

# BREEDING BEHAVIOR OF A POLYANDROUS TRIO OF HARRIS' HAWKS IN SOUTHERN ARIZONA

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**ABSTRACT.**—Nests of Harris' Hawks (*Parabuteo unicinctus*) in the Sonoran Desert of southern Arizona are commonly attended by three adults. In all four confirmed cases the trios have been composed of two males with a single female. Nesting behavior of one trio was intensively studied in 1977. Both males incubated eggs and brooded young and both provided food for the female and young. Copulations were approximately equally frequent for both males. The primary roles of the female were incubation of eggs and, later, feeding, shading, and brooding of the single chick. All three adults exchanged prey and commonly fed from the same prey item. The female was largest and dominated both males, while the larger male dominated the smaller. Female Harris' Hawks may derive clear benefits from such simultaneous polyandry, but the benefit for males is less apparent. Factors that may have been important in the evolution of frequent polyandry in this species include: (1) variations in habitat quality that force males to choose between already pair-bonded females in good habitat and lone or pair-bonded females in poor habitat, (2) unbalanced adult sex ratio with more males, and/or (3) possibly close kinship of males in trios. These possibilities have not been tested rigorously. Present evidence suggests that trios may have higher nest success than pairs because the extra males assist in nest attendance, food procurement, and nest defense. Also, an extra male insures against total nest failure if one adult should die during the breeding season. *Received 8 November 1977, accepted 23 April 1979.*

POLYANDRY is a rare mating system among vertebrates (Orians 1969, Jenni 1974, Emlen and Oring 1977). In birds it is known primarily in the Charadriiformes, in which it commonly occurs in a sequential manner. Among Falconiformes regular polyandry has been recorded only in the Galapagos Hawk, *Buteo galapagoensis* (see de Vries 1973), and Harris' Hawk, *Parabuteo unicinctus* (see Mader 1975a, b), in which two or more males have been observed copulating with a single female and cooperating with her in the raising of young. Such simultaneous polyandry is much less common than sequential polyandry in birds. Here I present detailed observations of one polyandrous trio of Harris' Hawks that provide some insight into the organization of this mating system.

## METHODS

The trio (two adult males and a color-banded adult female, first identified 8 February 1977) was observed in Pima County, Arizona. The female was banded as a nestling from the second nesting attempt of a pair in June 1975, approximately 5.2 km from the nest described here. Males were sexed by their much smaller size than the female (see Mader 1975a) and by their nearly invariable roles in copulations. Male 1 (M1) was slightly larger than Male 2 (M2), had a completely black breast and head, and had black spots on the white undertail coverts, while M2 had light brown streaks on the breast and head and clear white undertail coverts.

The trio rebuilt an old nest in a pine (*Pinus* sp.) in the front yard of an occupied house. The surrounding area was saguaro-palo verde (*Carnegiea gigantea-Cercidium* sp.) flatland (see Mader 1975a: 59) with a few houses intermittently spaced. The nest was 8.0 m from the ground and 14.2 m from the house. In 1976 the nest successfully fledged at least one chick, but identities of the adults were unknown. On 24 February 1977 the female was in an incubation posture in the nest. No adults were present at the nest on 21 February, so the female presumably started laying eggs shortly before or after the 24th. Three eggs were laid but only one hatched. It was pipped for 1.0 cm on 31 March and probably hatched on 1 April. This time interval (about 36 days) corresponds closely with the reported 35-day incubation period (Mader 1975a).

Observation periods were as follows: pre-incubation, a total of 25.6 h on 10 days between 8 and 21 February; incubation, a total of 9 full days (1, 5, 8, 12, 15, 19, 22, 26, and 29 March), each starting 0.5 h before sunrise and ending 0.5 h after sundown; and nestling, a total of 11 full days (2, 5, 9, 12, 16, 19, 23, 26, 30 April and 3, 7 May), each starting 0.5 h before sunrise and ending 0.5 h after sundown. During the pre-incubation period, observations were made from my car or on foot. On 19 February, a 4.1-m-high tower blind was built 29.3 m south of the nest. Blind observations started on 1 March. Observations after 1 March were made from the blind with the exception of 26 March, when I spent 7.5 h watching the nest from my car (29 m from the nest) because of heavy rains.

The blind was made out of wood and cloth and had a 29 cm-wide one-way mirror placed in front and holes on the side to allow observations from complete concealment. The hawks, especially the female, were very tolerant of humans. Children often played within 50 m of the nest without disturbing the hawks. This allowed me to relax outside of the blind periodically when there was no activity at the nest. During the nestling phase, I sometimes climbed to the nest to determine the size and species of prey brought in, after the female had temporarily left. Visits to the nest from the blind usually took less than 3 min and appeared to cause no significant disruption of adult activities.

I estimated the weight of each prey item by using known weights of comparably size specimens in the University of Arizona Museum. Weights of the desert spiny lizard (*Sceloporus magister*) were determined by equating snout-vent length (Parker and Pianka 1973) to body weight (about 57 g; C. Schwalbe pers. comm.). Data on daily temperatures were gathered from weather station records at the University of Arizona (33 km south of the nest, elevation 20 m less than the nest).

The term "nesting range" (Craighead and Craighead 1956: 247) represents the area and living requirements necessary for a nesting pair or trio. The term "nesting territory" is the area around the nest that is defended.

## RESULTS AND COMMENTS

*Pre-egg-laying phase.*—Prior to egg-laying, the trio of Harris' Hawks generally perched on saguaros and telephone poles near the nest and on occasion moved away as far as 1,200 m. The adults usually stayed within view of one another. Of 7 copulations in which I was able to identify the participating male, M1 copulated with the female 4 times, and M2 3 times. Copulations continued into the incubation period, but with a lower frequency. Of six copulations observed during early incubation only two were by M1. The two copulations seen during the nestling period, when the chick was 37 days old, were by M1. The duration of copulations averaged 13 s for M1 and 18 s for M2. This similarity, coupled with the comparable frequency of copulations by the two males, suggests that the chance of a given male fertilizing a given egg was near 50%.

All copulations observed were on saguaros or telephone poles. Chirp calls or slurred chirp calls (Mader 1975a) were sometimes given by both participants. In two cases, the copulations occurred as the female was holding prey. There was also one aberrant copulation by M2 with M1 while M1 was holding prey; the copulation movements of M2 appeared typical, and M1 only crouched during the copulation. In addition, I saw two instances of backstanding (see Mader 1975a: 74). In one instance M1 stood on the back of the female for 12 s, then immediately copulated for 8 s. In the other instance both M1 and M2 stood on the female's back simultaneously for 4 s. Backstanding was relatively infrequent prior to egg-laying, possibly because of a strong urge for males to copulate at this time.

Both males provided food for the female during the pre-incubation period. M1 was observed passing prey to her three times, and M2 once. Two of the prey exchanges took place at the nest and two about 800 m from the nest. In addition, M2 gave one prey to M1 at the nest, and on 14 February M1 gave an immature Harris' Hawk (not a member of the trio) a prey item 400 m from the nest, on top of a saguaro. This immature bird had just begun to molt secondary feathers and was

sighted continually in the area during the period of observations. Very likely it was an offspring from 1976 of one or more members of the trio. Although immature Harris' Hawks are often dependent on their parents for a period of 2–3 months, the apparent partial dependence of this immature must have continued for at least 8 months.

Both males commonly visited the nest during pre-incubation, and each made nest-shaping movements when the female was at the nest. In these movements the male flattened down into the nest with its head low and tail slightly elevated and moved its shoulders and primaries up and down. Nest-shaping movements by the males were also seen when the female perched near the nest; these movements may have some signal function to the female, as they were not given by males at the nest when the female was not in the vicinity. Both males and the female arranged sticks during their nest visits. When the female was at the nest with one of the males, reciprocal nibbling at one another's bill or cere sometimes occurred. On one occasion both males were at the nest simultaneously: M1 laid down in the nest cup while M2 stood on the rim.

*The incubation phase.*—All adults regularly visited the nest ( $\bar{x}$  = 19.1 visits per day) after the eggs were laid, but each had well-defined duties. Of 172 total visits, 18 (10.5%) were with sticks and 9 (5.2%) with prey. All brought sticks to the nest during the incubation and nestling phases. For 9 days of observation the female averaged 6.4 visits per day, M1 6.4, and M2 6.2. All adults were at the nest simultaneously 12 times.

The female incubated most of the day (Fig. 1). Only the female incubated at night. The hawks relieved one another of incubating an average of 12.5 times per day (range = 5–20). The average duration of the incubation bouts (the period of continuous incubation before the adult was relieved by another or voluntarily left the nest) decreased significantly as ambient temperatures increased ( $r = -0.72$ ,  $df = 7$ ,  $P < 0.05$ ; see Fig. 2). However, the total amount of incubation per day (daylight hours, 30 min before sunrise to 30 min after sunset) by all three birds collectively remained about the same ( $\bar{x}$  = 92.7%, range 81.6–99.5).

The males had three basic roles during incubation: (1) supplement the female's role of incubation, (2) supply food to the female, and (3) chase predators away from the nest area. Whenever M1 was temporarily absent and unable to cover the eggs after the female had left the nest, M2 immediately flew to the nest and incubated. When M1 returned to the nest area, he flew to M2 and relieved him. This allowed maximum coverage of the eggs and reduced the chances of nest failure due to excessive exposure to the weather and predation. Adequate covering of eggs by the adults may be especially important when ambient temperatures are high and the nest has little shade. For 9 days of observation the female incubated an average of 78.4% of the daylight hours per day ( $\bar{x}$  = 52 min per bout, range 1–319), while M1 averaged 12.0% ( $\bar{x}$  = 16 min per bout, range 2–83), and M2 2.3% ( $\bar{x}$  = 5 min per bout, range 1–28). The incubating hawks regularly relieved one another, with the female relieving M1 most often (Table 1). The frequency of visits per day decreased when rain fell and temperatures were low. Consequently, the number of times an incubating adult was relieved by another was significantly less ( $t = 2.7$ ,  $df = 6$ ,  $P < 0.025$ ) on the four coolest days of observation. The increased number of relief bouts on warm days seemed related to high ambient temperatures and not to an increase in prey transfers (presumably from more prey caught) from the males to the female, which would have resulted in more bouts.

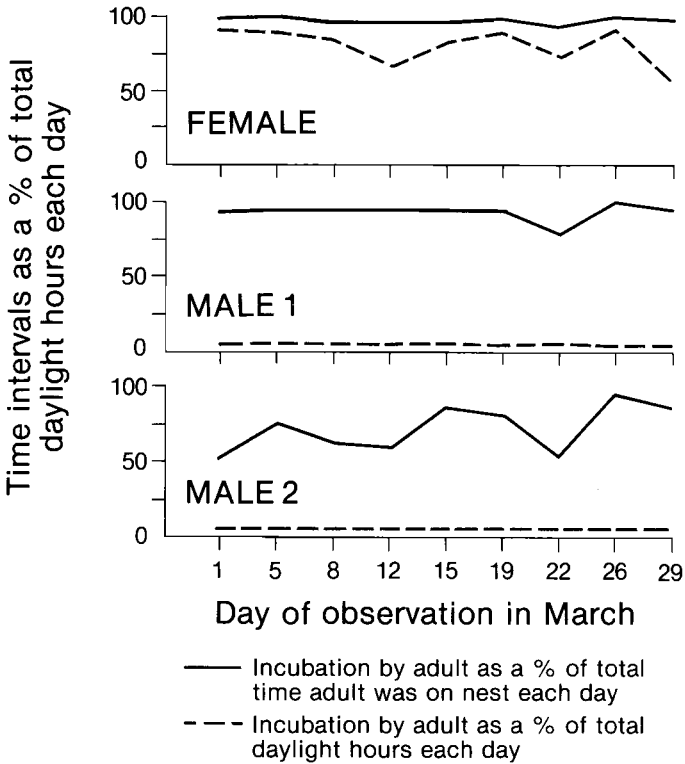


Fig. 1. The time partitioning of incubation duties in a polyandrous trio of Harris' Hawks during 9 days of observation. The total number of daylight hours each day includes the period from 0.5 h before sunup to 0.5 h after sundown. Three eggs were laid on about 24 February, but only one hatched, on 1 April.

The female dominated the males throughout incubation. Incubating males rose and let the female incubate when she arrived at the nest. In one instance, the female nibbled at the cere and bill of M2 until he quit incubating and stood up. The males did not try to displace and push the female from perches. M1 dominated the slightly smaller M2, however. Usually when M1 flew to the nest, and M2 was incubating, M1 nibbled at the cere and bill of M2 until M2 stood up and let M1 incubate. On three occasions, M1 stood on the back of M2 ( $\bar{x} = 3$  s) until M2 surrendered the perch. M1 also displaced M2 from perches ( $n = 13$ ) by extending his legs and feet at M2 as a threat when he approached the perch. Sometimes M1 gave an alarm call. In one instance M1 displaced M2 from a perch by nibbling at his cere and bill until M2 left. Except for once prior to egg laying, M2 did not stand on the back of the female or of M1, nor did he displace either one from perches.

Both males provided food for the female. She received 4 of the 5 prey items brought by M1 and 5 of the 7 brought by M2. The female did not catch any prey and received an average of 80 g of prey biomass per day from an average of 0.89 prey items per day from the males (Table 2). On 3 days she received no prey from the males and did not consume any food.

The three adults commonly exchanged prey with one another. When an item is

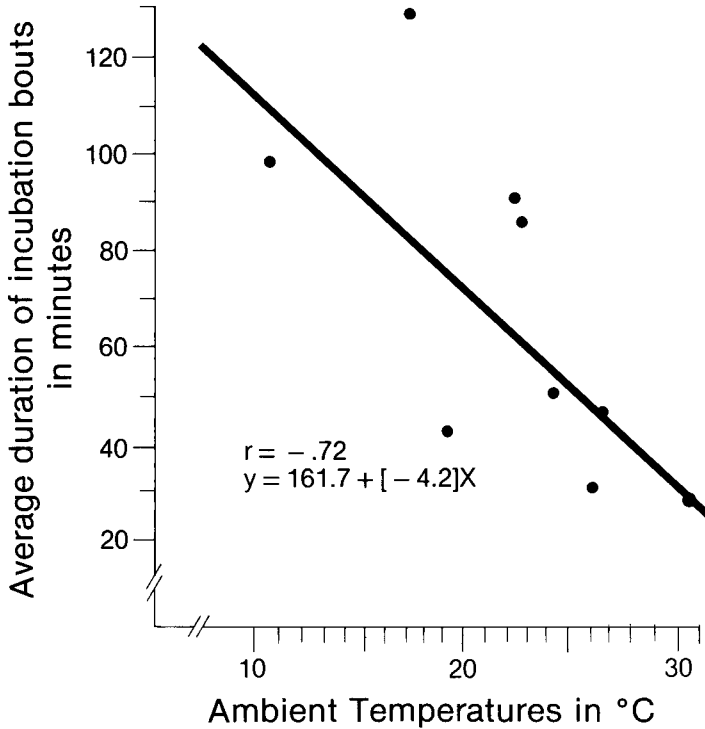


Fig. 2. The average duration of the female Harris' Hawk incubation bouts as a function of the highest recorded ambient temperature for 9 days of observation.

transferred directly from one hawk to another I term it a direct exchange. In indirect exchanges (including caching, in which prey is stored), a prey item is left at a perch or the nest and later picked up by another hawk. (Prey exchanges in Mader 1975a, Table 13 are direct.) During incubation I witnessed 11 (78.6%) direct and 3 (21.4%) indirect prey exchanges (Table 3); 6 (42.9%) occurred at the nest (all direct). Three (23.1%) of the total 13 prey items observed brought to the nest or surrounding area were received and partially consumed by all three adults (one was the result of indirect exchange). This estimate may be higher than the actual percentage, because the males might have consumed some unobserved prey items away from the nest.

*The nestling phase.*—All adults continued visiting the nest regularly ( $\bar{x} = 18.1$  visits per day) after the chick hatched, but nest roles were divided. Of 199 total visits to the nest, 20 (10.1%) were with sticks, and 47 (23.6%) with prey. For 11 days of observation the female averaged 10.5 visits per day, M1 3.6, and M2 3.9 per day. The averages for each adult were significantly different from their respective averages during incubation (female,  $t = 3.24$ ,  $df = 18$ ; M1,  $t = 2.82$ ,  $df = 18$ ; M2,  $t = 2.34$ ,  $df = 18$ ;  $P < 0.05$  for all). Average visits per day increased for the female during the nestling phase, while those of the males decreased. All three adults were at the nest at the same time on 20 occasions.

The female brooded, shaded, and fed the chick (Fig. 3). Her percent brooding per day increased when ambient temperatures were low (see days 9–19 in Fig. 3). The female shaded the chick five times ( $\bar{x} = 45$  min, range 2–120) when it was hot

TABLE 1. Number of times an incubating Harris' Hawk was relieved by another at nest<sup>a</sup>.

Date of observation	M1 relieved M2	M2 relieved M1	F relieved M1	F relieved M2	M2 relieved F	M1 relieved F	Number per day
March 1	1	0	3	0	1	0	5
5	5	2	3	0	3	0	13
8	5	0	5	0	3	1	14
12	3	0	4	0	4	1	12
15	5	1	8	0	3	3	20
19	5	1	5	1	6	1	19
22	3	0	4	0	3	2	12
26	1	0	3	0	1	2	7
29	3	2	2	1	2	1	11
Totals <sup>b</sup>	31 (27.4)	6 (5.3)	37 (32.7)	2 (1.8)	26 (23.0)	11 (9.7)	113

<sup>a</sup> Relieved means that the arriving hawk exchanged places with the incubating hawk. F represents Female; M1, Male 1 and M2, Male 2.

<sup>b</sup> Percentages of overall total in parentheses.

and the nest was in the sunlight. Although Harris' Hawk chicks are probably somewhat tolerant of high ambient temperatures, brooding and shading by the adults may still be necessary in preventing excessive dehydration and possible chick mortality. When the female did not care for the chick, she perched, preened, stretched, or fed herself at the nest or on nearby perches within 150 m of the nest.

M1 and M2 supplied all the prey to the nest and brooded the chick but did not feed or shade the chick. After the chick was 2 days old the amount of time spent at the nest by each male sharply decreased (Fig. 3). M1 brooded only on the first observation day, when the chick was 2 days old (1.4% of the daylight hours), while M2 brooded on the first (8.8%) and second days (0.1%, chick was 5 days old) of observation. In contrast to the incubation phase, M2 spent much more time (2.4% of daylight hours) on the nest than did M1 (0.8%). M1 still remained dominant over M2 and displaced M2 from 10 perches. On two occasions M1 landed next to M2 and then pushed it off the perch. Pushing was less aggressive than displacement, although both resulted in loss of the perch by the originally perched hawk. The female still dominated both males. She pushed both M1 and M2 off two perches.

Brooding adults were relieved by another adult only on the first day of observation. M1 relieved the female and M2 once, M2 relieved the female 4 times, and the female relieved M1 2 times and M2 3 times. Once when the female was brooding, M2 tore apart a prey item and fed the female 5 pieces of meat. Similarly, when M1 was brooding, the female tore apart a prey item and fed M1 nine pieces.

The female did not catch any prey and received all her food from the males. During the nestling phase, M1 caught 11 prey items and M2 27. M1 brought 5 (13.9%) prey items to the nest itself, M2 26 (72.2%), and the female 5 (13.9%). Direct prey exchanges during the nestling phase ( $n = 37$ ) occurred most frequently from M2 to the female, and to a lesser degree from M1 to the female and M2 to M1;

TABLE 2. Prey biomass received by female from males per day during incubation.

	Day of observation (in March)									Average per day
	1	5	8	12	15	19	22	26	29	
Biomass (g)	173	102	159	0	175	0	82	27	0	80
Number of prey items	1	1	2	0	2	0	1	1	0	0.89

TABLE 3. Prey exchanges between three adult Harris' Hawks at a nest and nearby vicinity during the incubation and nestling phases.

	Male 1 to female	Male 2 to female	Female to Male 1	Male 2 to Male 1	Male 1 to Male 2	Female to Male 2	Totals
<b>Direct exchanges<sup>a</sup></b>							
Number of exchanges	14	20	3	10	1	0	48
Exchanges at nest	7	16	0	6	0	0	29
Exchanges on saguaros	0	0	0	1	0	0	1
Exchanges on telephone poles	0	0	1	0	0	0	1
Exchanges in air	0	0	0	1	0	0	1
Exchange site unknown	7	4	2	2	1	0	16
<b>Indirect exchanges<sup>a</sup></b>							
Number of exchanges	1	4	2	2	3	2	14
Exchanges at nest	1	4	1	1	0	1	8
Exchanges on saguaros	0	0	1	0	0	0	1
Exchange site unknown	0	0	0	1	3	1	5

<sup>a</sup> A direct exchange is one in which a prey item is transferred directly from one hawk to the next. An indirect exchange is one in which a prey item is left at a perch or the nest and then picked up later by another hawk.

11 indirect prey exchanges were witnessed in which both adults were identified (Table 3) and 9 in which only the receiving adult was. All the exchanges took place within 150 m of the nest. Of 58 identified prey items (11 from incubation and 47 from nestling phase) observed brought to the nest or surrounding area, 77.6% were mammals, 13.8% were birds, and 8.6% were reptiles (Table 4). Six (12.8%) of the 47 prey items during the nestling phase were partially consumed by all three adults (four were the result of indirect prey exchanges). Again, this percentage is probably biased slightly high, because the males may have consumed some prey items before they came within view of the blind. Prey brought to the nest, including items left at the nest the previous night, averaged 4.1 items, or 418 g per day (Table 5).

Balgooyen (1976) suggested that food caching in Kestrels (*Falco sparverius*) allowed them to help insure a constant supply of energy during conditions of inclement weather, low food availability, and high production requirements. Indirect, direct, and "group" prey exchanges, when more than two adults consume prey, probably have the same function in Harris' Hawks.

Overall, the interactions between members of the trio seemed harmonious. This is in contrast to the tense interactions between pair members that have been described for other strongly dimorphic raptors (Snyder and Wiley 1976). The harmony and smooth execution of nest duties during incubation, brooding, and prey exchanges appeared to be, at least in part, a result of the dominant-subordinate relationship of the adults.

*Nest defense.*—I observed eight instances of nest defense against potential predators. In three cases, M1 and M2 uttered alarm calls at domestic cats, and then one or both dived at them until they left the nest area. M1 and M2 chased away a White-necked Raven (*Corvus cryptoleucus*) and a Cooper's Hawk (*Accipiter cooperii*) that came within 300 m of the nest. In the latter case M2 flew towards the hawk first, and then M1 quit incubating and left the nest to give chase. M1 and M2 also chased, dived at, and hit a Red-tailed Hawk (*Buteo jamaicensis*) that was about 1,200 m from the nest. Usually when M1 and M2 chased away intruders, the female was incubating eggs or brooding. Once when both males were absent the female quit incubating, gave alarm calls, and then chased a domestic cat away from the

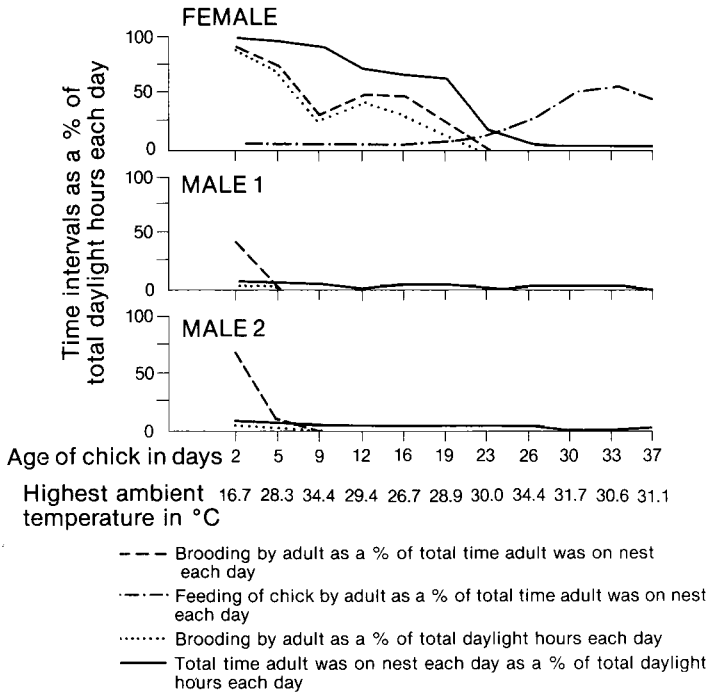


Fig. 3. The time partitioning of nest duties that the adults of a polyandrous trio of Harris' Hawks performed in the care of a chick at a nest during 11 days of observation. The total number of daylight hours each day includes the period from 0.5 h before sunup to 0.5 h after sundown.

nest area. Similarly, during the nestling phase the female left the nest at the approach of an unknown animal (probably a cat) and then dived at it a few minutes later when no males were present. It was clear that the absence of the males forced the female to expose the eggs or chick while she drove the predators from the nest area.

DISCUSSION

*Nest helping.*—Previously I suggested that nest helping (the helper could be male or female) among Harris' Hawks in Arizona might be common (Mader 1975a,b). My observations at three such nests indicated that the extra hawk served as a helper by either feeding the chicks and/or supplying prey at the nest. Nest helping may be an adaptation that increases nesting success due to better nest attentiveness and prey procurement in a desert environment where food resources are scattered and subject to seasonal or yearly fluctuations. Indeed, trios appeared to have greater reproductive success. I offered three hypotheses that attempted to explain why trios might be more successful than pairs. Below I discuss these hypotheses in light of new evidence and some possible selective pressures for the evolution of simultaneous polyandry.

*Hypothesis 1:* An extra adult could increase prey supplies at a nest, thereby insuring greater fledgling success in low prey years. Related to this I also suggested that group hunting by two or three adults might provide even more food by disproportionately increasing the success rates of capture attempts. Both males frequently



TABLE 4. Prey items observed brought to a Harris' Hawk nest and nest vicinity during the incubation and nestling phases.

	Number individuals	Percent individuals	Percent biomass
<b>MAMMALS</b>			
Cottontail rabbit, <i>Sylvilagus audubonii</i>	8	13.8	42.6
Round-tailed ground squirrel, <i>Spermophilus tereticaudus</i>	10	17.2	14.6
Harris ground squirrel, <i>Ammospermophilus harrisi</i>	11	19.0	13.9
Wood rat, <i>Neotoma albigula</i>	7	12.1	13.7
Unidentified rodents	9	15.5	5.5
Total mammals	45	77.6	90.3
<b>BIRDS</b>			
Gambel's Quail, <i>Lophortyx gambelii</i>	1	1.7	1.9
Curve-billed Thrasher, <i>Toxostoma curvirostre</i>	1	1.7	0.7
Roadrunner, <i>Geococcyx californianus</i>	1	1.7	2.6
Unidentified birds	5	8.7	2.2
Total birds	8	13.8	7.4
<b>REPTILES</b>			
Desert spiny lizard, <i>Sceloporus magister</i>	2	3.4	1.3
Unidentified lizards	3	5.2	1.0
Total reptiles	5	8.6	2.3
Total number of prey items	58	100.0	100.0

hunted and caught prey, and there was no evidence to indicate that any of the adults or the chick might have been stressed by lack of food, except during incubation. The incubating female did not receive food during 3 of the 9 days of observation and received an average of 80 g per day. On these 3 days her percent incubation for the day was low and may have been influenced by a lack of food and a greater urge to leave the nest. Four of the five prey-capture attempts by the female were on days when she received either no prey or very little.

Cooperative hunting and prey exchanges between the adults help to ensure an adequate food supply not only for the chicks but also for the adults. Cooperative hunting does not seem to increase prey captures (Mader 1975a: 80), but probably still provides more food for each adult than if each hunted singly. This is because the hawk that misses the prey commonly receives it later from the hawk that caught

TABLE 5. Prey biomass brought to a Harris' Hawk nest per day.

Age of chick (days)	Number of prey items left at nest the night before	Number of prey items brought to nest	Total items	Biomass (g)
2	0	3	3	270
5	1	2	3	418
9	0	3	3	236
12	1	3	4	394
16	1	4	5	547
19	1	4	5	658
23	1	3	4	635
26	0	2	2	257
30	0	3	3	341
33	0	6	6	339
37	3	4	7	499
Totals (%)	8 (17.8)	37 (82.2)	45	4,594
Average per day	0.73	3.36	4.1	417.6

it, when the prey is large enough to be eaten by more than one hawk. During incubation 23.1% of the prey items observed brought to the nest or the surrounding area were received and partially consumed by all three adults; for the nestling phase it was 12.8%. I have observed three-way prey exchanges in two other trios. It thus seems reasonable that a trio usually could supply more food than a pair, thereby insuring greater fledgling success in low prey years. Strong evidence that nest helpers increase reproductive success exists for the Superb Blue Wren, *Malurus cyaneus* (Rowley 1965), and the Florida Scurb Jay, *Aphelocoma c. coerulescens* (Woolfenden 1975).

*Hypothesis 2:* A third hunting adult would leave more time for the primary nest-attending hawk to "guard" the nest from predators. This seemed true for a trio I studied earlier (see Mader 1975a), in which the female primarily guarded the nest. In those birds reported herein, it was the role of the two males to chase predators away and the female's role to incubate the eggs and to feed, brood, and shade the chick. When the males were away hunting, the female twice defended the nest. Also, when M1 was temporarily absent and unable to cover the eggs during incubation after the female had left the nest, M2 covered them, thus presumably decreasing predation risk. De Vries (1973) noted that polyandrous trios of Galapagos Hawks were usually more successful in defending nest territories than were pairs. Taken together, these facts indicate that an extra adult provides for better nest attentiveness and defense but that this function does not rest always with only one particular adult.

*Hypothesis 3:* If one adult perished, the other two could shift their nest duties and avoid loss of the brood. In 1973 and 1974 I studied the same trio from a blind for 164 and 87 h, respectively. In 1974 I placed my blind too close to the nest (12 m), and although the nest successfully fledged three young, the female became so shy that she would not feed the chicks when I was in the blind. Consequently, M1 shifted his nest duties from feeding the chicks only 30.1% of the time (at the 1973 nest) to 100% in 1974 (10 feeding bouts for a total of 86 min); the difference is highly significant (corr.  $\chi^2 = 6.77$ ,  $df = 1$ ,  $P < 0.01$ ). Although M1 did not shade the chicks in 1973, he took over the shading duties of the chicks in 1974 (10 shading bouts for a total of 323 min). At the 1977 trio, the female and both males incubated and brooded. If one male had perished, the other could likely have readjusted his nest duties to avoid loss of the brood. On the other hand, if the female had died during incubation, the clutch might have been lost. If the female had disappeared during the nestling phase, it is possible that the chick would have survived by having one male feed it while the other became the primary food provider. M2 once fed the brooding female and probably would have been capable of feeding the chick. Therefore, depending on which sex perishes, the sex ratio within the trio, and when the adult dies in the breeding cycle, individual nest duties can sometimes be shifted and loss of the brood avoided.

*Simultaneous polyandry.*—Simultaneous polyandry in Harris' Hawks in Arizona appears to be common. I have documented four cases. Factors that may have been important in the evolution of frequent polyandry in this species are: (1) variations in habitat quality that force males to choose between already pair-bonded females in good habitat and lone or pair-bonded females in poor habitat, (2) an unbalanced adult sex ratio with more males, and (3) possibly close kinship of males in trios. For clarity, I have assumed that these factors are not interrelated, even though the final explanation may not be so simple.

In relation to the first factor, Harris' Hawks in Arizona appear to be restricted mostly to breeding in saguaro-palo verde desert in which food resources, though occasionally at moderate densities, are often temporally and spatially unpredictable (Mader 1975a, b, 1978). Poor food conditions may be common for most polyandrous species (Graul et al. 1977). Some parts of the Arizona desert are more arid than others. For example, complex habitat with saguaros, palo verdes, or ironwoods is less arid and probably has a greater prey base than peripheral areas dominated by creosotebush (*Larrea divaricata*) (see Tomoff 1974); Harris' Hawks are least common in the latter. Thus it may be more productive for a male to mate with an already pair-bonded female in the "best" desert available, rather than with a lone or pair-bonded female in very arid habitat where the chances of successful reproduction are less. This gains support in that most of the trios I saw were in relatively productive (complex) habitat.

Presumably, an initially monogamous male accepts a second male and his copulations with the female because the first has the most to gain in inclusive fitness. Indeed, this is true if the first male fertilizes most of the eggs. It may still be advantageous for the second male to remain, however, if his initial loss of fitness is compensated for by an increase in fecundity later, if the first male dies. But if the males father an equal number of chicks, any gains are reduced on a per-nest-attempt basis. This means that for every chick fertilized and cared for by M1 he will in turn "waste" care on a chick fertilized by M2. Under this strategy, one advantage to cooperating, breeding males may be better survival as members of trios versus pairs. There might be three reasons for this: (1) enhanced food sharing, (2) less stress on them in the breeding process, and (3) less predation. The latter is probably of least importance, as Harris' Hawks have so few predators.

Males seem to do slightly better in pairs on a per male basis in the population (1.2 young per male per nesting attempt) than in trios (1.0 young per male per nesting attempt), as far as success to fledging is concerned (Mader 1975b). However, my observation of an at least partially dependent 8-month-old immature receiving food from a male in a trio suggests that a major advantage of trio breeding could be that it allows more broods and offspring per unit time and longer parental care for juveniles after fledging. At another trio, I saw a male give prey to a crippled immature that was 4 months old and from a first brood when there were chicks in a nearby nest from the second brood (Mader 1975a: 78). This trio was also extremely productive over a 3-yr period, producing 14 fledglings (2.33 young per male per yr) (Mader 1977).

The foregoing suggests that polyandry may be linked to differences in habitat quality and that a male that chooses to breed cooperatively in superior habitat does so because he stands a better chance of increasing his fitness by: (1) increased fecundity after the first male has died, (2) better survival, and (3) greater net production of offspring to breeding age.

In support of the second factor, of 42 adult Harris' Hawks trapped in winter, 31 were males (Mader 1975a). This gives a ratio of 2.8 males per female and is in sharp contrast to a nestling sex ratio of 1.1 males per female ( $n = 107$ ). Although there is the chance that sexes differ in trap susceptibility, these data suggest that female mortality exceeds that of males in Arizona. Yom-Tov and Ollason (1976) postulated that sexual dimorphism and intrasexual competition over food might result in differential mortality and an uneven sex ratio in old age groups. Harris' Hawks are strongly dimorphic. The mean dimorphism index as based on wing,

culmen, and weight is 12.1 (Storer 1966, Snyder and Wiley 1976). Thus, the uneven sex ratio may be a local occurrence due to difficult prey conditions and problems of capture for females in a desert, although why this should be so remains unclear. Hamerstrom and Hamerstrom (1978) found a nearly even sex ratio of 1.2 males per female for 397 adult Harris' Hawks trapped in the mesquite grasslands of Texas. Polyandry also seems less frequent in Texas (Griffin 1976). Polyandry in Arizona, then, might be the result of a greater survival rate in males.

On the other hand, the secondary sex ratio may actually be even but the operational sex ratio (defined as the average ratio of fertilizable females to sexually active males at a given time, see Emlen and Oring 1977) uneven. Emlen and Oring concluded that the operational sex ratio in many polyandrous species is probably skewed (females fewer than males). A skewed ratio would increase the likelihood of simultaneous pair bonds to the same female. It also means, however, that some female Harris' Hawks will be unable to breed if pair bonds last through the breeding season. Some pair bonds in Harris' Hawks do last through the breeding season and others last up to 3 years (Mader 1977). Thus, if the operational sex ratio is uneven and selects for polyandry, the initial loss of fitness by nonbreeding females must, on the average, be compensated for by an increase in fecundity later.

Related to the third factor, Hamilton (1964) theorized that selection for altruistic traits in the genetic evolution of social behaviors should occur among close relatives. This seems to be accurate for some cooperative breeding jays, if not other species (Brown 1978). Simultaneous polyandry is prevalent in the Tasmanian Native Hen (*Tribonyx mortierii*) (Maynard Smith and Ridpath 1972) and in many respects resembles that in the Harris' Hawk. In both species the polyandrous group forms a cooperative breeding unit in which each member of the trio shares in copulation, nest construction, incubation, care of the young, and defense of the nest. Smith and Ridpath thought kin selection was operating because trios often consisted of two brothers with an unrelated female. It remains to be seen if a similar situation exists in the Harris' Hawk.

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