).

Intraspecific aggression usually involved a series of steps that occurred in a well-defined order from least to most intense (Table 1). Ag-

TABLE 2. Rates of social behaviors in groups and social aggregations of Harris' Hawks.

Behavior	Groups		Aggregations	
	<i>n</i>	Events/ 10 h	<i>n</i>	Events/ 10 h
Communal perching	593	2.9	31	1.6
Backstanding	78	0.4	0	—
Threat posturing	72	0.3	231	12.4
Supplanting	1,152	5.7	65	3.5
Direct attacking	0	—	18	1.0
Chasing	0	—	24	1.3
Foot grabbing	0	—	13	0.7

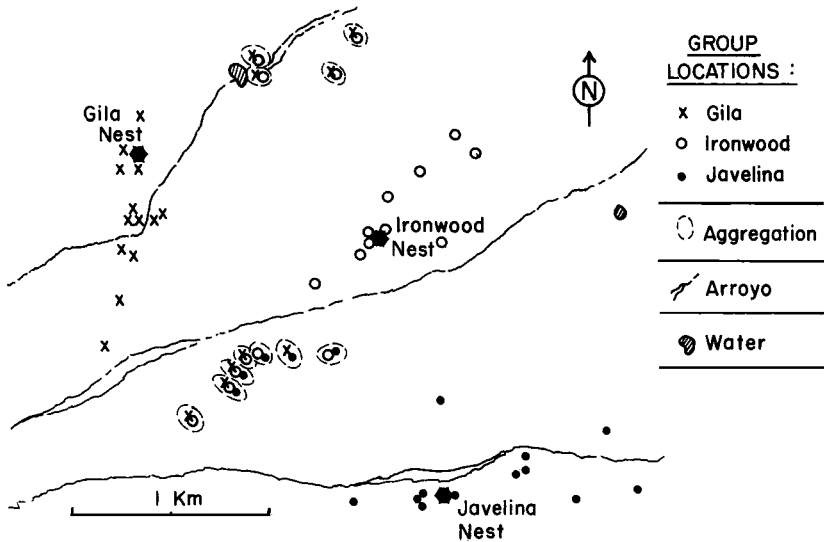


Fig. 3. Group locations showing aggregations of Harris' Hawks in 3 neighboring territories during a nonbreeding period. Data collected during 10-week period before egg laying.

gressive interactions generally involved only two hawks. All aggressive behaviors, except supplanting (see Dawson and Mannan 1991 for details of supplanting in groups), occurred more frequently in aggregations than in groups (Table 2). Behaviors that constituted intense aggression (such as attacking, chasing, and foot grabbing) were never observed in groups. We believe that aggressive interactions within aggregations occurred between hawks from different groups. We identified the hawks involved in 4 incidents of foot grabbing: 2 occurred between female breeders from different groups, 1 occurred between a male breeder and a male helper from different groups, and 1 occurred between a male breeder and an adult male transient.

*Territoriality during nonbreeding periods.*—We observed individuals and groups hunting up to 1.5 km from their previous nest during autumn and winter, but most locations (82.1%,  $n = 21,540$ ) were within 600 m of the old nest. Aggregations did not occur closer than 600 m of nest sites (Fig. 3) and usually formed in interstitial areas between core areas used by groups. Group locations were centered around nest areas, and groups did not use aggregation zones during their normal activities in nonbreeding periods. The spatial relationships between core areas and aggregation sites were similar among all groups we studied.

We observed members chasing a conspecific from the nest area during the nonbreeding period on 6 occasions in 5 different groups. All observations occurred in late autumn and early winter at least 2.5 months before nesting. The chases began within 70 m of the site of the previous nest and, in all 5 groups, members abandoned the chase ca. 500 m from the old nest. Of the 6 hawks that were chased, 4 were members of neighboring groups, and 2 were unidentified. In no instances did trespassers interact with residents near the nest without being expelled.

*Territoriality during breeding periods.*—Members of breeding groups rarely ranged beyond 0.8 km of the nest during nesting (except to visit sources of water), and we did not observe territory overlap in any of the groups studied (Fig. 4). Groups did not frequently use areas in which aggregations had been observed (Figs. 3, 4).

We observed 11 incidents (11 groups) in which hawks we believed to be nonmembers passed over nest areas but did not perch. Resident hawks responded by soaring with the nonmembers but did not attack or chase them. The circling hawks gradually moved higher and out of the nest area without attacks or chases. We observed known trespassers that perched near the nest on 2 occasions in 2 groups (1 was a transient and 1 was a member of an adjoining

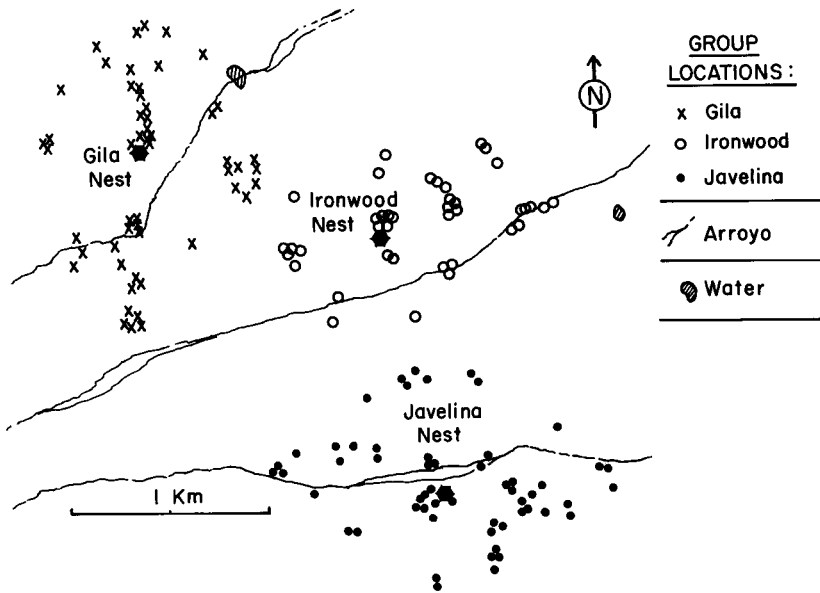


Fig. 4. Group locations of Harris' Hawks in 3 neighboring territories during a breeding period.

group). On both occasions, group members chased the trespassers from the nest area.

Groups also aggressively expelled trained hawks from the nest area at 13 of 14 nests (14 groups). Group sizes ranged from 2 to 7 hawks and stages of breeding ranged from 2 weeks before egg laying to the late nestling stage (nestling age = 37 days). We recorded aggressive behaviors including supplantations and chases at 13 nests, direct attacks at 9 nests, and foot-grabbing contests at 4 nests. The one exception occurred ca. 1.5 weeks before egg laying, at a nest attended by a pair. The pair did not respond aggressively to the trained immature female; they perched beside her and copulated once within 1 m of her. We released the same female at 2 other nests before eggs were laid, and residents chased her out of the area (at least 500 m from the nest). Both groups had >2 members.

Residents often did not expel the trained hawk immediately. Aggression was delayed at 10 of 13 nests and the time between release and initiation of aggression averaged 4.4 min ( $n = 13$ , range = 0.3–8.0 min). During this time, residents watched the trained hawk but did not approach. Either the dominant female or male in the resident group usually initiated aggression when the trained hawk left its initial perch, and other members joined the chase when the trespasser flew away. The time between release

and when the trained hawk was chased from the nest area (or at least beyond the range of visibility from blinds, 500 to 600 m from the nest) averaged 5.7 min (range = 1.1–20.3 min). When we recovered the trained hawks after release, they were usually hiding in dense cover, and residents were perched within 30 m of the cover (distance from nest ranged from 750 to 1,175 m from the nest,  $\bar{x} = 825$  m).

*Water sources.*—Harris' Hawks visited water sources daily in late spring and summer when daytime temperatures exceeded approx. 37°C. Hawks usually drank and bathed at water sources, and sometimes (4 incidents) stood with water covering their feet and tarsi from 0.7 to 3.4 h. Several groups usually shared the same water source. Twice, we observed members of different groups bathing and drinking at a cattle pond at the same time without conflict, but they did not perch or bathe together and usually stayed on opposite sides of the water source. Group members did not often perch for extended periods or hunt near water sources, but usually flew directly to the water source, used water, and then returned to the nest area. We identified the group affiliations of 9 hawks at water sources. For these 9 birds, the distances between their active nests and the water sources ranged from 0.7 to 2.8 km ( $\bar{x} = 1.1$  km). Distances between all active nests and water ranged from 0.65 to 3.0 km ( $\bar{x} = 1.2$  km,  $n = 105$  nests). The

number of young fledged (from 21 nests attended by groups of 3) was not correlated with the distance between nests and water sources (Pearson's  $r = 0.1074$ ,  $P = 0.322$ ).

*Permanency of territories.*—Breeding groups usually used the same territories in subsequent years. Territories were occupied continuously by 21 of 25 groups that were color-marked and monitored for 1 yr or more. In 50 breeding attempts, 46 nests were built within 200 m from the previous nest. Four new nests were built from 400 to 800 m of the previous site. Four groups disappeared from their territories between breeding attempts, and members of these groups were never relocated. In two instances, vacated territories were occupied the next year by pairs that raised offspring but were unoccupied again in the following year. The other two vacant territories remained unoccupied although, in one instance, a neighboring group shifted its territory and used part of the vacated territory.

#### DISCUSSION

*Levels of aggression.*—The social system of Harris' Hawks is characterized by low frequencies and low intensities of agonistic interactions, particularly within groups. It is similar, in a general sense, to sociality in other cooperative breeders (Brown 1987). However, the degree of harmony between Harris' Hawks in social aggregations contrasts with the vigorous displays and sometimes aggressive interactions reported for intergroup conflicts in some cooperatively breeding species (e.g. Kookaburras, *Dacelo gigas*, Parry 1971; Acorn Woodpeckers, *Melanerpes formicivorus*, Koenig 1981; Scrub Jays, *Aphelocoma coerulescens*, Woolfenden and Fitzpatrick 1977, 1984). Furthermore, sociality between neighboring territory holders is especially unusual in Falconiformes where territorial disputes between neighboring breeders are typically aggressive (Newton 1979) and sometimes fatal to combatants (e.g. Cash 1914, L. H. Brown 1955, Gargett 1971, Hall 1955, Willgoos 1961).

We propose that behavioral adaptations to reduce intraspecific aggression are highly evolved in the Harris' Hawk because the likelihood of inflicting serious injury during conflicts is higher in this hawk than in most social birds. Harris' Hawks settle conflicts between members of different groups through ritualized behaviors (Tinbergen 1951) that are relatively harmless,

such as foot-grabbing contests. Similarly, the suppression of aggression is most complete within groups where frequent conflicts could disrupt breeding activities.

*Territoriality.*—Harris' Hawks in our study area exhibited what Brown (1969, 1987) described as "group territoriality." Groups generally resided on nesting territories all year and continuously defended at least a portion of their home ranges, and all members participated somewhat in territorial defense. Hardy et al. (1981) reported that groups of San Blas Jays (*Cyanocorax sanblasianus*) rarely trespassed upon neighboring territories and maintained home ranges through mutual avoidance. We propose that similar behaviors are present in Harris' Hawks in Arizona because we saw very few trespassers in either breeding or nonbreeding periods, despite the high density of nests.

The behavior of Harris' Hawks toward trespassers can be defined as territoriality according to the widely cited criterion of "any defended area" (Howard 1920, Noble 1939, Hinde 1956, Brown 1969). Still, it is possible that our observations at active nests simply reflected the actions of members defending nestlings from predation rather than the defense of resources from conspecific competitors. Predation of nestling Harris' Hawks by a conspecific has never been reported, and we have 3 additional lines of evidence that argue against this idea. First, we observed territorial behavior in 6 instances during winter when the nest was empty, which implies that hawks were defending the nest site or area instead of the nest contents. Second, the responses of hawks toward conspecific trespassers were very different from the responses of hawks toward Great Horned Owls (*Bubo virginianus*), a known nestling predator (Dawson and Mannan 1991). Responses by residents toward conspecifics were delayed and involved ritualized behaviors. In contrast, residents immediately and vigorously attacked trespassing owls (Dawson and Mannan 1991). Third, we did not see overlap in areas used by adjacent groups when they foraged during the breeding season. We speculate that overlap would be common if groups were defending only nestlings, and we suggest that Harris' Hawks defend both nesting and foraging areas from trespassers.

Mader (1975) and Bednarz (1987) observed aggressive interactions between Harris' Hawks, but few of these observations contained critical details (e.g. the identities of supposed trespass-

ers). Mader (1975) reported that the responses of an adult trio ranged from playful to aggressive during 10 "boundary violations" by an immature hawk near the nest. He presumed the immature was the same individual in all observations. Mader (1975) also twice observed neighboring hawks that soared with resident adults ca. 120 m over the nest with no apparent aggression. Bednarz (1987) identified both participants in 1 of 5 observations of aggression at the nest. He did not establish the identities of hawks in the other 4 incidents, but felt that aggression was related to factors other than territorial behavior.

Our observations of aggression toward intruders at the nest are consistent with those reported previously, but contradict the assertion that Harris' Hawks "do not actively defend space or exhibit territorial behavior" (Bednarz and Ligon 1988: 1177). There are at least two potential explanations for the differences between our views and those of Bednarz (1986, 1987) and Bednarz and Ligon (1988). First, it is possible that reports of harmonious interactions between residents and trespassers were based on misinterpreted observations. We reported elsewhere (Dawson and Mannan 1989) that methods used previously to census Harris' Hawk groups (Mader 1975, Whaley 1985, Bednarz 1987) were inadequate in Arizona to record all group members. A hawk missed when a group was censused could be misidentified as a trespasser when it interacted with known members. Also, the ritualization of aggression in the Harris' Hawk renders some behaviors subtle and potentially misleading. For example, if hawks are observed during the interval (up to 8 min) between the arrival of a trespasser and the initiation of aggression, the interaction could be misinterpreted as harmonious. These factors caution against the rigorous interpretation of equivocal or incomplete observations of trespassing incidents.

Second, Harris' Hawks in New Mexico—where Bednarz (1987) worked—may behave differently than those in Arizona. Bednarz (1987) and Bednarz and Ligon (1988) studied Harris' Hawks in an area where density of nests was about 1 nest per 4.1 km<sup>2</sup>, and number of fledglings per successful nest was 1.9. Density of nests on our study area was 1 nest per 2.0 km<sup>2</sup>, and number of fledglings per successful nest was 2.1. The differences between the 2 sites suggest that the quality of the habitat in Arizona

was higher, and it is possible that the nature and level of territorial behavior in Harris' Hawks differs with habitat quality. We suspect that trespassing is very rare at low nesting densities and caution that territorial behavior under these conditions would be hard to document without a manipulative experiment. Variability in territorial behavior in Harris' Hawks will be difficult to describe until more information is obtained from nesting groups in other parts of the species range.

In Arizona, the responses of nesting hawks to trespassing conspecifics and the observed patterns of the use of space by groups strongly suggest that Harris' Hawks are territorial. Although direct aggression has been reduced through the evolution of ritualized behaviors, we suggest that territorial behavior is effective in maintaining exclusive use of areas by groups in Arizona.

*Aggregations.*—Winter aggregations or flocks have been reported for several avian cooperative breeders (see Skutch 1987 for review), but most of these species do not reside year-round on their breeding territories as do Harris' Hawks (Mader 1977, Whaley 1986). We observed a peak in the frequency of aggregations ca. 3 weeks before nesting and presume that Harris' Hawk aggregations serve a function associated with breeding.

Group displays or "rallies" may serve, in part, to advertise the presence of individuals in a flock to deter potential immigrants (Zack 1986). Harris' Hawk aggregations also may serve as a means by which a group advertises its composition, hierarchy, and status (e.g. open or closed to new members). In addition, groups are able to assess potential new members. The spatial arrangement of aggregations and core nesting areas allows potential immigrants to assess, and be assessed by, resident groups without being subject to territorial aggression. Observations of recruitment of new members into groups support this idea; new members initially associated with groups only in aggregations.

Cooperative hunting (Mader 1975, Bednarz 1988) by hawks in aggregations may provide an advantage that is not directly associated with breeding. We observed 14 attempts by aggregations to capture prey, and flushed aggregations 3 times from jackrabbit (2 *Lepus californicus*, 1 *L. alleni*) kills that apparently were being shared (Dawson 1988). Mader (1975) first documented and described cooperative hunting by Harris'



Hawks in Arizona, and Bednarz (1988) subsequently studied this behavior in New Mexico. Larger groups were more successful in capturing prey than single birds, and prey items were shared among hawks that hunted together in Arizona and New Mexico (Bednarz 1988, Dawson 1988). Cooperative hunting may enhance the survival of individuals that hunt together (Mader 1979, Bednarz 1988, Bednarz and Ligon 1988) and may affect reproductive success by enhancing the survival of offspring learning to hunt (Dawson and Mannan 1991). During non-breeding periods, a hawk may also profit by hunting with birds from nearby groups if the aggregation size is closer to optimum size for cooperative hunting than its group size is. The higher success rates attainable through cooperative hunting may be of greater importance during the winter when energetic demands are high and prey populations are low.

*Habitat saturation.*—Bednarz and Ligon (1988) examined several proposed explanations for the evolution of cooperative breeding in birds and found little support for the habitat saturation model (Selander 1964; Brown 1974, 1987; Woolfenden 1975; Zahavi 1976; Emlen 1978, 1981, 1982; Stacey 1979; Koenig and Pitelka 1981) in the Harris' Hawk. The assertions that Harris' Hawks did not actively defend space and that habitat was not limited in the New Mexico population are inconsistent with habitat saturation as a factor that promotes group living. Instead, Bednarz and Ligon (1988) proposed that the benefits derived from cooperative hunting form the most likely basis for the development of cooperative breeding in the Harris' Hawk.

We also suggest that cooperative hunting is a potentially important element of sociality in the Harris' Hawk (see Dawson 1988, Dawson and Mannan 1991; also see the discussion of aggregations) and may have led to the evolution of ritualized behaviors. We found, however, that Harris' Hawks are territorial, and our observations of territory use between years are consistent with habitat limitation. Some territories in our study area were abandoned and remained vacant, but in other instances, new territories were formed in areas that were previously unoccupied (Dawson unpubl. data). These observations tell little about habitat saturation because the effects of fluctuations in resource levels (i.e. habitat quality) in these territories were unknown. Because some Harris' Hawk territories remained unoccupied despite

the presence of transients that wandered through the study area, and because pairs that reoccupied vacant territories were present for only one breeding season, we believe that abandoned territories were either unsuitable for breeding or were lacking the resources needed for extended residency by groups and offspring. We suggest that the high nesting densities in the study area, the stability of most groups from year to year, and the many transients that wandered through the study area without staying are consistent with habitat limitation. In our opinion, the habitat saturation model remains a viable alternative explanation for the evolution of cooperative behavior in Harris' Hawks.

Habitat saturation is perhaps easiest to conceptualize when a required but limited feature of the environment is discrete and can be defended. The ecological constraints model (Koenig and Mumme 1987) proposes that such a habitat feature, whose presence is an essential criterion of habitat for a species, results in a lack of marginal habitat in which dispersing young can "wait" for an opening in suitable habitat. Bednarz and Ligon (1988) could not identify an ecological variable of Harris' Hawk habitat that was critically limited among the vegetation measurements and prey indices they examined in New Mexico. We did not measure habitat quality, but our observations of territoriality and an apparent dependence on water during breeding suggest that habitat suitability for Harris' Hawk in Arizona may be influenced by the availability of water. We speculate that sources of water may represent an ecological constraint that favors group living in the Harris' Hawk in the Sonoran Desert.

Water sources used by Harris' Hawks in Arizona were small (e.g. man-made ponds, tanks, and wildlife catchments) and represented a limited and discrete component of habitat. Daily use of water during nesting, particularly when temperatures exceeded 37°C, support Milsap's (1981) suggestion that water is an important resource for Harris' Hawks in the Sonoran Desert. Historic patterns of nesting in Arizona (Whaley 1979) suggest that Harris' Hawks initially nested near riparian zones and expanded into xeric areas following the construction of water sources for livestock. Water was not examined as an ecological variable by Bednarz and Ligon (1988), but frequent use of water was reported for the Harris' Hawk in New Mexico (Bednarz et al. 1988). We found that water

sources were shared rather than defended by groups, and this seems to be inconsistent with the ecological constraints model. Three factors suggest that groups may not have to—or be able to—defend water sources.

First, hawks usually visited water only once a day and drank to satiation in a few minutes. It would be somewhat easy for trespassers to “sneak” water unless the source of water was very close to the nest. Second, use of water by members was highest in early summer when most groups were feeding large nestlings. Defending a water source at this time would involve confronting many trespassers when food demands of the brood were high. Disruption of breeding activities by frequent trespassers may explain why groups did not nest closer than 600 m to a water source. Third, the amount of water was not limited at most sources, and it is unlikely that water use by one group had negative effects on the availability of water for other groups. Few direct benefits could thus be gained by a group defending a water source.

Harris’ Hawks can probably fly considerable distances to water but there is presumably a distance beyond which a required daily movement has energetic costs to an individual and indirect costs to reproduction (e.g. time lost from hunting and predator defense) that are prohibitively high. If water availability poses an ecological constraint on Harris’ Hawks, the area within some threshold distance from water would represent breeding habitat, whereas areas outside that threshold would be unsuitable. Alternatively, distance from water to nest sites could be negatively correlated with habitat quality. In the latter case, the habitat saturation model is not easily invoked. We did not find a negative correlation between distance of nests to water and number of young fledged, or a threshold distance beyond which nesting densities declined rapidly. We did not examine nests at distances > 2.8 km from water because of the many water sources in and near the study area.

Although the habitat saturation model has been widely accepted, Stacey and Ligon (1987) questioned habitat limitation as a factor leading to cooperative breeding. If water is a determinant of habitat quality for Harris’ Hawks, philopatry may enhance access to high-quality habitat and promote group living regardless of habitat saturation (Stacey and Ligon 1987). Additional research will be needed to clarify the importance of water dependency and other po-

tential benefits of group living such as reduced predation of young (Dawson and Mannan 1991) and cooperative hunting (Mader 1975, Bednarz 1987, Bednarz and Ligon 1988) in the evolution of sociality in the Harris’ Hawk.

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