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The influence of microtines on polygyny, productivity, age, and provisioning of breeding Northern Harriers: a 5-year study

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Breeding Northern Harriers, *Circus cyaneus*, and their principle prey, the vole *Microtus pennsylvanicus*, underwent synchronous fluctuations in New Brunswick between 1980 and 1984. Microtines were abundant in 1980 and 1983 and were significantly tracked by the number of nesting harriers ($r = 0.90$), the number of polygynous males ($r = 0.89$), the number of harem females ($r = 0.90$), and the mean clutch size ($r = 0.94$), but not the reproductive success of successful females ($r = 0.72$). Male nest defence likewise exhibited a strong relationship ($r = 0.99$, $n = 3$) with prey abundance, but nest predation did not. An unexpected association with prey abundance was the greater proportion of young females (≤ 2 years) breeding at vole lows; the reverse was true for yearling males. Young females that did breed at vole highs were significantly more productive than were old females breeding at highs. The difference arose principally through nest predation. Successful females also consistently reared significantly greater proportions of their hatchlings when voles were increasing than when they were decreasing. Our results suggest that New Brunswick harriers were affected by prey fluctuations in most aspects of their reproduction and population dynamics. Significant correlations between male food provisioning rates and clutch size and reproductive success over 3 years provide a proximate mechanism through which fecundity may vary annually. They may also provide a proximate pathway mediating for polygyny.

SIMMONS, R., P. BARNARD, B. MACWHIRTER et G. L. HANSEN. 1986. The influence of microtines on polygyny, productivity, age, and provisioning of breeding Northern Harriers: a 5-year study. Can. J. Zool. **64**: 2447–2456.

Les Busards des marais, *Circus cyaneus*, en période de reproduction et leurs proies principales, les campagnols *Microtus pennsylvanicus*, ont subi des fluctuations synchronisées de densité entre 1980 et 1984 au Nouveau-Brunswick. Les microtinés ont été abondants en 1980 et 1983 et leur nombre était en corrélation significative avec le nombre de busards en période de nidification ($r = 0,90$), le nombre de mâles polygynes ($r = 0,89$), le nombre de femelles dans le harem ($r = 0,90$), le nombre moyen d'oeufs par couvée ($r = 0,94$), mais pas avec le succès de la reproduction chez les femelles reproductrices ($r = 0,72$). De même, la défense du nid par les mâles était fortement reliée à l'abondance des proies ($r = 0,99$, $n = 3$), mais la prédation au nid ne l'était pas. Une relation assez étonnante a été constatée entre le nombre de jeunes femelles (<2 ans) et l'abondance des proies: la proportion de ces jeunes femelles était plus élevée lorsque la densité des campagnols était faible; la relation était cependant inversée dans le cas des mâles de 1 an. Les jeunes femelles qui se reproduisaient lorsque la densité des campagnols était élevée étaient significativement plus productives que les femelles âgées qui se reproduisaient dans les mêmes conditions, surtout à cause de la prédation exercée sur les nids. Les femelles reproductrices réussissaient toujours à élever une plus grande proportion de leur couvée lorsque la population de campagnols augmentait que lorsqu'elle diminuait. Nos résultats indiquent que les fluctuations dans la population de proies affectent la plupart des paramètres reliés à la reproduction et à la dynamique des populations des busards du Nouveau-Brunswick. Les corrélations significatives entre les taux d'approvisionnement de nourriture par les mâles, et le nombre d'oisillons par couvée et le succès de la reproduction évalué sur une période de 3 ans sont probablement une cause immédiate de variation annuelle de la fécondité. Ces corrélations peuvent être aussi directement responsables de la polygynie.

[Traduit par la revue]

Introduction

Avian predators specializing on single prey types make ideal subjects for studies of food-influenced reproduction. The nature of prey specializations dictates that when prey are scarce, breeding should be adversely affected. The most commonly cited avian–mammal examples are voles (*Microtus* spp.) and lemmings (*Lemmus* spp.) and their influence on the breeding of nocturnal and diurnal raptors (Falconiformes) (Pitelka et al. 1955; Hagen 1969; Galushin 1974). Effects range from changes in the size of the breeding population (Cavé 1968; Hagen 1969; Hamerstrom 1979; Village 1981) and clutches (Barth 1964; Hagen 1969; Wijnandts 1984) to changes in the nomadism of individuals (Lockie 1955; Galushin 1974; Mendelsohn 1983). In the most extreme interactions, plagues of rats (*Rattus villosissimus*) spark explosions of breeding in the Letter-winged

Kite (*Elanus scriptus*), large colonies form, birds breed at very young ages, and some females initiate second broods before their first broods are out of the nest (D. J. Baker-Gabb, in correspondence).

Despite the expanding literature on raptors and their effects on cyclic prey (Erlinge et al. 1983, 1984), there are few data on behavioural responses to increased prey abundance (Cavé 1968; Mendelsohn 1983), fewer on the effects of the phase of the prey cycle on individuals (Hagen 1969) and age structure, and no data on changes in mating system with changing prey abundance. In this paper we report on each of these aspects, including clutch size, fledging success, mating system, behaviour, and age structure, for a prey specialist, the Northern Harrier (*Circus cyaneus*). We also focus on proximate causes of changing harrier fecundity, in particular male food provisioning rates. These were studied for 3 of 5 years and our findings are related both to clutch sizes and to fledging success (the number of young reared to first flight).

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Study area and methods

We studied an average of 24 harrier nests per year from 1980 to 1984 on a 60-km² portion of the reclaimed Tantramar Marsh of New Brunswick (45°53′ N, 64°20′ W). This freshwater marsh has been partially drained for 300 years and lies on the shores of the Bay of Fundy. Marsh habitat and harrier nest sites are detailed in Simmons and Smith (1985). From 1980 to 1982, every nest in the study area was located and its initiation date, clutch size, fledging success, and harem position were noted (Simmons et al. 1986b). In 1983 and 1984, 46 nests were known, but 9 remained unstudied; these 9 are excluded from most further analyses. Also, any nests deserted shortly after our first visit or (in early years) when repeated visits had been made were removed from productivity analysis.

Female age

Two age-classes, "young" (1–2 years) and "old" (3+ years) were assigned to the majority of females on the basis of iris colour (Hamerstrom 1968; Picozzi 1981). All females were repeatedly assessed while they defended their nests. Three females were also caught and eye colour was assessed in the hand; two others were returns, banded as nestlings on the study area, and 11 females were observed from hides 3–6 m from their nests. Two females not aged by these criteria were classed as young because of light, unstreaked breasts and monosyllabic alarm calls, which were characteristics of other aged, young females. Each year between 54 and 92% of breeding females were of known age. Since this consitutes 75 of 103 females (73%), we feel they are representative of the entire population.

Male food provisioning

Provisioning rates were determined between 1980 and 1982 by direct observations, before and after hatch (562 h), for nine males per year. Detailed biomass data collected in 1983 and 1984 are to be presented elsewhere (R. B. MacWhirter and G. L. Hansen, in preparation). Provisioning rates are thought to be a good measure of biomass rates because within years we could discern no differences in the size of items delivered by different males. Nests were observed from ≥250 m, depending on the tolerance of the pair, for 3–50 h. In 1980 and 1981 pre- and post-hatch rates were combined to give a "seasonal" provisioning rate. The fewer nests in 1982 allowed more intensive observations and rates before and after hatch were independently correlated with clutch size and fledging success. The lumping of 1980 and 1981 data to give "seasonal" rates made no difference to our conclusions.

Male nest defence scores

Nest defence by males (see Simmons 1983a for a slightly different assessment for females) was scored according to male aggression during our nest visits. Employing only nests visited more than twice, we recorded the proportion of our visits on which males approached within 30 m, alarm calling or diving. Separating alarm calling and diving, proportions were scored as follows: 0%, 0 points; 1–9%, 1 point; 10–19%, 2 points ... 90–99%, 10 points; 100%, 11 points. Summing both categories gave maximum scores of 22 points for males calling (11 points) and diving (11 points) at us on every visit.

Because males whose nests fail before hatch automatically incur lower defence scores than successful males (Simmons et al. 1986a), we used only hatched nests for an analysis of defence in relation to prey abundance. This is a conservative analysis of nest defence, since natural predators placed near the nest elicit intense aggression from harriers (R. Simmons, in preparation).

Small mammal trapping

All small mammals identified as harrier prey on the Tantramar Marsh were sampled annually by line snap trapping in up to seven different habitats per year. Museum Specials® baited with a peanut butter – oat paste were set in May, June, July, and (or) August (Fig. 1), with one trap per station for three to five nights. Traps, placed every 10 m, were sensitive enough to sample the smallest shrews (5 g) and the largest voles (67 g). Abundance of small mammals, based on an average 1940 trap nights per year, are expressed as mammals caught per 100 trap
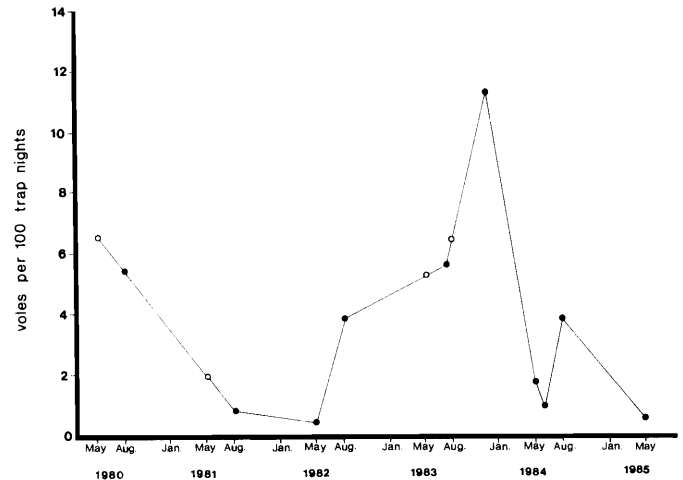

FIG. 1. Vole abundance measured over 5 years on the Tantramar Marsh of New Brunswick. Interpolations (○) between known indices (●) are given for some May values. The November 1983 peak and the May 1982 low were sampled by J. Watkins (unpublished data) and K. J. Turner (unpublished data). The May 1985 value (M. Saunders, unpublished data) indicates a continuing decline into 1985.

nights. Tantramar harriers were vole specialists as judged by dietary frequency and biomass (Barnard 1984; MacWhirter 1985). As an index of the dependence of harriers on alternative mammalian prey, we compared correlation coefficients based on Microtus alone and all small mammals (Table 2). In 3 of 5 years we did not trap in May and interpolated instead between known values closest to the May value. We justify the use of these interpolations by noting that (i) voles cycled uniformly and allowed correct predictions of the following years' vole and harrier populations (Simmons 1982, 1983b); (ii) we always trapped close to the peak (August) in each year; and (iii) vole populations do not invariably increase from May to August, particularly when they are in a declining phase (see Hagen 1969, Fig. 29). Therefore, downward interpolations are likely real, not artificial. Also, correlations computed without the most controversial of our interpolations (May 1980) lost significance in only one of five major correlations (eggs), while the coefficient (0.77) remained strong. Our results are presented both graphically and correlatively to satisfy our critics.

Results

Breeding

Nesting density

Within the 60-km² study area we located 119 nests in 5 years, the highest annual mean density (4 nests/10 km²) recorded in North America. There was a threefold increase in density from 12 nests in 1982 to 37 nests the following year. This variation paralleled indices of the Microtus population over 5 years (Table 1); the number of nests was significantly correlated ($p < 0.03$) with microtine abundance in May, the courtship and egg laying period (Fig. 2). The correlation with all small mammals was marginally poorer but remained significant (Table 2).

Timing of breeding

Males generally arrived on the study area in late March, followed shortly thereafter by females. Breeding began in early May in most years, depending partly on Microtus abundance (Table 3, Fig. 3). The unusual 1983 pattern probably arose from very late snowfall shortly after the first birds had laid (MacWhirter 1985). Despite these strong trends ($r = -0.56$ for mean laying date and $r = -0.70$ for the first egg), vole abundance did not significantly influence initiation dates.

Clutch size

Variations in clutch size are undocumented in North Amer-

TABLE 1. *Microtus* indices in May and August in relation to annual breeding parameters of Northern Harriers in New Brunswick, 1980–1984

|	*Microtus* index[a]			Polygynous		Young fledged by:	
Year	May	August	Nests[b]	Males	Females	all females[c]	successful females
1980	6.6	5.6	30	4	11	2.59 (27)[d]	3.33 (21)[d]
1981	1.9	1.1	22	1	2	1.75 (16)	2.80 (10)
1982	0.5[e]	3.9	12	2	4	2.00 (12)	2.67 (9)
1983	5.5	6.6	37	4	13	2.54 (26)	3.88 (17)
1984	1.8	4.2	18	2	4	1.38 (13)	2.57 (7)
Totals	—	—	119	13	34	2.19 (94)	3.22 (64)

[a]Number of voles caught per 100 trap nights.
[b]Includes all nest and renests in which at least one egg was laid.
[c]Excludes nests adversely affected by research activity.
[d]Sample sizes are given in parentheses.
[e]Data of K. J. Turner (unpublished).
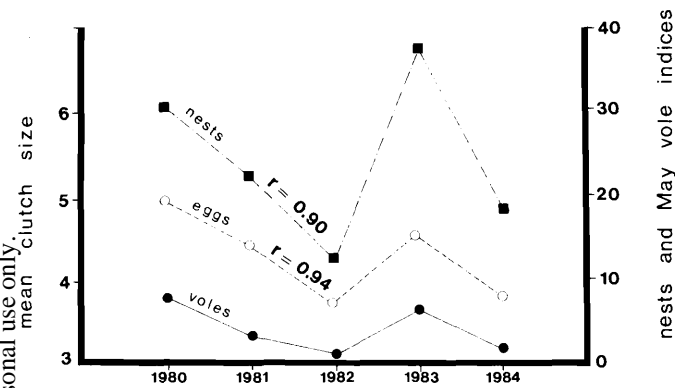
FIG. 2. Relationship between May vole abundance over 5 years and the number of nests and the mean clutch size for New Brunswick harriers. Both variables are significantly related to vole abundance.

TABLE 2. Comparison of correlation achieved with vole indices and all small mammal indices for harrier breeding, polygyny, and age-related statistics, 1980–1984

	Correlation with:		
	voles	all small mammals	Month
Nests	0.90*	0.89*	May
Clutch size	0.89*	0.97*	May
Polygynous males	0.89*	0.75ns	May
Harem females	0.90*	0.78ns	May
Productivity			
All females	0.68ns	0.34ns	Aug.
Successful females	0.72ns	0.43ns	Aug.
Breeding yearlings			
Males	0.87*	0.76ns	May
Young females	0.66ns	0.66ns	May

NOTE: *, significant at the 5% level, one-tailed test. ns, not significant.

ica, possibly because of the impression that Northern Harriers desert their clutches if visited during incubation (Hamerstrom 1969, 1979). Neither we nor Picozzi (1978, 1984) encountered this problem, although *C. cyaneus* may desert during early egg laying (Simmons 1984).

Mean clutch size was strongly and significantly correlated

TABLE 3. The influence of vole abundance on laying dates of New Brunswick harriers, 1980–1984

Year	May vole index	First egg	Mean laying date	Modal laying date (n)
1980	6.6	7 May	19 May	9 May (7)
1983	5.5	1 May	24 May	24 May (4)
1981	1.9	5 May	19 May	18 May (3)
1984	1.8	14 May	23 May	14 May (3)
1982	0.5	17 May	3 June	28 May (2)

NOTE: Years are ordered by decreasing vole abundance.

with May vole and all small mammal indices ($p < 0.01$: Table 2, Fig. 2). When voles were scarce, modal clutch size fell from four and five to three eggs, while mean clutch size was also about one egg lower (Table 4).

Reproductive success

Female fecundity was determined at four levels to judge the factors limiting success in the population: (*i*) the mean fledging success of *all* females, (*ii*) the mean fledging success of *successful* females, (*iii*) the proportion of females raising at least one young each year, and (*iv*) the proportion of hatchlings lost before fledging (a guide to starvation). Males could not be assessed in a similar fashion because of complications imposed by polygyny. We expected a priori that *Microtus* indices in August would be more closely related with fledging success, since the majority of harriers had large nestlings or still dependent young at that time.

Neither the success of *all* nor *successful* females was significantly related (Fig. 4) to vole (or all small mammal) abundance. Recent analyses of seasonality in prey selection (P. Barnard, B. MacWhirter, R. Simmons, G. L. Hansen, and P. C. Smith, in preparation) provide a clue to this anomaly (see Discussion). The third measure of success was used by Hamerstrom (1979) in Wisconsin to show that a greater proportion of harriers reared at least one young in high than in low vole years. This was not so in New Brunswick (Fig. 5).

The final measure of success realized some very strong associations with the phase of the prey cycle. Regardless of absolute abundance, females fledged significantly different proportions of their hatched young. Almost twice as many young perished in decreasing years as in increasing years (35% in 1980, 1981, 1984, vs. 19% in 1982, 1983; Table 5). These
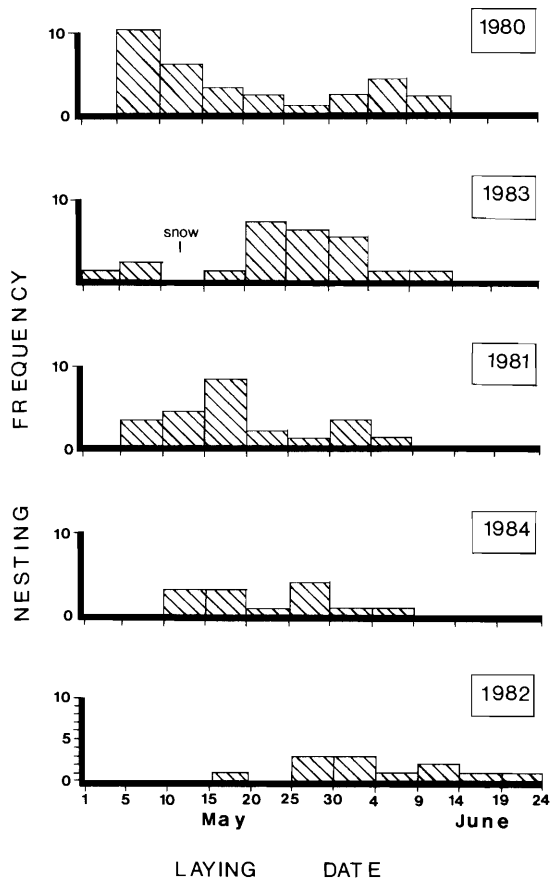
FIG. 3. Nesting frequency of Northern Harriers plotted in 5-day intervals arranged in decreasing order of May vole abundance. Note both the fewer nests and skew to the right in food-poor years. First eggs were found from May 1 to June 20.
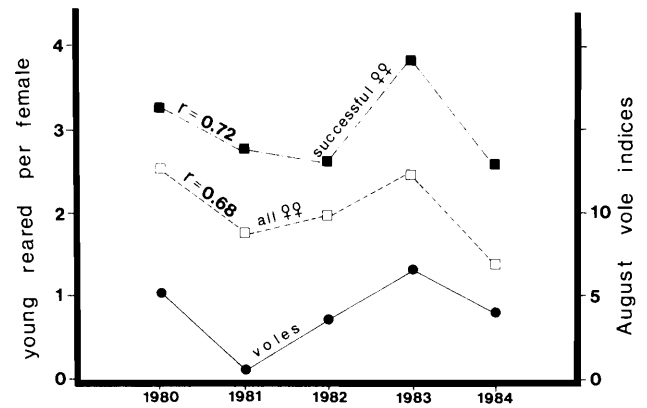
FIG. 4. Relationship between August vole abundance over 5 years and the average fledging success of all and successful female harriers. The success of successful and all females is not significantly related to vole abundance.
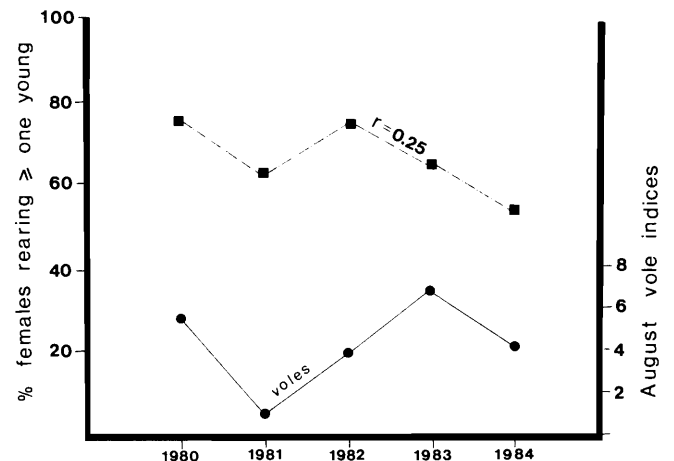
FIG. 5. Relationship between August vole abundance over 5 years and the proportion of female harriers fledging at least one young. No significant association occurs.

TABLE 4. Full clutch sizes over 5 years in New Brunswick

Year	May vole indices	No. of clutches of size:								Clutch size ($\bar{x} \pm 1$ SD)
		1	2	3	4	5	6	7	8	
1980	6.6	0	0	0	7	**9**	2	0	1	4.89±0.9
1983	5.5	1	2	2	8	**9**	4	0	1	4.44±1.4
1981	1.9	0	1	1	**5**	4	1	0	0	4.25±1.0
1984	1.8	0	1	**4**	3	1	1	0	0	3.70±1.3
1982	0.5	0	2	**4**	3	3	0	0	0	3.58±1.1
Totals	—	1	6	11	26	26	8	0	2	4.3±1.6

NOTE: Clutch size modes are given in bold face type and years are ordered by decreasing abundance of voles in May.

TABLE 5. Hatched young surviving to day 30 in relation to the phase of the vole cycle

	Cycle decrease	Cycle increase
No. of young surviving	93	88
No. of young perishing	51 (35%)	21 (19%)
	$\chi^2 = 7.92, p < 0.005$	

trends are not apparent in comparisons of high and low years, which may explain why they are only anecdotally documented (Hagen 1969).

Variations and causes of nest failure

All forms of nest failure were categorized (Table 1) to determine whether total nest failure was related to prey abundance. Annual nest failure varied between 25 and 46%, a nonsignificant difference ($\chi^2_4 = 2.98$, $p > 0.1$). Suspected predation varied more than failure from other causes (Table 6). Again, this variation was neither significant between years ($\chi^2_4 = 2.98$, $p > 0.1$) nor did it vary significantly with vole abundance ($r = -0.73$, $p > 0.1$). The negative correlation suggests that predation was normally low when voles were

abundant, in contrast to some studies (Lockie 1955; Pitelka et al. 1955) but consistent with findings in Wisconsin (Hamerstrom 1979).

Nests were assumed to have been abandoned naturally if feathered remains of chicks, unbroken skeletons, or eggs were present in the nest. Three of four nests found in 1980 and 1983 in this state belonged to late-settling polygynous females and probably arose from inadequate male food provisioning (Simmons et al. 1986b). Alternative reasons for nest abandonment were apparent in 1984. Many nestlings starved that year (MacWhirter 1985) and five females deserted their nests during prolonged rain. Inadequate provisioning again appeared to be the proximate cause of desertion (MacWhirter 1985). Other forms of nest

TABLE 6. Suspected causes of nest failure among New Brunswick harriers, 1980–1984

Year	August vole indices	Nests studied[a]	Predation	Abandoned	Disease	Infertile	?	Total
			Suspected cause of nest failure					
1983	6.6	26	4[b] (15%)	3[f]	0	1	1	9 (35%)
1980	5.5	28	5[c] (18%)	1[f]	1	0	0	7 (25%)
1984	4.0	13	1 (8%)	5	0	0	0	6 (46%)
1982	3.9	12	2 (17%)	0	1	0	0	3 (25%)
1981	0.9	16	6[d] (38%)[e]	0	0	0	0	6 (38%)
All years	—	95	18 (19%)	9	2	1	1	25 (26%)

NOTE: Years are ordered by decreasing August vole abundance.
[a]Excluding those affected by research activity.
[b]Three nests destroyed by *Canus latrans*.
[c]Eggs at two nests disappeared one by one.
[d]One nest destroyed by *Corvus corax*, one probably by *Bubo virginianus*.
[e]Six nests were excluded from the 1981 analysis because of research interference; the high percent predation probably arises from these exclusions.
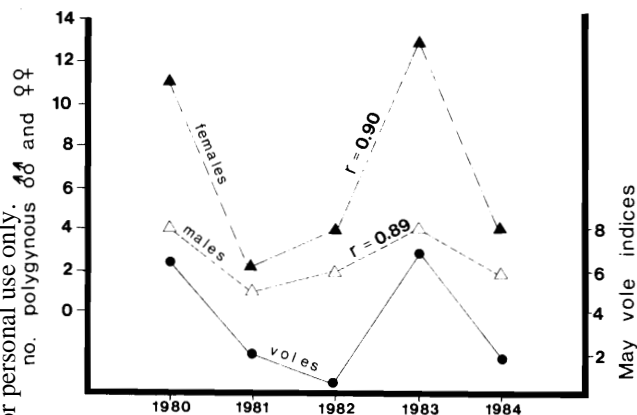[f]Three of the four nests were those of polygynous females.

FIG. 6. Relationship between May vole abundance over 5 years and the number of polygynous males and females in harems. Both variables are significantly related to vole abundance.

failure were rare; one clutch (of two) failed totally through nonhatching but partial nonhatching was fairly common and was associated with sperm depletion (R. Simmons, B. MacWhirter, and G. L. Hansen, in preparation).

Polygyny and Microtus *abundance*

We recently demonstrated (Simmons et al. 1986a) that male harriers display more often and intensely in food-rich than food-poor years. Because more females breed with males that display most frequently (R. Simmons, unpublished data), we predicted that high *Microtus* abundance would lead to more polygyny. This was verified. A significant ($p < 0.01$) correlation existed between male polygyny and vole abundance (Fig. 6) even though no more than four males controlled harems in any year. Similarly, the number of females in harems fluctuated in concert with vole abundance ($p < 0.01$; Fig. 6) despite varying by a factor of 6.5 between years (Table 1). As polygyny generally arose in May, these correlations were computed with May indices. In 1982, however, polygyny occurred in June; correlations incorporating the June 1982 index were stronger for both males and females ($r_\delta = 0.93$; $r_\varphi = 0.93$). Clearly, a close relationship existed between polygyny and food abundance.

Age

Age structure and Microtus *abundance*

In the abundant vole years of 1980 and 1983, a marginally

TABLE 7. Influence of May vole abundance on female age structure in New Brunswick, 1980–1984

	Vole abundance	
	High	Low
Young females	10	10
Old females	31	24
Proportion of young females (%)	24	29

NOTE: Low vole abundance is <4.5 *Microtus* per 100 trap nights. Young females are ≤2 years old.

lower proportion of young females (24%) bred than in vole-poor years (29%: Table 7). The difference was not significant ($\chi^2 = 0.25$).

Young males (aged by their brown rather than grey plumage) followed a more expected pattern relative to vole abundance. Five of six yearling males bred in high vole years (1980 and 1983), and a significant correlation existed between breeding yearlings and May vole indices (Table 2). Four of the six males bred with young females (the mate of one other yearling male was not aged).

Differential age-related productivity and Microtus *abundance*

On average, young females laid slightly smaller clutches than old females, yet in both success categories (*all* and *successful* females) young females were more successful than older birds (Table 8). This was not consistent between years because vole abundance differentially affected the two age-classes. For example, those young females that bred during vole highs (Table 7) were significantly more successful than old birds at these highs ($t = 1.85$, 36 df, $p < 0.05$). The converse was true at vole lows: old females were then significantly more successful than young birds ($t = 1.85$, 29 df, $p < 0.05$). This arose because the productivity of old females was generally unaffected by vole abundance (2.2 young per *all* females at lows and highs) while that of young females fluctuated widely with vole abundance (Table 9, a). Indeed, young females were significantly more successful at highs than at lows ($t = 3.68$, 17 df, $p < 0.005$). The difference was due to nest predation. Most nests of young females failed (60%) at vole lows but not one failed during vole highs. Old females were once again much more stable in this

TABLE 8. Effect of female age on clutch size and fledging success, 1980–1984[a]

| | | | Fledging success | | | |
| | Clutch size | | All females[b] | | Successful females | |
Year	Young	Old	Young	Old	Young	Old
1980	4.0 (2)[c]	5.3 (9)	3.2 (5)	2.1 (10)	3.2 (5)	3.0 (7)
1981	4.8 (4)	4.0 (5)	1.0 (4)	2.7 (6)	4.0 (1)	2.7 (6)
1982	3.8 (4)	3.7 (7)	2.0 (4)	2.3 (7)	2.7 (3)	2.7 (3)
1983	4.4 (5)	4.4 (19)	3.8 (4)	2.2 (19)	3.8 (4)	3.8 (11)
1984	3.5 (2)	4.0 (7)	0.0 (2)	1.9 (8)	—	2.5 (6)
Means	4.2 (17)	4.4 (47)	2.3 (19)	2.2 (50)	3.3 (13)	3.1 (36)

[a]Old females were not disadvantaged by harem membership, since the fledging success of young and old females was similar when harem status was controlled (all females: $\bar{x}$ = 2.4 and 2.2, respectively; successful females: $\bar{x}$ = 3.3 and 2.9). Too few young females were harem members (see Simmons et al. 1986b) to warrant a similar analysis.
[b]Excluding females affected by research activity.
[c]Number of females is given in parentheses.

TABLE 9. Age-related fledging success of (a) all young and old females in years of high and low August vole abundance, and (b) successful females in relation to vole abundance

| | Microtus index | |
	High	Low
(a) All females		
Old	2.2	2.2
Young	3.4	1.2
(b) Successful females		
Old	3.5	2.6
Young	3.4	3.0

NOTE: High vole abundance is >4.5 voles per 100 trap nights. High years, 1980 and 1983; low years, 1981, 1982, 1984.

TABLE 10. Nest site quality scores of young (1–2 years) and old (3+ years) harriers, 1980–1983

	Mean nest site quality	Range of scores	n
Young females	184	152–206	13
Old females	182	152–206	24

NOTE: Nest site quality is based on moisture, vegetation, and visibility at nest sites; for details see Simmons and Smith (1985). Kruskal–Wallis test, H = 0.44, p > 0.3; no significant differences were found in the means of the two groups.

regard, suffering only 14% and 38% failure at lows and highs, respectively (Table 9, b). The differential nest failure of old and young females could not be explained by nest site quality (see Simmons and Smith 1985) because no significant difference in quality existed between nest sites (Table 10).

Young males were also relatively successful. In six nesting attempts, yearlings reared an average 2.8 young, and *successful* birds reared 4.3 young per attempt. These samples are small and may change with further study.

Female age and initiation date

Because seasonal declines in productivity were found in each

TABLE 11. Mean laying dates of young and old females in relation to May vole abundance

| | Laying date | | No. of days by which old preceded young |
Year	Old females	Young females	
1980	16 May	1 June	16
1983	24 May	23 May	−1
1981	17 May	23 May	6
1984	20 May	2 June	13
1982	5 June	30 May	−6
Means	22 May	28 May	6

NOTE: Years are ordered by decreasing vole abundance. t = 2.2, 72 df, p < 0.02.

TABLE 12. Average male nest defence scores over 3 years, 1980–1982

Year	Nest defence score ($\bar{x}$ ± 1 SD)	No. of nests assessed
1980	10.6±7.9	10
1981	3.6±6.1	5
1982	3.9±3.8	7

NOTE: Scores are presented only for those males hatching young (see Methods).

year in New Brunswick (P. Barnard, B. MacWhirter, R. Simmons, G. L. Hansen, and P. C. Smith, in preparation), late-laying females and their relatively poor reproduction could account for the differential age trends reported above. In fact, this was not so. Vole abundance per se made no difference to the onset of breeding by the two age groups (Table 11). Lumping all data (i.e., disregarding vole abundance) indicated that there was a significant age-related difference in settling dates: older females preceded young ones by an average of 6 days. This implies that old females should reproduce better than young females, a reversal of that found (above).

Behavioural changes influenced by vole fluctuations

Defence scores obtained over 3 years showed strong associations (r = 0.99) with vole abundance in June of each year (Table 12). In the highest vole year of the three (1980), defence scores were about three times higher than in the lower years (Table 12), but the difference was not significant.
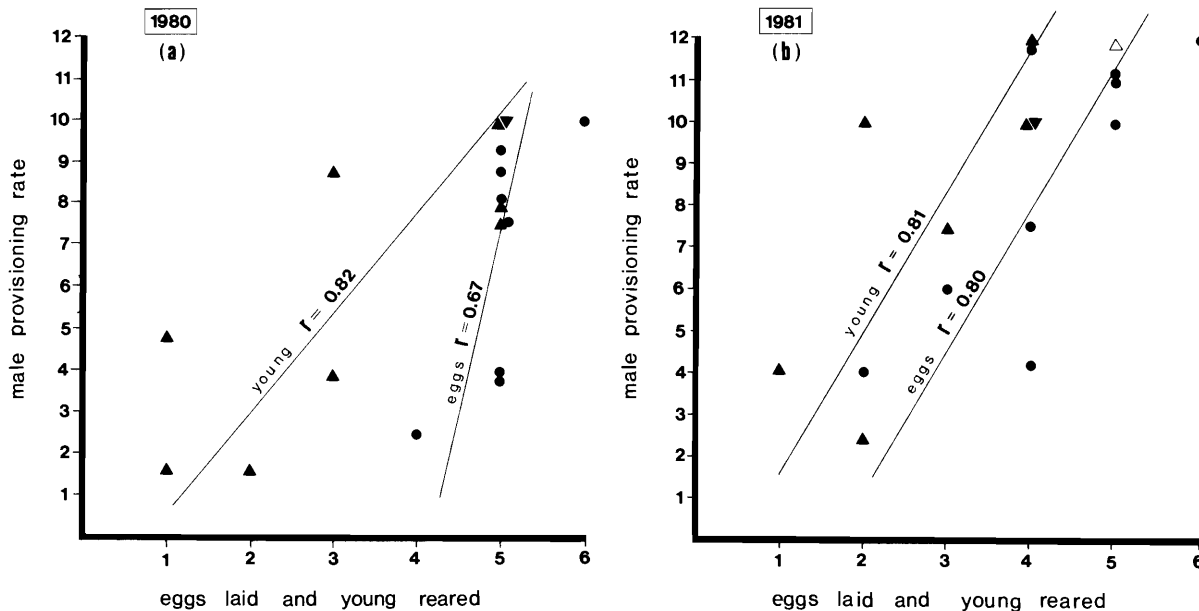
Food provisioning

Provisioning and vole abundance

Posthatch provisioning rates differed little between years (Simmons et al. 1986a), yet biomass per item did. In 1982 and 1980, high and rapidly increasing vole years, an average of 1.7 items and 3.0 items per 14-h day were needed to rear two chicks to fledging (derived from equations in Figs. 7 and 8). This rose to 4.9 items in the vole-poor August of 1981. Hence in food-rich or increasing years fewer items were required to raise a chick than in poor years. This is explicable if males ate less of their catch in food-rich years, and provisioned larger proportions.

Provisioning and clutch size

Female harriers obtain most of their food from their mates for 7 to 21 days before egg laying (Simmons et al. 1986a); thus male provisioning rates may affect clutch size if food and eggs are causally related (Newton and Marquiss 1981; Dijkstra et al. 1982). In 1980 and 1981, "seasonal" (pre- + post-hatch)

FIG. 7. Relationship between seasonal provisioning rates of male harriers (items per 14-h day) and clutch size (●) and fledging success (▲), 1980–1981. △, a failed nest destroyed within 5 days of fledging. The lines of best fit for clutches and young reared are as follows: $Eggs_{1980} = 4.14 + 0.12(food)$, $p < 0.02$; $Eggs_{1981} = 1.68 + 0.30(food)$, $p < 0.01$; $Young_{1980} = 0.71 + 0.42(food)$, $p < 0.01$; $Young_{1981} = 0.54 + 0.30(food)$, $p < 0.01$.
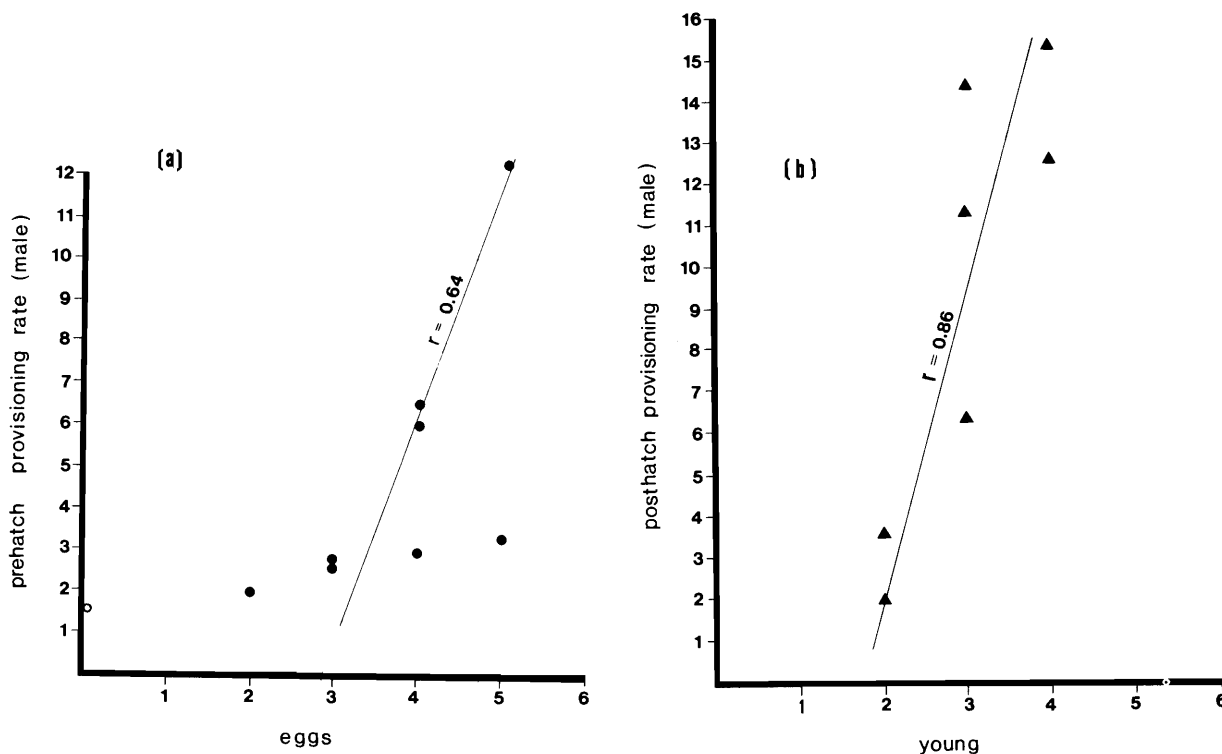

FIG. 8. Relationship between provisioning rates of male harriers (items per 14-h day) and fecundity in 1982: (a) prehatch provisioning and clutch size; (b) posthatch provisioning and fledging success. These data were derived from a year of low May vole abundance and rapidly increasing summer abundance; the steepness of graph b may be explained by the limiting effects of small clutches. ○, a female fed 1.5 items per day during courtship which subsequently deserted the nest. The lines of best fit are as follows: $Eggs_{1982} = 2.84 + 0.19(food)$, $p < 0.05$; $Young_{1982} = 1.78 + 0.13(food)$, $p < 0.01$.

provisioning rates were significantly related to clutch size ($p < 0.02$, Figs. 7a, 7b) as were more precisely monitored prehatch rates in 1982 ($p < 0.02$, Fig. 8). This occurred even though prey abundance in early 1982 was considerably lower than other years.

Provisioning and fledging success

In 1980 and 1981 we again found highly significant correlations ($p < 0.01$) between seasonal provisioning rates and fledging success. Using more precise measures in 1982, we again found significant correlations ($p < 0.01$) between

posthatch provisioning and fledging success (Fig. 8b). Our data thus support the idea that male provisioning is vital at all stages of the nesting cycle and that it can act as a proximate link between harrier production and vole fluctuations.

Discussion

The major conclusion of this 5-year study is that vole abundance had a marked affect on Northern Harrier breeding density, polygyny, clutch size, and age-related productivity, while the phase of the vole cycle had a significant effect on the survival of hatched young. That voles rather than all small mammals were influencing these trends seems clear from comparisons of correlations between voles and small mammals (Table 2).

There are, however, two drawbacks to studies of this kind: time and covariation. Our 5-year study yielded only five data points, rendering correlation analysis relatively weak. Fortunately the trends observed were sufficiently strong to be apparent with or without statistical testing. The second problem is more acute; with five data points, partial correlation analysis is inappropriate; hence, covariation may go undetected. Below, we investigate possible covariation of age, laying date, and reproduction, offer suggestions for the lack of association between vole abundance and fledging success, and explore the polygyny–food relationship further.

Timing of breeding, clutch size, and provisioning rates

In general, vole abundance explained an insignificant proportion of variation (~50%) in the onset of laying. This has been noted in European studies (Schipper 1978), and rain and low spring temperatures have been implicated as confounding influences (Schipper 1978; N. Picozzi, personal communication). The influence of both variables has recently been analysed for another temperate breeding raptor, the European Sparrowhawk, *Accipiter nisus*; both were found to be of roughly equal importance in explaining 80% of the variance in breeding initiation (Newton and Marquiss 1984). Proximately, these factors and their inhibiting effect can be explained through feeding rates. Rain invariably inhibits foraging in harriers (Schipper 1973; Belanger 1981) and dramatically decreases provisioning rates to nests (Barnard 1983; MacWhirter 1985). Poorly provisioned females or those unable to forage for themselves prior to breeding are more likely to delay breeding as a result. In New Brunswick, low temperatures have a similar effect on harrier foraging rates. Temperatures lower than 20°C significantly reduce provisioning rates of breeding males (MacWhirter 1985).

Data on male provisioning during large fluctuations in prey abundance indicated that females appeared to be in better condition for egg laying in food-rich years. We deduce this from the clutch size intercepts (Figs. 7 and 8) for females theoretically receiving no food from their mates. The difference was most marked in 1980 when voles were abundant and a value of four eggs was apparent. Despite these differences, females continued to exhibit strong male-dependent fecundity in all years. This was evident in both clutches and eventual success (Figs. 7 and 8). That females appeared to actively assess male effort prior to breeding was suggested by the desertion of one female, fed during courtship at a rate of 1.5 items per 14-h day (lower than any other female in that year). That she was probably capable of laying three eggs unaided (cf. intercept Fig. 8a) implies not only an assessment of male provisioning but a maximization of expected success.

Few other North American studies have provided a large sample of harrier clutches, but comparisons with those from North Dakota and Europe show that clutches in New Brunswick were smaller and ranges were larger ($\bar{x} = 4.3$, 1–8) than those in Hammond and Henry's study (1949) ($\bar{x} = 5.1$, 3–7), or Balfour's (1957) study ($\bar{x} = 4.6$, 3–8). Although we found no 10- to 12-egg clutches, we suspect that minimum clutches reported from elsewhere may not be inherently larger, but artifacts of policies to disregard clutches smaller than three as not "genuine." We question this because of the number of small clutches in our study (Table 4), the fact that they were frequently successful, and because western European studies (Schipper 1978) reveal means and ranges similar to our own ($\bar{x} = 4.6$, 2–9).

Female age, fledging success, and vole abundance

Female age greatly affected fledging success but not clutch size. More interestingly, young and old females were differentially affected by vole abundance, primarily through differential nest failure. Excluding nest failure from the analysis revealed that young females responded similarly to highs and lows (Table 9, b). This is unusual because young birds in several species typically reproduce less well than more experienced ones (Coulson and Horobin 1976; Davis 1975; Newton et al. 1981). Moreover, young harriers also laid their clutches later on average than older females (Table 11), and with seasonal declines in success might be expected to reproduce poorly. A plausible explanation for their relatively good success is that only the highest quality youngsters breed in their 1st or 2nd year. When their success is compared with old females, a group in which both high *and* low quality birds would probably be breeding, it is perhaps not surprising that youngsters equalled the reproduction of more experienced birds. Identical results for young harriers were reported by Burke (1979); young females breeding at vole lows were not only very successful but their success was higher than any other group at any other time.

Further comparisons of fledging success and prey abundance in New Brunswick, Wisconsin, and Europe show some unexpected disparities. Whereas Hamerstrom (1979) noted no variation in success with vole fluctuations and a correlation of $r = 0.13$ (derived from Burke 1979, Appendix I), Schipper (1978) noted a significant variation in fledging success ($p < 0.005$, no r value given), and we found a strong ($r = 0.72$) but nonsignificant variation between vole abundance and success. These comparisons are all the more unusual because each population feeds primarily on *Microtus* spp. We can explain our results because of a recently discovered prey shift evident at harrier hatch (R. Barnard, B. MacWhirter, R. Simmons, G. L. Hansen, and P. C. Smith, in preparation). Although harriers take mainly voles between May and August, a large, newly available prey source in the form of nestling and fledgling birds makes an important supplement to the diet just at the time harriers hatch their young in mid June. Indeed, New Brunswick harriers may time their breeding to coincide with this newly available prey source. We contend, therefore, that the nonsignificant vole – reproductive success result arises because juvenile passerines have a boosting effect on harrier reproduction, especially when voles are scarce, and smooth out expected lows in harrier productivity. Whether these trends exist for other harrier populations is unknown.

Reproductive success and phase of prey cycle

Like Hagen (1969), we noted that more hatchlings were fledged in years of increasing than decreasing vole abundance.

There are three plausible explanations for these trends. (*i*) Voles in increasing years are relatively abundant when compared with the number of harriers exploiting them. This is well illustrated in 1982 when only 12 females nested and the vole index in May was very low. By August, vole numbers had increased dramatically and the success of the small broods was correspondingly very high. That this was directly influenced by food provisioning is evident from the increase in provisioning rates between pre- and post-hatch periods. The rate was 2.5 times higher in 1982, the highest increase in the 3 years during which it was studied (Simmons et al. 1986a). (*ii*) Greater biomass: increased *Microtus* body mass at population peaks has been documented several times (Chitty 1960; Golley et al. 1975; Laine and Henttonen 1983). Thus by chance a harrier foraging at such times should catch larger voles. However, even though the largest voles trapped by us during highs and lows were of different weights (67 g and 45 g), mean weights differed little (MacWhirter 1985). In fact, harriers appeared to select smaller (more vulnerable?) voles than their frequency in the trapped population predicted (MacWhirter 1985). Thus, although variation in vole biomass may influence other populations, Tantramar harriers seemed unaffected in this regard. (*iii*) Juvenile vole dispersal: for vole populations to increase at all, large numbers of juveniles must be present. After independence this age-class disperses out of prime, well-covered habitat (Birney et al. 1976) into more marginal areas (Lidicker 1975). Juveniles may thereby be more vulnerable to predators, a supposition supported by MacWhirter's results (1985). In sum we suspect that the first and third factors were important in ensuring that more hatched harriers fledged in increasing vole years. These factors may also explain the unusual results of Village (1981) in which more hatchling *Asio atus* were reared in vole-poor years. Reinterpreting his data according to the *relative* spring to summer vole increase (supplied by A. Village, in correspondence) indicates that greater proportions of owls were reared in the years of highest relative increase (despite the year being ranked as "poor").

Polygyny and Microtus *abundance*

In a review of 23 published studies of prey abundance and polygyny (6 raptor and 17 passerine), we found only 2 that had directly assessed food abundance. Both Harmeson (1974) and Wittenberger (1980) found a strong relationship between polygyny and food richness. Experimental feedings would help elucidate causal pathways in these species.

That more harrier polygyny was evident in food-rich than in food-poor years may be proximately explained through male provisioning rate. Not only is greater biomass provisioned by males in food-rich years but it is a resource on which females and broods are highly dependent. Females can also assess provisioning potential through courtship feeding and male condition though display frequency (Simmons et al. 1986a) or nest defence (Table 12). As long as males maintain threshold courtship rates in food-rich years, their potential for attracting two females is high (R. Simmons, in preparation). Because high courtship provisioning rates to two females are probably impossible in food-poor years, polygyny is unlikely. Furthermore, the strong association between polygyny and food adds further support to the idea (Simmons et al. 1986b) that food, not skewed sex ratios (e.g., Picozzi 1984), is paramount in the evolution of polygyny, at least in North American harriers. Again experimental food supplements would help clarify the causal mechanisms.

In summary, 5 years' data from New Brunswick indicate that productivity, mating system, and male behaviours of Northern Harriers closely parallel changes in the harrier's principle prey, the meadow vole. The phase of the prey cycle likewise had a significant effect on productivity, which is best explained by the fact that males were preying on relatively abundant voles that may have been highly vulnerable as they dispersed into marginal habitat. Apparent anomalies in correlations between success and vole abundance may be explained by a prey switch to newly available passerine birds at the time of hatch. Male provisioning, which significantly affected both clutches and fledging success in all 3 years, provides a proximate link between fluctuating vole abundance and fluctuating harrier productivity. It also provides a proximate link between variations in polygyny and vole abundance.

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