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## Great Horned Owls

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Great horned owls (*Bubo virginianus* Gmelin) are large, long-lived, generalist predators. Diets of great horned owls are extremely variable and include a wide variety of species (ranging in size from insects to lagomorphs; Donazar et al. 1989), although the average prey size of great horned owls is larger than for smaller owl species (Marti 1974). Great horned owls typically ambush their prey from elevated perches and may be most successful in a mix of open and forested habitat (Johnson 1993, Rohner and Krebs 1996). Nevertheless, they are widely distributed in most landscapes across North and South America, including the whole range of boreal forest (Voous 1988, Houston et al. 1998; See figure 2.7). Great horned owls form lasting pair bonds and defend territories year-round (Petersen 1979, Rohner 1996). Great horned owls are the largest avian predators occurring widely at high densities in the boreal forest (body mass in June: 18 female adults,  $1.61 \pm 0.26$  kg, 4 male adults,  $1.23 \pm 0.07$  kg; C. Rohner, unpublished data).

Several links to the 10-year population cycle of snowshoe hares (*Lepus americanus*) have been recognized. Great horned owls include a higher proportion of hares in their diet and increase reproduction during the peak of the cycle, and irruptions of great horned owls into southern Canada and the northern United States occur during the decline phase (Rusch et al. 1972, McInville and Keith 1974, Adamcik et al. 1978, Houston 1987, Keith and Rusch 1988, Houston and Francis 1995). Maximum life span can exceed 20 years (Houston and Francis 1995); therefore, these predators may survive more than one snowshoe hare cycle. So far, radio-telemetry and experimental approaches have not been used to address the population ecology and social structure of great horned owls in the boreal forest.

In this chapter, we complement the main experiments of the project with more specific results on the mechanism of population processes that are relevant in the context of trophic interactions in the boreal forest, and we provide data that are essential for modeling this predator as a component in the food web of the vertebrate community (see chapter 18).

First, we address the question of how great horned owls respond in their demography to changing hare densities. In particular, we examine the “numerical response” (Holling 1959) in relation to social status, and we directly estimate the size of the pool of secretive, nonterritorial floaters.

Second, we focus on the question of how the diet of great horned owls varied during the course of the snowshoe hare cycle. More specifically, we used estimates of prey density to calculate the preferences for different prey, and we integrated the available information to construct functional responses (Holling 1965, Fujii et al. 1986) by great horned owls to varying hare densities. Much is known about how predators optimize their foraging decisions (e.g., review in Stephens and Krebs 1986), but most implications on population dynamics were derived from functional responses of predators to prey density (Holling 1959, Fujii et al. 1986). It is particularly the distinction between opportunistic foraging (type-2 response) and prey switching (type-3 response) that changes the dynamics of predator–prey interactions (e.g., Rosenzweig and MacArthur 1963, Holling 1965, Murdoch and Oaten 1975; examples in Messier 1994, Caughley and Sinclair 1994).

Third, we investigated the social structure of great horned owls and examined the question of how individual behavior related to population processes. In particular, we addressed the question of whether territorial behavior (social exclusion) limited population

growth and breeding density in great horned owls (see also Newton 1992) or whether food was sufficient to explain the dynamics of demographic change. We further demonstrate that individual behavior is necessary to explain the time lag of this predator to a prey cycle.

Finally, we asked at what spatial scale great horned owls responded to the large-scale manipulations of prey densities (chapter 8). Predators can concentrate their foraging effort or even aggregate in hot spots of high prey density, and spatially shifting predators have been hypothesized to synchronize population cycles in small mammals (e.g., Pitelka et al. 1955, Angelstam et al. 1984, Lindström et al. 1987, Ydenberg 1987, Ims and Steen 1990, Korpimäki and Norrdahl 1991, Korpimäki 1994). Few empirical data are available on such aggregative responses, and we discuss our findings in the context of whether territoriality can act as a social fence (see also Hestbeck 1982), which limits access and spatial aggregations of predators where prey is locally abundant.

## 15.1 Methods

### 15.1.1 Population Census

The population data for great horned owls span the years 1988–1996, with the most intensive monitoring and additional studies from 1989–1992. Great horned owls were censused in late winter and early spring on a 100-km<sup>2</sup> plot within the main study area (see CD-ROM frame 68). Individual pairs were identified when hooting simultaneously with neighbors at dawn and dusk, and obvious disputes between hooting males or pairs were used to map territorial boundaries. When necessary, we used playbacks of calls to elicit territorial responses of owners and their neighbors. Most males were individually known, not only because of radio tagging but also because of their distinctly different hoots. These differences were later verified with sonograms from recordings at the nest (C. Rohner unpublished data; method as used for *Strix aluco*, Galeotti 1990). Observations of territorial activity were made almost daily from early February until late April (at least 300 h in each year). Details on owl territories are given in Rohner (1997).

We intensively monitored a subsample of territories to assess reproductive parameters. The proportion of owl pairs that did not breed or failed early before producing nestlings was established from two methods: (1) monitoring breeding activities by females with radio transmitters (checked at least twice per week), and (2) systematic search for nests by triangulation of hooting owls according to Rohner and Doyle (1992). A search for breeding activity was recorded negative if no nest was found within 5 h of systematic search and if searches for begging calls of fledglings at a later stage were also negative.

To avoid possible effects of disturbance, we only checked nests when chicks were estimated to be at least 1 week old. A total of 116 nestlings were measured during 1989–1991, and their ages were determined from feather measurements (Rohner and Hunter 1996). Clutch initiation was back-calculated using the oldest chick, assuming that incubation commenced with the first egg and required 33 days until hatching (review in Houston et al. 1998). We determined postfledging survival according to Rohner and Hunter (1996).

### 15.1.2 Monitoring Diets

In May and June, nestlings were transferred shortly before fledging to elevated tethering platforms (Petersen and Keir 1976), where the parents kept feeding them, and they were systematically monitored for about 5 weeks (CD-ROM frame 33). This method allowed short-term brood size manipulations and collection of data on diets (details in Rohner 1995, Rohner and Hunter 1996, Rohner and Smith 1996).

We sampled summer diets of territorial owls during May–July, when pellets were collected from breeding birds at nests and at roost sites of owls located by telemetry. The results of pellet analysis were expressed as the percentage of a prey species of the total biomass, calculated by adding up diagnostic bones of each prey species for a minimum estimate of prey items (details in Rohner 1995). Because sample sizes were small for winter diets and for the summer diets in 1993–1995, the number of diagnostic bones may not have been large enough to avoid rounding errors. Therefore, we directly estimated for each pellet the proportion of different prey species based on all bones and fur encountered, and then calculated the proportion of prey species as an average across pellets. A test on subsamples confirmed that results of the two methods can be directly compared (details in Rohner 1995).

### 15.1.3 Radio Telemetry

Survival estimates and information on movements were based on individual great horned owls monitored by radio telemetry. We captured 21 territorial adult owls with mist nets and cage traps (CD-ROM frame 32) and equipped 55 owlets with radio transmitters before they fledged (breakdown of sample sizes in table 15.1, figure 15.2b). Successful dispersers were later monitored intensively (3 born in 1988, 11 in 1989, and 16 in 1990), and 9 remained as nonterritorial floaters in the study area (details in Rohner 1996, 1997). The radios weighed 50 g including a shoulder harness of teflon ribbon for attachment as a backpack (<5% of body weight, Kenward 1985; See CD-ROM frame 39). Battery life was 2–2.5 years. The radios were equipped with a two-phase activity switch (sensitive to movement and change of angle).

All floaters and territory holders with transmitters were normally monitored once per week (for the presentation of weekly data, locations in addition to the weekly sampling intervals were excluded). Most checks were conducted with handheld equipment from the Alaska Highway, which follows the valley bottom for the whole length of the study area (see CD-ROM frame 40). In addition, the entire area and its surroundings were searched for radio signals from helicopter or fixed-wing aircraft at least twice per year (in autumn after dispersal and in spring after the onset of breeding).

Telemetry work on space use of great horned owls concentrated on periods of 3 weeks (20–21 days) for each year, with locations obtained on consecutive nights for each bird if possible (this was not achieved in the first year of data collection, thus the total monitoring periods for each bird in 1989 were 27, 28, and 41 days). These periods of intensive monitoring were conducted 24 July–8 September 1989, 7–26 September 1990, 5–26 September 1991, and 12 June–3 July 1992. A detailed breakdown of sample sizes is presented in table 15.1. All of the territorial owls were females, except in 1992, when female no. 503 emigrated from the study area and her mate, no. 564, was monitored instead (details in Rohner and Krebs 1998).

Table 15.1 Summary of sample sizes and precision of telemetry locations used for specific comparisons (see text for details).

	<i>Floaters</i>		<i>Territory Holders</i>			
	1990	1991	1989	1990	1991	1992
<i>All Locations</i>						
<i>N</i> owls	6	8	—	15	20	—
<i>N</i> locations/owl (mean ± SE)	80.3 ± 12.2	61.3 ± 7.8	—	17.3 ± 3.1	35.1 ± 5.4	—
95% Error area (median, km <sup>2</sup> )	0.46	0.21	—	0.08	0.07	—
95% Error area (quartiles, km <sup>2</sup> )	0.14–1.79	0.08–0.84	—	0.02–0.28	0.02–0.19	—
<i>Weekly Locations</i>						
<i>N</i> owls	6	8	—	—	—	—
<i>N</i> locations/owl (mean ± SE)	42.7 ± 2.6	36.9 ± 2.0	—	—	—	—
95% Error area (median, km <sup>2</sup> )	0.58	0.25	—	—	—	—
95% Error area (quartiles, km <sup>2</sup> )	0.19–1.79	0.09–1.45	—	—	—	—
<i>September (3 weeks)</i>						
<i>N</i> owls	4	3	3	5	5	6
<i>N</i> locations/owl (mean ± SE)	19.8 ± 0.25	17.3 ± 2.2	18.7 ± 1.2	20.0 ± 0.0	20.0 ± 0.0	21.0 ± 0.0
95% Error area (median, km <sup>2</sup> )	0.15	0.13	0.19	0.10	0.09	0.05
95% Error area (quartiles, km <sup>2</sup> )	0.05–0.34	0.13–0.29	0.05–0.37	0.02–0.26	0.03–0.20	0.02–0.15

### 15.1.4 Analysis of Telemetry Data

Telemetry locations were obtained by triangulating owls with handheld equipment. We used topographical maps in the field to plot the locations and assess the number of bearings needed for reliable estimates. The triangulations were then analyzed with the program Locate II (Nams 1990) for calculating exact locations and distances. Median 95% error ellipses (Lenth estimator; Saltz and White 1990) are given in table 15.1 to allow an assessment of precision for telemetry locations. The accuracy of telemetry locations was assessed by triangulating five transmitters that were placed in trees at a height of 4.5–5.5 m. The deviation of these telemetry locations (error area of  $0.052 \pm 0.018$  km) from the site coordinates obtained by GPS (Global Positioning System) was  $0.101 \pm 0.027$  km.

Space use was measured by utilization distributions based on clustering methods, and all calculations were performed using the program Ranges IV (Kenward 1990). From a center of closest locations, an increasing percentage of nearest-neighbor locations were added, resulting in a cumulative increase of core area used. Mononuclear clustering was

centered around the harmonic mean location only, whereas multinuclear clustering allowed for separate clusters of closest locations. Home range sizes were then derived for different levels of core percentages (Kenward 1987). Patchiness was calculated as “part areas,” which are the areas used at a specific core percentage and expressed as a portion of the total area (details in Kenward 1987). These procedures allowed a more sensitive approach to recognizing biases due to outliers and different patterns of space use. For the monitoring period in September 1991, we excluded three territorial owls from analysis because of extreme long-distance movements during several days (these extraterritorial movements are described in Rohner 1996).

### 15.1.5 Statistical Analyses

All arithmetic means are reported with standard errors and all probabilities are two-tailed unless otherwise specified. We calculated correlation coefficients as Spearman rank correlations. For statistical testing, nonparametric tests were used wherever possible (all analyses of variance were calculated with log-transformed data, or with arcsine-transformed data for percentages). The testing of bootstrap hypotheses followed the guidelines of Hall and Wilson (1991), and two-sided probabilities were derived from 500 simulations (see also Rohner 1997).

## 15.2 Demography

### 15.2.1 Reproduction and Population Productivity

Great horned owls showed a strong reproductive response to the snowshoe hare cycle (figure 15.1, table 15.2). During peak densities of hares in 1989 and 1990, 1.7 offspring per resident pair were estimated to reach independence in autumn. As hare density started to decline in 1991, productivity fell by 82% to 0.3 offspring per pair, and during the lowest phase from 1992 to 1994 reproduction of great horned owls ceased altogether. From 1995 onward, owl productivity recovered along with increasing hare densities. The calculations of population productivity are provided in table 15.2, and more details on the reproductive parameters involved are described in the following paragraphs (see also Rohner 1996, Rohner and Hunter 1996).

The proportion of pairs breeding successfully not only had the greatest effect on population productivity but was also the parameter most closely related to snowshoe hare densities (figure 15.1B). During 1989–1991, 14–22% of territorial owl pairs did not breed or failed early, with results from radio-tagged owls and systematic searches for breeding activity in monitored territories being similar (Rohner 1996). Of 17 females that did not produce young and were monitored by radio telemetry in 1989–1992, only 2 (11%) laid eggs, indicating that inhibition of breeding activity occurred at a very early stage. In 1992, there were no signs of nesting attempts, and mates of three monitored pairs did not even roost together, as typically found in reproductive years (Petersen 1979, Rohner and Doyle 1992). This drop in the proportion of owl pairs producing young from 1989–1991 to 1992 was statistically significant ( $\chi^2 = 17.5$ ,  $df = 1$ ,  $p < .001$ ,  $n = 123$ ). The situation remained unchanged during the lowest phase of the cycle during 1993 and 1994, with only one

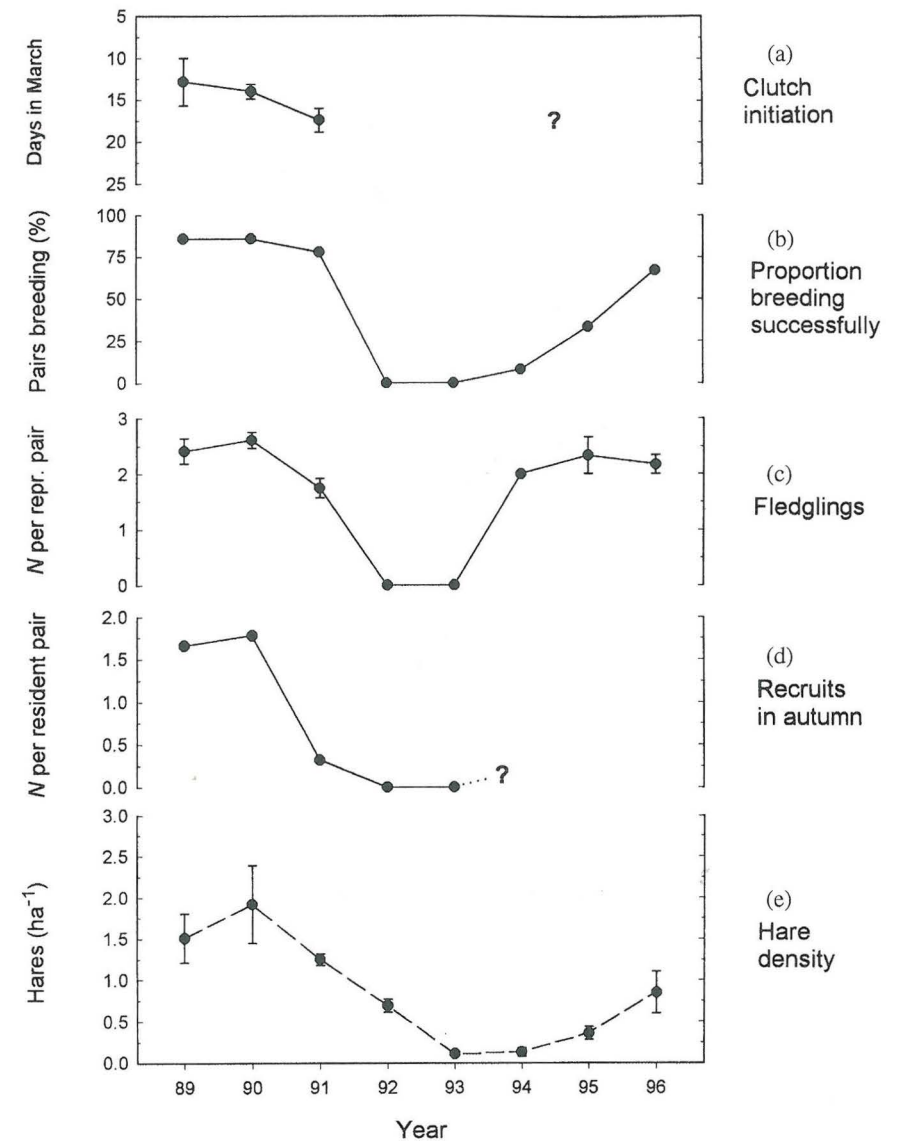


Figure 15.1 Breeding performance of great horned owls and the snowshoe hare cycle at Klunane Lake, southwestern Yukon (sample sizes in table 15.2; time periods with missing data are indicated by question marks). (a) Laying day in March; (b) breeding rate (proportion of territorial pairs producing nestlings), measured 1989–1992 only; (c) number of fledglings per successful nest; (d) number of juveniles (per resident pair) reaching independence and dispersing in autumn, measured 1989–1992 only; (e) snowshoe hare densities (winter estimates  $\pm$  SE). Modified from Rohner (1996).

Table 15.2 Reproductive parameters and estimation of the autumn recruitment rate of great horned owls at Kluane Lake, Yukon, during 1989–1996.

Reproductive Parameter	1989	1990	1991	1992	1993	1994	1995	1996
Number of owl pairs monitored	14	21	27	25	17	13	12	9
Proportion of pairs with successful nests ( $b_i$ )	0.86	0.86	0.74	0.00	0.00	0.008	0.33	0.67
Fledglings per successful nest ( $FL_i$ ) $\pm$ SE	0.242 $\pm$ 0.21	2.61 $\pm$ 0.13	1.75 $\pm$ 0.15	—	—	2.00	2.33 $\pm$ 0.33	2.17 $\pm$ 0.17
Number of fledglings radio tagged	15	22	18	—	—	0	0	0
Postfledgling survival ( $s_{FL_i}$ ) (20 weeks) $\pm$ SE	0.800 $\pm$ 0.208	0.795 $\pm$ 0.090	0.232 $\pm$ 0.077	—	—	NA	NA	NA
Autumn recruitment rate (offspring per resident pair; $R_i$ )	1.66	1.78	0.32	0.00	0.00	NA	NA	NA

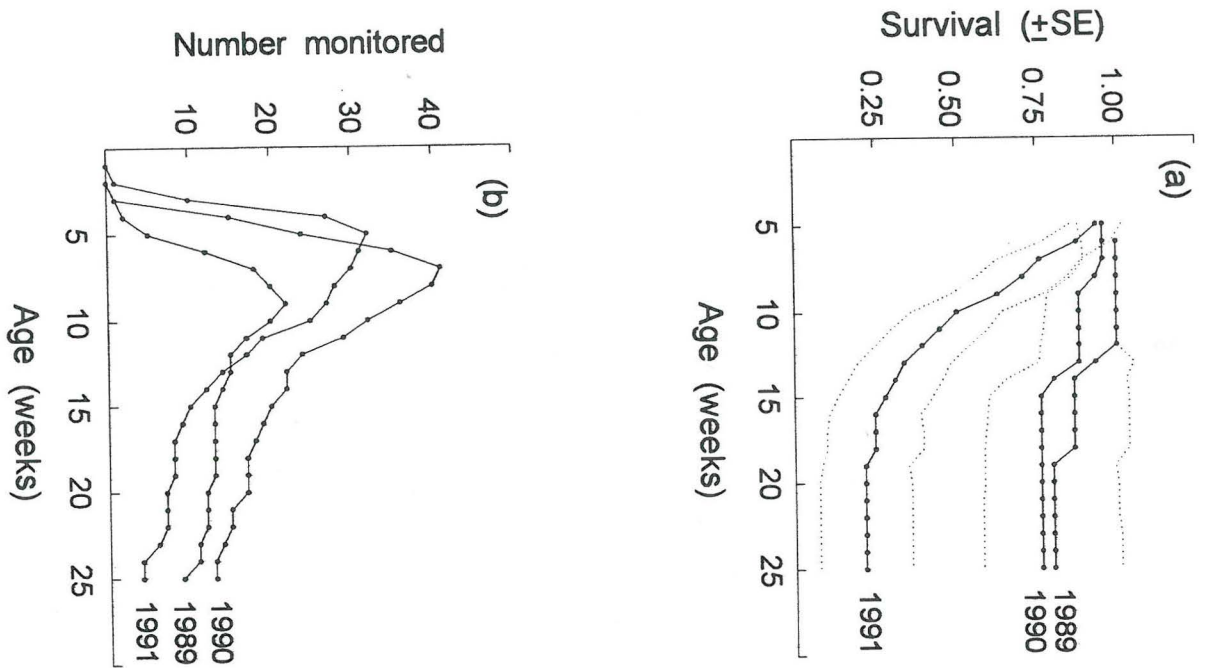


Figure 15.2 Postfledging survival rates of juvenile great horned owls, 1989–1991. (a) Survival curves with 95% confidence limits (combined for 1989 and 1990); (b) sample sizes for each time interval. From Rohner and Hunter (1996).

Table 15.3 Causes of mortality of juvenile great horned owls older than 35 days (from Rohner and Hunter 1996).

Cause of Mortality	1989	1990	1991
High levels of parasitism	0	3	10
Predation or signs of scavenging	0	0	11
Found intact (disease, starvation, unknown)	3	3	3
Traffic mortalities (road kills)	1	3	2
Total mortalities	4	9	26
Total no. juveniles monitored	24	36	34

breeding pair (3% of population). Breeding attempts rose again to 42% in 1995 and 89% in 1996 (some of these attempts failed early; table 15.2).

There was a trend toward later clutch initiation from 1989 to 1991 (figure 15.1A), but this result was not significant statistically. In 1991, brood size was lower, and nestling mortalities increased (Rohner and Hunter 1996). This resulted in fewer fledglings produced per successful nest in 1991 compared to 1989–1990 ( $1.75 \pm 0.79$  SD,  $n = 27$ ,  $p < .005$ ,  $df = 2$ ; Kruskal-Wallis test; figure 15.1C). But note that the number of fledglings per successful nest was relatively constant at whatever hare densities owls attempted to breed. The most dramatic change of reproductive parameters in 1991 occurred between fledging and dispersal, when survival fell to 29% of previous levels (figure 15.2). The causes of mortality during this period are presented in table 15.3. It is interesting that only few owlets died of starvation, but extreme damage by blood-sucking flies (*Simuliidae*) and a blood parasite (*Leucocytozoon ziemanni*) were common (details in Hunter et al. 1997). The effect on birds by black flies and diseases transmitted by them in the boreal forest may have been underestimated. Great horned owls tried to escape black flies by roosting closer to the ground and more in the open (Rohner et al. 2000), although survival rates dropped despite this change in behavior. The main cause of proximate mortality was likely an interaction between food shortage and parasitism (Rohner and Hunter 1996). For information on dispersal and age at first breeding, see Rohner (1996).

To test whether great horned owls typically fail to reproduce during the cyclic low of snowshoe hares in the boreal forest, an external set of data was used. By 1978, D. Mossop (Renewable Resources, Yukon territorial government) had established routine inspections of raptors and owls that were found injured or dead and reported to conservation officers. This information is based on the area of the entire Yukon and covers two snowshoe hare peaks (replication over space and time). The same pattern as in our study area was apparent (figure 15.3). Although injured or dead adult owls were reported throughout the entire length of the cycle, there were no juveniles during the years of lowest hare densities during 1984–1986.

### 15.2.2 Survival and Emigration

Survival of both territorial owls and floaters was high during the peak phase of the cycle (table 15.4). Territorial adults survived at a yearly rate of 95.1% ( $\pm 3.4\%$  SE) in 1989–1990 and 1990–1991. Floaters in their first or second year of life had an equally high sur-

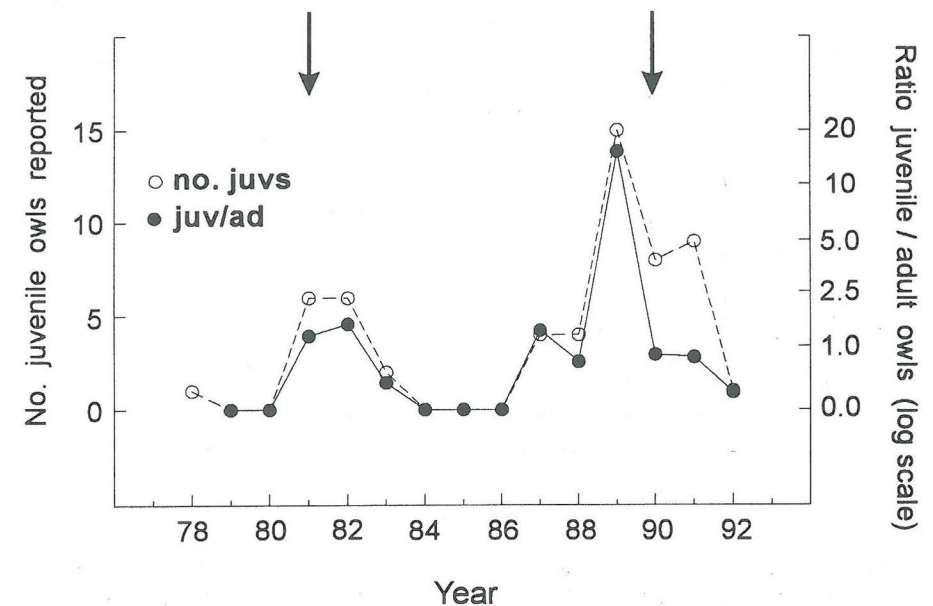


Figure 15.3 Occurrence of juvenile great horned owls during two peaks of the snowshoe hare cycle in the Yukon (56 juveniles, 70 adults, arrows indicate years of highest hare density in Kluane); based on numbers of injured and dead great horned owls that were reported to Renewable Resources, Yukon territorial government (data from D. Mossop, personal communication).

Table 15.4 Survival and emigration of great horned owls at Kluane Lake, Yukon, as determined by radio telemetry from autumn 1989 to autumn 1992.

Time Period	Hare Density	Social Class	Survival $\pm$ SE	Residency $\pm$ SE	Total No. Monitored (weekly avg.)
1989–90	Peak	Territorial	0.947 $\pm$ 0.051	1.000	19 (14)
		Floater	1.000	1.000	8 (8)
1990–91	First year decline	Territorial	0.955 $\pm$ 0.047	0.950 $\pm$ 0.049 <sup>a</sup>	22 (19)
		Floater	1.000	0.696 $\pm$ 0.136 <sup>a,b</sup>	19 (13)
1991–92	Second year decline	Territorial	0.819 $\pm$ 0.132 <sup>a</sup>	0.668 $\pm$ 0.136 <sup>a,b</sup>	18 (13)
		Floater	0.400 $\pm$ 0.219 <sup>a,b</sup>	0.600 $\pm$ 0.268	10 (4)
1989–92	Overall	Territorial	0.905 $\pm$ 0.073	0.860 $\pm$ 0.136	22 (16)
		Floater	0.701 $\pm$ 0.174	0.748 $\pm$ 0.225	19 (8)

Given are yearly survival rates ( $s_T$  and  $s_{FT}$ ) and yearly residency rates ( $e_T$  and  $e_{FT}$ ) for territorial owls and floaters. Survival rates are (1–mortality); residency rates are (1–emigration). All rates (including overall calculations) are annual rates. From Rohner (1996).

<sup>a</sup> $p < .05$  for difference between social classes (within individual years).

<sup>b</sup> $p < .05$  for difference to previous year (within social classes).

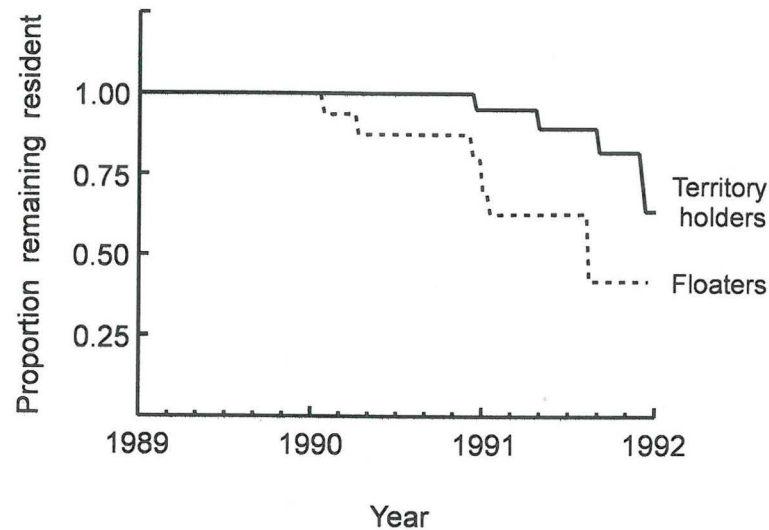


Figure 15.4 Emigration of adult owls (territorial) and young owls (first and second year, floaters) based on radio telemetry. Presented is the residency rate (1 = all owls remain resident; 0 = all owls emigrate). Sample sizes are given in figure 15.2b. From Rohner (1996).

vival rate during peak hare densities. The values in table 15.4 even exceed those for adult owls, but this is likely the result of a slight rounding error because the sample size for young birds was too small to detect survival differences of <5%.

Hare densities did not recover during summer 1991 and continued to decline in the following years. The survival of territory owners decreased by 13.2% in 1991–1992 compared to previous levels (table 15.4; difference 1990–1991 versus 1991–1992,  $p = .12$ ). During the same time, the survival of floaters dropped by >60% (table 15.4, difference 1990–1991 versus 1991–1992,  $p < .01$ ). This sharper decline in survival of floaters was also reflected in a significant difference in survival between floaters and territorial owls in 1991 ( $p = .02$ ).

Territory holders showed extreme site fidelity during highest hare densities, but an increase in extraterritorial movements was observed as the hare population declined in 1991–1992 (Rohner 1996). None of 18 territorial owls was recorded outside its territory during 1989 and 1990. Extraterritorial movements first occurred in September 1991, when three females moved 15 km, 28 km, and >30 km away. These birds returned within 2–14 days to their territories. By October 1992, 37% of monitored territory owners (7 of 19) had shown extraterritorial movements (difference between years: Fisher's Exact test,  $df = 1$ ,  $p = .03$ ).

A similar trend for increased movements when hare densities declined was observed for emigration rates (proportion of owls leaving the study area permanently, figure 15.4). None of the territory holders and floaters monitored in the study area left during the peak of the hare cycle before autumn 1990. Consistent with the trend in the survival data (table 15.4), floaters were affected before territorial owls. In 1990, emigration of floaters was

significantly higher than in territorial owls ( $p = .02$ ), and the first territory owners started to emigrate with a 1-year time lag relative to floaters (figure 15.4).

### 15.2.3 Estimating Numerical Responses

The density of nonterritorial floaters was estimated based on productivity, survival, and emigration (tables 15.2, 15.4; population model in Rohner 1996). The results are shown in figure 15.5A. Even when assuming that no floaters were present in spring 1988 for a minimum estimate, the numbers rose quickly from zero to densities similar to territorial owls (figure 15.5B). The beginning of the hare decline in the winter of 1990–1991 resulted in an immediate reduction in population growth due to emigration and lowered production of recruits by territorial pairs. Floater densities reached a peak with a time lag of 1 year relative to the hare cycle, and then dropped sharply from 1991 onward because of increased emigration and mortality and because no additional juveniles were produced locally that could have compensated for losses in the nonterritorial segment of the population.

The number of territorial owls in the study area increased almost linearly from 1988 to 1992 (figure 15.5B). Even when the hare population started to decline in 1990–1991, the number of owl territories kept rising until spring 1992. Then, with a time lag of 2 years relative to the hare cycle, the number of territories dropped from 22–25 pairs/100 km<sup>2</sup> to 7–14 pairs/100 km<sup>2</sup> in 1993. The decline of territorial owls appears to have leveled off at 10–11 pairs/100 km<sup>2</sup> during 1994–1995, and the density was still at 10 pairs/100 km<sup>2</sup> in 1996.

The numerical response of the total population of great horned owls during 1988–1993 is given in figure 15.5B. Because the territorial segment represented a nearly linear component, the sum of densities or overall pattern more closely resembled the floater response with (1) an immediate reduction in population growth as hare densities declined, and (2) with a decline that was delayed by 1 year relative to the hare cycle.

## 15.3 Foraging Behavior

### 15.3.1 Diet

Great horned owls foraged on a wide variety of prey species from the size of a beetle, dragonfly, or warbler (<15 g) to prey of the size of a snowshoe hare, muskrat (*Ondatra zibethica*), or mallard (*Anas platyrhynchos*) (all >1.2 kg). Snowshoe hares were clearly the predominant prey in summer diets during the peak of the cycle (83.2–90.1% during 1989–1991) but declined to 18.8–27.4% during the low phase in the summers of 1992–1994 (figure 15.6A; a more detailed account is given for 1989–1992 in table 15.5). During this time, hares were mostly substituted by voles (11.7–59.1%), red squirrels (*Tamiasciurus hudsonicus*; 1.8–33.4%), ground squirrels (*Spermophilus parryii*; 1.7–22.5%), birds (9.3–19.6%), and other mammals such as muskrats, woodrats (*Neotoma* sp.), northern flying squirrels (*Glaucomys sabrinus*), and least weasels (*Mustela nivalis*; 0–10.4%). Among birds, all major groups were represented including ducks, grouse, shorebirds, corvids, woodpeckers, and other owls and raptors (see also Rohner and Doyle 1992, Rohner et al. 1995). It appears that waterfowl migration in spring made up a substantial portion in the diet of breeding great horned owls.

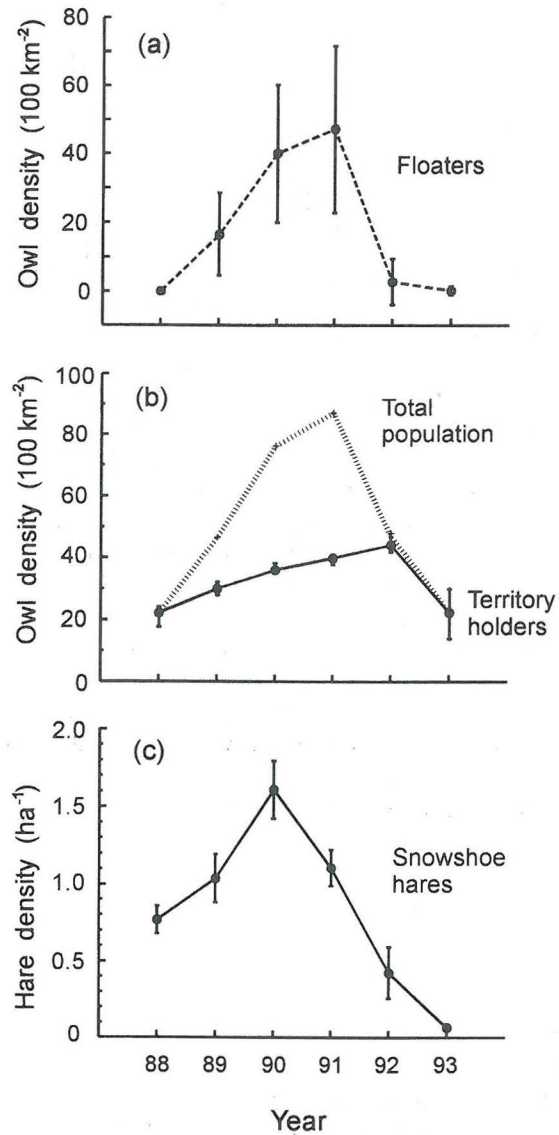


Figure 15.5 Numerical response of great horned owls (spring densities) to the snowshoe hare cycle. (a) Density of nonterritorial owls (floaters) estimated by the population model (with standard deviation); (b) census of the territorial owl population (with minimum and maximum estimates) and estimate of the total population (sum of territorial and nonterritorial owls); (c) spring densities of snowshoe hares (with SEs) from live trapping. From Rohner (1996).

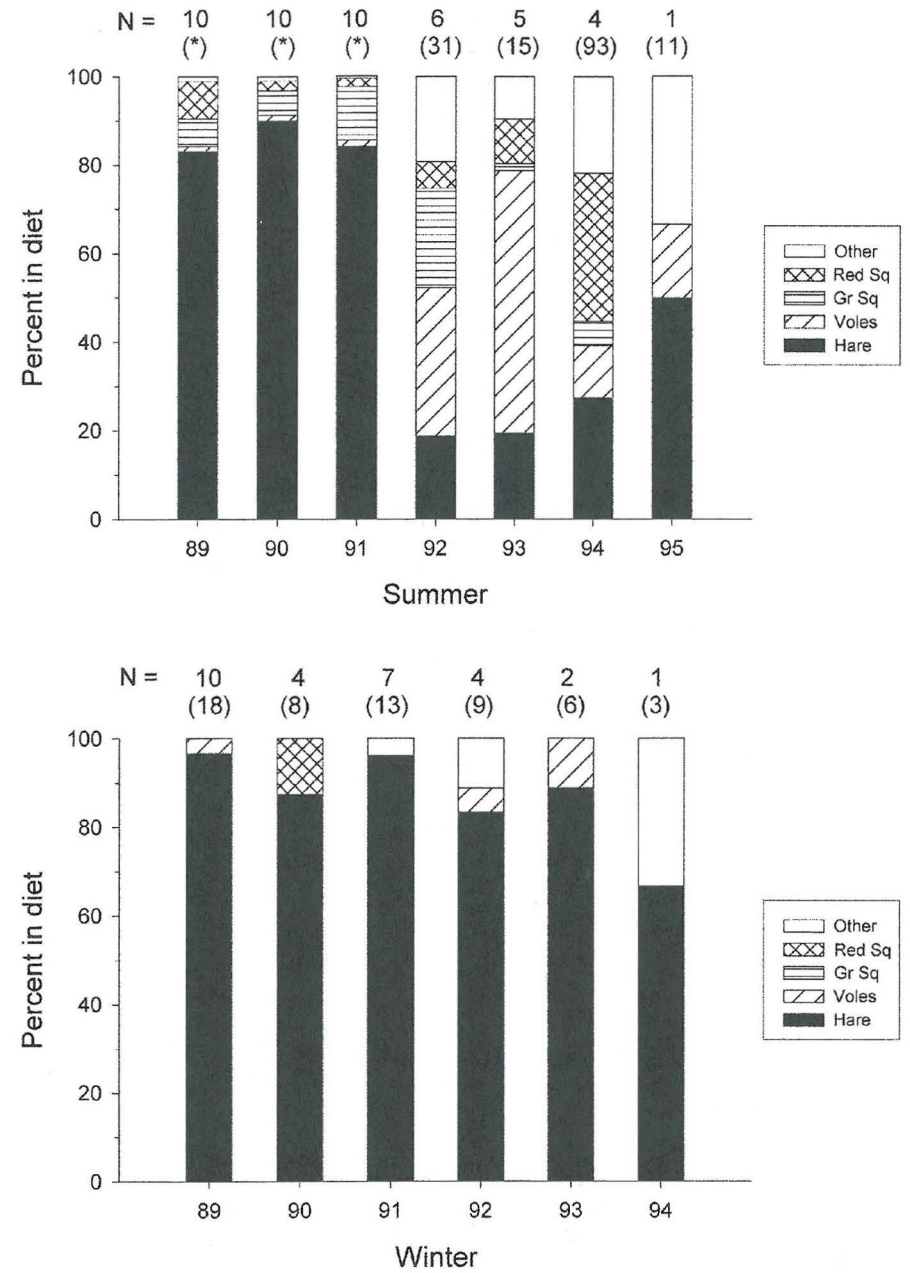


Figure 15.6 Proportions of main prey species in the diet of great horned owls in the boreal forest at Kluane Lake Yukon, during 1989–1995, based on pellet analysis. Sample sizes (number of territories sampled, with total number of pellets collected in parentheses) are given above the bars. Asterisks refer to years with >500 pellets and the total prey biomass accounted for in table 15.5. (a) Summer diet (mid-April–mid-October); (b) winter diet (mid-October–mid-April).



Table 15.5 Great horned owl diet, 1989–1992 at Kluane Lake, Yukon, according to minimum counts of prey species from pellets collected during the breeding season (10 territories 1989–1991, 6 territories 1992).

Prey Species	% Mass (n)				
	1989	1990	1991	1992	1989–92
Adult hares	53.8 (47)	42.8 (42)	50.5 (33)	0 (0)	48.0 (122)
Juvenile hares	29.3 (163)	47.3 (295)	33.7 (140)	18.8 (4)	37.2 (602)
Ground squirrels	6.3 (22)	5.6 (22)	12.2 (32)	22.5 (3)	7.8 (79)
Red squirrels	8.5 (37)	2.2 (11)	1.8 (6)	6.0 (1)	4.3 (55)
Voies	1.1 (44)	1.2 (54)	1.4 (42)	33.4 (52)	1.6 (192)
Birds	1.0 (4)	0.9 (4)	0.3 (1)	19.3 (3)	1.0 (12)
Total	100 (317)	100 (428)	100 (254)	100 (63)	100 (1062)

Proportions of prey categories are expressed as the percentage of total prey mass in the diet (number of prey items in parentheses).

Winter diets of great horned owls were remarkably different from summer diets. The proportion of snowshoe hares in winter diets was similar to that in summer diets as long as hare densities were high, but an important difference was observed during the hare decline (figure 15.6B). In winter, the proportion of hares remained high (66.7–96.2%) despite the low hare numbers. Apparently, in the boreal forest at this latitude, alternative prey is difficult to find in winter. Most birds have migrated to southern climates, and most small mammals are either hibernating or active under the snow (see also Pruitt 1978). We suspect that we may have somewhat underestimated the proportion of less frequent prey items, such as grouse because our small sample sizes were likely to result in rounding errors of small fractions. Most pellets were collected in the last part of winter, and more information on early winter diets is desirable.

### 15.3.2 Prey Preferences

Although great horned owls are known as generalist predators, there were pronounced differences in the selectivity of certain prey species by great horned owls (table 15.6). Snowshoe hares were 1.8 times more prevalent in the diet than expected from the relative availability in the environment. Voies were taken approximately in proportion to measured densities, and ground squirrels were slightly avoided. Red squirrels were the least preferred species and were 9.2 times less prevalent than snowshoe hares (table 15.6). There were strong differences between seasons.

During summer, the values of Manly's alpha (preference index) were  $0.44 \pm 0.11$  and  $0.32 \pm 0.06$  for voies and hares, respectively (table 15.6). When plotting use versus availability, this resulted in a convex curve above the line of equal representation (figure 15.7). For hares, the data points at low densities are close to the line of equal representation, and prey switching (*sensu* Murdoch and Daten 1975) may occur. To establish the vulnerability of juvenile and adult hares to predation by great horned owls, we calculated Manly's alpha for diet samples from 30 territories during the summers of 1989–1991 (14 different territories) and compared these data to a more detailed estimation of age-specific hare

Table 15.6 Prey selection by great horned owls in the boreal forest at Kluane Lake in southwestern Yukon.

Prey Category	Summer (n = 7)		Winter (n = 6)		All Seasons
	Factor <sup>a</sup>	Manly's $\alpha$	Factor <sup>a</sup>	Manly's $\alpha$	Factor <sup>a</sup>
Snowshoe hares	1.27	$0.32 \pm 0.06$	2.51	$0.83 \pm 0.09$	$1.84 \pm 0.25$
Voies	1.78	$0.44 \pm 0.11$	1.13	$0.12 \pm 0.09$	$1.13 \pm 0.32$
Red squirrels	0.24	$0.06 \pm 0.02$	0.20	$0.05 \pm 0.05$	$0.20 \pm 0.08$
Ground squirrels	0.71	$0.18 \pm 0.06$	0.71	—	$0.71 \pm 0.22$

Given are means and standard errors for summers (1989–1995), winters (1989–1994), and both seasons pooled (numbers of territories and pellets as in figure 15.7). Manly's  $\alpha$  is an index describing the relative preference for prey categories in each season (sum = 1). The preference factor describes deviations from equal representation in diet and environment and is comparable across seasons (preference >1, avoidance <1).

<sup>a</sup>Factor =  $(\alpha_i / \sum \alpha_i / m_i)$ , where  $m_i$  = number of prey categories.

densities in summer (Rohner and Krebs 1996). The preference of great horned owls for juvenile hares was much higher than the preference for adult hares (juvenile,  $\alpha = 0.68$  vs. adult,  $\alpha = 0.32$ , SE = 0.04,  $p < .001$ ; Wilcoxon rank test for paired samples).

Ground squirrels were taken at similar proportions as available during summer (Manly's  $\alpha = 0.18 \pm 0.06$ , slightly below the neutral  $\alpha$  of 0.25). Red squirrels were the least preferred of these prey species (table 15.6), resulting in a clearly concave curve below the line of equal proportions (figure 15.7).

Winter results were remarkably different (table 15.6). As illustrated in figure 15.8, there was a strong preference for snowshoe hares ( $\alpha = 0.83 \pm 0.09$ , factor 2.5), whereas voies were underrepresented in winter diets ( $\alpha = 0.12 \pm 0.09$ , factor 0.4), presumably because they were less accessible due to snow cover. Red squirrels were selected for 1.5 times less than in summer, possibly due to the reduced activity of red squirrels in winter.

### 15.3.3 Estimating Functional Responses and Predation Impact

Functional responses predict specific kill rates of predators in relation to changing prey densities (e.g., Holling 1959). Such measurements of the number of prey killed by a predator per unit time are extremely difficult to obtain for elusive species such as great horned owls. We estimated the kill rate, KR, of a prey type  $i$  as

$$KR_i = D_i M_c A R W_i t, \quad (1)$$

where  $D_i$  = proportion of prey type  $i$  in diet,  $M_c$  = average biomass consumed per day,  $A$  = activity level,  $R$  = increase needed for reproduction (e.g., mass delivered to dependent young),  $W_i$  = wastage of prey type  $i$  (parts of kill that are not consumed), and  $t$  = number of days over which kill rate is calculated. A minimum estimate of  $M_c$  can be obtained from studies of existence metabolism in captive owls. Data from allometric equations, specific metabolic measurements, and feeding trials indicate a daily consumption of approximately 0.15 kg live prey mass per owl (Craighead and Craighead 1956, Kendeigh et

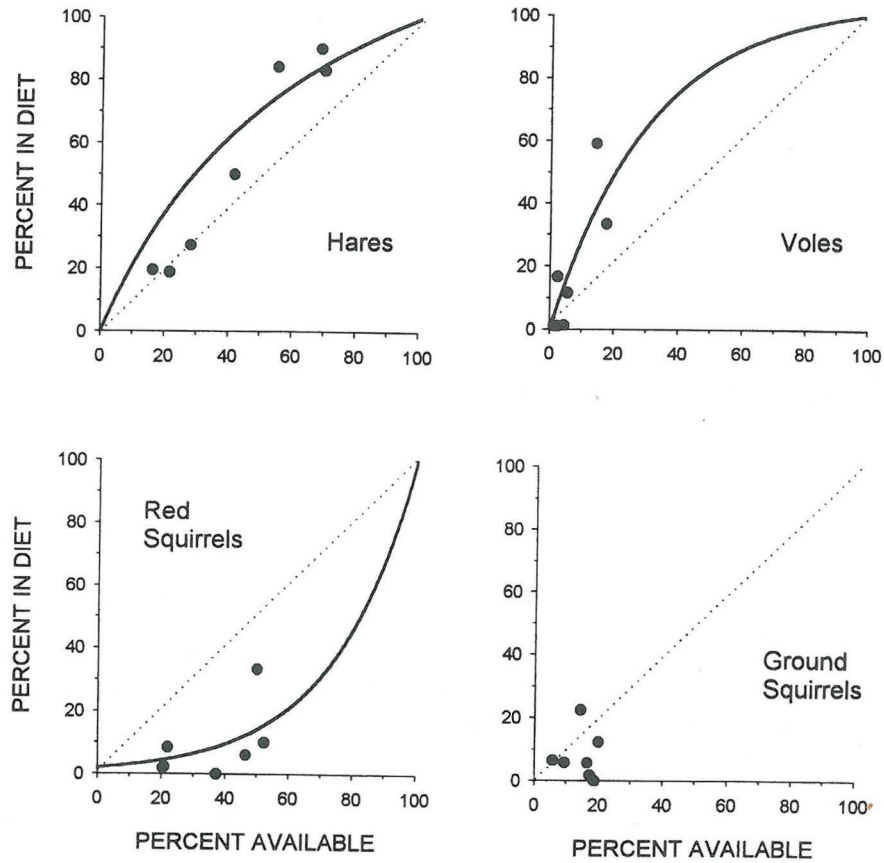


Figure 15.7 Responses in summer diets of great horned owls to changes in relative availability of the major prey species. Preference for a prey type is indicated when points lie above the line of equal representation; avoidance is indicated when points are below the line. A change from underrepresentation at low prey densities to overrepresentation at high densities is evidence for prey switching.

al. 1977, Kasparie 1983). This consumption is further modified by the costs of reproduction,  $R$ , and other increases of activity levels in the field (e.g., cost of flight;  $A$  has been estimated from 1.01 to 2.5; Kasparie 1983, Wijnandts 1984). We approximated  $R$  by calculating the number of fledglings per territorial owl (table 15.2). Because data are not available on  $A$  and  $W$  for great horned owls, we did not use these parameters in our calculations. Therefore, the functional responses presented are minimum estimates.

Overall, great horned owls showed a strong functional response to the snowshoe hare cycle (figure 15.9c) and closely followed the theoretical prediction of a type-2 functional response (Holling 1959, Fujii et al. 1986):

$$KR = a N_0 / (1 + a T_H N_0) \quad \text{with } T_H = 1/A_{\max}, \quad (2)$$

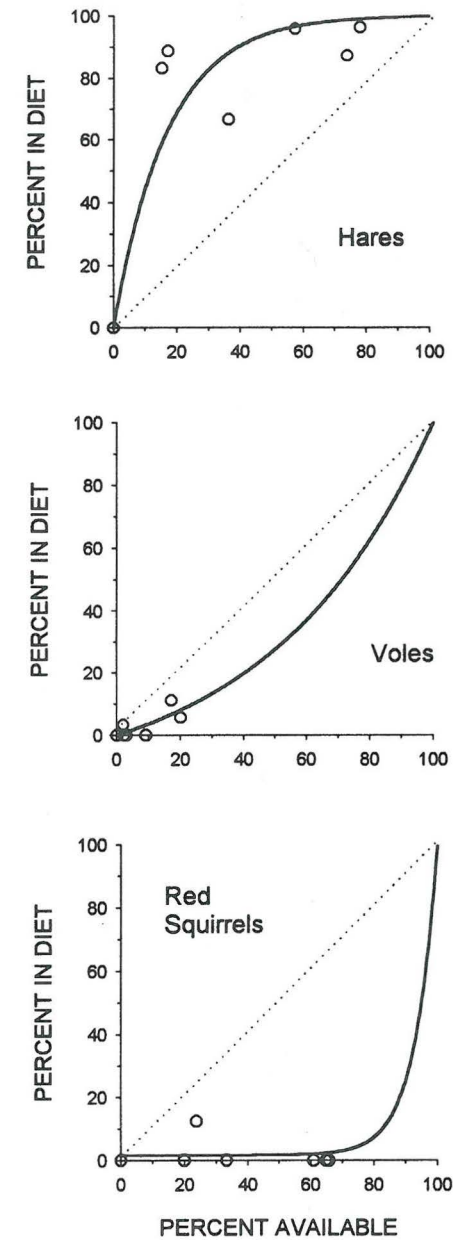


Figure 15.8 Responses in winter diets of great horned owls to changes in relative availability of the major prey species. Preference for a prey type is indicated when points lie above the line of equal representation; avoidance is indicated when points are below the line. A change from underrepresentation at low prey densities to overrepresentation at high densities is evidence for prey switching.

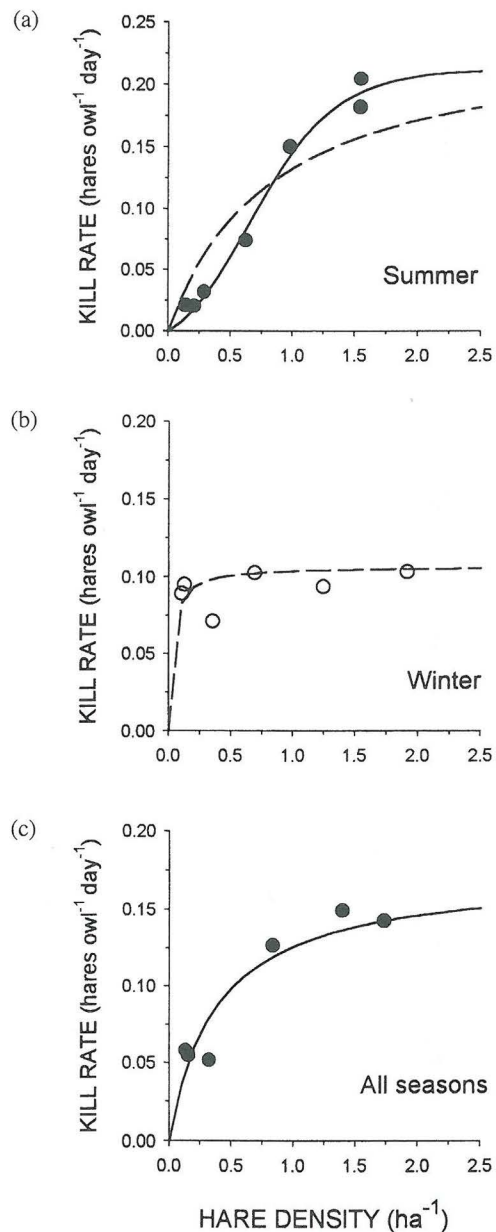


Figure 15.9 Minimum estimates of functional responses by great horned owls (kills per owl per day) to changing snowshoe densities, with curves from Holling's disc equation fitted to the data (Fujii et al. 1986). (a) Summer (mid-April–mid-October, average of hare densities in spring and autumn); (b) winter (mid-October–mid-April, average of hare densities in autumn and spring); (c) all seasons (average of summer and winter).

whereas  $N_0$  = hare density/(ha<sup>-1</sup>),  $a$  = 0.456 (coefficient indicating prey preference),  $A_{\max}$  = 0.174 hares(owl<sup>-1</sup>day<sup>-1</sup>), asymptotic maximum of kill rate, KR. In other words, the handling time,  $T_H$  (or time interval between kills), was estimated at 5.7 days on average throughout the year. But figure 15.9 also shows a strong difference in the functional responses during summer and winter.

During summer, the kill rate of great horned owls responded strongly to changing snowshoe hare densities. We estimated  $A_{\max}$  at 0.24 hares(owl<sup>-1</sup>day<sup>-1</sup>) from a maximum increase,  $M_c$ , of 2.5 fledglings per owl pair, and using a type-2 functional response, curve fitting yielded  $a$  = 0.297 ( $n$  = 7,  $r^2$  = 0.84). However, a sigmoid type-3 (Holling 1959, Fujii et al. 1986) provided a better fit to the data:

$$KR = a N_0 / [a N_0 / A_{\max} + \exp(-2 N_0)], \quad (3)$$

with a parameter estimation for both  $a$  = 0.063 and  $A_{\max}$  = 0.213 hares(owl<sup>-1</sup>day<sup>-1</sup>) ( $n$  = 7,  $r^2$  = 0.98). A different approach to estimate the kill rate during breeding consisted of calculating the prey biomass from remains found in pellets (table 15.5). The daily biomass brought to owlets during 1989–1991 was  $353 \pm 50$  g,  $375 \pm 58$  g, and  $192 \pm 43$  g, respectively. This translates into a kill rate of 0.21, 0.24, and 0.12 hares per day, and these results were similar to the estimates based on energetic demands (figure 15.9a) of 0.18, 0.20, and 0.15 hares per day. A third method based on the dry weight of pellets yielded somewhat higher estimates. In 1989,  $26.2 \pm 4.2$  g of dry pellet mass were delivered daily to tethered owlets. Assuming the assimilation efficiency measured by Kasparie (1983), this translates into a total of 502 g of live prey, or an estimated kill rate of 0.30 hares per day.

During winter, great horned owls were almost entirely dependent on snowshoe hares as their main diet, resulting in a flat curve with estimated kill rates close to the asymptote throughout the hare cycle ( $a$  = 3.678,  $A_{\max}$  = 0.11,  $n$  = 6,  $r^2$  = .98).

These kill rates from functional responses were then combined with the numerical response (figure 15.5) to produce a minimum estimate of the predation impact on the snowshoe hare population (table 15.7). The results indicate that great horned owls killed at least 5–10% of the hare population in peak winters, and possibly had an even larger impact during declining and low densities.

Table 15.7 Estimates of predation impact by great horned owls on snowshoe hares during winter at Kluane Lake, Yukon (see text for details).

Year	Hares/km <sup>2</sup>	Kill Rate (hares/owl/day)	Owls/km <sup>2</sup>	Days Exposed	Hares Killed/ km <sup>2</sup>	Predation Impact (%)
1988–89	228	0.10	0.53	180	9.85	4.3
1989–90	235	0.09	0.78	180	13.15	5.6
1990–91	162	0.10	0.94	180	17.35	10.7
1991–92	109	0.09	0.49	180	7.92	7.3
1992–93	13	0.10	0.29	180	4.97	38.2
1993–94	20	0.07	0.21	180	2.72	13.6

## 15.4 Social Organization

### 15.4.1 Social Status and Vocal Activity

The long life spans of radio transmitters allowed us to examine the integration of fledglings into the breeding population. Only 15% (3 of 20) settled in territories before the end of their first year of life (for details, see Rohner 1996). None of the 9 owls that were further monitored in the study area to the end of their second year of life settled during that time, or showed any sign of hooting or other territorial defense. To test whether these non-territorial floaters would normally be included in a census, we monitored a number of radio-tagged owls within hearing range to record their hooting activity from 3 March to 27 April 1990. Hooting activity was measured as the duration of bouts, each of them considered to be finished when more than 5 min elapsed between hoots.

Almost all territorial males, and often also females, gave territorial challenges at least for a short time, particularly at dusk and dawn (see also Rohner and Doyle 1992). In 11 territories that were monitored for a total of 32.0 h between dusk and midnight, all males were recorded giving territorial challenges. Their hooting bouts lasted 26.7% of the total time. Of six individual floaters that were monitored for a total of 16.8 h between dusk and midnight, none of them gave a territorial challenge or any other call.

During the same time period, known territorial and nonterritorial owls were tested for their responsiveness to playback. Territorial challenges were broadcast at irregular intervals for a total duration of 20 minutes from a tape-recorder, and each individual was tested in one trial. Seventeen out of 24 territorial males (70.8%) responded vocally. Two out of six floaters approached the speaker as concluded from telemetry readings, but none of them responded with a vocal signal that would have allowed their detection during a standard census (Fisher's Exact test,  $p < .01$ ,  $df = 1$ ,  $n = 30$ ).

### 15.4.2 Stability and Size of Home Ranges

In contrast to territorial owls, which formed stable pairs on distinct territories, floaters showed a variety of movement patterns (Rohner 1997). Some individuals concentrated their space use more than others, brief long-distance movements occurred, and one floater shifted its home range  $>20$  km. Despite this variation, there was a consistent pattern of stable home ranges with occasional movements beyond the area normally used. Median shifts in the centers of activity between subsequent 4-month periods ranged from 2.1 to 4.1 km for floaters, but were only 0.2–0.9 km for territorial owls (Mann-Whitney  $p < .05$  for all 4-month periods,  $n > 5$ ). As a comparison, we also calculated median shifts in home range centers for the entire monitoring periods of individual birds (average  $12.6 \pm 0.6$  months per owl). These shifts ranged from 0.6 to 28.3 km (median 5.8 km) for floaters and from 0.2 to 3.11 km (median 1.2 km) for territorial birds ( $p = .006$ , Mann-Whitney  $U = 128$ ,  $n_1 = 9$ ,  $n_2 = 17$ ).

Territory sizes were much smaller than floater home ranges. Based on weekly locations, floaters covered a 90% area of 12.0–48.3 km<sup>2</sup> in 1990 and 4.75–69.4 km<sup>2</sup> in 1991. On average, these values were  $26.1 \pm 5.7$  km<sup>2</sup> and  $24.8 \pm 8.1$  km<sup>2</sup> (details in Rohner 1997). In contrast, there were 18–19 territorial pairs per 100 km<sup>2</sup> in 1990 (Rohner 1996; i.e., average territory size was 5.26–5.56 km<sup>2</sup>). In 1991, the boundaries of 16 territories

were mapped by observing encounters of hooting males. Territory sizes ranged from 2.30 to 8.83 km<sup>2</sup>, with an average of  $4.83 \pm 0.40$  km<sup>2</sup>.

A more direct comparison of space use between territorial and nonterritorial owls consisted of a 3-week period in September 1990 and 1991 with locations for each night (Rohner 1997). There was a significant effect of social class not only for 90% areas but throughout different core percentages, while patchiness in space use and year effects were not significant (Rohner 1997).

Home range sizes of territorial owls decreased from 1989 to 1992 ( $r = -.64$ ,  $n = 19$ ,  $p < .001$ , details in Rohner and Krebs 1998). Because hare densities declined during the same time, it is an obvious hypothesis that the observed changes in space use are a direct function of varying prey density. Hare density, however, explained only a small portion of the variance in home range size ( $r^2 = .163$ ,  $F_{1,2} = 0.39$ ,  $p = .59$ ). At the same time, the owl population increased, leading to a more densely packed array of territories in the study area. Thus, declining territory size explained considerably more of the variation in space use of these owls than prey density ( $r^2 = .846$ ,  $F_{1,2} = 10.95$ ,  $p = .08$ , details in Rohner and Krebs 1998).

### 15.4.3 Effect of Territoriality on Spacing of Owls

Nonterritorial owls overlapped broadly with other owls of the same social class (figure 15.10). On average, mononuclear 90% areas overlapped by  $23.3 \pm 4.8\%$  and multinuclear 90% areas overlapped by  $28.8 \pm 6.4\%$  ( $n = 23$  overlappers and  $n = 18$  overlappers, respectively, only for combinations of floaters that were monitored simultaneously and had  $>1\%$  overlap). There were no consistent differences between 1990 and 1991. Some overlapped with up to four other monitored floaters (figure 15.10), and the highest overlap observed with one other floater was 87.8% (mononuclear 90% area in 1991).

Floaters were not restricted to areas outside of established territories and intruded widely into several territories (all mononuclear 90% ranges of figure 15.10 overlapped with at least five territories in the area of figure 15.11 where territorial boundaries were known). On a finer scale, however, some spatial segregation became apparent (figure 15.11). Four of five floaters were located significantly closer to territorial boundaries than expected from a random pattern (Rohner 1997). The median distance of random points to territorial boundaries was 0.343 km, the overall median of the results for individual floaters (not the median of the pooled data) was 0.229 km. This deviation of 33% was significantly different from random (bootstrap  $p < .001$ ).

### 15.4.4 Territorial Behavior and Limitation of Population Increase

Predators are usually larger, live longer, and have fewer offspring than their prey (Taylor 1984, Stearns 1992). This translates into a lower rate of increase for populations of long-lived species, as illustrated in figure 15.12. The yearly finite rate of increase at Klunane was  $\lambda = 1.22$  for great horned owls in comparison to  $\lambda = 1.5$ –1.8 for snowshoe hares (details of calculation in Rohner 1995). An almost identical pattern was found in Rochester, Alberta, during an earlier cycle with peak hare densities in 1971 (analysis of data from Adamcik et al. 1978; figure 15.12B). Although the values for absolute densities

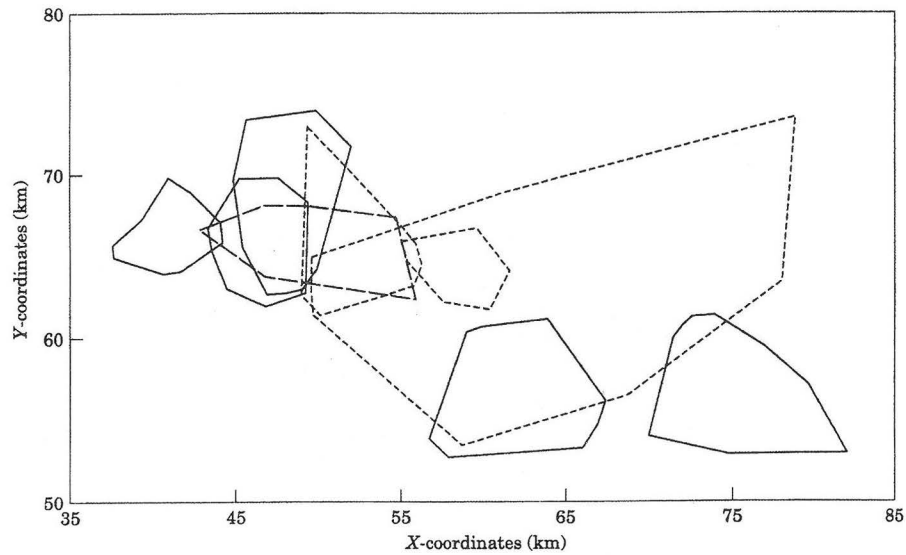


Figure 15.10 Spatial overlap among nonterritorial owls in the study area. The home ranges presented are based on 90% areas calculated by mononuclear clustering. Five owls monitored both in 1990 and in 1991 are identified by solid lines, one owl monitored only in 1990 by a broken line, and three owls monitored only in 1991 by dotted lines. From Rohner (1997).

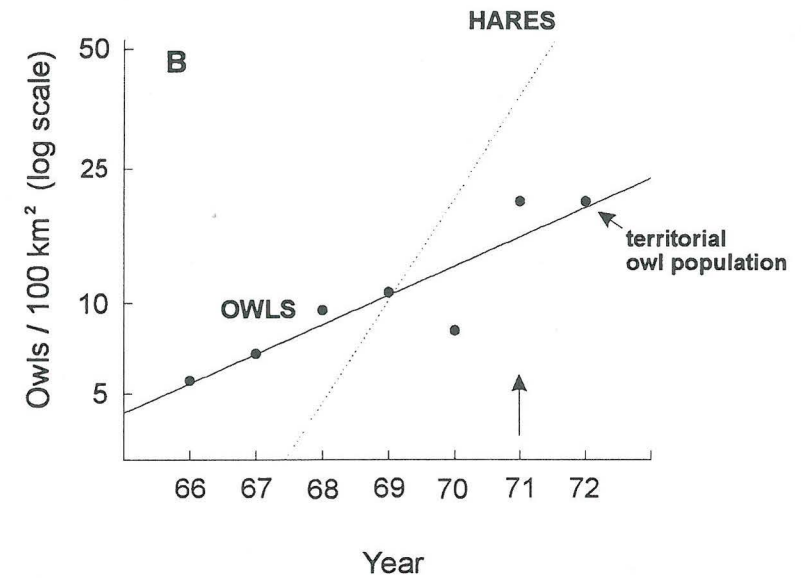
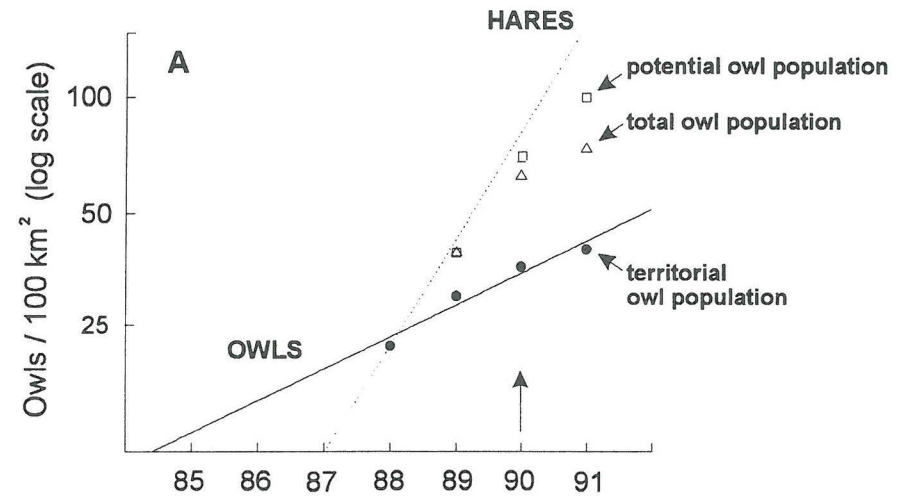


Figure 15.12 Annual rates of increase (slopes) in populations of great horned owls (solid line, symbols) and snowshoe hares (broken line, slope overlaid onto owl scale). Years of peak hare densities are indicated by arrows. (a) Kluane, Yukon; (b) Rochester, Alberta (data from Adamcik et al. 1978). From Rohner (1995).

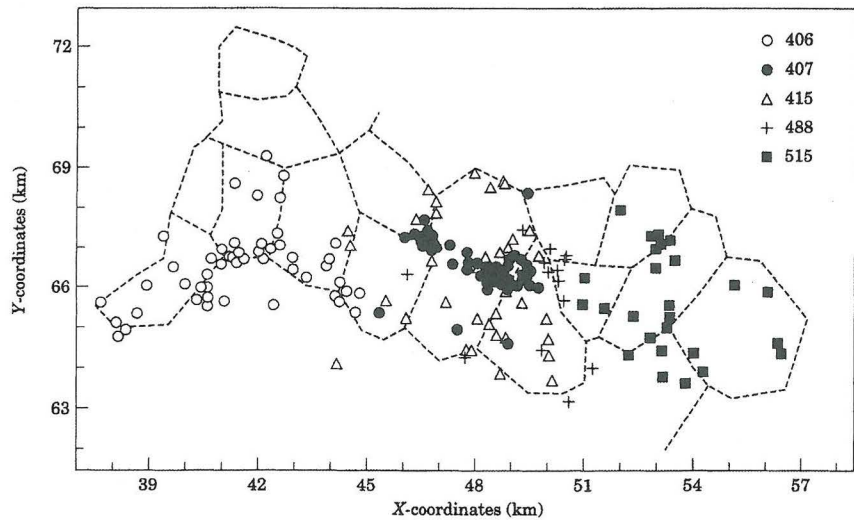


Figure 15.11 Locations of floaters relative to territorial boundaries during the period of September 1990–June 1991. Five individual floaters (see table 15.8) are represented with different symbols and a total of 198 locations. All locations are shown within the minimum convex polygon that connects the outermost corners of these known territories. Less precise locations with 95% error areas  $>0.5 \text{ km}^2$  were excluded. From Rohner (1997).

were somewhat different, the rates of increase were similar, with  $\lambda = 1.26$  for owls and  $\lambda = 1.8$  for hares.

This result may not be surprising, but it is interesting that the differences in population growth almost disappeared when nonterritorial floaters were taken into account ( $\lambda = 1.5$ ; figure 15.12A). This phenomenon is even more pronounced when a population model is used to simulate the potential rate of increase under the assumption that young owls (which in reality became floaters) could establish territories and breed as yearlings ( $\lambda = 1.66$ ).

These findings suggest that territoriality, or, more precisely, the social exclusion from breeding, limited the increase of the predator population. This can also be illustrated by testing demographic parameters for density dependence. In agreement with the hypothesis of social exclusion, the population growth of territorial owls declined with increasing density of territories already established (figure 15.13A). Meanwhile, the floater pool of nonterritorial owls increased as territories became packed more densely (figure 15.13B).

The best evidence for the limitation of breeding densities by social exclusion is drawn from removal experiments (reviews in Watson and Moss 1970, Newton 1992). While monitoring radio-marked birds, we observed six vacancies in territories, which served as natural removal experiments. Territory holders either died or emigrated, and we recorded whether these vacancies were filled with new birds. In at least five of six vacancies, such replacements occurred (details in Rohner 1995).

All of the above results indicate that competition among owls was severe, and that this predator population was food limited even at extremely high prey densities. Usually, predators have been assumed to experience superabundant food in peak years of cyclic prey (e.g., Lack 1946). A combination of brood-size manipulations and food additions, however, suggested that this was not the case (Rohner and Smith 1996). Owlets in temporarily enlarged broods lost weight, apparently because their parents could not easily increase provision rates (Rohner and Smith 1996). In addition, mothers of enlarged broods ranged farther away from nests, probably because they were forced to hunt under food stress (Rohner and Smith 1996). In agreement with this hypothesis, food additions to enlarged broods rapidly returned the parental behavior to normal (Rohner and Smith 1996).

#### 15.4.5 Social Behavior and the Time Lag in the Numerical Response

Predator populations often decline with a time lag after the peak of prey cycles. This delay can be explained by two hypotheses (Rohner 1995): densities of the main prey species are extremely high, leave predators with superabundant food, and buffer their decline (single prey hypothesis, SPH). Alternatively, the availability of other prey is high and thus delays the decline of generalist predators (multiple prey hypothesis, MPH).

Social exclusion among owls seemed to set a ceiling to their peak densities (figure 15.5B). This situation is in agreement with the SPH, but the presence of a large floater pool, the complete failure to breed during the prey decline (figure 15.1, table 15.2), and indications of food stress during the brood-size manipulations suggest that food was not superabundant when great horned owls showed a time lag in their numerical response to the decline of snowshoe hares.

The predictions of the MPH were met for summer diets, when great horned owls took

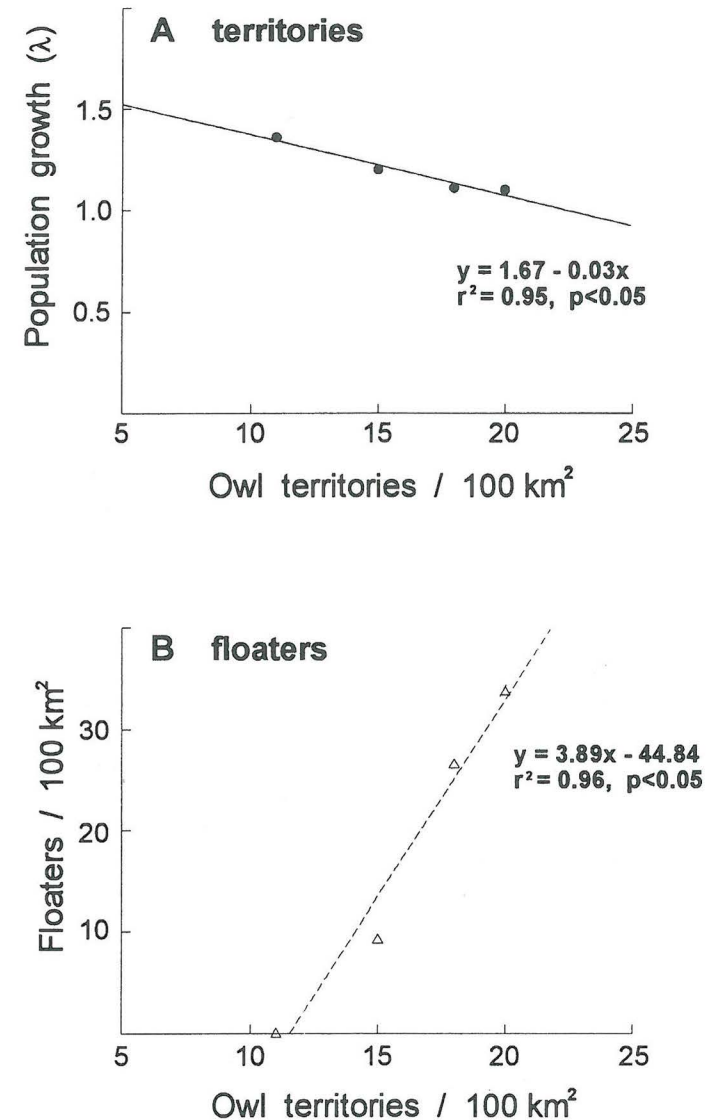


Figure 15.13 Social behavior and the limitation of population growth in great horned owls at Kluane, Yukon. (A) Growth rates of the territorial population decline as numbers of owl territories increase in the area (inverse density-dependent growth rate); (B) numbers of nonterritorial floaters increase as territories are packed more densely (density-dependent increase). From Rohner (1995).

more alternative prey and fewer hares during the low phase of the cycle (figure 15.6A). But during winter, the proportion of hares as the main prey remained high throughout the cycle (figure 15.6B), probably due to a lack of other available prey at these northern latitudes. This result emphasizes the dependence of great horned owls on snowshoe hares.

Therefore, neither the SPH nor the MPH are satisfactory explanations for the delayed decline of great horned owls relative to the snowshoe hare cycle. The key to understanding the processes involved seems to lie in the behavior of individuals (see 15.6.4).

## 15.5 Responses to Large-Scale Experiments

### 15.5.1 Space Use in Territories with Experimental Hot Spots of Prey

The contrast between prey density on artificially created hot spots and on the study area in general increased drastically from 3.8- to 10.3-fold as the decline of the snowshoe hare cycle progressed (Rohner and Krebs 1998; see chapter 8). Therefore, we investigated owls on two experimental territories that were accessible for telemetry work in more detail in 1992, when the response of predators was expected to be greatest. Food shortages for great horned owls during this year were indicated by a complete lack of breeding attempts and elevated rates of emigration and mortality by resident owls (details in Rohner 1996).

Results from experimental owls did not confirm a direct effect of prey density on home range use. Owls on territories with hot spots did not differ in home range size from owls on control territories (ANCOVA,  $F_{1,16} < 0.1$ ,  $p = 0.99$ ; details in Rohner and Krebs 1998). However, a more powerful randomization test revealed clear concentrations in space use of owls on territories with experimental hot spots. We modeled the null hypothesis of uniform space use by randomly generating 5000 points within the known boundaries of these territories. The distances of these points to the center of the territory (geometric mean) were then calculated and grouped into classes of 200 m, thus representing an expected frequency distribution of uniform space use within a territory. The actual telemetry locations of experimental owls were then compared to this expected distribution. If the owls behaved according to the null hypothesis, no systematic and significant deviation from the expected distribution should occur. This, however, was not the case. The results showed regions that were used more frequently than expected for both experimental owls. For owl no. 544, the mean of positive deviation from the expected values was 5.35 ( $p < .01$ ); for owl no. 503 this mean was 9.20 ( $p = .02$ ).

Were these concentrations in space use related to hot spots in hare abundance? Telemetry locations were compared to the experimental blocks of manipulated prey densities, and the distances to the center of these 1-km<sup>2</sup> blocks were calculated (figure 15.14). Both experimental owls showed a positive response when compared to the expected distributions as calculated from points randomly generated within the boundaries of their territories. For owl no. 544, the distance was  $0.846 \pm 0.050$  km ( $n = 152$ ) from the center of the hot spot (mean expected distance 1.534 km, bootstrap  $p < .001$ ). For owl no. 503, this distance was  $0.741 \pm 0.087$  km ( $n = 41$ , mean expected distance 1.179 km, bootstrap  $p < .001$ ).

Data from pellet analysis of territorial owls support that these concentrations in space use were related to foraging activity. Summer diets of great horned owls consisted of

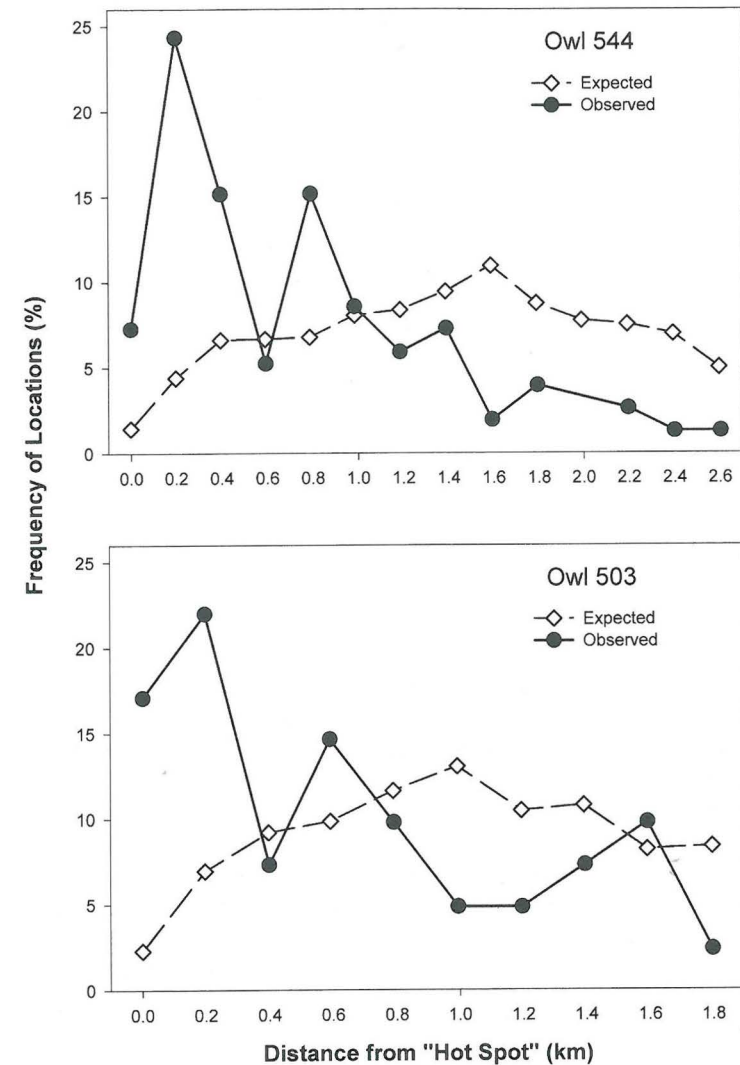


Figure 15.14 Concentrations in space use of two experimental owls relative to the center of 1-km<sup>2</sup> blocks with increased prey density. Locations were grouped into distance classes and shown as frequency distribution of observed locations (filled symbols) and expected frequencies from random locations in the specific territories (open symbols). From Rohner and Krebs (1998).

82.6–86.0% snowshoe hares in 1989–1991 when hare abundance was high ( $n = 13$  different territories; see also pooled data in figure 15.6). In 1992, this portion dropped to  $12.7 \pm 8.5\%$  (range 0–42.3%,  $n = 5$  territories). We were able to collect pellets from one experimental owl in summer 1992. In contrast to controls, the diet of experimental owl no. 544 consisted of a high portion (64.7%) of snowshoe hares (see also figure 15.6).

Table 15.8 Shifts in space use by nonterritorial great horned owls in relation to experimental hot spots of high prey density.

Individual	$N_1$	$N_2$	$D_1$ (km)	$D_2$ (km)	$D_2 - D_1$ (km)	$p$
406	71	20	10.858	11.070	0.211	.153
407	61	5	5.221	7.091	1.876	.092
415	72	14	4.454	4.967	0.513	.674
417	25	22	4.564	3.545	-1.019	.258
425	52	15	8.723	11.380	2.657	.003
433	60	13	5.178	6.115	0.937	.076
505	25	31	4.890	12.700	7.810	.001
515	38	19	1.800	3.667	1.868	.021

For each monitored owl, the median distances of weekly telemetry locations to the center of the closest experimental block are shown for the peak ( $D_1$ , January 1990–May 1991) and decline phase of the snowshoe hare cycle ( $D_2$ , June 1991–September 1992), with sample sizes of telemetry locations ( $N_1$ ,  $N_2$ ) and levels of significance for the difference  $D_1 - D_2$  (U-test, two-tailed). From Rohner and Krebs (1998).

### 15.5.2 Predator Movements from Poor Patches to Rich Patches

During the decline phase of the hare cycle, territorial owls were predicted to abandon poor territories and intrude at least temporarily into territories with hot spots of high prey abundance. Despite intensive monitoring, we did not observe any owners leaving their territories to use food-addition blocks or changing to a nomadic strategy on the >350 km<sup>2</sup> study area (for details, see Rohner 1996).

Although nonterritorial floaters were present in the study area, these owls did not aggregate in areas with food enrichment, and despite intensive monitoring, we were unable to detect an association of floaters with hot spots of high prey abundance. Table 15.8 summarizes the results on potential shifts of 8 nonterritorial owls toward hot spots during a time when the abundance of hares in these patches increased from 3.8- to 10.3-fold compared to control levels in the study area (see Rohner and Krebs 1998). There was no distinct pattern, and the only significant shifts in space use by three owls were opposite to the predicted direction.

## 15.6 Discussion

### 15.6.1 Large Floating Population When Resources Are Abundant

This study demonstrates a profound effect of resource availability on reproduction, juvenile survival, and emigration in a predator of cyclic prey. The fraction of nonterritorial owls rose to 40–50% of the population during years of high food abundance. The numerical responses of territorial and nonterritorial birds were qualitatively different, and the notion that such a high proportion of secretive floaters can occur may require a re-

assessment of results that are entirely based on the territorial and therefore visible fraction of a population (Rohner 1996).

In considering both academic research and applied management questions, many studies have attempted to examine the impact of predators on prey populations (review in Krebs 1994). A common method is to census predator and prey populations, identify the diet of predators, and calculate the predation mortality among prey (e.g., Craighead and Craighead 1956, Keith et al. 1977, Petersen 1979, Angelstam et al. 1984, Trostel et al. 1987, Korpimäki and Norrdahl 1991, Korpimäki 1993). In this study, the proportion of secretive floaters was high, and predation pressure on prey would have been severely underestimated when taking only territorial birds into account. This problem may also arise in other systems where floaters are difficult to detect.

Our results also demonstrate how a large proportion of secretive floaters can delay the detection of population declines in conservation studies. When, as here, floaters are more affected by decreasing habitat quality than are territorial birds, traditional monitoring programs based on censusing territories will not reveal these declines at an early stage (Wilcove and Terborgh 1984). For example, in a scenario for spotted owl populations, Franklin (1992) estimated that declines in territorial owls could not be detected for 15 or more years when floaters were present even at low densities.

### 15.6.2 Factors Affecting Functional Responses and Predation Impact

Great horned owls showed strong preferences for specific prey species, mostly for snowshoe hares and voles and, among vole species, *Microtus* over *Clethrionomys* (see also Rohner et al. 1995). A major behavioral mechanism accounting for these differences lies in the habitat selection of both predator and prey. The hunting success of great horned owls on snowshoe hares was highest in open habitat with shrub and tree cover below average (Rohner and Krebs 1996), and snowshoe hares appear to select for dense cover as an antipredator behavior (Hik 1995). Voles are less accessible to great horned owls during winter because they are active below snow cover, and, at the same time, the loss of leaves reduces shrub cover for snowshoe hares outside the growing period and exposes them to higher predation by owls (see also Sonerud 1986). Several lines of evidence suggest that great horned owls prefer to hunt in open habitat (Rohner and Krebs 1996), and since field voles (in particular *Microtus pennsylvanicus*) prefer open grassy habitat, this may also account for the surprisingly low representation of the forest-dwelling red-backed voles (*Clethrionomys rutilus*) in the diet of great horned owls. We assume that this basic pattern based on habitat is further modified by other antipredator behavior of specific prey species. For example, ground squirrels use social alert calls and burrows to escape predation, and red squirrels are more agile than a pursuing owl in spiraling branches and tree trunks (K. McKeever, personal observation).

The shape of the functional response of great horned owls to changing hare densities deviated from a typical type-2 curve in summer and suggested that there may be an element of active prey switching (type-3 response, sensu Holling 1959, Fujii et al. 1986). In figure 15.7, the data points at low hare densities do not clearly cross the line of equal representation as predicted by prey switching (Murdoch and Oaten 1975), but they are nev-



ertheless close. However, a minor bias in our calculations may account for this result. Because snowshoe hares are the largest portion of vertebrate biomass in the boreal forest and we only included the four major prey groups to calculate relative availabilities, a complete array of prey species would reduce the relative portion of snowshoe hares at low densities and shift the data points closer to the convex curve that is expected with no active change in behavior.

More significantly, prey switching in summer may be caused by the active change in breeding behavior. At low hare densities, great horned owls do not attempt to breed, whereas they switch to producing large broods at high hare abundance. This increases the energy requirements dramatically, and hunting males providing for families will show higher kill rates than predicted by a simple type-2 curve (figure 15.9). Furthermore, breeding central-place foragers may ignore small prey such as voles and actively select for larger prey (i.e., snowshoe hares) when provisioning young, but not when they are refraining from reproduction (e.g., Stephens and Krebs 1986, Sonnerud 1992). We find it interesting that others have also reported almost linear (and not typical type-2) functional responses of avian predators in summer (e.g., McInville and Keith 1974, Korpimäki and Norrdahl 1991), and we add that such elongated or quasi-type-3 responses should be expected on theoretical grounds in avian predators that adjust their breeding effort in relation to prey density.

The flat shape of our type-2 functional response in winter is probably a result of sampling limitations. We calculated the asymptote  $A_{\max}$  based on energetic considerations, and, lacking actual data, we assumed that the energetic requirements are constant through the whole range of hare densities. However, this is not very likely. At high snowshoe hare densities, we observed in the field that considerable wastage or surplus killing of snowshoe hares occurs and that territorial and courtship activity was considerably elevated compared to the low phase of the cycle, therefore indicating that  $A_{\max}$  in figure 15.9B is an underestimate. At low hare densities, great horned owls may reduce their energy demands drastically (Kasparie 1983), and the functional response in great horned owls may increase more gradually than we assumed. In addition, great horned owls may sample hares more efficiently than we did and hunt at patches of above average density, and the observed high values at extremely low hare densities may correspond to somewhat higher densities than we measured by live-trapping grids that are relatively small compared to an owl territory.

Overall, our functional responses were similar to those measured by Keith's group (McInville and Keith 1974, Keith et al. 1977), with an asymptotic kill rate of 0.2–0.3 hares/day during April–May and similar limitations in estimating procedures. Our cross-comparison with biomass brought to nests indicated that we also measured minimum estimates in summer (calculations based on diagnostic bones underestimate the actual number of prey, and our pellet samples at nests did not include the consumption by the parents). Although data are not currently available, we conservatively speculate that our functional responses underestimate the real kill rates by a factor of 1.5–3.

Minimum predation rates of 5–10% of the hare population at high densities are considerable and may add substantially to the effect of other predators (see chapter 13). In contrast to other predators, the numerical response of great horned owls is only three- to fourfold. This means that a generalist predator will remain at relatively high densities dur-

ing low hare densities, with potentially high predation impacts on snowshoe hares and alternative prey species during the low phase of the snowshoe hare cycle (see chapter 8).

### 15.6.3 Limitation of Population Growth at Peaks of Cyclic Prey

This study provides several lines of evidence that territorial behavior excluded subordinate owls from breeding even at peak abundance of prey. Floaters were located more often than expected at the periphery of established territories, indicating that territorial behavior restricted their movements (Rohner 1996). Furthermore, replacements of territorial vacancies were in agreement with the hypothesis that social behavior limited the number of owl territories; there were inverse density-dependent growth rates in the territorial population, and the accumulation of floaters was density dependent (Rohner 1995). A combination of brood-size manipulations and food additions suggested that there was competition over limited resources even at peak densities of the snowshoe hare cycle (Rohner and Smith 1996).

It is now well established that territorial behavior limits the breeding density of many raptors and owls (Southern 1970, Newton 1976, Village 1983, Hirons 1985, Newton 1992). It is interesting that not only stable populations, but also fluctuating populations linked to prey cycles of extreme amplitude may reach population ceilings without superabundant food. A similar situation was suggested for Tengmalm's owls (*Aegolius funereus*) responding to vole cycles in Fennoscandia (Korpimäki 1988, 1989). Such ceilings in the numerical response of predators self-regulation of predator populations, or social interference among predators have rarely been demonstrated empirically, although they have been assumed for models of predator-prey dynamics, and their consequences on stability in population interactions and on cascading effects in trophic levels of communities have been discussed (e.g., Rosenzweig and MacArthur 1963, Arditi and Ginzburg 1989, Hanski 1991, Caughley and Sinclair 1994).

### 15.6.4 Time Lag in the Numerical Response of a Predator of Cyclic Prey

Time lags are an important feature of theoretical models addressing the causes of population cycles (e.g., Ginzburg and Taneyhill 1994, review in Krebs 1994). Several hypotheses can explain why predators of cyclic prey should decline with a time lag relative to prey populations. This study suggests that time lags in some vertebrate predators may not be caused by an excess of food but a change in individual strategy. Territorial great horned owls monopolized a disproportionate amount of resources, while others were excluded. These "family territories" allowed not only a high reproductive success during optimal conditions, but also a sufficient overhead of prey when owls switched off reproduction and adopted a more conservative strategy during the decline phase of the cycle (Rohner 1995, see also Kasparie 1983). In agreement with this hypothesis, the prey decline affected survival and emigration rates of subordinate owls before those of territory holders (Rohner 1996).

The importance of behavioral changes in causing the time lag in the numerical response

may also apply to other vertebrate predators. For example, avian predators with less pronounced territorial behavior showed no delay in their numerical response to vole cycles in Finland (Korpimäki and Norrdahl 1991, Korpimäki 1994). Goshawks (*Accipiter gentilis*), which may not have the option of conserving much energy because fast flights are essential to their search and hunting success (Kenward 1982, Widén 1984), also responded immediately to the decline of snowshoe hares both at Rochester and Kluane (Keith et al. 1977, Doyle and Smith 1994; see chapter 16).

#### 15.6.5 Factors Limiting Spatial Aggregation of Predators

Experimental owls on food-enriched territories concentrated their foraging effort on experimental hot spots. Although conventional methods of estimating home range size and patchiness in space use failed to detect a difference between experiments and controls, more specific measurements showed a clear response. Both the distribution of owl locations within known territory boundaries and the distance of locations in relation to the food-addition blocks were significantly different from a random prediction in two replicates. Differences in the use of snowshoe hares in the diet by experimental versus control owls confirmed the concentration of foraging effort on food-enriched patches within a territory.

At a larger scale, however, neither territorial owls nor floaters showed any tendency to leave poorer patches and move towards hot spots, and the territorial system of great horned owls was robust to extreme variations in prey density. The spatial scale of the experimental hot spots may not have been large enough to present a detectable patch (or a patch of sufficient rewards) to attract great horned owls other than the specific territory owners, but nonterritorial floaters ranged widely in the study area and were temporarily located at many different sites.

More likely, great horned owls did not follow an ideal free distribution (sensu Fretwell 1972, review in Milinski and Parker 1991), and territory holders prevented aggregations of other owls on hot spots. According to territory economics and the threshold model of territoriality (Brown 1964, Davies 1980, Carpenter 1987), short-term feeding territories should be abandoned when food and intruder pressure increase beyond an upper threshold where the cost of defense exceeds the benefits of exclusive access. Despite extreme variations in prey density, this was not the case for great horned owls. Although intrusions by nonterritorial owls were frequent, this robust territorial system did not only impose self-regulation (sensu Caughley and Sinclair 1994) on the growth of a predator population, but also represented a ceiling to spatial aggregations of predators where prey was abundant.

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