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SYNCHRONOUS AND DELAYED NUMERICAL RESPONSES OF A PREDATORY BIRD COMMUNITY TO A VOLE OUTBREAK ON THE CANADIAN PRAIRIES

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ABSTRACT.—In 1997, meadow vole (*Microtus pennsylvanicus*) populations reached abnormally high levels in the grasslands of Saskatchewan. From 1996–98 on the Regina Plain, we studied the numerical responses of eight predatory birds to the meadow vole outbreak. Populations of Loggerhead Shrikes (*Lanius ludovicianus*) and American Kestrels (*Falco sparverius*) were unaffected by the high-vole year, but six other species exhibited significant numerical responses. Populations of Short-eared Owls (*Asio flammeus*) and Ferruginous Hawks (*Buteo regalis*) changed in synchrony with the availability of small mammals. Short-eared Owls were apparently nomadic, as they were common on our study area during the vole high, but were not observed the year before or the year after. In contrast, the Burrowing Owl (*Athene cunicularia*) population reached a historical low the year that voles were most abundant, but increased substantially in the following year. This was the only annual population increase observed for Burrowing Owls in our study area for at least a decade. Sightings of Red-tailed Hawks (*B. jamaicensis*), Swainson's Hawks (*B. swainsoni*), and Northern Harriers (*Circus cyaneus*) increased in the year of the vole outbreak and remained at elevated levels in the following year. Immature buteos were seldom seen before or after the vole peak, but during the vole peak, immatures were common, roosting together in large groups in fields.

KEY WORDS: *raptors; hawks; owls; Burrowing Owl;* Athene cunicularia; *Loggerhead Shrike; meadow vole; numerical response; grassland.*

Respuetas numericas subcronicas y retardadas de una comunidad depredadora de aves a una erupción de ratones de campo en las praderas canadienses

RESUMEN.—En 1997, las poblaciones del ratón de pradera (*Microtus pennsylvanicus*) alcanzaron niveles anormalmente altos en los pastizales de Saskatchewan. Desde 1996–98 en la Llanura de Regina, estudiamos las respuestas numéricas de ocho aves depredadoras a la proliferación de ratones de la pradera. Las poblaciones de Alcaudón Tonto (*Lanius ludovicianus*) y Cernicalos (*Falco sparverius*) no fueron afectadas por el año de alta abundancia de ratones, pero otras seis especies exhibieron respuestas numéricas significativas. Las poblaciones del Búho de Orejas Cortas (*Asio flammeus*) y del Gavilán ferruginoso (*Buteo regalis*) cambiaron sincrónicamente con la disponibilidad de los pequeños mamíferos. Los Búhos de Orejas Cortas aparentemente fueron nómadas, tanto así que fueron comunes en nuestra área de estudio durante la gran abundancia, pero no fueron observados el año anterior o al año siguiente. En contraste, la población del Búho Cavador (*Athene cunicularia*) alcanzó una baja histórica el año en que los ratones fueron mas abundantes, pero aumentaron sustancialmente al año siguiente. Este fue el único incremento poblacional anual observado en los Búhos Cavadores en nuestra área de estudio por lo menos en una década. Los avistamientos de Gavilanes de Cola Roja (*B. jamaicensis*), Gavilanes de Swainson (*B. swainsoni*) y Aguiluchos Norteños (*Circus cyaneus*) aumentaron en el año de explosión de ratones y permanecieron en niveles elevados al año siguiente. Los búteos inmaduros fueron vistos rara vez antes o después del pico de abundancia de ratones, pero durante el pico, los inmaduros fueron comunes, perchando juntos en grandes grupos en los campos.

[Traducción de Victor Vanegas y César Márquez]

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Table 1. Summary of search effort employed to survey birds of prey on the Regina Plain, Saskatchewan. Each day that a party recorded raptor sightings from a truck is considered one 'search day.' Thus, two trucks covering different routes on the same day were counted as two search days.

RANGE OF DATES	NO. OF SEARCH DAYS	TOTAL NO. OF HOURS SEARCHED	MEAN NO. OF HOURS PER SEARCH DAY	TOTAL DISTANCE SEARCHED (km)	MEAN DISTANCE PER SEARCH DAY (km)
19 Apr–13 Aug 1996	152	1101	7.2 ± 0.14	41 873	275 ± 7.3
21 Apr–19 Aug 1997	158	1028	6.5 ± 0.21	32 397	205 ± 7.2
14 Apr–20 Aug 1998	146	1005	6.9 ± 0.15	31 644	216 ± 5.7

Breeding densities of many raptor species vary from year to year because of annual fluctuations in their prey (Newton 1976). Such numerical responses of predators can be either in synchrony (S) with their prey, showing no obvious time lags, or delayed (D) by one or more years (Galushin 1974). Numerous examples of synchronous and delayed numerical responses to prey have been recorded for raptor species in a variety of habitats: in tundra, Rough-legged Hawk (*Buteo lagopus*) (S) (e.g., Virkkola 1992), Gyrfalcon (*Falco rusticolus*) (D) (Nielsen 1999), Short-eared Owl (*Asio flammeus*) (S) (Andersson 1981), and Snowy Owl (*Nyctea scandiaca*) (S) (Wiklund and Stigh 1986); in boreal, Northern Harrier (*Circus cyaneus*) (S) (Hamerstrom 1979), Northern Hawk-Owl (*Surnia ulula*) (S) (Rohner et al. 1995), Boreal Owl (*Aegolius funereus*) (S or D) (Korpimaki 1992), Great Horned Owl (*Bubo virginianus*) (D) (Rohner 1996), and Northern Goshawk (*Accipiter gentilis*) (S) (Doyle and Smith 2001); in semidesert, Harris' Hawk (*Parabuteo unicinctus*) (S), Red-backed Hawk (*Buteo polyosoma*) (S), and Black-chested Eagle (*Geranoaetus melanoleucus*) (S) (Jaksic et al. 1992); and in the tropics, Barn Owl (*Tyto alba*) (S) (Wilson et al. 1986).

Few studies have attempted to relate numerical changes of breeding raptors to annual food variation in grassland habitats (Schmutz and Hungle 1989, Steenhof et al. 1997). In the present study, we recorded patterns of inter-annual variation in population indices of eight species of predatory birds on the Regina Plain in southern Saskatchewan, Canada. We also estimated small mammal availability before, during, and after a meadow vole (*Microtus pennsylvanicus*) peak in the study area. Our effort and methods for obtaining population indices remained consistent within each species among years. However, given that the proportion of the population detected undoubtedly varied among species because of differences in size, behavior, and survey techniques (Millsap and LeFranc 1988), we made no attempt to compare population indices among species.

Four of our eight study species, including the endangered Burrowing Owl (*Athene cunicularia*, Wellicome and Haug 1995), are designated as a Species at Risk in Canada (Rothfels et al. 1999). Hopefully, an improved understanding of factors influencing populations of these species will also aid in their conservation.

METHODS

Study Area. This study was conducted in the grassland ecoregion of Saskatchewan (Harris et al. 1983), in an area roughly bounded by the cities of Regina (50°25'N, 104°39'W), Moose Jaw (50°23'N, 105°32'W), and Weyburn (49°41'N, 103°52'W). The study site encompassed 12 000 km^2 of predominantly cultivated land. Over 90% of the original grassland in the area has been converted to cropland (James et al. 1990). European settlement and farming in the region has resulted in roads, usually spaced by 3.2–6.4 km, running east-west and north-south in a grid across the study area.

Raptor Survey. To estimate the relative abundance of birds of prey (other than Burrowing Owls) in the study area, we counted Short-eared Owls, Northern Harriers, American Kestrels (*Falco sparverius*), Loggerhead Shrikes (*Lanius ludovicianus*), Ferruginous Hawks (*Buteo regalis*), Red-tailed Hawks (*B. jamaicensis*), and Swainson's Hawks (*B. swainsoni*) that we observed while driving in the study area each day. We also counted Prairie Falcons (*Falco mexicanus*), Merlins (*F. columbarius*), Great Horned Owls, and Golden Eagles (*Aquila chrysaetos*), but they were too rare for analysis. Field vehicles contained tally sheets on which investigators recorded observations of predatory birds, along with the number of km driven and hours worked each day (Hochachka et al. 2000). Young-of-the-year were not included for any species, and migrating individuals were excluded by the dates of our surveys (Table 1). Also, raptor species that migrate through, but do not breed in our study area (e.g., Rough-legged Hawk, Snowy Owl, and Gyrfalcon), were excluded from our analysis. Distant buteos that could not be identified to species were recorded as 'unknown buteos.' We did not record the sex or breeding status of birds, so non-breeding adults (e.g., second-year Red-tailed Hawks) were included in the overall abundance indices. Individuals may sometimes have been counted more than once per day because the same area was occasionally driven more than once in a day. However, such errors were likely consistent among years, so our method provided useful indices for comparing among-year population changes within species.

Our work was conducted during daylight hours, typically between 0900 H and 1800 H. Total search effort was similar among years (Table 1). To account for any variation in search effort, however, estimates of bird abundances were expressed as the mean number of individuals observed per 100 km traveled per census day. Among-year variation in these population indices was assessed for each species using one-way analysis of variance and significant differences were identified with post-hoc Tukey tests. All analyses were conducted with an alpha value of 0.05.

Burrowing Owl Census. Burrowing Owls were rarer than the other birds of prey in our study area, so we used a more intensive method to estimate changes in their population. Beginning in the second or third week of April (1996–98), all sites known to have Burrowing Owls in the previous 5 yr (James et al. 1997, Wellicome et al. 1997) were searched for signs of occupancy. We slowly drove or walked transects, spaced at ca. 25 m, through suitable nesting areas (i.e., non-cultivated fields), scanning each Richardson's ground squirrel (*Spermophilus richardsonii*) or badger (*Taxidea taxus*) burrow for signs of owls, owl pellets, or whitewash. In addition to our searches, the Operation Burrowing Owl program in Saskatchewan had a toll-free telephone number that other biologists and members of the general public were encouraged to use to report Burrowing Owl sightings (Skeel et al. 2001). We investigated each reported sighting within our study area.

We are confident that our census was accurate because nesting pastures were small and work on Burrowing Owls had been ongoing since 1987 in the area (James et al. 1997, Wellicome et al. 1997). However, as an accuracy check, we randomly chose five of the 28 townships (each 9.6 km × 9.6 km) that contained owls in 1995, and searched all grassland fragments and roadside ditches (regardless of whether the sites had any previous records of owls) within this subset of townships in 1996. We searched all suitable habitat within these townships by driving slowly along ditches and walking transects in pastures and other grasslands. No new owls were found using this intensive search, suggesting that the estimated population size obtained from our usual census technique was close to 100% of the actual population (see Wellicome et al. 1997 for details).

Small Mammals. Burrowing Owls are generalist hunters that capture prey species in the same proportions as are available in the environment (Green et al. 1993, Plumpton and Lutz 1993, Silva et al. 1995, but see Jaksic et al. 1992). On the Regina Plain study area, vertebrate prey made up between 85–97% of total prey volume measured in food pellets annually during the breeding season (Wellicome 2000). We obtained an index of small mammal availability by counting the number of small mammals cached inside Burrowing Owl nests, as average annual cache size has been shown to reflect annual relative prey abundance in our study area (measured by small mammal trapping over a 4-yr period; Wellicome 2000). To determine cache sizes, we opened all Burrowing Owl nests that were in artificial nest boxes. Artificial nest boxes allowed us to access nest chambers to count and mark all stored prey items without disturbing the physical structure of the nest (Wellicome et al. 1997, Wellicome 2000). For analyses, we used prey-cache data collected up until 2 wk after the first egg was laid in each nest because this laying period had the highest rate of prey caching within each season (Wellicome 2000). Cache size was measured as the mean number of prey items found in each nest, provided the nest had been visited at least twice during pre-laying and laying. The mean of all nests was then calculated to obtain an index of relative abundance of small mammals in the study area for each year between 1992–98.

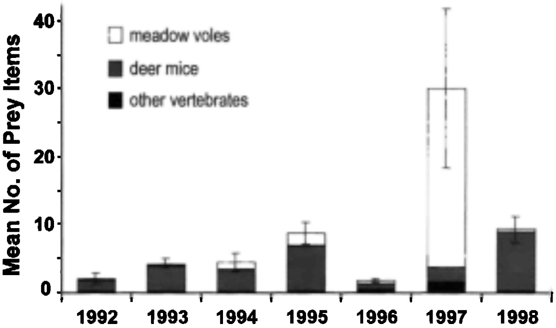

Figure 1. Mean number of vertebrates cached by Burrowing Owl pairs in each of 7 yr. Values were calculated for each pair by averaging the number of prey counted in nest stores during checks in both the pre-laying and laying periods. Bars indicate annual means of all vertebrate prey cached and error bars show SE. 'Other vertebrate prey' include sagebrush voles, house mice, shrews, passerines, and tiger salamanders. Prey-cache data were collected from 13, 24, 16, 26, 17, 18, and 17 pairs in 1992–98, respectively (adapted from Wellicome 2000).

RESULTS

Almost all cached vertebrate prey were either deer mice (*Peromyscus maniculatus*) or meadow voles. Other vertebrate prey included sagebrush voles (*Lemmiscus curtatus*), house mice (*Mus musculus*), shrews (*Sorex* spp.), passerines, and tiger salamanders (*Ambystoma tigrinum*). Excluding 1997, a mean of 70% (range = 40–87%) of the vertebrate prey items found in Burrowing Owl nests were deer mice, and only 19% (range = 7–32%) of prey items were meadow voles (Fig. 1). In 1997, general field observations and snap-trapping data (Wellicome 2000, Sissons et al. 2001) suggested that the small mammal population reached extremely high levels. Such a high abundance of small mammals

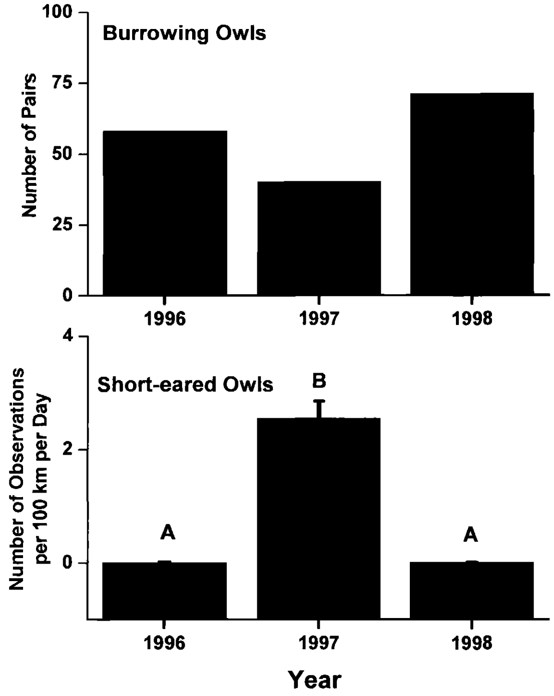

Figure 2. Total number of Burrowing Owl pairs on the study area, and Short-eared Owl population index ([mean No./100 km/search day] ± SE) in three separate years. The Burrowing Owl population had a delayed response to the high abundance of small mammals in 1997, but the Short-eared Owl population had a synchronous response. For Short-eared Owls, results from Tukey tests are shown with letters above each bar; differing letters indicate that among-year differences in observation rates were significant.

was evidently a rare occurrence, as populations had not been this plentiful since 1969 (Houston 1997). In 1997, 87% of cached prey items were meadow voles, making the mean total number of prey items per nest between three and 16 times higher in 1997 than in the other years (Fig. 1).

Data have been collected on the population size of Burrowing Owls in a portion of our study area since 1987 and there was a decline in every year except 1998 (James et al. 1997, Wellicome et al. 1997). The only recorded increase in the number of Burrowing Owls was between 1997–98 (Fig. 2) and the fewest Burrowing Owls in the past decade occurred in 1997, the year of the meadow vole outbreak.

Neither Loggerhead Shrikes ($F = 0.08$, df = 2, $N = 453$, $P = 0.93$) nor American Kestrels ($F = 1.7$, df = 2, $N = 453$, $P = 0.17$) showed significant population responses to the 1997 vole increase. The mean number of individuals (±SE) observed per 100 km per search-day from 1996–98, were 0.17 ± 0.03, 0.16 ± 0.03, and 0.18 ± 0.03 for shrikes, and 0.15 ± 0.03, 0.09 ± 0.03, and 0.17 ± 0.04 for kestrels, respectively.

There was a highly-significant difference in the number of Short-eared Owls observed among years ($F = 68.4$, df = 2, $N = 453$, $P < 0.001$; Fig. 2). In both 1996 and 1998 (years with normal small mammal populations), we observed this species on only two occasions; whereas, in 1997 (the peak vole year), we recorded a total of 604 observations of this species.

There was significant annual variation in the number of Swainson's Hawks ($F = 56.92$, df = 2, $N = 453$, $P < 0.001$), Red-tailed Hawks ($F = 29.1$, df = 2, $N = 453$, $P < 0.001$), Ferruginous Hawks ($F = 13.7$, df = 2, $N = 453$, $P < 0.001$), and total buteos (including unknown; $F = 49.897$, df = 2, $N = 453$, $P < 0.000$) observed per 100 km per day. For each of the three species, there were significantly more observations during the year of the vole outbreak (Fig. 3). In the year following the vole outbreak, when prey numbers returned to a normal level, both Swainson's and Red-tailed Hawk populations remained significantly higher than they were in the year prior to the vole outbreak. However, observations of Ferruginous Hawks did not remain elevated in the year following the vole peak. For all buteos combined (unidentified, Red-tailed, Swainson's, and Ferruginous Hawks), there were eight times more observations in 1997 (3413), and four times more observations in 1998 (1667), than there were in 1996 (416). Although the numbers of adult vs. immature birds were not recorded, there was an obvious increase in the frequency of immature buteos in 1997. Most observations of buteos in 1997 were of 1-yr-old Swainson's and Red-tailed Hawks, but in 1996 and 1998 almost all observations were of adult, breeding birds (pers. observ.).

There was significant annual variation in the number of Northern Harriers observed per 100 km per day ($F = 51.3$, df = 2453, $P < 0.001$; Fig. 3). Harriers were much more abundant in 1997 than in 1996, but did not decrease in 1998 to 1996 levels.

DISCUSSION

Two of the eight avian predators in this study showed no significant numerical response to the

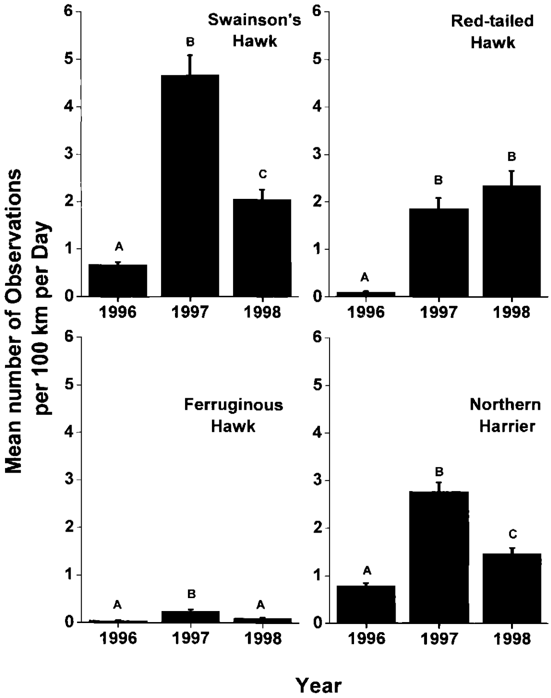

Figure 3. Population indices ([mean No./100 km/search day] ± SE) for Swainson's Hawks, Red-tailed Hawks, Ferruginous Hawks, and Northern Harriers. All four species exhibited a synchronous response to the high abundance of small mammals in 1997 and all species except the Ferruginous Hawk were higher in 1998 than in 1996. Results from Tukey tests are shown with letters above each bar; differing letters indicate that among-year differences in observation rates were significant. Note that patterns of change in population indices among years can be compared, but that indices should not be compared among species, as detectability likely differed among species.

small mammal high in 1997; populations of Loggerhead Shrikes and American Kestrels remained stable over all three survey years. This lack of response might have been an artifact of the relatively small populations of these two species in our study area. Alternatively, it is possible that these two species relied heavily on prey items other than small mammals. For example, they may have fed predominantly on insects. Another possibility is that, rather than food supply, availability of nesting sites limited their populations. This explanation might be plausible for kestrels, as they are obligate secondary-cavity nesters (Bent 1938), but seems less likely for shrikes, as they construct their own stick nests in shrubs or small trees (Yosef 1996).

The remaining six avian predators in this grassland study showed significant numerical responses to the vole high in 1997. In general, local increases in bird populations in response to elevated prey numbers can result from increased reproductive output *in situ* and/or immigration from peripheral populations (Solomon 1949). The numerical response of the Short-eared Owl to prey can undoubtedly be attributed to immigration because Short-eared Owls were rare on the study area in 1996, but suddenly became very common in 1997 with the increase in voles. Such synchronous responses are characteristic of species with nomadic lifestyles (Galushin 1974). In concordance with our results in the grasslands, the Short-eared Owl has been described as nomadic also in boreal (Korpimaki and Norrdahl 1991) and tundra habitats (Andersson 1981). The species' specialized diet, simple nest-site requirements, and large clutch size seem to make it particularly well suited to a lifestyle of nomadism (Holt and Leasure 1993).

Although the Burrowing Owl shares some of these general characteristics with the Short-eared Owl, it exhibited an opposite response to the prey high. Burrowing Owls in our study were at their lowest during the vole peak but increased in the subsequent year (Fig. 2). The 1-yr delay in the population's response to the vole outbreak suggests that these owls are not nomadic, as they do not search actively for nesting sites based on the current availability of prey in an area, at least not at a large geographic scale. Given that the species is not nomadic then, other mechanisms must explain its observed numerical response to the prey high. Although clutch size was no higher for Burrowing Owls during the vole high in 1997, both nestling survival and fledging success were substantially elevated in that year compared to other years (Wellicome 2000). In addition, post-fledging survival was significantly higher in 1997 than it was in years following (Todd 2001) or preceding the vole high (Clayton 1997). Furthermore, the percent of fledglings from 1997 that returned to breed in the population in 1998 was twice that of returns from other years (R. Poulin, T. Wellicome, and L. Todd unpubl. data). These factors, alone or in combination, seem to have contributed to the delayed numerical response exhibited by Burrowing Owls to the vole high. Interestingly, the only study other than ours to examine the reaction of a Burrowing

Owl population to a prey high, showed that owls in a Chilean semi-desert also exhibited a delayed numerical response (Jaksic et al. 1997).

Unlike Short-eared Owls, Burrowing Owls consume a wide variety of prey items, and their diet often changes depending on the availability of prey in the environment (Green et al. 1993, Plumpton and Lutz 1993, Silva et al. 1995, Jaksic et al. 1992). Thus, Burrowing Owls are not overly reliant on any one type of prey, and can switch to take advantage of peaks in several prey species (Fig. 1).

Ferruginous Hawks showed a synchronous response to the vole outbreak, reaching their highest relative population size in 1997. A nomadic tendency has been suggested for breeding populations of this species (Schmutz and Hungle 1989, Bechard and Schmutz 1995). However, unlike Short-eared Owls, Ferruginous Hawks did not appear to react strongly to the voles and remained an uncommon species through the course of our study (Fig. 3). We did not examine reproduction, but if Ferruginous Hawks fledged more young in 1997 than in other years, we might not expect to see an increase in the breeding population until 1999 when those fledglings reached breeding age (Bechard and Schmutz 1995). Alternatively, perhaps these hawks specialized on Richardson's ground squirrels in our area, as has been noted in other studies (e.g., Schmutz and Hungle 1989), in which case Ferruginous Hawks would be expected to show little reaction to vole populations.

Populations of Red-tailed and Swainson's Hawks showed elements of both synchronous and delayed responses. We noted, though, that most of the hawks in the high-food year were non-breeding, immature birds. It was common in the 1997 breeding season to see dozens of immature buteos roosting communally in fields. In 1996 and 1998, the only similar densities of hawks occurred when adults congregated to feed near tractors that were tilling fields, and those observations were comparatively rare. This raises the intriguing possibility that different age-classes of these species might use different strategies for distributing themselves geographically with respect to prey. That is, adults may choose to be faithful to nesting sites (which may be limited), returning to the same territories each year regardless of prey; whereas, immature buteos may opt for a nomadic lifestyle, searching at a large geographic scale and settling in areas with high prey availability. In this scenario, immature hawks could specialize on hunting voles wherever they were most plentiful on the landscape; whereas, adults would be forced to be generalists, eating whatever prey was available in their breeding territories each year. Further research is needed to test this hypothesis because, although studies suggest that adult breeders in these species are generalist predators faithful to their breeding sites, little is known about the ranging behavior of immature hawks (Preston and Beane 1993, England et al. 1997).

The above scenario does not explain why Red-tailed and Swainson's Hawk numbers were higher in 1998 than they were in 1996. This delayed partial response to the vole high could have been caused by an increase in adult survivorship, by an increase in breeding fidelity, or by a number of immature birds from 1997 returning to breed in the study area in 1998.

Northern Harriers showed a synchronous increase with the meadow vole peak in our study. This is in agreement with the results of a long-term study in Wisconsin, which found that harriers fluctuated in synchrony with meadow voles during a 16-yr period (Hamerstrom 1979). However, similar to the populations of Swainson's and Red-tailed Hawks, the population of Northern Harriers remained at higher levels in 1998 than in 1996, suggesting that perhaps they experienced high productivity in 1997 and/or high survivorship and site fidelity over the winter of 1997–98. Northern Harriers commonly feed on meadow voles, but they also supplement their diet with several other prey species (MacWhirter and Bildstein 1996). Unlike Short-eared Owls, the more generalized diet of harriers likely allows them to remain on the Regina Plain as a resident population in years of more moderate vole abundance.

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