PAIR AND GROUP REPRODUCTIVE SUCCESS, POLYANDRY, AND COOPERATIVE BREEDING IN HARRIS' HAWKS

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ABSTRACT.—The average size of Harris' Hawk (*Parabuteo unicinctus*) social units in New Mexico was 2.7 individuals, and pairs were most common (49%; $n = 61$). Groups of more than two hawks included both adult- (74%) and immature-plumaged (26%) members ($n = 76$). Immatures rarely provided food to nestlings, but adult supernumeraries did. Electrophoretic analyses of two groups containing two adult-plumaged males did not suggest polyandry. At least in southeastern New Mexico, Harris' Hawk groups consist primarily of a monogamous pair with "helpers." Pairs and groups showed no differences in clutch size, number of young produced per successful nest, or number of offspring fledged per year. Pair nests failed less often (16%) than group nests (46%) during the incubation period. Groups reared larger offspring and tended to initiate second nests more frequently than pairs. The overall lack of correlation between reproductive output and group size suggests that kin selection has not been a major influence in the evolution of the Harris' Hawk breeding system. *Received 6 June 1986, accepted 22 December 1986.*

MADER (1975a, b) described a breeding population of Harris' Hawks (*Parabuteo unicinctus*) in Arizona that consisted both of pairs and of putatively polyandrous trios. Since publication of Mader's work, the Harris' Hawk often has been cited as one of only a few species known to exhibit polyandry or a cooperatively polyandrous breeding system (e.g. Woolfenden 1976; Brown 1978, 1983; Faaborg and Patterson 1981; Koenig and Pitelka 1981; Ligon 1983; Woolfenden and Fitzpatrick 1984; Oring 1986). In contrast, 18 of 19 (95%) Harris' Hawk nests in Texas were tended only by pairs, suggesting that polyandry and cooperative breeding are rare in at least one Texas population (Griffin 1976).

Cooperative breeding should entail some fitness advantage over available alternative strategies. Benefits resulting from cooperation may be shared mutually by all group members or biased toward those individuals of the group that have greater behavioral leverage (Emlen and Vehrencamp 1983). These advantages may be expressed in terms of increased reproductive success, improved quality of young (e.g. production of healthier or heavier fledglings), decreased stress on breeders (Morton and Parry 1974, Ricklefs 1980, Emlen 1984), or increased probability of survival (Woolfenden and Fitzpatrick 1984, Faaborg 1986).

Because survival probabilities and stress are difficult to measure, most fieldworkers have concentrated on obtaining estimates of reproductive success. Data on reproductive success show that, in general, large groups produce more fledglings than smaller groups of the same species (Brown 1978; Emlen 1978, 1984). There are exceptions, however, and in many cases this positive relationship is not significant. Koenig (1981) compared productivity measures for 15 species and found that per-capita reproductive success tended to decrease with increased group size.

Enhanced inclusive fitness (Hamilton 1964) has been suggested as an important factor favoring the evolution of cooperative breeding (Maynard Smith and Ridpath 1972; Brown 1974, 1978; Reyer 1984). In systems significantly influenced by kin selection, groups should exhibit greater reproductive success than pairs, and supernumeraries should be related to breeders (Brown 1983). These patterns, however, also can result from other processes (Ligon 1980, 1983; Woolfenden and Fitzpatrick 1984). If these conditions are not present, resource limitation (Koenig and Pitelka 1981), other ecological constraints (Emlen 1982a), or cooperation *per se* (Ligon 1983) may have been more important than kin selection in the evolution of a particular cooperative system.

I describe here the social system of the Harris' Hawk in New Mexico, based on 3 yr of observations, and compare the reproductive success of pairs and groups. The results are then considered with regard to the expectations of kin-

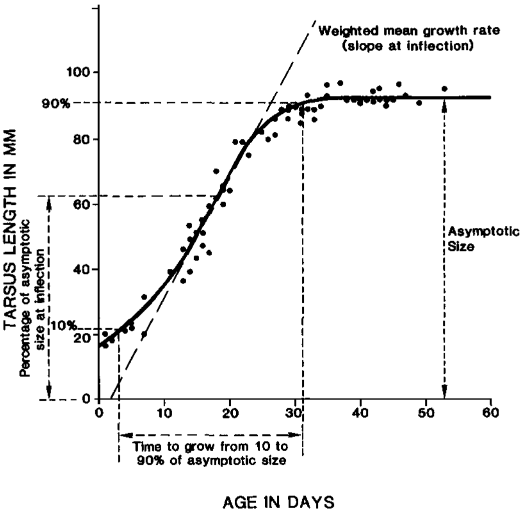

Fig. 1. Growth of tarsus length of females reared by pairs of Harris' Hawks ($n = 8$ individuals and 77 measurements). The four growth parameters used in the statistical analysis are illustrated.

selection theory and with alternative explanations for the evolution of cooperation in birds.

METHODS

The study area was in the shinnery-oak (*Quercus havardii*) shrublands of southeastern New Mexico and has been described previously (Bednarz 1987). Topography varies from level to rolling sand dunes. Local habitats include sparse grasslands, creosote (*Larrea tridentata*) shrub associations on level caliche soils, and oak-mesquite (*Prosopis glandulosa*) associations on sand substrates. Harris' Hawks nest in small (4-7 m) mesquite or soapberry trees (*Sapindus drummondi*), which are scattered throughout the study area.

Because of the prolonged breeding season (Bednarz 1987), all known nesting ranges were searched for active nests at least three times per year (once each in spring, summer, and autumn). The nesting range is the area where members of a specific group are usually observed and within which nests occur. I use the term nesting range because the Harris' Hawk makes little effort to defend space (see Results). If no nests were found in a given range during any of the seasonal searches, that range was reexamined repeatedly until I was sure no nesting attempt had been initiated during that season.

I classified a nest as being tended by a pair if I visited it at least 5 times and no more than 2 hawks were ever seen in the vicinity. All pairs visited more than 5 times (85 additional visits at 19 pair nests) were not found to have a previously undetected supernumerary. When 3 or more hawks were observed together in the vicinity of a nest, they were classified as a group. The exact size of the group, however, was unknown except at intensively watched nests or where some or all group members were marked. Only nests visited 5 or more times were included in the analyses.

I considered the maximum number of hawks observed in the vicinity of nests during the first breeding effort of the year to be the size of the social unit. The technique is subject to some error; in particular, wary members may have been missed and occasional transients may have been counted inadvertently. I was careful, however, to count as group members only hawks that seemed to stay together during nest visits, and not to include birds that apparently were vagrants.

Data were compared primarily between pairs and larger social units (hereafter "groups"), although in many cases the exact size of groups was unknown. Because pairs made up 49% of all breeding units, these analyses should reveal any trends related to social-unit size.

In 1982 and 1983, all members of breeding units were classified as adult- or immature-plumaged based on the presence or absence of obvious white patches under the wings, which mostly disappear when hawks are about 1 yr of age (pers. obs.).

Nest success was calculated by the Mayfield (1961, 1975) method, with the standard error estimates proposed by Johnson (1979). This technique avoids overestimates of breeding success that result because some early nesting failures probably are undetected (Steenhof and Kochert 1982). The incubation and brood-rearing periods used for the Mayfield analysis were 34 and 46 days, respectively. Hatching dates were estimated by a regression method (Bednarz 1987). Conventional measures of reproductive success (clutch size and fledgling success) also are reported. Young hawks were recorded as having fledged successfully only if they were observed after leaving the nest.

Adults and nestlings were banded with unique color combinations of vinyl tarsus bands. Adults were trapped with bal-chatri (Berger and Mueller 1959) and padded steel leg traps. I color-marked a total of 163 hawks during the study. By November 1983 about half of the estimated 75 adult-plumaged hawks in the population were color-marked.

Paternity analysis was done by the paternity-exclusion method using blood and muscle allozymes (Hanken and Sherman 1981). Blood (Joste et al. 1985; collected with heparin-treated syringes) and muscle samples (Baker 1981) were taken from 50 captured hawks. Standard starch-gel electrophoretic analyses (Smith 1976) were done by Dr. Donald C. Morizot (Univ. Texas System Cancer Center, Smithville, Texas). Of the 43 blood and muscle allozymes surveyed, 4 pectoral muscle loci [glycerol-3-phosphate dehydrogenase (GPD, E.C. 1.1.1.8), peptidase glycyl-leucine (PEP-GL, 3.4.11 or 13), phosphoglyceromutase (PGAM, 2.7.5.3), and glutamate-pyruvate transami-

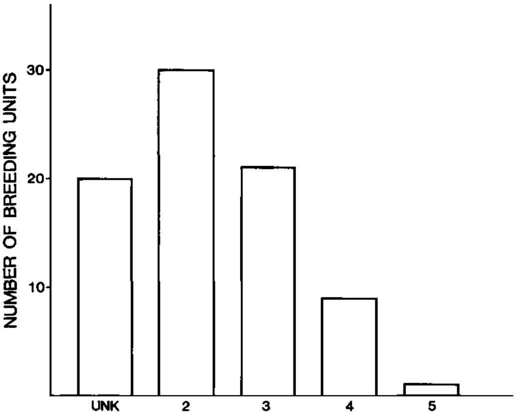

Fig. 2. Estimated social-unit size of Harris' Hawks based on the number of hawks observed in the vicinity of the first nesting attempt of the year (see Methods).

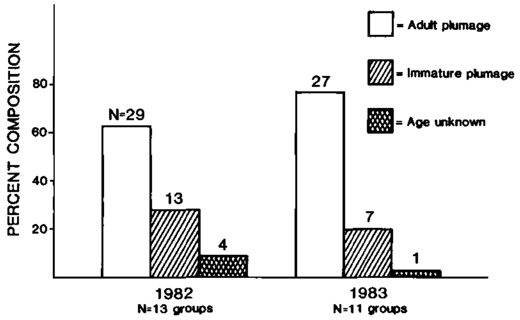

Fig. 3. Age composition of groups in 1982 and 1983, as determined from hawks observed in the vicinity of the nest during the first successful nesting attempt of the year.

nase (GPT, 2.6.1.2)] showed adequate variability to be useful in the paternity analysis. A Mendelian mode of inheritance was assumed for the genetic loci examined. Although data were limited, comparison of allozymic patterns of 12 offspring and 9 putative parents ($n = 7$ social units) was consistent with this assumption.

Growth patterns of nestlings reared by pairs and larger groups were compared by fitting data to the Richards' (1959) growth curve and calculating jackknife confidence intervals (Bradley et al. 1984). With this technique, four parameters that describe the general growth pattern were calculated: asymptotic size, weighted mean growth rate, percentage of asymptotic size achieved at curve inflection, and time period in days to grow from 10 to 90% of asymptotic size (Richards 1959, Ricklefs 1967, Bradley et al. 1984; see Fig. 1). These four parameters were compared for three measures of growth taken from known-age nestlings, (i.e. at nests that were visited at or within 24 h after hatching) so that all nestlings could be assigned hatch dates no more than 1 day in error. The three growth variables used in the analysis were mass, tarsus length from the bend in the intertarsal joint to the bend of the toes, and extended toe-pad length (with the toe-pad held approximately perpendicular to the tarsus and the toes spread open to their maximum extension, the pad is measured from the tip of toe 3 to the tip of the hallux). Growth patterns were described separately for each sex because of sexual dimorphism (Hamerstrom 1978).

Nest attentiveness was determined by time-lapse photography. Kodak analyst super-8 movie cameras were placed 2-8 m from nests and adjusted to take photographs at intervals of 11-14 s. In 1983 I attempted to photograph all nests that survived beyond hatching. In 1981 and 1982 only a few nests, selected primarily for ease of camera placement, were filmed. Activity in frames was classified into one of four categories: (1) adults absent, (2) adults present (in nest or on nearby branch), (3) adult covering young (brooding or shading), and (4) adults(s) feeding young.

Cameras were either set up at sunrise and operated until sunset (10-14 h of activity recorded, depending on the season) or placed at the nest in the middle of the day with a photo switch that shut the camera off at sunset and resumed photography at first light. Both of these approaches included early-morning and late-afternoon activities and were considered to be one film-day. To standardize for any initial disturbance the camera set had on the nest attendants, I included in the analysis only those frames after the first attendant returned and departed from the nest for each film-day. A total of 56,220 frames from 32 film-days was analyzed. Because patterns of nest visitation changed with the ages and the needs of nestlings (Mader 1979, Newton 1979), such activities are presented in 5-day age periods. I combined data into one 10-day age period (nestling age 11-20 days, $n = 16$ film-days) and one 5-day period (nestling age 26-30 days, $n = 14$ film-days) to allow an adequate sample size for statistical comparison. Proportional data (arcsine transformed) for each of the four behavior categories described above were compared using analysis of variance (Sokal and Rohlf 1981) between pairs and groups and between years.

RESULTS

Group size and composition.—Harris' Hawk social units averaged 2.7 individuals ($n = 61$; Fig. 2). Pairs were most common (49.4%, $n = 61$); larger groups usually were trios (34.4%), but I recorded 9 groups of four (14.8%) and 1 of five (1.6%). After nestlings fledged, social units often increased to five or six members. Such groups were common in late autumn and during the

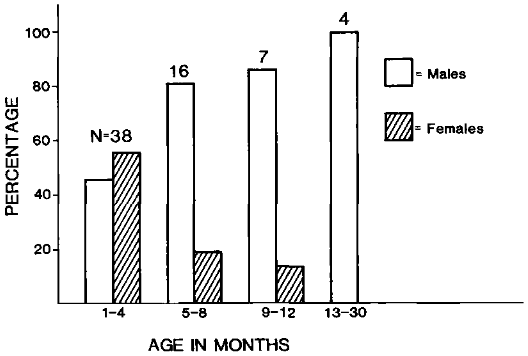

Fig. 4. Sex composition of Harris' Hawks marked as nestlings and later observed on their natal breeding range [$\chi^2 = 11.2$, $P = 0.004$, df = 2; data in two oldest age classes (9–30 months) combined].

short nonbreeding period (December–January). By March or April, unit size declined, probably because of dispersal and mortality of some group members.

Adult-plumaged birds comprised 69.1% of group members in 1982 and 1983 (Fig. 3), with a mean of 2.4 adult-plumaged hawks per group ($n = 23$ units with 3 or more members). Group membership included 24.7% immature-plumaged hawks (0.9 immature members/group) and 6.2% of unknown age. All banded immature supernumeraries observed ($n = 39$; fledged during the previous year) were in the vicinity of their natal ranges and associated with the adults tending the active nest in that range. Immature auxiliaries commonly perched with adults adjacent to nest trees, screamed at nest intruders, and shared prey with other group members.

Immature hawks were recorded at or adjacent to nests during 2 of 9 film-days at sites with known immature auxiliaries. A 9-month-old supernumerary repeatedly perched (during 1 film-day) beside an active nest and seemed to be ignored by the adult female that often was present. The second case involved a 6-month-old female that delivered an unidentified object (probably prey) to an active nest and then immediately departed.These observations suggest that delivery of prey to nests by immature auxiliaries is rare.

Side-by-side observations of adults in 5 groups suggested that all consisted of 2 or more apparent males and only 1 female. This was later confirmed for 3 of these groups when all members or both males were trapped. Overall, the sex ratio of immature-plumaged auxiliaries was biased toward males (60.1%, $n = 56$; $\chi^2 = 0.6$, $P = 0.4$, df = 1). Significantly more males, however, were noted in the older age classes ($\chi^2 = 11.2$, $P = 0.004$, df = 2; Fig. 4), suggesting that male offspring associate with their parents for longer periods than do females. Of banded nestlings, only males ($n = 4$) were known to associate with adults on their natal range beyond 1 yr of age.

Adult-plumaged auxiliaries commonly perched at nests and brought food. I could not determine the frequency of visits among adult males within groups. Two adult males (20–24 months of age) banded as nestlings in two different groups provided prey to nests within their natal ranges (determined by time-lapse photography). I was unable to ascertain whether two other males observed on their natal range for more than 13 months provided food to nestlings.

Paternity analysis.—Harris' Hawk group 12 contained 2 adult males, 1 adult female, and 1 immature female. The PEP-GL locus excluded adult male 810 as a possible father of the two nestlings in 1983, so the other adult male (not sampled) may be inferred to be the male parent. The allozyme data for adult female 565 were compatible with her being the mother of both offspring. Male 810, who actively provided food to the young, was hatched in the same range in 1981. Because the adults were not banded in 1981, it is not known whether this bird was assisting its genetic parents in 1983.

All three adults (2 males, 1 female), in addi-

TABLE 1. Mean clutch sizes for pairs and groups of Harris' Hawks.

	Pairs			Groups			Groups of unknown size		
	n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
1981	11	2.91	0.83	10	3.30	0.67	6	2.83	0.98
1982	6	3.00	0.89	12	2.92	0.51	8	3.25	1.04
1983	12	2.92	0.67	9	3.11	0.33	4	2.75	0.50
1981–1983	29	2.93	0.75	31	3.10	0.54	18	3.00	0.91

TABLE 2. Mean number of fledglings reared per successful nest attempt by pairs and groups of Harris' Hawks.

	Pairs			Groups			Groups of unknown size		
	n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
1981	10	1.80	1.03	8	2.00	0.76	7	1.71	0.76
1982	6	1.83	0.75	13	2.08	0.76	6	2.17	0.75
1983	14	2.00	0.96	9	1.78	0.83	1	2.00	—
1981-1983	30	1.90	0.92	30	1.97	0.76	14	1.93	0.73

tion to the two nestlings, were sampled in range No. 18. All five hawks had identical allozyme patterns, so either male could have sired the offspring. One of the adult males (842) was reared on this range in 1981 and provided prey to the nestlings. The adults were not banded in 1981, so I do not know if this male was assisting his parents.

Group 20 consisted of 2 adult males, 1 female, and 2 nestlings. The two adult males were homozygous for different alleles at the GPD and the PGAM presumptive loci. Male 563 could not have sired either offspring, while male 562 was compatible electrophoretically with both nestlings. Moreover, the electrophoretic results indicated that the two adult males (562 and 563) were not father and son.

Territoriality.—Harris' Hawks make little or no effort to defend the area around their nest from conspecifics. In 3 yr I witnessed only five intraspecific aggressive interactions. In two instances the interaction was probably between members of the same group, possibly one hawk asserting dominance over another. Another observation involved a female that screamed and chased a transient Harris' Hawk that had flown close to the female's nest, which contained small nestlings. The female returned to its nest after pursuing the intruder for less than 500 m. The context of the other observed aggressions was undetermined, but territorial behavior seemed unlikely.

Harris' Hawks seemed to move freely through their neighbors' nesting ranges without being challenged. On two occasions I observed banded hawks from adjacent groups peacefully perched within 5 m of each other. In one case immature hawks from two different social units (9 and 17) perched on a windmill that breeding unit 9 traditionally used for nesting. Two weeks later the adult female of unit 9 was incubating a complete clutch of eggs on the windmill nest.

In one instance, two social units of Harris' Hawks inhabiting adjacent ranges swapped nesting core areas. In 1983 unit 26 nested in an area that had previously been used by unit 7. Unit 7, in turn, bred in the range formerly oc-

TABLE 3. Estimated proportion of successful breeding attempts of pairs and groups of Harris' Hawks. Proportions were determined by the Mayfield method (see Methods). CI = confidence interval.

	Pairs	Groups
1981		
Proportion	0.80	0.55
95% CI	0.59-1.00	0.32-0.94
n	12	13
1982		
Proportion	1.00	0.74
95% CI	—[a]	0.53-1.00
n	7	15
1983		
Proportion	0.85	0.68
95% CI	0.67-1.00	0.46-1.00
n	19	13

[a] Confidence intervals cannot be calculated when all nests monitored were successful.

TABLE 4. Estimated proportion of breeding attempts successful at different nesting stages of Harris' Hawk pairs and groups, 1981-1983. Sample size (*n*) represents the number of nests usable in Mayfield analysis (see Methods). CI = confidence interval.

	Pairs	Groups
Incubation period		
Proportion	0.84	0.54
95% CI	0.65-1.00	0.37-0.78
n	18	21
Brood-rearing period		
Proportion	0.92	0.94
95% CI	0.82-1.00	0.84-1.00
n	36	30
Combined incubation and brood-rearing period		
Proportion	0.86	0.66
95% CI	0.74-1.00	0.52-0.84
n	38	41

TABLE 5. Mean number of fledglings reared by pairs and groups of Harris' Hawks per year.

	Pairs			Groups			Groups of unknown size		
	n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
1981	7	2.29	0.95	8	2.00	1.31	8	1.50	1.69
1982	6	1.83	0.75	12	2.17	1.80	9	1.33	1.32
1983	16	1.69	1.20	10	1.70	1.06	3	0.67	1.15
1981–1983	29	1.86	1.06	30	1.97	1.43	20	1.30	1.42
Per capita	29	0.93	0.52	30	0.60	0.47			

cupied by unit 26. In addition, active nests were commonly located within 500 m of each other in open habitat, and I never observed aggressive interactions between two breeding units rearing young within view of each other. In New Mexico these birds seem to make no effort to defend their breeding or foraging ranges from conspecifics, except to challenge intruders in the vicinity of nests with young.

Reproductive success.—Clutch sizes produced by females of pairs and groups of Harris' Hawk did not differ (Wilcoxon test, $z = 0.83$, $P > 0.2$) and was about 3 eggs in all 3 yr (Table 1). The number of fledglings produced from successful nests of pairs and groups likewise did not differ (Wilcoxon test, $z = 0.23$, $P > 0.2$) and was about 2 in all years (Table 2). The proportion of successful nests, however, was greater for pairs in all years (Table 3). When these data were combined (Table 4), pairs were significantly more successful (86%) than groups (66%). After separating the incubation and brood-rearing periods, group nests failed significantly more often ($P < 0.05$) during the incubation period than did those of pairs (Table 4). There were no differences in success between pairs (92%) and groups (94%) during the brood-rearing period.

At least one egg failed to hatch in 52% of pair nests ($n = 25$) and 47% ($n = 15$) of group nests. Many of these eggs disappeared before hatching (42%, $n = 26$). Losses of complete clutches accounted for the majority of the eggs laid that did not hatch. This was a relatively rare occurrence for pairs (2 of 31 nesting attempts, both attributed to severe weather). Clutch losses were more frequent for group nests (12/27); in 10 cases the cause could not be determined. Severe weather was probably responsible for the failure of two group nests during the incubation period.

Harris' Hawks can successfully rear two broods to fledging in 1 yr, and one unit that fledged two broods attempted a third nest (Bednarz 1987). Groups showed a greater tendency to produce a second brood (40%, $n = 20$) than did pairs (12.5%, $n = 24$). This tendency was significant ($\chi^2 = 4.4$, $P = 0.03$, df = 1) when data from all years were combined. Social units that failed in their first nesting attempt were excluded from this analysis because their second nesting attempt was considered a replacement clutch or brood. Three pairs attempted second broods only in 1981, when prey populations were at a peak (Bednarz 1987). Groups attempted to rear second broods in all 3 yr of the study (2 groups in 1981, 5 in 1982, and 1 in 1983).

The increased tendency of groups to double-brood partially offset their nest failures during the incubation period (Table 4). Groups produced slightly, but not significantly (Wilcoxon test, $z = 0.55$, $P > 0.2$), more fledglings per year than did pairs (Table 5). However, per-capita production of fledglings per year was significantly greater (Wilcoxon test, $z = 2.62$, $P < 0.01$) for members of pairs (mean = 0.93) than for members of groups (mean = 0.60).

Growth analysis.—Estimates of asymptotic size of the three growth variables measured were consistently larger for nestlings reared by groups, except for male toe-pad length (Table 6). This difference was significant ($P < 0.05$) for tarsus lengths of both males and females. The group male data were based on only two individuals and must be considered preliminary. Female nestlings reared by pairs exhibited faster growth rates and shorter primary growth periods than those reared by groups (Table 7). Male data (not shown) exhibited a similar pattern. Only for female tarsus length (Table 7) was the duration of the primary growth period significantly different ($P < 0.05$) between pairs (estimate = 33.5 days) and groups (estimate = 38.0 days).

Estimates of the percentage of asymptotic size reached at inflection revealed no consistent differences in nestling growth patterns between

TABLE 6. Asymptotic size estimates of nestlings reared by pairs and groups of Harris' Hawks. Sample size (n) represents the number of nestlings included in the analysis. CI = confidence interval.

	Pairs	(n)	Groups	(n)
Female mass				
Asymptotic size	780.1	(9)	882.7	(5)
95% CI	699.5–870.0		664.7–1,172.4	
Male mass				
Asymptotic size	587.9	(9)	605.0	(2)
95% CI	559.7–617.6		359.1–1,019.2	
Female tarsus length				
Asymptotic size	93.9	(8)	97.9	(5)
95% CI	91.5–96.3		93.9–102.1	
Male tarsus length				
Asymptotic size	91.0	(9)	93.5	(2)
95% CI	89.2–92.7		93.2–93.9	
Female toe-pad length				
Asymptotic size	96.9	(8)	98.1	(5)
95% CI	94.0–99.9		95.4–100.8	
Male toe-pad length				
Asymptotic size	86.5	(9)	86.3	(2)
95% CI	84.8–88.3		66.0–112.6	

nests of pairs and nests of groups. Estimates of this parameter, which may be considered an indicator of growth-curve shape (Bradley et al. 1984), were similar between young birds produced by pairs and groups (Table 7).

All differences between pairs and groups probably can be attributed to the different asymptotic sizes reached by fledglings rather than to actual differences in growth rates. More rapid growth-rate indices for pairs (Table 7), as calculated by the Richards' growth curve method, probably were the result of young hawks terminating growth sooner than the nestlings of groups. Weighted mean growth rates were inversely related and primary growth periods were directly related to the estimates of asymptotic size (Tables 6 and 7; Bradley et al. 1984).

Based on a limited sample, the consistent trends of this analysis suggest that a difference exists in the growth pattern of nestlings reared by groups and pairs. Offspring reared by groups continued to grow for a longer period and hence

TABLE 7. Estimates of growth parameters[a] for three variables of female Harris' Hawk nestlings reared by pairs and groups.

	Pairs	(n)	Groups	(n)
Female mass				
Mean growth rate	0.096	(9)	0.071	(5)
Duration of growth period (days)	23.1	(9)	34.2	(5)
Percentage of asymptotic size	49	(9)	43	(5)
Female tarsus length				
Mean growth rate	0.059	(8)	0.052	(5)
Duration of growth period (days)[b]	33.5*	(8)	38.0*	(5)
Percentage of asymptotic size	68	(8)	73	(5)
Female toe-pad length				
Mean growth rate	0.061	(8)	0.055	(5)
Duration of growth period (days)	32.8	(8)	36.3	(5)
Percentage of asymptotic size	71	(8)	70	(5)

[a] See Methods.

[b] Asterisks indicate estimates were significantly different at $P < 0.05$.

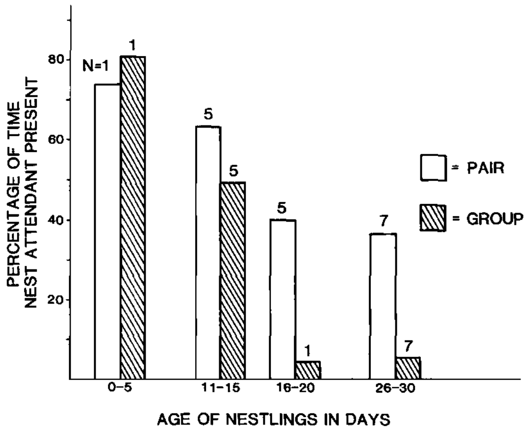

Fig. 5. Percentage of time that one or more member of pairs and groups was present at the nest during various nestling age intervals.

Table 8. Percentage of time that an adult attended nestlings for pairs and groups of Harris' Hawks. P values are based on an analysis of variance of arcsine-transformed data. Sample size (n) represents the number of film-days.

	Pairs	Groups	P^a
Nestlings 11-20 days old	$n = 10$	$n = 6$	
Attendant feeding	9.8	9.8	0.67
Attendant covering	26.8	28.8	0.79
Attendant present	53.9	47.3	0.68
Attendant absent	46.1	52.7	0.49
Nestlings 26-30 days old	$n = 7$	$n = 7$	
Attendant feeding	9.6	3.1	0.03*
Attendant covering	8.6	0.0	0.07
Attendant present	37.3	5.1	0.01*
Attendant absent	62.7	94.9	<0.01*

[a] Asterisks indicate significant differences between pairs and groups.

achieved a slightly larger asymptotic size at fledging than did those reared by pairs.

Nest attendance.—Time-lapse photography indicated that groups attended nestlings no more often than pairs did when nestlings were 0-15 days old (Fig. 5). For pairs, however, an adult was present significantly more often ($P < 0.05$) than for groups when nestlings were 26-30 days old. Feeding ($P = 0.03$) and covering ($P = 0.07$) of young by adults also were recorded more often at nests of pairs than those of groups after 26 days, whereas no difference was observed during the 11-20-day nestling period (Table 8). After young are approximately 20 days old, they are capable of self-feeding on the prey provided. The proportion of time an adult was observed feeding older nestlings therefore probably bears no relationship to the quantity of food brought to the nest. In the later stages of the brood-rearing period, adults most often deliver food and depart. In addition, 25-day-old young probably do not need to be covered except during episodes of extreme weather. Because no harsh weather occurred when nests were being photographed, it is unclear how feeding or covering behavior exhibited by pairs benefited nestlings over 25 days of age.

Discussion

The paternity data presented here do not support the occurrence of genetic polyandry in two Harris' Hawk groups. All members of the third group examined (group 18; see Results) had identical allozyme patterns (homozygous for the 4 presumptive loci examined); thus, paternity was inconclusive. However, this result is consistent with the pattern expected if the male offspring of 1981 was assisting his parents in 1983. Group 20, on the other hand, consisted of two males that could not be father and son, and were probably not brothers ($P < 0.008$, assuming independent assortment in a Mendelian manner). Whether male 563, which was excluded as the father of both offspring, attempted to copulate with the female is unknown.

Of the 26 Harris' Hawk social units monitored (5 or more visits) in 1983, only 7 included three or more adult-plumaged hawks; 3 of these groups were either unsuccessful (2) or fledged one young (1). Electrophoretic analyses provided no evidence of shared paternity in two of the remaining four groups. Thus, only 27% of the social units in the study population were potentially polyandrous, and actual genetic polyandry could have occurred in no more than two groups (7.7%).

The results of this study indicate that cooperative polyandry (Faaborg and Patterson 1981) does not seem to be the prevalent mating strategy within the groups of Harris' Hawks I studied in New Mexico (cf. Mader 1975b, 1979). Further, juveniles do not seem to pursue a classical helping strategy. Rather, this system primarily involves the retention of male offspring, which do not actively help during the first year. This system, in which juveniles associate with breeders but do not actively aid in rearing the current brood, is unusual among cooperative breeders (Brown 1978, Emlen 1978). It may represent an elementary stage of group breeding that, when exposed to some set of ecological conditions, may develop into a cooperative system in which helping is common (Brown 1974, Gaston 1978). Retention of young that do not help was reported in the Green Jay (*Cyanocorax yncas*) by Gayou (1986), who argued that this system represents an early evolutionary step in the development of cooperative breeding. Retention of offspring may be a parental strategy to improve their offspring's chances of survival and subsequent ability to acquire breeding status (Ligon 1981, Woolfenden and Fitzpatrick 1984). If so, offspring may assist parents actively only if their inclusive fitness is increased by enhancing their parents' reproductive output or they gain some other benefit [e.g. repayment of their help (Ligon 1983) or improved probability of obtaining breeding space (Woolfenden and Fitzpatrick 1984)], or a combination of these.

Why do some Harris' Hawks, specifically adult-plumaged males previously reared in the breeding range, actively assist the primary breeders? Several theoretical treatments (Vehrencamp 1980, Emlen 1982b, Stacey 1982) suggest that shared copulations or "forfeiture of fitness" by the alpha male may induce auxiliary individuals to provide care for broods. Mader's (1979) observations suggest that male Harris' Hawks may share paternity in the brood. Assuming that polyandry is a potential strategy, the extra males observed helping in my study may have resulted from one of several possible situations. First, males may pursue a polyandrous strategy and breed within their natal range if both parents have disappeared; otherwise they should disperse. Second, the male may help if its mother is replaced, so there may be cooperation between father and son. Third, the male supernumerary may be mating incestuously with his mother and cooperating with his father or an unrelated male. Finally, the 2-yr-old male helpers may gain some other unknown benefit by assisting parents, young, or both.

The first strategy is a possibility, as one trio included two males that were not a father-son pair. I rarely observed Harris' Hawks copulate and therefore do not know if both males attempted to sire offspring in the brood. The third strategy, incestuous mating between mother and son, seems unlikely given the apparent intentional avoidance of offspring-parent mating observed in other cooperative systems (e.g. Woolfenden and Fitzpatrick 1978, Koenig and Pitelka 1979, Johnson and Brown 1980). Alternatively, helping may be selectively neutral, possibly a hormonally induced response (see Woolfenden and Fitzpatrick 1984).

During the third year of my study, I found that some adult-plumaged supernumeraries, which actively helped with broods, were 2-yr-old hawks that had remained in their natal range. This requires a minimum of 3 yr of fieldwork to establish because nestlings banded in the first field season will not attain full adult plumage until the third season of work. The origin of auxiliary hawks in Arizona was not determined by Mader (1975a, b). Rather, he observed two cases of different males copulating with the same female during a 2-yr population study and inferred that polyandry explained the existence of groups (Mader 1975b). Later Mader (1979) reported intensive observations of one trio of Harris' Hawks that supported the existence of cooperative polyandry. The widely cited notion that Harris' Hawks mate polyandrously is therefore based on observations of only a few groups. Mader (1975b) also noted the presence of immature-plumaged hawks that did not help in the vicinity of nests, similar to what I found in New Mexico. Taken together, Mader's and my work indicate that both polyandry and the retention of offspring as active helpers may occur in the Harris' Hawk. I suggest that the retention of offspring is the more important process leading to the development of breeding groups in New Mexico and could also account for many of the groups observed in Arizona. In Texas, both Griffin (1976) and Brannon (1980) recorded a lower incidence of groups in their study populations (5%, $n = 19$ and 13%, $n = 16$, respectively) than I found in New Mexico (51%, $n = 61$). These observations suggest that some differences in behavior and social system exist among geographical areas; thus, it seems that the Harris' Hawk breeding system is flexible and responds to variations in environmental conditions.

A relatively high proportion of group nests failed during the incubation period (46%) compared with simple pairs (16%). Whether this is related to the decreased hatchability associated with an increased complexity of social structure

(Koenig 1982) is unknown. Most eggs that did not hatch simply disappeared.

The high incidence of nest failure during incubation by groups was compensated by their tendency to double-brood more frequently than pairs. This suggests that supernumerary birds may decrease the stress of nesting on breeders. Positive assistance from helpers has been implicated in improving breeder survivorship in several cooperatively breeding species (Morton and Parry 1974, Stallcup and Woolfenden 1978, Vehrencamp 1978, Woolfenden and Fitzpatrick 1984).

Overall, pairs and groups did not differ in productivity. Moreover, the per-capita reproductive success of groups was far less than that of pairs. Koenig (1981, pers. comm.) suggested that examination of reproductive success on a per-capita basis is a useful preliminary test of whether mutualistic benefits (prediction: groups should have enhanced reproductive success) or ecological constraints (prediction: pairs should have enhanced reproductive success) are driving a specific cooperative-breeding system. According to this reasoning, resource localization may be a more important influence on the maintenance of group living in the Harris' Hawk than possible cooperative benefits such as exploitation of food resources or group defense against predators. Woolfenden and Fitzpatrick (1984), however, pointed out that the importance of such mutualistic benefits could not be clearly ruled out until information on individual lifetime reproductive success and fitness are known.

The pattern of reproductive output I found for Harris' Hawks in New Mexico differs from those reported for most other cooperative breeders (e.g. Brown 1978, Emlen 1978, Koenig 1981, Woolfenden and Fitzpatrick 1984), possibly including the Harris' Hawk in Arizona (Mader 1975b). The absence of a correlation between reproductive success and group size should not occur if the Harris' Hawk system was substantially influenced by kin selection (Brown 1983, Woolfenden and Fitzpatrick 1984). Rather, other factors such as ecological (e.g. resource localization; Koenig and Pitelka 1981) or demographic constraints (e.g. survivorship, availability of mates; Reyer 1980, Emlen 1982a, Faaborg 1986) or cooperation (Ligon 1983) probably account for the social system of this species in New Mexico.

I detected two possible reproductive advantages of groups. First, groups tend to double-brood more frequently than pairs do; second, offspring reared by groups are slightly larger at fledging than those of pairs. Whether greater size at fledging yields any fitness advantages in Harris' Hawks is unknown. Fledging mass of Florida Scrub Jays (*Aphelocoma coerulescens*) was not correlated with survival to 1 yr of age (Woolfenden and Fitzpatrick 1984), which is contrary to the traditional pattern (e.g. Lack 1968). The differences noted above between groups and pairs of Harris' Hawks cannot be attributed to differences in nest attentiveness or to differences in habitat or prey-resource populations between areas occupied by groups and those occupied by pairs (Bednarz 1986). Rather, groups may have some foraging advantage over pairs. For example, Mader (1979) suggested that cooperative hunting by Harris' Hawks may result in increased success in capturing prey.

The previously published information on the breeding system of the Harris' Hawk should be interpreted with caution. Supernumerary Harris' Hawks in southeastern New Mexico are primarily birds that remain in their natal ranges. Most auxiliaries are males that may assist in the rearing of broods after they molt into adult plumage. Groups of Harris' Hawks had no detectable reproductive advantage over pairs, suggesting that kin selection probably was not a causal factor in the evolution of this bird's breeding system.

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ERRATUM

In "Lek organization in Sage Grouse: variations on a territorial theme" by R. M. Gibson and J. W. Bradbury (1987, Auk 104: 77-84), the definition (p. 78) and computed values (p. 81) for Arnold and Wade's (1984) opportunity for selection should read (corrected words/numbers are in boldface): "Skew in male mating success in each season was measured by the ratio of its variance to its mean **squared**" (p. 78); and "skew in male mating success . . . was greater in 1983 (I = **4.239**) than in any of the years 1984-1986 . . . (I = **1.212-1.784**) . . ." (p. 81).