

EFFECT OF VOLES ON MATING SYSTEMS IN A CENTRAL WISCONSIN POPULATION OF HARRIERS

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Polygyny has been reported among harriers (*Circus cyaneus*), and the circumstances under which it occurs have been the subject of some speculation. Before Balfour and Cadbury (1975) there were so few accounts of this phenomenon that it was deemed aberrant.

In North America, Reindahl (1941) found five harrier nests within a radius of half a mile. A male that defended two of these nests was believed to have mated with both females. Yocum (1944) reported two nests 400 yards apart in an 80-acre tract in Washington, both vigorously defended by one male. In Manitoba, Hecht (1951) observed unmarked birds at 11 nests, and clearly demonstrated that one male was a bigamist. Hamerstrom (1969) reported polygyny among color-marked harriers in Wisconsin.

In Britain, polygyny in Hen Harriers (*Circus c. cyaneus*) was first recognized in Orkney by J. Douglas in 1931 (Watson 1977), and seems to appear more frequently there following population increases (Balfour and Cadbury 1975, 1979). Polygyny has also been reported in Kincardineshire, Scotland (N. Picozzi, pers. comm. in Balfour and Cadbury 1975) and the Netherlands (van der Kraan and van Strien 1969). It has been suggested that polygyny in harriers may be the result of an unbalanced sex ratio in breeding adults both at Delta, Manitoba (Hecht 1951), and in Orkney (Balfour and Cadbury 1975, 1979).

In this paper we discuss mating systems of *C. c. hudsonius* in Wisconsin and show that polygyny is not aberrant but occurs regularly, and further that it is tied to vole (*Microtus pennsylvanicus*) abundance.

STUDY AREA

The study area is in and on the edges of the Buena Vista Marsh, in Portage County, and the northern part of the Leola Marsh in Adams County, Wisconsin. It encompasses 51,830 acres (20,732 ha), subdivided into two parts, the core area and the periphery (Fig. 1). The core area consists of the best nesting habitat, and all but three nests found since the study began in 1959 have been within it. The core area totals 41,718 acres (16,687 ha) and corresponds to the figure of "approximately 40,000 acres" that has been used in earlier papers and theses (e.g., Hamerstrom 1969). The peripheral zone of 10,112 acres (4045 ha) is less clearly defined and is used by harriers mainly for hunting.

Farming is common on both the sandy interior islands and edges and on the muck and peat of the two drained marshes. The lowest areas tend to become sedge (*Carex* spp.) and

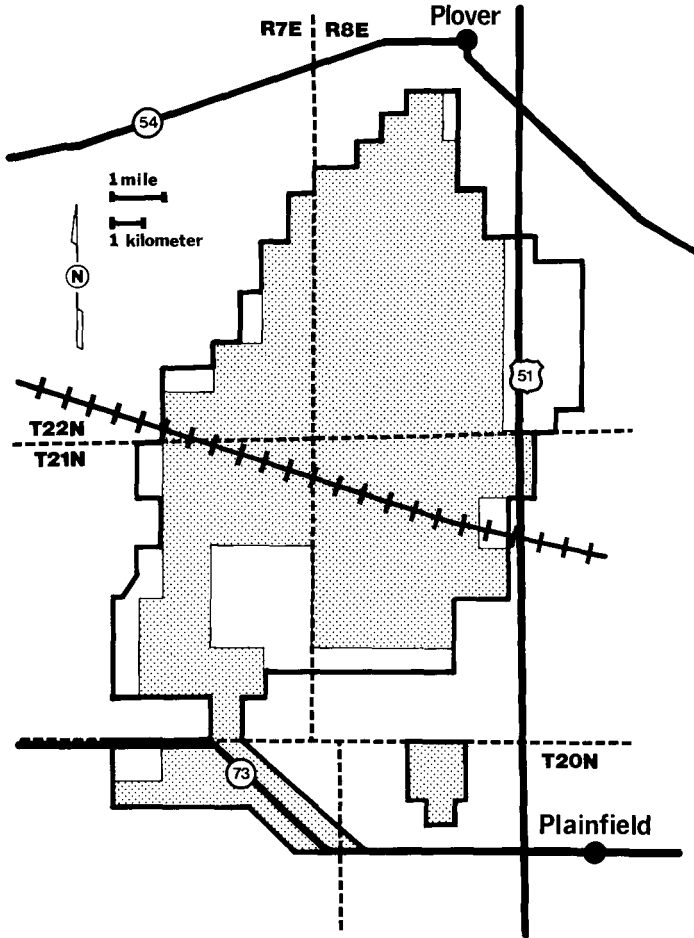


FIG. 1. The study area. The "core area" is stippled; the rest, inside the heavy boundary line, is the "peripheral area." The railroad crossing the area is now abandoned.

willow (*Salix* spp.) swales. For a more detailed description, see Hamerstrom and Hamerstrom (1973).

Approximately 11,377 acres (4551 ha) are managed as grasslands for the Greater Prairie Chicken (*Tympanuchus cupido pinnatus*), with important repercussions for the harrier (Hamerstrom 1974).

METHODS

The study began in 1959, when only part of the area was searched for nests. Full coverage began in 1960 and continued through 1983. Data for 1959 are usable for *totals*—e.g.,

numbers of nests and young—as in Tables 1–3, but are excluded from comparisons among years, e.g., Table 4 and all figures.

Banding, with U.S. Fish and Wildlife Service bands, and color marking have been critical elements in the study, both for keeping track of individuals in the field and in the analysis of data.

Trapping techniques.—In spring, before harriers were on breeding territories, we used bal-chattris baited with European Starlings (*Sturnus vulgaris*) (Berger and Hamerstrom 1962). Breeding adults were caught in a dho-gaza over a stuffed or live tame Great Horned Owl (*Bubo virginianus*) (Hamerstrom 1963).

We devised a new method of trapping breeding adults that were poor reactors to the dho-gaza set. A “nest dome” was placed over the young in the nest. The nest dome is flattened quonset-shaped, measures 63 × 18 cm at the base and 27 cm high, and is made of 1 in. welded wire with about 200, 40-lb test monofilament nooses, 5 cm in diameter, tied to its top. In essence, the nest dome acts as a bal-chattri with the nestling harriers as bait.

Banding and color marking.—Breeding adults were aged, sexed, weighed, measured, banded, and color marked. Colored feathers impied into the wings enabled us to recognize individuals with the unaided eye at distances up to 0.4 km (Hamerstrom 1969). After 1961, all breeders were also given colored jesses, which enabled individual recognition in later years without retrapping. The jesses were made of brightly colored strong plastic, and were attached around the tarsi with rivets.

In all, 231 breeding harriers were banded, 220 of which were also color marked. An additional 70 incoming or passage birds were banded in spring and not retrapped as breeders; 57 of these were impied but none was jessed. Six hundred forty-seven nestlings were sexed, measured, aged, and banded but not color marked.

Nest finding.—Harriers were watched with spotting scopes and binoculars. Methods of nest finding are described in Hamerstrom (1969). After the first few years, because we feared that harriers would desert if nests were disturbed during incubation, we normally made our first nest visits after the eggs had hatched. As a result, some nests that failed before hatching may have been missed. Except in 1959, all successful nests (i.e., nests in which at least one young fledged) were found, either before the young had fledged or, in some cases, after fledging when the young are conspicuous and remain in the close vicinity of their nests for several weeks (Hamerstrom 1969). Including the latter, 330 nests have been found. By our definition, a nest had to contain an egg or evidence that an egg had been present. We made five exceptions to this rule, one in 1962 and four in 1969; all were parts of polygynist menages. In each case, the behavior of the female led experienced observers to be confident that nests actually were present.

Marked individuals enabled identification of monogamous and polygynous birds. Polygynous males were those that fed or defended nests with two or more females.

Sixteen of 27 bigamous males were color marked; 11 bigamist males could not be trapped but were identified by plumage. Of 54 females involved in bigamy, 35 were color marked; 19 could not be trapped but were seen accepting food transfers from or having their nests defended by known bigamist males.

Of eight trigamous males, seven were color marked. One could not be trapped but was seen feeding three (two color marked and one unmarked) females within one hour. Fifteen of 24 females involved in trigamy were color marked; nine were not, but were seen accepting food from or having their nests defended by a known trigamist male.

Potential breeders, nonbreeders, sex ratio.—A determined effort was made to find nonbreeders. At least two trained observers covered the marshes from early June, after the incoming migrants had settled in, until early July when a small influx of harriers from other areas is to be expected. Each observer tallied or mapped his sight records independently,

after which a consensus was reached as to total numbers of potential breeders—the summer population—and sex ratio. Agreement was generally within two or three birds. These tallies were aided by marked birds, some impeded in spring, and some color jessed in earlier years. The actual breeders and the nonbreeders were sorted out as the summer progressed.

Vole index.—An index to vole abundance has been conducted since 1960 (Hamerstrom 1979). From 1960 through 1967 D. Q. Thompson (pers. comm.) provided an index to regional vole abundance based on stems cut by voles in Wisconsin and neighboring states; in 1964 we began a local index based on break-back trapping, using peanut butter as bait, on the study area. An objective of 1080 (1200 after 1972) trap nights per breeding season has been met or exceeded each year except 1969 (745 trap nights). The curve shown in Figs. 2 and 3 is derived from the number of voles caught each year, divided by the number of trap nights, multiplied by 1000. (This is the actual formula used in Hamerstrom 1979:371, rather than the formula given there; the 1979 graph itself is correct.)

RESULTS AND DISCUSSION

Most harriers were monogamous, but polygyny played a consistent role. To understand fully the mating systems of the central Wisconsin harrier population, however, one must go beyond vital statistics and look at the relationship between harrier nesting and vole abundance.

Number of nests and nesting success.—We do not know exactly when the first vole cyclic period (ca 1960–1964) began, and it is less clearly defined in that we used a regional, rather than the later local, vole index (Figs. 2 and 3). There seem to have been three moderate peaks of vole abundance during this first period, at least one of which, 1963, we believe to be well documented (see Hamerstrom 1979). The still incomplete last period shows a plateau in 1981–1983 rather than a rise to a high.

The years 1960–1978 have been detailed in Hamerstrom (1979). We now add another peak and plateau in numbers of both voles and harrier nests (Figs. 2 and 3). Except for the aberrant low number of nests in 1966, which we attribute to DDT, the correlation between the numbers of voles and harrier nests is at once obvious. In a way, the two plateaus in nesting at intermediate vole numbers (1977, 1978, 1981–1983) are even more convincing than the highs and lows: the two periods of intermediate vole abundance are faithfully mirrored by numbers of harrier nests.

Two hundred fifty-two of 330 nests (76%) were of monogamous pairs (Table 1). Monogamy was thus the more common situation and the only one to occur every year (Fig. 3). Monogamous nests were more successful (76%) than polygynous nests (64%), and they fledged the greatest number of young in total (588 of 726) and per female (2.3); successful monogamous females averaged 3.1 young (Table 1).

There were 27 instances of bigamy and eight of trigamy during 15 of the 25 years. Trigamy occurred without bigamy only in 1970. Bigamous matings occurred in 14 years and fledged 100 young; trigamous matings

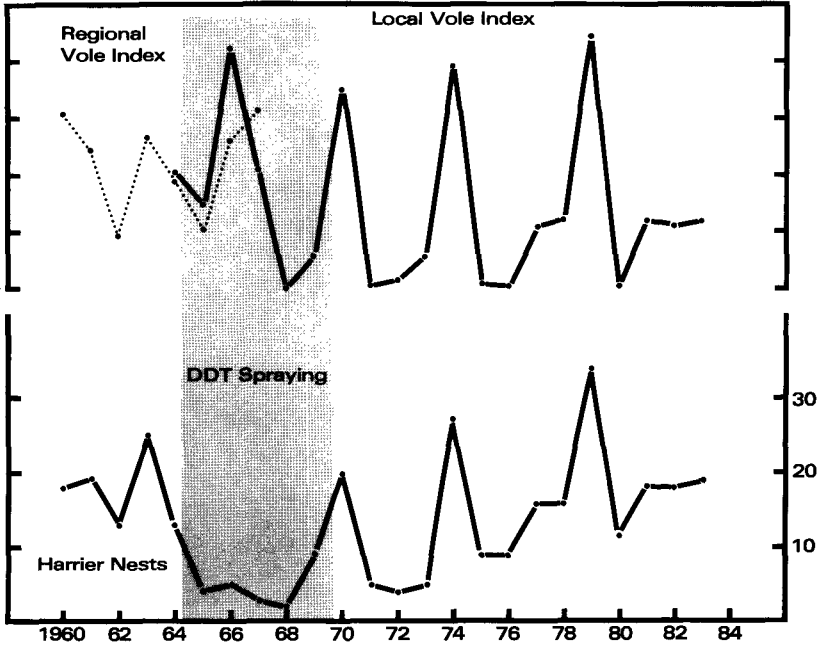


FIG. 2. Harrier nests in relation to vole abundance, 1960–1983.

during six years fledged 38 young. Bigamous females were less successful than trigamists (61% vs 71%) in terms of nests that fledged at least one young, but averaged higher productivity per female (1.9 vs 1.6 young); the number of nests, however, is small (Table 1).

Alan Beske (pers. comm.) kept track of a radioed male trigamist that mated with three females, all of whose nests were found, and that also copulated with a fourth female. No nesting resulted in this last instance, and we have not included the fourth female in our calculations.

Number of potential breeders. — Except for two years, there were always more potential breeders than actual nesters. In 1974 and 1979, both years with many nests, the estimated number of potential breeders equalled the number of actual breeders. Of the two years, 1979 was the year with the highest-ever number of polygynous nests, 21, as against two in 1974. Both 1979 and 1974 were high vole years (Fig. 3). In short, neither the annual number of nests nor the extent of polygyny seems to have been caused by a shortage of potential partners.

Sex ratio. — The sex ratio of the population might be expected to influence breeding behavior, and the occurrence of monogamy and polygyny.

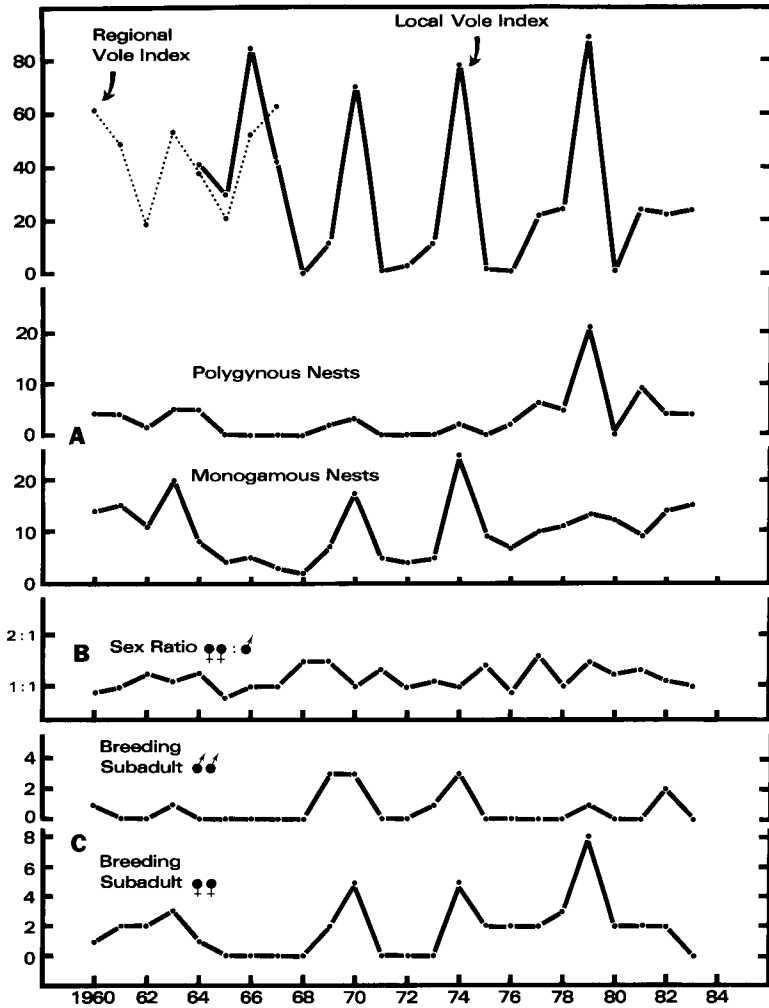


FIG. 3. Harrier vital statistics shown in relation to vole abundance: A. incidence of polygyny and monogamy; B. sex ratio; C. nesting by subadults.

In harriers the two sexes do not appear to contribute equally to the nesting effort. The female lays and incubates the eggs; the male brings most of the female's food during incubation and shortly after the eggs hatch, then both bring food to the nestlings; but only the female tears it into pieces small enough for helpless young to swallow. Some males desert before the young are fully fledged. There are many instances of abandoned females successfully fledging young, but we have only one example of a

TABLE 1
 HARRIER BREEDING PERFORMANCE IN RELATION TO MATING SYSTEM, 1959-1983

	Monogamy	Bigamy	Trigamy	Total
Number (%) of all nests	252 (76)	54 (16)	24 (7)	330
Percent of nests successful ^a	76	61	71	73
Number of successful nests:				
Per female	0.8	0.6	0.7	0.7
Per male	0.8	1.2	2.1	0.8
Percent of males successful	76	85	100	77
Number (%) of young fledged	588 (81)	100 (14)	38 (5)	726
Mean \pm SD per female ^b	2.3 \pm 1.6	1.9 \pm 1.7	1.6 \pm 1.5	2.2 \pm 1.7
Mean \pm SD per successful female	3.1 \pm 1.1	3.0 \pm 1.0	2.2 \pm 1.3	3.0 \pm 1.1
Mean \pm SD per male	2.3 \pm 1.6	3.7 \pm 2.4 ^c	4.8 \pm 1.7 ^d	2.5 \pm 1.8
Mean \pm SD per successful male	3.1 \pm 1.1	4.4 \pm 2.0	4.8 \pm 1.7	3.3 \pm 1.3

^a Successful nests fledged at least one young. In addition to young seen on the wing, birds banded shortly before fledging time were presumed to have fledged.

^b Number fledged per nest ranged from one to five in all mating systems. Five young were fledged by 8% of monogamous pairs, but by only 2% of bigamous nestings and 4% of trigamous nestings.

^c Range 1-8.

^d Range 2-7.

TABLE 2
BREEDING PERFORMANCE OF MONOGAMISTS, AGE OF BOTH PARTNERS KNOWN, 1959–1983^a

Age of females	Subadult males	Adult males	Total
Subadults^b			
Number of nests	4	22	26
Percent of nests successful	100	82	85
Number of young fledged	11	56	67
Mean ± SD per female	2.8 ± 1.3	2.6 ± 1.7	2.6 ± 1.6
Mean ± SD per successful female	2.8 ± 1.3	3.1 ± 1.2	3.0 ± 1.2
Adults			
Number of nests	8	123	131
Percent of nests successful	62	78	77
Number of young fledged	13	320	333
Mean ± SD per female	1.6 ± 1.4	2.6 ± 1.7	2.5 ± 1.7
Mean ± SD per successful female	2.6 ± 0.6	3.3 ± 1.0	3.3 ± 1.0

^a Ninety-five nests, involving 40 males and 75 females for which the age of only one partner is known, are omitted (including four subadult males and four subadult females).

^b Subadults are birds that hatched the year before. Adults are birds that hatched at least two years before.

male fledging young after disappearance of the female; those young were old enough to tear food for themselves when left motherless.

Over the 24-year period 1960–1983, the ratio of females to males among the potential breeders was 1.1:1, with a range of 0.8–1.6:1 (Fig. 3). The year-to-year variation shows no relationship to vole numbers (Fig. 3).

Polygyny occurred in eight years when there was an excess of females among potential breeders. The highest incidence was in 1979, when the ratio of females to males was 1.5:1; however, only three of those eight years were conspicuously above an even sex ratio, and four above-even years showed no polygyny (DDT years are excluded). There were seven years when the sex ratio was 1:1 or lower, but in which polygyny nevertheless occurred. Clearly, polygyny was not caused by an excess of females.

Age of breeding birds.—The role of subadults (birds hatched the year before) in breeding populations of harriers has only recently come to light (Hamerstrom 1969, Balfour and Cadbury 1979). During 24 years of study in Wisconsin, 60 subadults bred, 16 males and 44 females. To distinguish between adult and subadult females during the breeding season, one must determine eye color (i.e., either catch the bird, or get close enough to it to see eye color) (Hamerstrom 1968). Because we were not always able to do this, some females were not aged. However, of those females that were recognizably subadults, we know of none that was not breeding. It is thus quite possible that most Wisconsin females breed at one year.

TABLE 3
BREEDING PERFORMANCE OF POLYGYNISTS, AGE OF ALL PARTNERS KNOWN, 1959–1983^a

	Bigamy		Trigamy	
	Subadult females	Adult females	Subadult females	Adult females
Number of nests	10	25	4	13
Percent of nests successful	60	76	50	92
Number of young fledged	16	61	3	27
Mean ± SD per female	1.6 ± 1.6	2.4 ± 1.7	0.8 ± 0.8	2.1 ± 1.2
Mean ± SD per successful female	2.7 ± 1.0	3.2 ± 1.1	1.5 ± 0.5	2.3 ± 1.1
Mean ± SD per male	— ^b	4.5 ± 2.4	— ^c	5.5 ± 0.7
Mean ± SD per successful male	—	5.1 ± 1.8	—	5.5 ± 0.7

^a Fifteen bigamous and seven trigamous nests, accounting for 16 and eight young, respectively, have been excluded because the females were not aged. Four bigamous nests (seven young) have been excluded because their two males were not aged. All males in the table were adults.

^b No polygynous males were known to have had only subadult mates. Five adult males with one subadult and one adult female each averaged fewer young (4.3 ± 2.6 per successful male) than the eight with two adult mates (5.1 ± 1.8 per successful male).

^c For only two males (both adults) could all three females (all adults) be aged. Failed nests gave fewer chances to determine the female's age, biasing the results toward apparent failure. All harems with females of unknown age are therefore omitted; three of them did include subadult females.

It is difficult to assess the importance of age in relation to nesting and nesting success, for the members of a monogamous pair or polygynous menage were often not of the same age. In a few cases, the age of all partners was known. Among 157 such monogamous pairs there were 4 pairs of breeding subadults all of which were successful (Table 2). There is an indication that productivity increased with age, especially among monogamous males. Subadult females fledged fewer young when mated with trigamist males than with bigamists (Table 3) and those mated with bigamists fledged fewer young than those mated with monogamists (Table 2). Productivity of polygynous males varied erratically in our small samples, but averaged highest for both bigamist and trigamist males when they were mated with adult females.

Individual nesting success, whether or not the age of the partner(s) was known, for 44 subadult females was slightly lower than that for 171 adults (75% and 78%, respectively); the number fledged per successful nest was similarly close (2.8 and 3.1, respectively). In short, we find few substantial age-related differences among females in nesting success or fledging rates. This was not so with the males. Despite the almost even sex ratio, fewer males than females bred in their first year (16 vs 44). None were polygynists. Subadult males nested in only 9 of the 24 years, as opposed to 16 of 24 years for subadult females (Fig. 3). They did, however, show a high rate of nesting success, 88%.

Effect of voles on population structure.—In order to deal with our best data on “normal behavior,” we here omit all but 1963 of the first cyclic period and the aberrant DDT years, 1965–1968. We include 1969 because the harrier population was then beginning to recover. During this period of best data, vole abundance powerfully affected the occurrence of polygyny (Fig. 3). Polygyny occurred at all four vole highs—averaging 7.8 nests per high—and during each of the five years of intermediate vole abundance with an average of 5.6 nests. During the seven low years, however, polygyny occurred only twice, with only two nests each time. Monogamous nesting generally increased even more sharply at the vole highs but there was a curious exception in 1979, when monogamous nests rose only to 13 as compared to their highest number, 25, while polygynous nests numbered 21, far above their next highest, 9.

Nesting success during the 16 years under discussion was highest during vole highs but not strongly so, averaging 78% during the four vole highs, 71% during the five intermediate years, and 75% during the seven low years. The number of young fledged per successful nest was essentially the same during vole highs (3.0 ± 1.1), in intermediate years (2.8 ± 1.1), and at vole lows (3.1 ± 1.1); the average for these 16 years and for the entire study was 3.0 ± 1.1 . Total annual production of young followed the vole index very closely.

Table 4 records our data for these 16 “best” years to show the performance of known-age females in relation to both vole numbers and type of mating system. The samples are so small that the data are no more than suggestive, but it is the largest body of such data at present available and should be useful as a starting point for later studies. The relative scarcity of polygynous females, and especially subadults, at vole lows, is apparent. For monogamous females nest success was essentially the same at lows and highs, with some increase during intermediate years. Polygynous adults showed increasing nesting success from lows to highs (67% during lows, 79% during intermediate years, 100% during highs); however, the average number of young fledged per successful female was highest during the lows (3.5 ± 0.7). Among adult females, average production of successful monogamists and polygynists differed by no more than 0.3 young (Table 4).

In short, high vole numbers led to (1) first and foremost, a marked increase in the total number of harriers nesting in a given year; (2) an increase in the number of subadults nesting; and (3) an increase in polygyny. These effects were far more pronounced than changes in nesting success or the number of young fledged.

The polygyny threshold model.—Polygyny was an advantage to participating males: more young were fledged per male and the chance of being

TABLE 4
NESTING OF KNOWN-AGE FEMALES, AGE OF PARTNER NOT ALWAYS KNOWN, IN RELATION TO VOLE ABUNDANCE^a

	Low years		Intermediate years		High years	
	Subadults	Adults	Subadults	Adults	Subadults	Adults
Number of nests						
Monogamous	7	19	4	39	12	40
Polygynous	1	3	5	14	8	12
Percent of nests successful						
Monogamous	86	79	75	87	92	80
Polygynous	100	67	40	79	63	100
Number of young fledged						
Monogamous	19	50	7	98	35	104
Polygynous	3	7	5	28	11	36
Mean ± SD fledged						
Per female						
Monogamous	2.7 ± 1.7	2.6 ± 1.6	1.8 ± 1.5	2.5 ± 1.4	2.7 ± 1.3	2.6 ± 1.7
Polygynous	3.0 ± 0.0	2.3 ± 2.1	1.0 ± 1.4	2.0 ± 1.5	1.4 ± 1.5	3.0 ± 1.3
Per successful female						
Monogamous	3.2 ± 1.3	3.3 ± 0.9	2.3 ± 1.2	2.9 ± 1.0	2.9 ± 1.1	3.3 ± 1.1
Polygynous	3.0 ± 0.0	3.5 ± 0.7	2.5 ± 0.7	2.6 ± 1.1	2.2 ± 1.3	3.0 ± 1.3

^a The vole index is a measure of vole abundance: an index of less than 15 is a low year, 15–45 an intermediate year, more than 45 a high year. See Figs. 2 and 3. The table summarizes the 16 years of "best" data: see text for details.

a successful breeder increased numerically (Table 1). For individual females, however, the chance of successful breeding decreased, as did the number of young fledged. Balfour and Cadbury (1979) found that male Hen Harriers in Orkney mated to 3–4 females brought off more young than monogamous males.

Both Hecht (1951) and Dent (1939) were able to identify females in polygynous groups that were favored by their males and were apparently dominant over the other females. Newton (1979) has discussed such “alpha females” in detail. We have occasionally recognized favoritism in polygynous groups, but have been unable to detect a stable female hierarchy. The logistics of our field work has kept us from learning the order in which females settled in a polygynous male’s territory. In most cases polygyny has been simultaneous, rather than serial, for most of the nesting period.

Oring (1982) has summarized the considerable amount of research in recent years on polygyny, most of it on passerines. He adduces three kinds of polygyny: (1) resource-defense polygyny, in which males defend resources critical to female reproductive success, such as food and cover; (2) direct defense of grouped females; and (3) male-dominance polygyny, based on competition, which allows females to choose on the basis of male quality (not otherwise defined). We cannot place harrier polygyny within this scheme because we have so seldom seen any evidence of territorial defense, defense of mate, or male-male tests of dominance through fighting or even a show of aggression. In fact, territoriality in the harrier has not been well defined, and its influence on breeding behavior is obscure. Harriers defend their nests (or nest area) against other species (including man), but defense against conspecifics has been less well documented. We have found few specifically described instances of it (Errington 1930, Watson 1977:125–126, Craig *et al.* 1982) and have seen no clear evidence ourselves. By inference, a mechanism for conspecific territoriality probably exists, but it must be remarkably subtle. For the present, we speak of territory as the area near the nest defended against intruders.

Darwin (1871) suggested that the choice of mate is made by the female. Under what conditions does a female choose a male that is already mated? Assuming that the best habitat has already been usurped, she may do better with an already mated male on superior habitat than with a monogamous male on inferior habitat, where her chance of success may be lower (Orians 1969); “monogamy with a pauper vs. polygyny with a tycoon” (Mock 1983). This difference in quality of habitats is a key factor, and is described as the “polygyny threshold” (Verner and Willson 1966, Garson *et al.* 1981). Furthermore, polygyny is expected to evolve only

when this difference in quality of habitats regularly presents itself (Orians 1969).

Once a female harrier is incubating, the male usually does essentially all the hunting. During incubation, females rarely leave the nest except for food transfers and brief periods of preening and flying. When voles are scarce, a male with one incubating female may be able to transfer food to her only two or three times a day (K. L. Bildstein, pers. comm.). But during high vole years males are able to present food more frequently—or to more females.

In 1979, during a vole high, we sometimes saw polygynous males circling above their nests calling to the females in what appeared to be attempts to draw them off the nest to accept food. But the incubating females, presumably sated, did not leave their nests. After failing to call the female off, the males usually flew to nearby perches. There they tore at the food, sometimes eating it, called to the female, or made short flights around the nest area. It is likely that unmated females may recognize such behavior as an index of the high quality of the male's territory.

In fact, 18 times (23%) successful females in polygyny fledged more young than the average number fledged by successful monogamous females for a given year, although monogamous females were generally more productive. This suggests that those harem females had indeed selected superior males or superior habitat.

There is need for a closer study of polygyny in harriers, but our data suggest that harriers fit the polygyny threshold model, with voles as the key factor. This would seem to be Oring's (1982) resource defense type of polygyny, but the mechanism of defense is not clear.

SUMMARY

This 25-year study on a 51,830 acre (20,732 ha) area in central Wisconsin is based on 231 banded breeding harriers (*Circus cyaneus hudsonius*), 330 nests, and 726 fledged young of which 647 were banded. Harriers were most commonly monogamous but polygyny (including both bigamy and trigamy) accounted for 24% of the nests and 19% of young fledged. Polygynous males sired more young than monogamous males. The reverse was true of harem females. The number of harrier nests closely mirrored the course of the vole (*Microtus pennsylvanicus*) population cycle, except during a period (1965–1968) of heavy aerial spraying of DDT. Vole abundance, not an excess of females or shortage of breeders, also triggered increased polygyny. Subadult females commonly bred and were involved in polygyny when voles were abundant. Subadult males bred less commonly than subadult females, and were never polygynists; they, too, bred more often during periods of vole abundance but to a lesser degree than subadult females. The data fit the polygyny threshold model with vole abundance a key factor. In short, the abundance of the prey—voles—governed not only the abundance of the predator, but also its mating systems.

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