

DOMINANCE HIERARCHIES AND HELPER CONTRIBUTIONS IN HARRIS' HAWKS

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ABSTRACT.—We examined dominance hierarchies, mating relationships, and helping by individually marked Harris' Hawks (*Parabuteo unicinctus*) at 64 nests in Arizona (1984–1988). Dominance hierarchies were linear and always contained an adult female as the most dominant member. We placed hawks into three dominance categories (alpha, beta, and gamma) based on frequencies of supplanting. Pairs without helpers (16%, $n = 64$) and groups that contained a beta male helper (63%) were the most common social structures. Some groups (11%) contained a second alpha female (alpha-2) that was subordinate to the alpha female and dominant over the alpha male. Of 68 observations of copulatory behavior, 45 (66%) were copulations between alpha males and alpha females. Beta males attempted to copulate with alpha females (23 observations; 34%) but were unsuccessful because of a lack of female compliance. Observations of movements by marked hawks suggested that most gamma helpers were offspring of the alpha pair and that beta males and alpha-2 females were probably unrelated to the alpha pair. Alpha hawks restricted access to the nest by both beta and gamma helpers, but beta males were tolerated closer to the nest than were gamma helpers. Consequently, beta and gamma helpers rarely participated in the direct care of eggs and young but were active in procuring prey, transporting prey to the nest area, and defending the nest from predation by Great Horned Owls (*Bubo virginianus*). Received 29 May 1990, accepted 15 January 1991.

COOPERATIVE breeding occurs in diverse avian groups but is unusual among Falconiformes (Newton 1979, Brown 1987, Skutch 1987). Only the Galapagos Hawk (*Buteo galapagoensis*) and Harris' Hawk (*Parabuteo unicinctus*) are reported to breed regularly in cooperative units (de Vries 1973, Mader 1975b, Faaborg et al. 1980, Faaborg and Patterson 1981). Sociality in the latter species extends to breeding and nonbreeding periods and has been the subject of several studies (Mader 1975a, Griffin 1976, Brannon 1980, Whaley 1986, Bednarz 1987). Harris' Hawks reside on and defend their territories year round (Dawson and Mannan 1991). In Arizona, breeding is seasonal and occurs primarily in spring and summer. Sociality during nonbreeding periods includes the formation of social aggregations composed of >1 breeding group in undefended zones between territories. Breeding groups range in size from 2 to 7 individuals and average 3.8 hawks per nest in Arizona (Dawson and Mannan 1989). Group composition is skewed toward adult males (Mader 1975a, Bednarz 1987), although adult females regularly occur as helpers in the Arizona population (Dawson and Mannan 1991).

Among cooperatively breeding birds, the kinds and amounts of aid provided by helpers

toward reproduction vary. *Alloparental behavior* (i.e. parental behavior by a nonparent) comprises all parental-type behaviors in some species (e.g. Woolfenden and Fitzpatrick 1984) but is apparently lacking in others (e.g. Carrick 1972). The role of extra hawks at Harris' Hawk nests is not well documented. Bednarz (1987) used time-lapse photography to record the presence of hawks on the nest. He concluded that adult males must "actively assist" breeders at nests. Mader (1979) reported that an adult male aided the adult pair by incubating eggs and delivering food to the nest. His observations of nesting behavior were detailed but were limited to only a single nest in Arizona.

Similarly, the role of dominance in the social organization of breeding groups of Harris' Hawks has never been studied. Aggression is relatively restrained in species that breed in cooperative units, and dominance hierarchies have been described for most species that have been studied in detail (reviewed in Brown 1987). Breeding status is invariably linked with dominance status in cooperative groups, prompting the suggestion that social competition influences cooperation (Emlen 1984). Concepts of parent-offspring conflict (Trivers 1974) have been applied to cooperative breeding and mod-

els of conflict between breeder and helper have been proposed (Brown 1978, Vehrencamp 1977, Emlen 1984). Manipulation or suppression of helpers by breeders has been proposed as a social factor underlying nonbreeding and aid-giving by helpers (e.g. Craig 1980).

We studied the social organization of Harris' Hawks in Arizona (Dawson and Mannan 1989) and report here on dominance hierarchies at the nest, helper relatedness to breeders, copulatory behavior, and the influence of dominance on helping. We also report on potential contributions by helpers toward reproduction. Intergroup behaviors such as territoriality and social aggregations are discussed elsewhere (Dawson and Mannan 1991).

STUDY AREA AND METHODS

We studied Harris' Hawks in a 48-km² study area 50 km north of Tucson in Pinal County, Arizona, from 1984–1988. Topography and vegetation in the study area are typical of the Arizona Upland Subdivision of the Sonoran Desert (Turner and Brown 1982) and were described by Dawson and Mannan (1991).

In this paper, *group* describes a breeding unit that was present in the study area for at least 1 yr. We considered a group to be the same group between years if one or more of the top three ranking hawks remained present. *Nest* describes a breeding attempt defined by the presence of eggs or young. We studied behavior at the nest in 29 groups that produced 64 nests from 1984 to 1987, and we monitored membership in groups from 1984 to the present.

We arbitrarily named each group after a distinctive landmark or habitat feature in its territory. Methods used to estimate group sizes, evaluate group affiliations, locate nests, and trap hawks were described by Dawson and Mannan (1989). Hawks were categorized as males or females based on body weight and were categorized as adult or immature, based on plumage characteristics (see Dawson and Mannan 1989 for description of methods). We color-banded all group members and nestlings using 3 plastic leg bands and 1 numbered metal band in 91% of 64 nests; one hawk was not marked at 6% of nests and 2 hawks were not marked at 3% of nests.

We observed behavior at nests from April to August, 1984–1987, for a minimum of 10 h at each nest (\bar{x} = 48.8, n = 64 nests, total observations = 3,125 h). We used 30× spotting scopes and 10 × 50 binoculars to observe nesting behavior from elevated blinds (Dawson and Mannan 1989). We used watches, tape recorders, and an ethogram code that consisted of 48 alphanumeric elements to record behavior. The code helped to simplify data collection on several hawks at once and to obtain consistent data from different observers. Most elements in the code represented

common nesting behaviors (e.g. brooding, shading, and feeding young) or social behaviors of this species (e.g. group hunting, communal perching, and back-standing).

We placed colored flagging at known distances (25, 50, 100, 150, 200, 250, 300, and 400 m) from nests and measured distances from preferred saguaro perches to nests to help observers in estimating distances of perch sites to the nest. During behavioral observations, we scanned the area around the nest (a radius of 375–600 m) every 5 min and recorded the behaviors and positions of group members relative to the nest. We used all-occurrences sampling (Altmann 1974) to record selected behaviors associated with mating, dominance, and nesting (e.g. food deliveries and exchanges). Prolonged behaviors such as incubating eggs, feeding young, hunting, and predator harassment were continuously monitored.

Obvious aggressive interactions were uncommon between Harris' Hawks of the same group but supplanting was common near the nest (Dawson and Mannan 1991). *Supplanting* occurred when a hawk approached a second hawk, which left its perch site as the first hawk arrived. We constructed a dominance hierarchy for each group by recording the outcomes of supplanting interactions. Supplanting provided a useful way to assess dominance because supplanting was frequent and usually occurred on the tops of saguaro cacti (≤ 80 m from the blind) where participants could be easily identified.

Harris' Hawks usually copulated on saguaros at 10 to 100 m from the blind. During copulation apparent cloacal contact is accompanied by the male leaning back and positioning his tail to one side underneath the tail of the female (Mader 1975a). We used this posture to assess the outcome of copulatory behavior and recorded a *copulation* when a male positioned his tail under the tail of the female. When a male mounted a female, performed copulatory behavior, but did not position his tail under the tail of the female, we recorded an *attempted copulation*.

The distributions of reported variables were tested for normality and were, in some instances, not normal. Therefore, we have reported median values and used Mann-Whitney-Wilcoxon tests when distributions were not normal. Mean values were reported and comparisons were made using *t*-tests for variables with normal distributions (Gibbons 1985).

RESULTS

DOMINANCE AT THE NEST

Supplanting was frequent near the nest and often occurred in *bouts* that involved a series of supplantations of a subordinate by a dominant until the subordinate left the nest area. Supplanting rates in bouts between the same two hawks ranged from 1 to 21 per minute (\bar{x} = 7.7

TABLE 1. Supplanting matrix for Harris' Hawks in the Gato 4 group, 1986, that contained an adult male as the most dominant helper. Data taken from 79 hours of observation.

Supplanter	Age	Sex	Supplantee				
			XWGR	WRXW	GKXK	WXRR	BXWK
XWGR	Adult	Female	—	1	10	7	3
WRXW	Adult	Male	0	—	39	16	7
GKXK	Adult	Male	0	0	—	4	1
WXRR	Adult	Male	0	9	0	—	0
BXWK	Immature	Female	0	9	0	0	—

supplantations/min, $n = 692$ supplanting bouts). We monitored supplanting at 4 nests throughout the nesting cycle and found that supplanting relationships remained consistent during the nesting period. Reversals in the role of an individual as a supplanter or supplantee did not occur during the nesting period.

Dominance hierarchies based on supplanting were linear, "peck-right" (Schjelderup-Ebbe 1935) systems in which the top hawk was dominant over the other group members, the second from the top was submissive to the top hawk and was dominant over the other group members, and so on. We ranked each hawk in a group according to the outcomes of supplantings and found that frequencies of supplantings between ranks differed. Interactions in which the dominant hawk (ranked as 1) supplanted the second hawk in the hierarchy (ranked as 2), represented here as $1 > 2$, were relatively infrequent (median = 0.6 per 10 hours of observation; $n = 29$ groups, 64 nests, 110 observations). Supplantings between $4 > 5-7$ were also infrequent (median = 0.5 per 10 hours of observation; $n = 8$ groups, 18 nests, 174 observations).

Supplanting was most frequent in the $2 > 3$ dyad (median = 2.3 per 10 hours of observation; $n = 23$ groups, 54 nests, 636 observations) and the $2 > 4-7$ dyad (median = 5.0 per 10 hours observation; $n = 8$ groups, 18 nests, 516 observations). Differences in frequencies of supplanting were significant between dyads $2 > 3$ and $1 > 2$ (Mann-Whitney U -test by groups, $P = 0.000$) and between dyads $2 > 4-7$ and $4 > 5-7$ (Mann-Whitney U -test, $P = 0.000$). Hawks that ranked 3 in groups also actively supplanted subordinates (median = 2.5; $n = 8$ groups, 18 nests, 285 observations), and frequencies differed significantly between $3 > 4-7$ and $1 > 2$ dyads (Mann-Whitney U -test, $P < 0.05$).

The differences in dominance relationships provided obvious groupings within a breeding

unit. We grouped together consecutive ranks with low frequencies of dominance interactions and placed each hawk into 1 of 3 levels: alpha, beta, and gamma (in descending order of rank). Most groups of 3 contained alpha and beta levels, and most groups of > 4 contained all three levels.

Social organization of groups.—An alpha female was the most dominant member in all groups studied. However, 3 social structures that differed at alpha and beta levels were evident among breeding units attending nests. First, a simple pair with no helpers occurred at 16% of 64 nests studied. Percentages of simple pairs ranged from 11 to 17 ($\bar{x} = 14$) in the 4 yr of study. Second, the most common social structure (63% of total nests, range over years = 56–80%, $\bar{x} = 66\%$) contained an adult male (beta male) that was subordinate to an alpha female and male (Table 1) plus 0 to 4 gamma hawks. The third social structure featured a second adult female (alpha-2) that was subordinate to the alpha female, but dominant over the alpha male (Table 2). Alpha-2 females were present at 11% of the nests studied (range over years = 0–20%, $\bar{x} = 9\%$).

All alpha and beta hawks were adults with the exception of one immature alpha female in a group of 3. Among gamma hawks, 22% were adults and 78% were immatures. We recorded only males at the beta level (Table 3) and, with the exception of alpha-2 females, extra females were subordinate to beta males. The beta level differed from both alpha or gamma in that it was occupied by only one hawk per group. Beta males were absent from 6 groups of 3 hawks that contained helpers. We classified helpers in the latter groups as gamma based on supplantings and behavior at the nest (see nesting roles). Gamma hawks were adult or immature, male or female, and groups contained up to 4 gamma hawks. Within the gamma level, dominance ap-

TABLE 2. Supplanting matrix for the Gato 1 group, 1984, that contained an adult female as the most dominant helper. Data taken from 138 hours of observation.

Supplanter	Age	Sex	Supplantee				
			GWXG	WXGG	BRXR	RWXR	XWBW
GWXG	Adult	Female	—	4	2	7	15
WXGG	Adult	Female	0	—	8	28	12
BRXR	Adult	Male	0	0	—	12	32
RWXR	Adult	Female	0	0	0	—	3
XWBW	Immature	Male	0	0	0	0	—

peared to be age-related (adults dominate immatures) and secondarily sex-rated (females dominate males).

Relatedness of helpers.—The majority of immature hawks were offspring (\bar{x} = 76%, range = 75–78% for 1985–1988) that were helping their parental group. The remaining immature hawks (\bar{x} = 24%, range = 23–25%) were hawks that left natal groups and joined unrelated groups as gamma helpers. We found that both related and unrelated adult helpers occurred in groups. Male hawks color-banded as nestlings often remained as adult gamma helpers in their natal territories for up to 3 yr. We recorded presence of offspring in 17 groups that were monitored for 4 yr (1984–1988). Of 21 males color-banded in 1984, 16 (58%) were present in their natal groups through their first year, 10 (48%) in their second year, 4 (19%) in their third year, and 0 in the fourth year. Of 18 females, 5 (28%) were present in their first year, 1 (6%) in the second year, and 0 by the third year.

We recorded dispersal from natal groups by 6 hawks that assumed gamma positions in non-natal groups. We also observed 3 instances in which an adult male (banded as a nestling) obtained beta status by joining an unrelated group. We did not observe the attainment of beta or

alpha status by hawks within their natal groups or territories. Thus, some gamma helpers and probably most beta helpers were unrelated to alpha members.

Copulatory behavior.—Harris' Hawks engaged in copulatory behavior throughout the nesting cycle, and we observed peaks in copulations and attempted copulations before and after egg laying (Fig. 1). We observed 44 copulations and 23 attempted copulations (20 nests, n = 15 groups). Copulations were obtained only by alpha males, but beta males (91.3%) and alpha males (8.7%) attempted copulations. Sexual behavior was always directed toward the dominant female in a group with one exception, when an alpha male copulated with an alpha-2 female.

We observed apparent cloacal contact during 44 copulations within 0.25–5.00 min (\bar{x} = 1.25 min) after the male perched on the female. Females did not engage in copulatory behavior during attempted copulations. Males attempting copulation, however, usually continued copulatory behavior until females left or threatened them. Consequently, the duration of attempted copulations (\bar{x} = 5.33 min) was significantly longer than the duration of copulations (\bar{x} = 2.79 min; t = 2.82, df = 65, P < 0.005).

TABLE 3. Sex, age, and status level of Harris' Hawks (n = 243) in 64 groups, 1984–1988. Capitalized letters (F, M) are adults and lowercase letters (f, m) are immatures.

Group size	No. of groups	No. of indiv.	Alpha				Beta		Gamma			
			F	M	f	-2F	M	F	M	f	m	
2	10	20	10	10	—	—	—	—	—	—	—	
3	21	63	20	21	1	1	13	—	2	1	4	
4	15	60	15	15	—	3	13	1	1	5	7	
5	10	50	10	10	—	2	7	1	4	7	9	
6	6	36	6	6	—	0	6	1	3	6	8	
7	2	14	2	2	—	1	2	1	1	2	3	
Total	64	243	63	64	1	7	41	4	11	21	31	

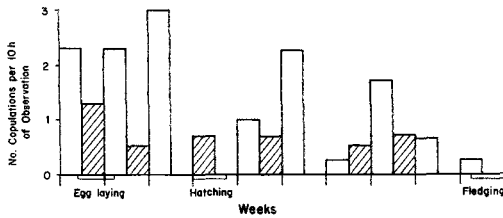


Fig. 1. Rates and frequency of copulatory behavior by Harris' Hawks in relation to stage of nesting at 20 nests, 15 groups, 1984–1986. Open bars show copulations ($n = 44$), and hatched bars show attempted copulations ($n = 23$).

CONTRIBUTIONS TO NESTING

Helper access to the nest.—In pairs, dominance by alpha females did not appear to affect parental behavior by alpha males; supplanting bouts were usually limited to a single event and did not serve to drive the alpha male away. Interactions that were more intense were expressed by an alpha female toward an alpha male in only 9 instances (6 groups) when she forcibly took food from the male while he was perched near the nest. Males in pairs freely entered the nest and participated in all categories of parental-type behavior.

In groups, access to the nest by beta and gamma hawks was directly affected by dominance. Although beta and gamma hawks often approached and perched near or in the nest, alpha males—and sometimes alpha females—supplanted them repeatedly until the subordinate left the nest area. Harassment by dominants was related to the nest site. Alpha males and helpers perched and hunted together in relative harmony at locations >400 m from the nest.

Alpha males showed a differential tolerance of beta and gamma hawks near the nest in 3 ways. First, supplanting of beta males was most frequent when they perched within 50 m of the nest, and supplanting of gamma hawks was most frequent when they perched within 150 m of the nest (Fig. 2). Supplanting declined when beta and gamma members perched beyond the 50-m and 150-m zones, respectively. Second, time intervals between the arrival of a helper within 50 m of the nest and supplanting by the alpha male were higher for beta males (median = 2.3 min; $n = 636$ observations, 23 groups) than for gamma hawks (median = 0.9 min; $n = 516$ observations, 21 groups; Mann-Whitney U -test, $P = 0.000$). Intervals between arrival and sup-

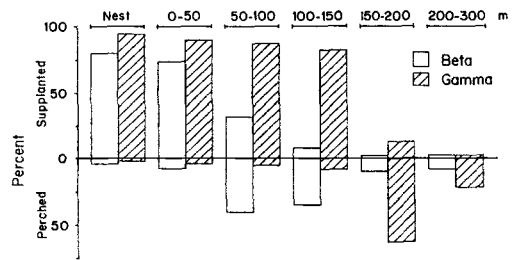


Fig. 2. Relationship between perching distance from the nest and supplanting for beta and gamma helpers in 23 Harris' Hawk groups. Upper axis shows mean percentages of perching events ($n = 1,139$) in which supplanting occurred, and lower axis shows mean percentage of perching time near the nest (total of 925.2 h).

plantation were not significantly different for beta males in groups containing gamma hawks ($n = 322$, 8 groups) and for beta males in groups without gamma hawks ($n = 164$, 15 groups; Mann-Whitney U -test, $P = 0.215$). Similarly, time intervals for supplanting of gamma hawks did not differ significantly in groups with a beta male ($n = 330$ observations, 8 groups) and in groups without a beta male ($n = 120$, 14 groups; Mann-Whitney U -test, $P = 0.264$). Third, alpha males allowed beta males to remain on the nest (9.2% of 710 observations) more often than gamma hawks (2.7% of 351 observations).

Alpha females were generally less aggressive toward helpers at the nest than were alpha males. Most instances (66%, $n = 90$ observations) of helpers perching uninterrupted on the nest occurred when an alpha female was present and the alpha male was absent. Alpha females usually perched alongside of helpers on the nest momentarily before supplanting them. Behavior of alpha-2 females toward helpers was similar to that of alpha females.

Nesting behaviors.—Alpha females stayed near the nest most of the time and left for brief periods to take food from helpers or to visit water sources. Nest attendance by other group members (Table 4) reflected dominance relationships. Alpha-2 females also closely attended the nest and rarely joined other members in hunting forays away from the nest area. Although alpha males often hunted with helpers, they also spent the majority of time perched near the nest. Attendance by beta and gamma helpers reflected supplanting by alpha males.

We found that in pairs, females and males participated in most parental behaviors exam-

TABLE 4. Percentage of time spent attending the nest (perched ≤ 100 m) by Harris' Hawks ($n = 223$) in 54 groups of > 2 .

Status	Sex	<i>n</i>	Observation (h)	Time near nest (%)
Alpha	F	54	2,620.8	92.3
	M	54	2,620.8	64.0
Alpha-2	F	7	311.0	86.9
Beta	M	41	1,704.0	32.1
Gamma	F	25	917.5	10.1
	M	42	988.0	16.0

ined. Hunting and harassment of predators—behaviors often performed by > 1 hawk in breeding groups—were, in pairs, performed primarily by the male alone while the female remained at the nest. In groups of ≥ 3 hawks, alpha females and males also provided most of the direct parental care such as incubating, brooding, shading, and feeding nestlings (Table 5). We observed beta males participating in at least one of these behaviors in 54.1% of nests attended by groups that contained a beta male. Among all groups, we observed the highest involvement by a beta male in direct parental care in the Ocotillo group (1984 nest). The beta male incubated the eggs 3 times and accounted for 11.3% of total incubation time ($n = 18$ hours of observation during the incubation period) compared with 28.1% for the alpha male and 60.6% for the alpha female. The beta male fed the young on 1 of 7 feeding events observed ($n = 10$ hours of observation when nestling age = 11 days).

Groups that contained 2 alpha females differed from other groups, in terms of nest-duty partitioning, only at the alpha level. Incubation, brooding, shading, and feeding were shared by alpha and alpha-2 females. For example, in Gato group, 1984 nest (supplanting hierarchy in Ta-

ble 2), the alpha female performed the majority of female incubation (66%, $n = 12$ observations), and brooding/shading the young (51.8%, $n = 27$ observations), whereas the alpha-2 female performed most of the feeding duties (55%, $n = 51$ observations).

Incubation and feeding of nestlings by gamma members was rare and occurred when the alpha male was absent. We observed incubation by a gamma immature female on only 1 occasion for 7 min. She was supplanted by the alpha male when he returned. Gamma males tried to feed young on 8 occasions at 5 nests, but the alpha female immediately flew to the nest and took the prey in 6 of the observations. We observed immature gamma females feed nestlings without interruption on 6 occasions at 3 nests.

Provisioning the brood.—Harris' Hawks captured prey by hunting alone or with other hawks in cooperative units (Mader 1975a, Bednarz 1988, Dawson 1988). Helpers sometimes shared food at kill sites and delivered food to the nest area. Food deliveries to the nest often took a circuitous route of prey exchanges that ascended through the dominance hierarchy before being delivered to the nest. We examined the provisioning of the brood and alpha female by dividing the task into 3 components: capturing prey, transporting food to the nest, and feeding nestlings.

At nests attended by a simple pair, alpha males usually hunted alone while alpha females remained near the nest. Consequently, cooperative hunting was common only at nests attended by ≥ 3 hawks. We observed both cooperative hunting and solo hunting by hawks in breeding groups. To estimate the frequency of cooperative versus solo hunting by Harris' Hawks during breeding, we included only observations from groups. We also excluded those infrequent solo attempts by alpha females while they were alone at the nest ($n = 22$ observations) in order

TABLE 5. Observations of behaviors associated with nesting by Harris' Hawks in 54 groups, 1984–1988.

Behavior	<i>n</i>	Alpha		Beta		Gamma	
		Female	Male	-2 Female	Male	Female	Male
Incubate	278	194	52	21	10	1	0
Brood/shade	323	210	83	26	13	0	0
Feed	988	681	203	40	48	6	10
Maintain nest	76	26	22	17	9	2	0
Hunt	2,201	112	459	36	601	439	554
Detect/harass predators	426	110	123	21	75	49	50

to restrict our estimate to members that had the options of cooperative or solo hunting (i.e. alpha males and beta and gamma hawks). Of 204 observations of prey capture attempts, 36 (17.7%) were solo attempts and 168 (82.3%) were cooperative attempts.

Harris' Hawks generally fed together on large prey animals and delivered prey to the nest only after feeding first at the kill site. In a sample of 23 kills of desert cottontails (*Sylvilagus auduboni*) by the North Star group (6 members) in 1985, 14 were delivered to the nest. The remaining 9 were consumed at the kill site.

Although beta and gamma members often flew to the nest area with prey, they rarely were allowed to deliver prey directly to the nest. Prey was taken from them by a dominant member who took it to the nest. A sample of prey deliveries to the nest area (within 50 m) was taken from 4 breeding groups of identical sizes and sex, age, and hierarchy compositions (Fig. 3). Beta males accounted for the highest percentage of total deliveries of prey, followed by alpha males, and then by gamma males. Gamma females rarely delivered prey to the nearest area.

Mean prey delivery rates to nests during the period when nestlings were actively fed (1–18 days of age) ranged from 2 to 18 per day ($\bar{x} = 4.9$ per day; $n = 74$ days, 29 groups, 64 nests). The alpha female fed nestlings from a prey item until they were satiated or the prey was consumed. Alpha females often ate part of the prey item before or after feeding the nestlings. Large prey items (e.g. the hindquarters of a cottontail rabbit) that were not entirely consumed were left in the nest and were fed to the brood several hours later.

Detecting and harassing potential predators.—The role of helpers in harassing predators that came into the nest area was conspicuous. Harris' Hawks became excited and used the alarm-call (Mader 1975a) repeatedly when a potential predator came within 150 m of the nest. Alarm-calling drew other members into the area, and they usually perched on saguaros near the predator and continued to vocalize until the predator left.

We found evidence of predation of a fledgling by a coyote (*Canis latrans*), and we once observed a Common Raven (*Corvus corax*) take a Harris' Hawk egg. Interspecific conflict was greatest between Harris' Hawks and Great Horned Owls (*Bubo virginianus*). The nesting density of Great Horned Owls in the study area

(1 nest/1.9 km²) was higher than that of Harris' Hawks (Dawson and Mannan 1991). Owls commonly nested within 500 m of active Harris' Hawk nests (in 45 of 64 nesting territories) and sometimes nested as close as 12 meters. Consequently, incidents of aggression by hawks toward owls were common.

We found evidence of 25 instances of Great Horned Owl predation on nestlings. Great Horned Owl predation occurred only in the sixth week of the nestling stage and early in the postfledgling period (up to 6 weeks after fledging). Owls took the entire brood at 3 nests; a nestling was taken on consecutive nights until the nest was empty.

The roles of group members in attacking and harassing Great Horned Owls in the Cholla Grove group (1986) were typical of most large groups (group size = 5) (Table 6). The number of hawks that harassed an owl ranged from 2 to 5 ($\bar{x} = 2.9$ hawks). The alpha male was the most aggressive member followed by the beta male, the gamma male, and the gamma female. The alpha female left the nest and actively harassed owls only when she was alone at the nest or when the owl was within 100 m. Both the alpha and beta males were initially aggressive toward owls, but strikes (i.e. physical contact between hawk and owl) were made primarily by the alpha male. All members participated to some degree in chases, but only the alpha and beta males always chased owls.

DISCUSSION

Breeding status and dominance.—The social organization of Harris' Hawks in Arizona includes pairs, groups consisting of an alpha pair and helpers, and groups consisting of 2 alpha females and an alpha male plus helpers. Our observations of copulatory behavior did not support multiple paternity in groups and are consistent with the electrophoretic evidence of monogamy in 2 groups in New Mexico (Bednarz 1987). However, polygamy in Harris' Hawk groups was recently confirmed by DNA fingerprinting (R. Sheehy, J. Dawson, and K. Oishi unpubl. data). Polyandry, polygyny, and monogamy were documented in groups that contained >2 adults. Harris' Hawks can be, therefore, described as a communal breeding (Emlen 1984) or mate-sharing species (Brown 1987, Koenig and Mumme 1987). Genetic evidence also revealed that observations of copu-

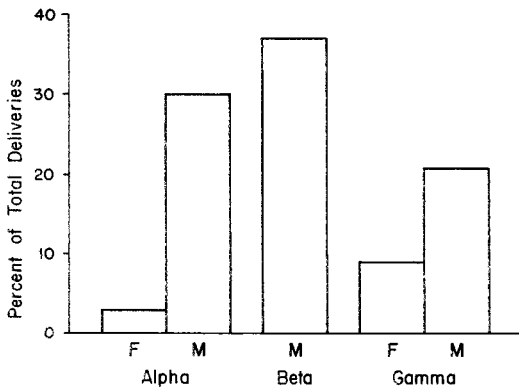


Fig. 3. Deliveries of prey ($n = 136$) to the nest area by Harris' Hawks. Data taken from 4 groups that contained identical compositions.

latory behavior provided a poor way to assess mating systems in groups (R. Sheehy, J. Dawson, and K. Oishi unpubl. data). The alpha-2 females and beta males that we studied may have been breeders or nonbreeders.

If parental investment is positively correlated with genetic investment (Dow 1978, Vehrencamp 1977, Joste et al. 1982), our observations of parental behaviors suggest that monogamy is the most common mating system in Harris' Hawk groups. The nesting roles of alpha-2 females (i.e. levels of parental care nearly equal to that of alpha females) strongly suggested that they were breeding, but groups with alpha-2 females were relatively rare. The most common group structure contained a beta adult male, but parental behavior by most beta males did not suggest genetic investment in broods. Assuming that paternity of young in a brood could be

divided equally between alpha and beta males, parental care also should be equally shared by males at some nests. In a trio of Harris' Hawks, Mader (1979) reported that participation in parental duties at the nest and copulations was similar for both males. His conclusion that the trio was polyandrous was probably correct. In contrast, we found that parental behavior of beta males, if present at all, was always well below that provided by alpha males.

Woolfenden and Fitzpatrick (1977) found that hierarchies in groups of Scrub Jays (*Aphelocoma coerulescens*) were male-dominated to the extent that male helpers dominated female breeders. Although female dominance at the alpha level was the rule in groups of Harris' Hawks, we did not observe absolute dominance of one sex over the other. Also, we did not observe independent hierarchies among the sexes (i.e. separate male and female hierarchies). Dominance within a status level usually conformed to sex and age conventions, but relationships between hawks in different levels often did not. For example, adult males (alpha and beta) often were dominant over extra adult females (gamma) in groups. Other factors must therefore overlay age- and sex-related dominance. Seniority, breeding experience, established associations with dominants, and relatedness to dominants also may affect position within a group hierarchy.

Our division of hierarchies into alpha, beta, and gamma levels was supported by differences in nesting roles among levels. These levels represent at least 2 stages of helping. The gamma level is composed of immatures and adults of both sexes, most of which are offspring helping

TABLE 6. Responses of Harris' Hawks in the Cholla Grove Group, 1986, to Great Horned Owls in the nest area ($n = 34$ incidents of trespassing by Great Horned Owls, 151 hours of observation). Abbreviations: Adult = A, immature = I, male = M, and female = F.)

Dominance status	Age/sex	n^a	Percentage of n			
			Active response ^b	Initial attack ^c	Chase ^d	Strike ^e
Alpha	A/F	34	26.5	14.7	26.5	11.8
	A/M	27	100.0	55.5	100.0	25.9
Beta	A/M	24	100.0	50.0	100.0	8.3
Gamma	A/M	9	77.7	22.2	55.5	0.0
	I/F	6	66.6	0.0	50.0	0.0

^a Number of observations of owl harassment in which a member was present.

^b Movement from a perch toward an owl.

^c The first closing flight toward an owl.

^d Chases were often performed by >1 hawk per observation.

^e Any physical contact between a hawk and an owl.

their parents. All offspring apparently disperse from their natal ranges by their fourth year, and young Harris' Hawks do not appear to use inheritance of the natal territory as the usual route to breeding.

We suggest that gamma helpers, many of which are offspring of alpha members, do not actively pursue a breeding position in natal groups or territories. Gamma hawks showed a complete lack of sexual behavior and immature helpers, all of which were gamma hawks, have levels of breeding hormones lower than those of adult helpers, many of which were beta males (Mays et al. 1991). Intolerance by alpha males of gamma hawks near the nest further suggests that breeding is unlikely at the gamma level. It is possible that gamma hawks remain on natal territories until a position in an unrelated group can be found. Dispersal from their natal groups may represent the shortest route to breeding for young Harris' Hawks, a relatively long-lived species with stable breeding groups over time. Alternatively, dispersal patterns in the Harris' Hawk may be due to selection to avoid inbreeding (Mays et al. 1991).

In contrast, alpha-2 females, beta males, and some gamma hawks are probably unrelated to the alpha pair. From nesting roles, sexual behavior, and instances in which helpers ascended in hierarchies (Dawson unpubl. data), we suggest that extra adults at the alpha and beta levels actively pursue a breeding position within groups.

Dominance and helper contributions.—We found that Harris' Hawk helpers actively captured and transported prey to the nest, harassed predators, and defended the territory from conspecific trespassers (Dawson and Mannan 1991). When helpers attempted to participate in parental-type behaviors at the nest, they were prevented from doing so by the dominant breeders.

These observations are consistent with concepts of social manipulation of subordinates by breeders or parents. Suppression of breeding in helpers has been a prominent concept in models of the evolution of sociality (Michener and Brothers 1974, Alexander 1974, Emlen 1982, Vehrencamp 1983) and has been suggested in several species that breed cooperatively (Reyer et al. 1986, Vehrencamp 1977, Carrick 1972).

Copulatory behavior by Harris' Hawk beta males implies that they are physiologically capable of breeding, a suggestion supported by hormonal evidence (Mays et al. 1991). Partici-

pation in nesting activities (i.e. exposure to eggs and begging young) may be necessary to induce breeding condition in helpers. This idea has been proposed in various forms to account for copulations by female breeders with male helpers in several species (Dow 1978; Craig 1980; Stacey 1979; Emlen 1982, 1984). Perhaps Harris' Hawk breeders must allow helpers to occasionally enter the nest to encourage helper participation in providing food to the nest and in territorial defense. Partial exclusion from the nest may prevent helpers from attaining full breeding condition. A helper in full breeding condition could have negative effects on reproduction through increased intragroup conflict or emigration from the group (Vehrencamp 1977).

Differential tolerance in the nest and differences in levels of participation in parental behaviors by beta and gamma hawks lend support to breeder manipulation of helpers. Beta males are allowed greater access to the nest than gamma hawks, and are tolerated by alpha males and females during attempted copulations. Beta males also show higher participation in cooperative hunting, food transport, and harassment of predators. In monogamous groups, alpha males may sacrifice little in terms of exclusive paternity by allowing beta males to engage in copulatory behavior. Despite the lack of mate guarding by males, confidence of paternity by alpha males may be maintained via noncooperation by alpha females during copulatory attempts. As in mate-sharing species in which male dominance is the rule, the outcome of extrapair copulatory behavior in Harris' Hawks is controlled by the most dominant members of groups—alpha females.

Beta males may increase their status by forming the beginnings of pair bonds with alpha females. Rudimentary pair bonds may allow a beta male to more quickly establish a breeding relationship with the alpha female when the alpha male is lost from the group. This may offer advantages in a species that can breed year-round, often produces several broods per year, can initiate another brood less than a month after the first has fledged, and has a sex ratio skewed toward adult males. Also, the presence of cooperative polyandry in some groups suggests that the costs of lost reproductive opportunities to a male serving in a beta position may be mitigated by mate sharing.

Exclusion of helpers from most parental-type

behaviors would appear to reduce potential fitness benefits to breeders that could be gained through increased care of the offspring or "load-sharing" of nest duties among all members of a group (Brown 1987). In particular, *allofeeding* (feeding of nestlings by a nonparent) is common among cooperative breeders (Brown 1987, Skutch 1987) yet it is conspicuously lacking in Harris' Hawks.

Allofeeding may not be important in a species that relies on relatively large prey that are difficult to capture. Harris' Hawks in Arizona use prey species that range widely in size, but rely heavily on 2 relatively large species—the desert cottontail and Gambel's Quail (*Callipepla gambelii*). Insectivorous birds that are cooperative breeders rely on numerous small prey items to feed nestlings. Stallcup and Woolfenden (1978) found that feeding rates in the Scrub Jay averaged 8 per hour. Food delivery rates for other species range from 3 per hour in the Kookaburra (*Dacelo gigas*) to >20 per hour in the Noisy Miner (*Manorina melanocephala*) and Green Woodhoopoe (*Phoeniculus purpureus*) (Parry 1973, Dow 1970, Grimes 1975). In these species, the energy costs to breeders of entering the nest and placing food in the mouth of a nestling on each delivery must be high. Helpers usually make significant contributions to this chore (Stallcup and Woolfenden 1978, Brown 1972, Rabenold 1984).

In contrast, Harris' Hawks make fewer deliveries (ca. 5 per day) but deliver a large amount of food each time. Often an entire brood can be satiated with food contained in one food delivery. Because nestlings can be fed a number of times from a single prey item and only a few deliveries are made each day, the task of tearing food into small pieces and placing it into the mouth of a nestling can be accomplished for the entire brood by a single adult. Furthermore, nestlings can eat unaided by an adult at 1.5–2.5 weeks of age (nestling period = ca. 6.4 weeks) and food is often placed in the nest without being fed to the nestlings. Consequently, allofeeding would probably have little effect on the amount of food or the frequency of nestling meals. Both factors may be influenced by the efforts of helpers in capturing and transporting prey to the nest (Mader 1975a, Brown 1987).

Predator detection and deterrence.—Increased protection from predators has been proposed as a benefit of cooperative breeding in the Striped-backed Wren (*Campylorhynchus nuchalis*), the

Purple Gallinule (*Porphyryla martinica*), and the Scrub Jay (Rabenold 1984, Hunter 1985, Woolfenden 1978). Mader (1979) proposed that the load sharing of hunting duties by a third adult Harris' Hawk may increase nest attentiveness and defense against predators, although he did not identify predation as a significant factor of nestling mortality. We found that Great Horned Owls posed the greatest threat of predation to young Harris' Hawks in our study area. We suggest that hawks were effective in driving owls from the nest area during the day but were unable to prevent owls from taking young at night. We also found evidence that most young hawks were killed during the late nestling and early fledgling stages. We suspect that young hawks were most vulnerable to predation by owls during this period because hawks stopped brooding nestlings at night about 1 week before fledging. Likewise, recently fledged hawks roosted alone in small trees near the nest and were not yet skilled enough at flight to evade owls.

We speculate that harassment by groups of hawks may influence the choice of a nest site by owls in relation to an active hawk territory. The aggressive nature of harassment suggests that owls could be injured or killed by hawks, although we did not see this during our study. These factors might reduce the threat posed by owls in the territory before hawk nestlings reach the vulnerable stage of development. The presence of helpers probably increased the likelihood that predators were detected in the territory and increased the duration and intensity of harassment (Woolfenden and Fitzpatrick 1984, Brown 1987).

We proposed elsewhere that group living in the Harris' Hawk is related to an ecological constraint (Koenig and Mumme 1987) imposed by the scarcity of open water sources in the desert (Dawson and Mannan 1991). The behavior of hawks at the nest suggests the helpers may influence reproductive success in at least 3 ways. First, the survival of nestling and fledgling hawks may be increased through predator deterrence. Second, helpers also defend the territory from conspecifics (Dawson and Mannan 1991). Third, the efforts of helpers to procure and deliver food to the nest area may increase the amount and frequency of deliveries to the nest area (Mader 1975a, Brown 1987). Cooperative hunting, first reported for the Harris' Hawk by Mader (1975a), is generally more successful

than hunting alone (Bednarz 1988, Dawson 1988). Whether or not this activity results in increased food supplies at the nest has yet to be established. It is possible that the benefits of cooperative hunting are accrued primarily by the individual hawks in a successful hunting party (Bednarz 1988, Bednarz and Ligon 1989). In this situation, reproductive enhancement may occur after offspring leave the nest and become proficient enough at flight to follow and eventually join hunting parties. Offspring survival may be higher for young that hunt (i.e. share kills) with older group members during the period after active provisioning has stopped and before young have developed adequate hunting skills.

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