

## RESPONSE OF GREAT HORNED OWLS TO EXPERIMENTAL “HOT SPOTS” OF SNOWSHOE HARE DENSITY

CHRISTOPH ROHNER<sup>1</sup> AND CHARLES J. KREBS

Centre for Biodiversity Research, Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

**ABSTRACT.**—Predators that aggregate in “hot spots” of high prey density have been hypothesized to synchronize population cycles of small mammals. During a peak and decline in a snowshoe hare (*Lepus americanus*) cycle, we created artificial hot spots of increased hare abundance by adding food and excluding mammalian predators on three 1-km<sup>2</sup> blocks and then recorded the response of radio-marked Great Horned Owls (*Bubo virginianus*) to these food additions. Territorial owls showed a decrease in home range size and patchiness of spatial use as hare densities peaked and declined, although this was better explained by smaller territory sizes due to a growing owl population rather than a direct behavioral response to changing food density. Experimental owls on food-enriched territories did not show a difference in conventional measurements of home-range size and patchiness of spatial use compared with controls, but the distances of owl locations to treatment blocks revealed concentrations of spatial use on experimental hot spots. At a larger scale, neither territorial owls nor nonterritorial floaters showed a tendency to leave poorer patches and move toward hot spots, and the territorial system of Great Horned Owls was largely resistant to extreme variations in prey density. The effect of social interference between predators has been assumed for several models of predator-prey interactions, but empirical evidence has rarely been demonstrated. Our results suggest that territorial behavior, in addition to limiting the growth of a predator population, also prevents large aggregations of predators at an intermediate spatial scale. Received 3 July 1997, accepted 29 December 1997.

TO WHAT DEGREE do predators exploit local concentrations of prey, and what are the limitations of plasticity in their behavioral response to “hot spots” of prey abundance? These questions have been of intense interest in studies of predator-prey relationships for several decades. For example, differences in predator-prey dynamics have been related to variation in predator foraging behavior. Most implications for population dynamics were derived from analyses of functional responses of predators to prey density (Holling 1959, Fujii et al. 1986). It is particularly the distinction between the convex type-II response and the sigmoid type-III response that changes the dynamics of predator-prey interactions (Rosenzweig and MacArthur 1963, Holling 1965, Murdoch and Oaten 1975, Caughley and Sinclair 1994).

On the other hand, variations in social behavior of predators can affect the dynamics of predator-prey relationships. Nomadic predators that are socially tolerant of one another may track hot spots of peak densities of prey rapidly and aggregate in such areas, depress

prey abundances, and therefore synchronize the dynamics of cyclic prey populations over large regions (e.g. Pitelka et al. 1955, Angelstam et al. 1984, Lindström et al. 1987, Ydenberg 1987, Ims and Steen 1990, Korpimäki 1994, Steen 1995, Norrdahl and Korpimäki 1996). Also, possible interference between socially intolerant predators may require changes in the assumptions for classic predator-prey isoclines, for example allowing the predator isocline to vary according to a ratio-dependent model (e.g. Arditi and Ginzburg 1989, Hanski 1991).

Much work has focused on how predators optimize their foraging decisions (see Stephens and Krebs 1986). Beside choosing optimal prey items (Pulliam 1974), animals in a heterogeneous environment are confronted with spatial decisions about where to go and how long to stay in specific patches (Charnov 1976). Several foraging models have provided a mechanistic approach to explain different functional responses in this context (Abrams 1982, 1987, Mitchell and Brown 1990, Brown and Morgan 1995). Other models have analyzed the temporal and spatial distribution of resources that

<sup>1</sup> E-mail: rohner@zoology.ubc.ca

will favor the evolution of nomadic or site-tenacious life styles in predators (Andersson 1980).

Although aggregative responses of predators may have a profound effect on predator-prey interactions and community structure (Hassell and May 1974, Holt and Lawton 1994), very little empirical information exists about the spatial and temporal scales of such responses (e.g. Keith and Rusch 1988, Korpimäki 1994), and limitations of predator responses due to social interference have rarely been demonstrated empirically. At present, there is virtually no information on large carnivores from food-supplementation experiments (Boutin 1990).

In this paper, we examine whether Great Horned Owls (*Bubo virginianus*) exhibit a spatial response in foraging effort to changes in numbers of cyclic snowshoe hares (*Lepus americanus*) in the boreal forest of the southwestern Yukon, Canada. Our approach was twofold. First, we asked how size and patchiness in use of space by radio-marked owls changed over the peak and decline of a snowshoe hare cycle, and what correlative factors best explained these changes. Second, we increased prey densities by providing food for snowshoe hares and by excluding mammalian predators (Krebs et al. 1995) and then recorded the behavioral responses of owls to these artificially created hot spots on 1-km<sup>2</sup> blocks (ca. 20 to 30% of an average owl territory; Rohner 1997). Lagomorphs are preferred prey items for *Bubo* owls (Donazar et al. 1989), and snowshoe hares comprised 83 to 92% of the diet of Great Horned Owls during the peak of the hare population cycle in our study area (Rohner 1995). According to the hypothesis that predators concentrate their foraging effort at hot spots of prey density at any spatial scale, we address the following predictions: (1) owls on territories with hot spots will decrease home-range size (i.e. the area used within a territory during a given time will decrease); (2) patchiness in use of space by territorial owls on enriched territories will increase; (3) telemetry locations of owls on enriched territories will be closer to food-addition blocks than expected from random locations; (4) experimental owls with hot spots will have a higher portion of snowshoe hares in their diets than do control owls; and (5) territorial and nonterritorial owls will leave poorer patches

and move closer to hot spots as hare densities decline in the study area.

#### STUDY AREA AND METHODS

*Study system.*—Great Horned Owls are large, long-lived predators that feed mainly on lagomorphs and are territorial year-round (Donazar et al. 1989, Rohner 1995, 1996). Great Horned Owls reach high densities in the Nearctic boreal forest, where they exhibit a numerical response to the snowshoe hare cycle (Rusch et al. 1972, McInville and Keith 1974, Adamcik et al. 1978, Houston 1987, Houston and Francis 1995, Rohner 1996).

Snowshoe hares show a regular 10-year population cycle across northern North America (Keith 1963). They can have more than three litters per year and at peak numbers represent a higher biomass than that of any other herbivore in boreal forests (O'Donoghue and Krebs 1992, Boutin et al. 1995). In our study area, hare densities recovered from a low in the mid-1980s, increased more than 50-fold in abundance to peak levels in 1989 and 1990, and then declined rapidly from the winter of 1990–91 onwards (see Krebs et al. 1995).

We worked at Kluane Lake (60°57'N, 138°12'W) in the southwestern Yukon, Canada. The study area comprised 350 km<sup>2</sup> of the Shakwak Trench, a broad glacial valley bounded by alpine areas to the northwest and southeast. The valley bottom averages about 900 m above sea level and is covered mostly with spruce forest (*Picea glauca*), shrub thickets (*Salix* spp.), aspen forest (*Populus tremuloides*), grassy meadows with low shrubs (*Betula glandulosa*), old burns, eskers, marshes, small lakes, and ponds.

*Definition of terms.*—Territorial owls were sedentary, paired, and occupied long-term territories year-round (Rohner 1996, 1997). Nonterritorial owls, or floaters, were owls that were radio-marked as fledglings and monitored for up to 2.5 years, during which time they did not acquire a territory and did not breed (see Rohner 1997). Experimental blocks, food supplementation, and food addition were manipulations of prey densities as described in the next section. Control blocks were other places in the study area where control prey densities were sampled for comparison (see below). Experimental owls were territory owners with food supplementation (provided for hares) within their territories. Control owls were all other territorial owls with active radio transmitters, independent of whether their territories included a sampling site of control densities of prey. Territory size was defined as the total area used by a pair throughout the year. Territory sizes can be measured by mapping hooting males and delineating territorial boundaries in spring when territorial activity is most pronounced. Here, we used an approximation of territory size that was calculated from the

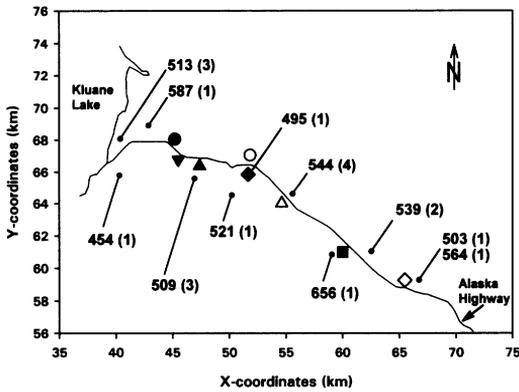


FIG. 1. Study area at Kluane Lake, southwestern Yukon, with blocks of manipulated snowshoe hare densities (open symbols), blocks of control measurements of hare densities, and location of territorial owls (identification code, with number of years monitored in parentheses).

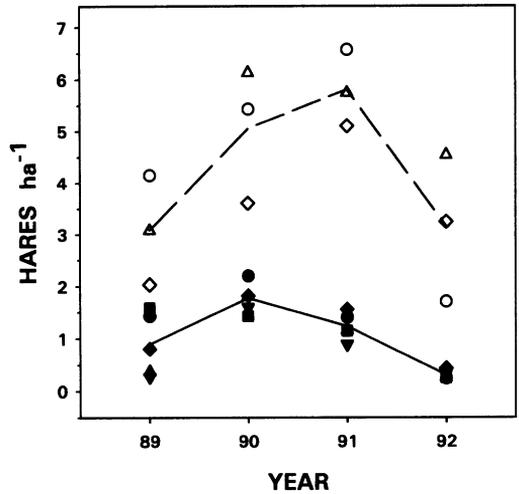


FIG. 2. Manipulations of snowshoe hare densities on 1-km<sup>2</sup> blocks at Kluane Lake, Yukon. Shown are hare densities in spring on three experimental blocks (open symbols) and five controls (filled symbols), with average densities connected by lines. Symbols as in Figure 1.

known population density within 100 km<sup>2</sup> (which was similar to mapped values; see Rohner 1997). We defined home range as the fraction of a defended territory that was actually used within a specified time period. Home-range size was calculated from telemetry locations using standard methods (see below).

**Manipulation of prey densities.**—We chose several 1-km<sup>2</sup> blocks of undisturbed boreal forest for treatments and strived to intersperse treatments and controls in the study area (Fig. 1). Three experimental areas were provided with supplemental food (commercial rabbit chow, 16% protein, added weekly) *ad libitum* year-round, and one of those was protected by an electric fence 2.2 m in height to exclude mammalian predators (fence checked daily for performance). All treatments were “press” experiments (sensu Bender et al. 1984) that lasted throughout the study period reported in this paper. Hare densities on blocks were estimated by mark-recapture live trapping during four to five days in late March and early April. Trapping was conducted on permanent, 36-ha grids on all blocks. We present an average of the density estimates from the program Capture and from the Jolly-Seber method (Pollock et al. 1990). Hare numbers on the three experimental blocks increased dramatically and on average were 2.8 to 10.3 times higher than those on control blocks (Fig. 2). Five controls consisted of two untreated blocks and three blocks treated with fertilizer and other treatments that did not result in strongly elevated hare numbers. Details are given in Krebs et al. (1995) and Boutin et al. (1995).

**Field techniques for owl data.**—Great Horned Owls were censused in late winter and early spring on a 100-km<sup>2</sup> plot within the main study area. 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 territory boundaries. When necessary, playbacks were used to elicit responses of territory owners and their neighbors. Most males were individually known because of radio tagging and because of their distinct vocalizations. Vocal differences were later verified with sonagrams from recordings at the nest (C. Rohner unpubl. data). Observations of territorial activity were made almost daily from early February until late April ( $\geq 300$  h each year).

Nests were found according to Rohner and Doyle (1992), and during 1988 to 1991, radio transmitters were attached to 55 owlets before fledging. Of those, the successful dispersers were later monitored intensively (3 born in 1988, 11 in 1989, and 16 in 1990), and nine remained as nonterritorial floaters in the area during this study (see Rohner 1996, 1997). Radio transmitters weighed 50 g, including a shoulder harness of Teflon ribbon for attachment as a backpack (<5% of body mass; Kenward 1985); transmitters functioned for 2 to 2.5 years.

In addition to juvenile birds, 21 territorial adult owls were captured with mist nets and cage traps and equipped with radio transmitters. The effective sample size of territorial owls used in each year varied and was smaller than the total sample size because of logistical difficulties. We were able to work with one to three experimental owls and two to six controls in each of the four years of study (see Table 1, Fig. 3). To allow for better comparisons, we used only females for telemetry studies, except in 1992,

TABLE 1. Summary of sample sizes and precision for telemetry locations of territorial Great Horned Owls at Kluane Lake, Yukon (including experimental and control owls; see Methods).

Year	No. of owls	No. of locations per owl <sup>a</sup>	95%-error area (median, km <sup>2</sup> )	95%-error area (quartiles, km <sup>2</sup> )
1989	3	18.7 ± 1.2	0.19	0.05 to 0.37
1990	5	20.0 ± 0.0	0.10	0.02 to 0.26
1991	5	20.0 ± 0.0	0.09	0.03 to 0.20
1992	6	21.0 ± 0.0	0.05	0.02 to 0.15

<sup>a</sup>  $\bar{x} \pm SE$ .

when female no. 503 emigrated from the study area and its mate (no. 564) was monitored instead.

Telemetry work on use of space by territorial owls was concentrated during periods of three weeks each year, with locations obtained on consecutive nights for each bird if possible (not achieved in the first year; thus, the total monitoring periods for each bird in 1989 were 27, 28, and 41 days). These periods of intensive monitoring were conducted from 24 July to 8 September 1989, 7 to 26 September 1990, 5 to 26 September 1991, and 12 June to 3 July 1992. For more specific measurements of experimental owls no. 544 and 503 during the decline phase of the hare cycle, all telemetry locations taken on nights between September 1991 and September 1992 were used. Telemetry work to assess the distance of nine nonterritorial floaters from experimental grids involved weekly locations from January 1990 to September 1992 (see Rohner 1997).

Telemetry locations were obtained by triangulation using hand-held equipment. Topographic maps were used in the field to plot the locations and assess the number of bearings needed for reliable estimates. The triangulations were 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 1. The accuracy of telemetry locations was assessed by triangulation on five transmitters that were placed in trees at heights of 4.5 to 5.5 m. The deviation of these locations (error of  $0.052 \pm SE$  of  $0.018 \text{ km}^2$ ) from the site coordinates obtained by a global positioning system was  $0.101 \pm 0.027 \text{ km}$ .

Summer diets of territorial owls were sampled during May to July (nine territories from 1989 to 1991, six territories in 1992). Pellets were collected from breeding birds at nests and at roost sites located by telemetry. The results of pellet analysis were expressed as the percentage of a prey species in the total prey biomass (see Rohner 1995).

*Analysis of telemetry data.*—Calculations were performed using Ranges IV software (Kenward 1990).

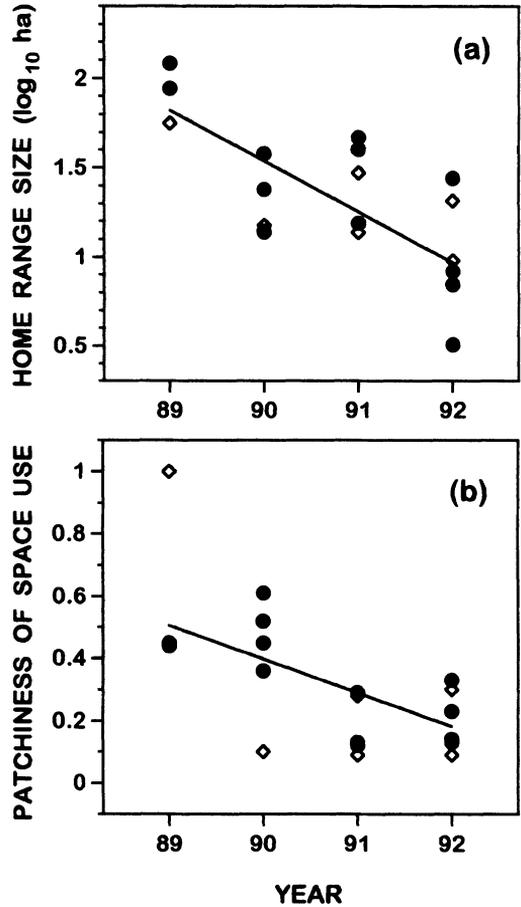


FIG. 3. Characteristics in use of space by Great Horned Owls monitored by radio telemetry during three-week periods in each year. Filled symbols are controls, open symbols are experimental owls on food-enriched territories (sample sizes in Table 1). Regression lines include only controls: (A) Home-range size, expressed as a minimum convex polygon of the innermost 70% of locations. (B) Patchiness in space use (expressed as the portion of the multinuclear 70% clusters relative to the mononuclear convex polygon given in [A]; see Kenward 1987).

Use of space was measured by utilization distributions based on clustering methods. From a center of closest locations, an increasing percentage of nearest-neighbor locations was added, resulting in a cumulative increase of core area used. Mononuclear clustering was centered around the harmonic mean location, whereas multinuclear clustering allowed for separate clusters wherever distances between locations were closest. Home-range size was 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 per-

centage and expressed as a portion of the total area (see Kenward 1987). These procedures allowed a more sensitive approach to recognizing biases due to outliers and different patterns of spatial use. For the monitoring period in September 1991, three of eight territorial owls were excluded from analysis because of extreme long-distance movements during several days (these extraterritorial movements are described in Rohner 1996).

*Statistical procedures.*—All arithmetic means are reported  $\pm$  one SE, and all probabilities are two-tailed unless otherwise specified. Correlation coefficients were calculated as Spearman rank correlations. For statistical testing, nonparametric tests were used wherever possible (ANOVAs were calculated with log-transformed data, or with arcsine-transformed data for percentages). The testing of bootstrap hypotheses followed Hall and Wilson (1991), and two-sided probabilities were derived from 500 simulations (see Rohner 1997).

## RESULTS

*Use of space: Home-range size and patchiness.*—Home-range sizes of territorial owls decreased from 1989 to 1992 ( $r_s = -0.64$ ,  $n = 19$ ,  $P < 0.001$ ; Fig. 3A). Because home-range estimates are sensitive to outliers (Kenward 1987), a range of different core percentages was analyzed. The same trend was consistent for core percentages of 60 to 95%, and we chose a level of 70% (i.e. discarding the outermost 30% of locations) for presentation in Figure 3A to ensure a conservative and robust result. This trend was also significant when experimental owls were excluded from analysis ( $r_s = -0.63$ ,  $n = 13$ ,  $P < 0.05$ ).

A similar trend was found for patchiness in use of space (Fig. 3B). Not only did Great Horned Owls use smaller areas within a given time, they also used this smaller space more uniformly ( $r_s = -0.60$ ,  $n = 19$ ,  $P < 0.01$ ). This trend was also significant for control owls only ( $r_s = -0.70$ ,  $n = 13$ ,  $P < 0.01$ ).

Because hare densities declined from 1990 to 1992 (Fig. 2), one obvious hypothesis is that the observed changes in use of space by owls were a direct function of varying prey density. Hare density, however, explained only a small portion of the variance in home-range size ( $r^2 = 0.16$ ,  $F = 0.39$ ,  $df = 1$  and  $2$ ,  $P = 0.59$ ). But at the same time, the number of owls increased, leading to a more densely packed array of territories in the study area, which is equivalent to a decrease in territory size over time (Fig. 4).

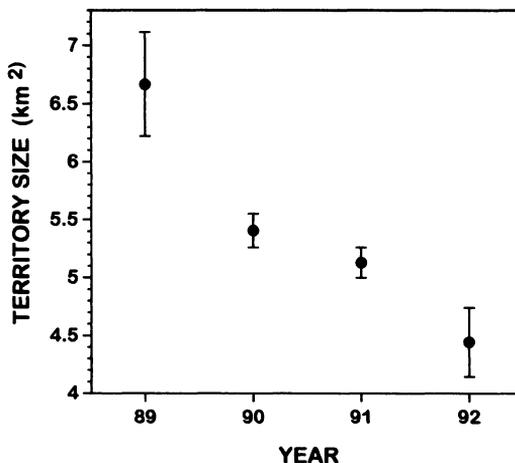


FIG. 4. Average territory size of Great Horned Owls during a peak and decline of snowshoe hares. Mean territory sizes (filled circles) were calculated from a census of owl territories on 100 km<sup>2</sup> of the main study area (vertical bars are minimum and maximum estimates, numbers of territories ranging from 14 to 15 in 1989 to 21 to 24 in 1992; Rohner 1996).

Interestingly, the decline in territory size explained considerably more of the variation in use of space by these owls ( $r^2 = 0.85$ ,  $F = 11.0$ ,  $df = 1$  and  $2$ ,  $P = 0.08$ ). Because the sample size of only four years was small, and collinearity in hare density and territory size of owls was high for all but one year, this correlative approach cannot be taken as strong support for the lack of a relationship between prey density and use of space by owls.

Results from experimental owls did not confirm a direct effect of prey density on home-range use. Mean home-range size of owls on territories with hot spots did not differ from that of owls on control territories (ANCOVA,  $F < 0.1$ ,  $df = 1$  and  $16$ ,  $P = 0.99$ ; Fig. 3A). Also, patchiness in use of space did not differ between experimental and control owls (ANCOVA,  $F = 0.52$ ,  $df = 1$  and  $16$ ,  $P = 0.48$ ; Fig. 3B). Although hare densities were 2.8 to 10.3 times higher at treatment sites than at control sites, with no apparent effect on owl home-range size, it should be noted that the statistical power for demonstrating a difference was low.

*Use of hot spots in experimental territories.*—The contrast between prey density on the study area in general and on artificially created hot spots increased drastically as the decline phase of the snowshoe hare cycle progressed (Fig. 2).

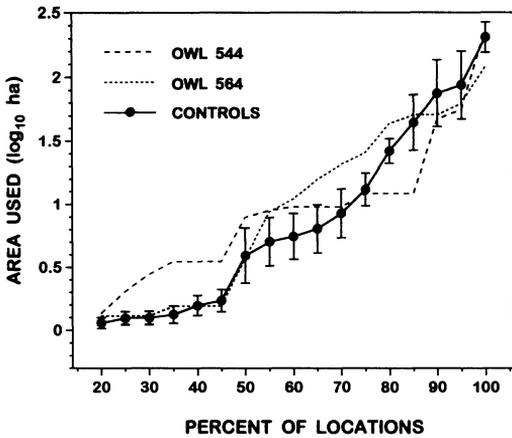


FIG. 5. Home range sizes of two experimental owls during June 1992 compared with four controls ( $\bar{x} \pm SE$ ), as determined from telemetry locations. The area of the maximum convex polygon are shown as a function of an increasing core percentage of innermost locations.

Therefore, we investigated owls on two experimental territories that were accessible for 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 in resident owls (see Rohner 1996). A more detailed analysis of home-range size was performed across all core percentages (Fig. 5). As we found in the multiyear analysis, there were no consistent differences between experimental and control owls (repeated-measures ANOVA,  $F = 0.21$ ,  $df = 1$  and  $4$ ,  $P = 0.67$ ).

A less conventional and more specific approach was taken to detect potential concentrations in use of space. A null hypothesis of uniform spatial use was modeled by randomly generating 5,000 points within the known boundaries of these territories. The distances from 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 spatial use within a territory. The actual telemetry locations of experimental owls were then compared with this expected distribution. The results clearly showed that some regions were used more frequently than expected for both experimental owls. For owl no. 544, the

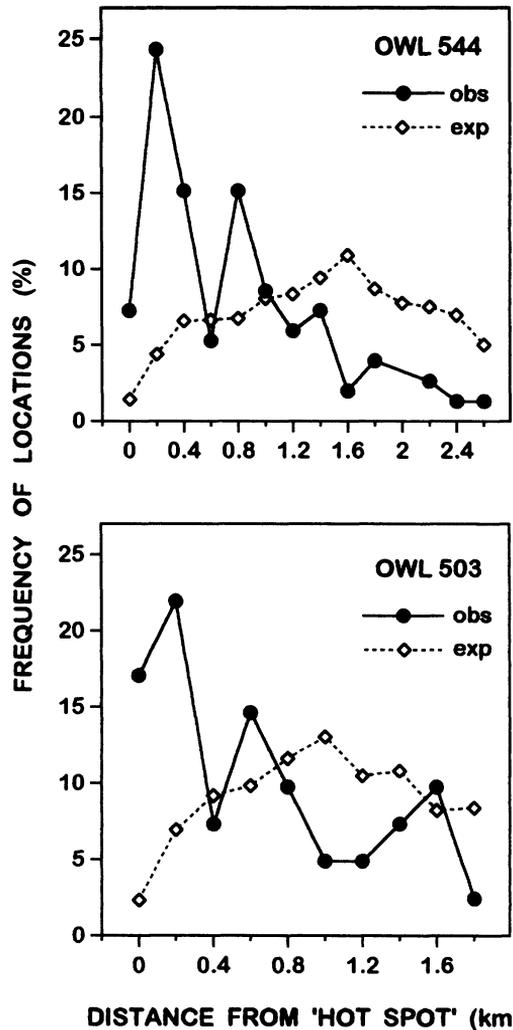


FIG. 6. Concentrations in space use of two experimental owls relative to the center of 1-km<sup>2</sup> blocks with increased prey density. Locations were grouped into distance classes, and shown as frequency distribution of observed locations (filled symbols) and expected frequencies from random locations in the specific territories (open symbols).

mean of positive deviations from the expected values was 5.35 ( $P < 0.01$ ); for owl no. 503 this mean was 9.20 ( $P = 0.02$ ).

Were these concentrations in use of space related to hot spots in hare abundance? Telemetry locations were then 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 (Fig. 6). Both experimental owls showed a positive response compared with the expected distributions as cal-

culated 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  $P < 0.001$ ). For owl no. 503, this distance was  $0.741 \pm 0.087$  km ( $n = 41$ , mean expected distance 1.179 km; bootstrap  $P < 0.001$ ).

Data from pellet analysis supported the notion that concentrations in use of space were related to foraging activity. Summer diets of Great Horned Owls consisted of 83 to 86% snowshoe hares from 1989 to 1991, when hare abundance was high ( $n = 13$  territories; see Rohner 1995). In 1992, the proportion of hares in the diet dropped to  $13 \pm 9\%$  (range 0 to 42%,  $n = 5$  territories). We collected pellets from one experimental owl during summer 1992. In contrast to control owls, the diet of experimental owl no. 544 consisted of a high proportion (65%) of hares.

*Predator movements from poor patches to rich patches.*—During the decline phase of the hare cycle, we predicted that territorial owls would abandon poor territories and intrude (at least temporarily) into territories with hot spots of prey abundance. Despite intensive monitoring, we did not observe any owls that had vacated their territories to use food-addition blocks or changed to a nomadic strategy on the study area (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 prey abundance. Table 2 summarizes the results on potential shifts of eight nonterritorial owls toward hot spots during a time when the abundance of hares in these patches increased by 3.8 to 10.3 times compared with control levels in the study area (see Fig. 2). There was no distinct pattern, and the only significant shifts in use of space by three owls were opposite to the predicted direction.

## DISCUSSION

*Responses of territorial owls and measures of spatial use.*—Home-range sizes of many animals are thought to vary inversely with food density (e.g. Myers et al. 1979, Davies 1980, Carpenter 1987b, Temeles 1987, Boutin 1990; but see Eber-

TABLE 2. Shifts in use of space by nonterritorial Great Horned Owls relative to experimental "hot spots" of snowshoe hares. Values are median distances (km) of weekly telemetry locations to the center of the closest experimental block during the peak ( $D_1$ ; January 1990 to May 1991) and decline ( $D_2$ ; June 1991 to September 1992) phases of the snowshoe hare cycle.

Owl no.	$n_1^a$	$n_2^a$	$D_1$	$D_2$	$D_2 - D_1$	$P^b$
406	71	20	10.858	11.070	0.211	0.153
407	61	5	5.221	7.091	1.876	0.092
415	72	14	4.454	4.967	0.513	0.674
417	25	22	4.564	3.545	-1.019	0.258
425	52	15	8.723	11.380	2.657	0.003
433	60	13	5.178	6.115	0.937	0.076
505	25	31	4.890	12.700	7.810	0.001
515	38	19	1.800	3.667	1.868	0.021

<sup>a</sup> Number of telemetry locations during peak ( $n_1$ ) and decline ( $n_2$ ) phases of hare cycle.

<sup>b</sup>  $P$ -value from two-tailed Mann-Whitney  $U$ -tests based on  $D_2 - D_1$ .

sole 1980, Schoener 1983). In contrast to this prediction, an analysis based on conventional measures of home-range size and patchiness in use of space suggested that Great Horned Owls decreased their use of space in response to decreasing prey density. However, a more specific examination led to a somewhat different result. During the first year of the hare decline, Great Horned Owl numbers were increasing because the response of owls to increasing hare densities occurred with a two-year time lag (Rohner 1995, 1996). Consequently, during the decline in hare numbers, the home-range size of settled owls actually decreased (contrary to theory) because of the more densely packed array of owl territories. Large territories may allow owls to be more selective for good patches over a larger area, but losses in territory size to newcomers may then force owls to hunt more evenly in a smaller area (see also Village 1982).

A preference for prey concentrations within a predator's territory is supported by the response of Great Horned Owls to experimental hot spots on their territories. Although conventional methods of estimating home-range size and patchiness in use of space failed to detect a difference between experimental and control owls, direct measurements of owl distances to hot spots showed a clear response. The distribution of owl locations within known territory boundaries and the distance of locations relative to food-addition blocks were significantly different from a random prediction in two rep-

licates. In support of a concentration of hunting effort at hot spots, the proportion of snowshoe hares in the diet of one experimental owl was much higher than that of control owls, according to pellet analysis.

However, these results have to be considered with some caution. First, our sample sizes were very small, and although we succeeded in replicating our experiments, further evidence from other studies would be desirable to confirm such responses to hot spots of prey within a predator's territory. Second, we have presented the null hypothesis that use of space by experimental owls is uniform if not influenced by food hot spots. Many other factors, such as vegetation structure, distribution of favored perched sites, or proximity to potential intruders, may influence the spatial distribution of raptors (e.g. Janes 1985). Although we found that owl locations were concentrated at food hot spots, alternative interpretations must be kept in mind. For future studies, the best procedure to test our preliminary results would consist of temporal controls, i.e. by monitoring experimental owls before (and possibly after) manipulations of food density (e.g. Rohner and Smith 1996). As a third concern, we address the relationship between hare abundance and hare availability. Previous studies have shown that prey abundance and prey availability to raptors do not always vary directly (e.g. Southern and Lowe 1968, Bechard 1982, Preston 1990). Snowshoe hares are more vulnerable to predation by Great Horned Owls in open habitats (Rohner and Krebs 1996), and because hares tend to use open habitats less frequently at low densities (Hik 1995), they may be less available to owls at the low phase of the population cycle. However, in both replicates, the distribution of owls was concentrated at hot spots of hare abundance, suggesting that hare availability did not deviate substantially from hare abundance.

The logistical effort required to create experimental hot spots of prey at a scale meaningful to raptors is enormous. Because many conservation and management projects rely on telemetry data, this raises concern about the detectability of responses of organisms to environmental change. We strongly advocate the use of specific questions and experiments instead of the application of standard analyses of home-range size. If manipulations are not possible, then management actions and conservation

measures may be designed as experiments (e.g. Walters 1986, Caughley and Sinclair 1994).

*Territoriality and spatial aggregation of predators.*—We did not observe any aggregations of Great Horned Owls at experimental hot spots. Also, we did not observe any movements by owls in the vicinity that suggested elevated visitation rates, which possibly could have increased predation rates due to predators being attracted to these rich patches. We cannot exclude the possibility that owls other than our marked individuals aggregated at hot spots. Assuming that these other owls did not behave differently from our monitored birds, however, our sample size of marked animals was sufficient at least to detect such movements had they taken place.

Two explanations can account for this result. First, the spatial scale of our 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. Although this explanation may apply to neighboring territory holders, nonterritorial floaters ranged widely in the study area and were temporarily located at many different sites, including at or near hot spots for short periods of time.

A more likely explanation is that Great Horned Owls did not follow an ideal free distribution (sensu Fretwell 1972, Milinski and Parker 1991), and territory holders prevented aggregations of other owls at hot spots. Although floaters overlapped broadly with each other and with established territory holders, they occurred more often at the periphery of territories than expected by chance (Rohner 1997). Other evidence also suggests that territorial behavior affected subordinate birds. For example, during 1988 to 1993, inverse density-dependent growth rates in the territorial population, density-dependent accumulation of floaters in the study area, and replacements of territorial vacancies confirmed the hypothesis that social behavior limited the number of owl territories (Rohner 1995; see also Newton 1992). Stability in the number of breeding pairs despite large variation in prey density was also observed for Tawny Owls (*Strix aluco*) in temperate forests (Jedrzejewski et al. 1996).

Although some theoretical models have assumed that interference between predators will reduce predation rates (e.g. Arditi and Ginz-

burg 1989, Hanski 1991, Caughley and Sinclair 1994), such effects have rarely been demonstrated empirically. Our data suggest that the territorial structure of Great Horned Owls is robust to extreme variations in prey density, and that interference between predators was common both at peak densities of a prey cycle (see Rohner and Smith 1996) and at artificially created hot spots of food abundance. According to territory economics and the threshold model of territoriality (Brown 1964, Davies 1980, Carpenter 1987a), territories should be abandoned when food and intruder pressure increase beyond an upper threshold where the costs of defense exceed the benefits of exclusive access. Evidence suggests that immature Golden Eagles (*Aquila chrysaetos*) aggregate in alpine areas where ungulate carcasses occur frequently, thus creating such a high intruder pressure that these hot spots cannot be defended by territorial eagles (Jenny 1992). In the case of Great Horned Owls, this was not observed (see Rohner 1996). Although intrusions by nonterritorial owls were frequent, the robust territorial system of the owls imposed self regulation (*sensu* Caughley and Sinclair 1994) on the growth of their population and also represented a ceiling to spatial aggregation of predators where prey was very abundant.

*Evidence for the predator hot spot hypothesis?*—The aggregative response of Great Horned Owls to hot spots of prey density was dependent on spatial scale. At the smallest scale of an individual territory, owls appeared to concentrate their foraging effort on experimental patches, as predicted. At an intermediate spatial scale of 350 km<sup>2</sup>, neither territorial owls nor nonterritorial floaters aggregated near experimental hot spots. Although intrusions occurred regularly, it is likely that resource defense by territory owners prevented large aggregations of Great Horned Owls. At this intermediate scale, snowshoe hare densities are synchronous (Fig. 2), and it is unlikely that natural hot spots that exceeded our experimental densities occurred elsewhere near the study area. We cannot exclude aggregative responses at the very large scale of whole regions within the boreal forest, particularly because substantial emigration of owls occurred as hare densities declined to very low levels (Rohner 1996). Such emigrations are also documented from Saskatchewan (Houston and Francis 1995), and

irruptive movements of Northern Goshawks (*Accipiter gentilis*) and Great Horned Owls may cause elevated predation rates in southern Canada and the northern United States (Keith and Rusch 1988). Although a considerable proportion of nonterritorial owls can live in an area with established territories (Rohner 1996), and predation rates may increase considerably when turnover rates of nomadic owls are high, this has not been demonstrated empirically.

Limitations to aggregative responses by social interference may not apply to other predators. Korpimäki (1994) found that avian predators in Finland tracked peaks in vole cycles rapidly and reached very high breeding densities without delay, and experimental reductions of breeding pairs resulted in elevated prey densities (Norrdahl and Korpimäki 1996; but see Steen 1995). In our study area, the number of Great Horned Owl territories dropped with a time lag of two years after the hare peak, but Northern Goshawks responded immediately with declining numbers (Doyle and Smith 1994). Northern Goshawks can have large and overlapping home ranges and may show aggregative responses to hot spots of prey density (Kenward et al. 1981). Comparisons of aggregative responses of predators with different social systems deserve more study. This direction also seems promising for mammalian predators that respond to prey cycles, because many of them are highly mobile and can be socially intolerant even between species (e.g. Keith et al. 1977, Ward and Krebs 1985, Litvaitis et al. 1986, Thompson and Colgan 1987, Gese et al. 1988, Frafjord et al. 1989, Breitenmoser et al. 1993, O'Donoghue et al. 1997).

#### ACKNOWLEDGMENTS

This research is part of a collaborative project, and we thank all members of the Klauene team for their tireless effort, particularly for setting up and maintaining the manipulations of hare densities and for assisting with live-trapping of hares. Frank Doyle, C. Schmid, P. Heaven, J. Stroman, B. Zimmermann, S. Wagnière, B. Delehanty, C. Kullberg, T. Wellicome, K. Russenberger, R. Mueller, and C. and U. Breitenmoser helped with the telemetry work. We thank Tony Sinclair and Deb Wilson for inspiring discussions, and B. Kotler, D. Ward, C. Preston, and an anonymous reviewer for helpful comments on the manuscript. Funding was provided by the Natural Sciences and Engineering Council of Canada (grants to C.J. Krebs and J.N.M. Smith), a J. R. Thompson Wild-

life Fellowship, and a Graduate Fellowship from the University of British Columbia. The manuscript was completed with support of the Swiss Academy of Sciences. This is publication number 120 of the Klunane Boreal Forest Ecosystem Project.

## LITERATURE CITED

- ABRAMS, P. A. 1982. Functional responses of optimal foragers. *American Naturalist* 120:382–391.
- ABRAMS, P. A. 1987. The functional responses of adaptive consumers of two resources. *Theoretical Population Biology* 33:262–288.
- ADAMCIK, R. S., A. W. TODD, AND L. B. KEITH. 1978. Demographic and dietary responses of Great Horned Owls during a snowshoe hare cycle. *Canadian Field-Naturalist* 92:156–166.
- ANDERSSON, M. 1980. Nomadism and nest site tenacity as alternative reproductive tactics in birds. *Journal of Animal Ecology* 49:175–184.
- ANGELSTAM, P., E. LINDSTRÖM, AND P. WIDÉN. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* 62:199–208.
- ARDITL, R., AND L. R. GINZBURG. 1989. Coupling in predator-prey dynamics: Ratio-dependence. *Journal of Theoretical Biology* 139:311–326.
- BECHARD, M. J. 1982. Effect of vegetative cover on foraging site selection by Swainson's Hawk. *Condor* 84:153–159.
- BENDER, E. A., T. J. CASE, AND M. E. GILPIN. 1984. Perturbation experiments in community ecology: Theory and practice. *Ecology* 65:1–13.
- BOUTIN, S. 1990. Food supplementation experiments with terrestrial vertebrates: Patterns, problems, and the future. *Canadian Journal of Zoology* 68:203–220.
- BOUTIN, S., C. J. KREBS, R. BOONSTRA, M. R. T. DALE, S. J. HANNON, K. MARTIN, A. R. E. SINCLAIR, J. N. M. SMITH, R. TURKINGTON, M. BLOWER, A. BYRON, F. I. DOYLE, C. DOYLE, D. HIK, L. HOFER, A. HUBBS, T. KARELS, D. L. MURRAY, V. NAMS, M. O'DONOGHUE, C. ROHNER, AND S. SCHWEIGER. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos* 74:69–80.
- BREITENMOSER, U., B. G. SLOUGH, AND C. BREITENMOSER-WÜRSTEN. 1993. Predators of cyclic prey: Is the Canada lynx victim or profiteer of the snowshoe hare cycle? *Oikos* 66:551–554.
- BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bulletin* 76:160–169.
- BROWN, J. S., AND R. A. MORGAN. 1995. Effects of foraging behavior and spatial scale on diet selectivity: A test with fox squirrels. *Oikos* 74:122–136.
- CARPENTER, F. L. 1987a. Food abundance and territoriality: To defend or not to defend? *American Zoologist* 27:387–399.
- CARPENTER, F. L. 1987b. The study of territoriality: Complexities and future directions. *American Zoologist* 27:401–409.
- CAUGHLEY, G., AND A. R. E. SINCLAIR. 1994. *Wildlife ecology and management*. Blackwell Scientific Publications, Oxford.
- CHARNOV, E. L. 1976. Optimal foraging and the marginal value theorem. *Theoretical Population Biology* 9:129–136.
- DAVIES, N. B. 1980. The economics of territorial behaviour in birds. *Ardea* 68:63–74.
- DONAZAR, J. A., F. HIRALDO, M. DELIBES, AND R. R. ESTRELLA. 1989. Comparative food habits of the Eagle Owl *Bubo bubo* and the Great Horned Owl *Bubo virginianus* in six Palearctic and Nearctic biomes. *Ornis Scandinavica* 20:298–306.
- DOYLE, F. I., AND J. N. M. SMITH. 1994. Population responses of Northern Goshawks to the 10-year cycle in numbers of snowshoe hares. *Studies in Avian Biology* 16:122–129.
- EBERSOLE, J. P. 1980. Food density and territory size: An alternative model and a test on the reef fish *Eupomacentrus leucostictus*. *American Naturalist* 115:492–509.
- FRAFJORD, K., D. BECKER, AND A. ANGERBJÖRN. 1989. Interactions between arctic and red foxes in Scandinavia—Predation and aggression. *Arctic* 42:354–356.
- FRETWELL, S. D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton, New Jersey.
- FUJII, K., C. S. HOLLING, AND P. M. MACE. 1986. A simple generalized model of attack by predators and parasites. *Ecological Research* 1:141–156.
- GESE, E. M., O. J. RONGSTAD, AND W. R. MYTTON. 1988. Home range and habitat use of coyotes in southeastern Colorado. *Journal of Wildlife Management* 52:640–646.
- HALL, P., AND S. R. WILSON. 1991. Two guidelines for bootstrap hypothesis testing. *Biometrics* 47:757–762.
- HANSKI, I. 1991. The functional response of predators: Worries about scale. *Trends in Ecology and Evolution* 6:141–142.
- HASSELL, M. P., AND R. M. MAY. 1974. Aggregation of predators and insect parasites and its effects on stability. *Journal of Animal Ecology* 43:567–594.
- HIK, D. S. 1995. Does risk of predation influence population dynamics? Evidence from the cyclic decline of snowshoe hares. *Wildlife Research* 22:115–129.
- HOLLING, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91:385–398.
- HOLLING, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* 45:1–60.
- HOLT, R. D., AND J. H. LAWTON. 1994. The ecological

- consequences of shared natural enemies. *Annual Review of Ecology and Systematics* 25:495–520.
- HOUSTON, C. S. 1987. Nearly synchronous cycles of the Great Horned Owl and snowshoe hare in Saskatchewan. Pages 56–58 in *Biology and conservation of northern forest owls* (R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, Eds.). United States Forest Service General Technical Report RM-142.
- HOUSTON, C. S., AND C. M. FRANCIS. 1995. Survival of Great Horned Owls in relation to the snowshoe hare cycle. *Auk* 112:44–59.
- IMS, R. A., AND H. STEEN. 1990. Geographical synchrony in microtine population cycles: A theoretical evaluation of the role of nomadic avian predators. *Oikos* 57:381–387.
- JANES, S.W. 1985. Habitat selection in raptorial birds. Pages 159–188 in *Habitat selection in birds* (M.L. Cody, Ed.). Academic Press, Orlando, Florida.
- JEDRZEJEWSKI, W., B. JEDRZEJEWSKA, A. SZYMURA, AND K. ZUB. 1996. Tawny Owl (*Strix aluco*) predation in a pristine deciduous forest (Bialowieza National Park, Poland). *Journal of Animal Ecology* 65:105–120.
- JENNY, D. 1992. Bruterfolg und Bestandsregulation einer alpinen Population des Steinadlers *Aquila chrysaetos*. *Der Ornithologische Beobachter* 89:1–43.
- KEITH, L. B. 1963. *Wildlife's ten year cycle*. University of Wisconsin Press, Madison.
- KEITH, L. B., AND D. H. RUSCH. 1988. Predation's role in the cyclic fluctuations Ruffed Grouse. Pages 699–732 in *Acta XIX Congressus Internationalis Ornithologici* (H. Ouellet, Ed.). Ottawa, Ontario, 1986. National Museum of Natural Sciences, Ottawa.
- KEITH, L. B., A. W. TODD, C. J. BRAND, R. S. ADAMCİK, AND D. H. RUSCH. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. *Proceedings of the International Congress of Game Biologists* 13:151–175.
- KENWARD, R. E. 1985. Raptor radio-tracking and telemetry. *ICBP Technical Publication* 5:409–420.
- KENWARD, R. E. 1987. *Wildlife radio-tagging: Equipment, field techniques, and data analysis*. Academic Press, London.
- KENWARD, R. E. 1990. *Ranges IV*. Institute of Terrestrial Ecology, Furzebrook, Wareham United Kingdom.
- KENWARD, R. E., V. MARCSTRÖM, AND M. KARLBOM. 1981. Goshawk winter ecology in Swedish pheasant habitats. *Journal of Wildlife Management* 45:397–408.
- KORPIMÄKI, E. 1994. Rapid or delayed tracking of multi-annual vole cycles by avian predators? *Journal of Animal Ecology* 63:619–628.
- KREBS, C. J., S. BOUTIN, R. BOONSTRA, A. R. E. SINCLAIR, J. N. M. SMITH, R. T. DALE, K. MARTIN, AND R. TURKINGTON. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269:1112–1115.
- LINDSTRÖM, E., P. ANGELSTAM, P. WIDÉN, AND H. ANDRÉN. 1987. Do predators synchronize vole and grouse fluctuations?—An experiment. *Oikos* 48:121–124.
- LITVAITIS, J. A., J. A. SHERBURNE, AND J. A. BISSONNETTE. 1986. Bobcat habitat use and home range size in relation to prey density. *Journal of Wildlife Management* 50:110–117.
- MCINVALLE, W. B., AND L. B. KEITH. 1974. Predator-prey relations and breeding biology of the Great Horned Owl and Red-tailed Hawk in central Alberta. *Canadian Field-Naturalist* 88:1–20.
- MILINSKI, M., AND G. A. PARKER. 1991. Competition for resources. Pages 137–168 in *Behavioural ecology: An evolutionary approach*, 3rd ed. (J. R. Krebs and N. B. Davies, Eds.). Blackwell Scientific Publications, Oxford.
- MITCHELL, W. A., AND J. S. BROWN. 1990. Density-dependent harvest rates by optimal foragers. *Oikos* 57:180–190.
- MURDOCH, M. W., AND A. OATEN. 1975. Predation and population stability. *Advances in Ecological Research* 9:2–131.
- MYERS, J. P., P. G. CONNORS, AND F. PITELKA. 1979. Territory size in wintering Sanderlings: The effects of prey abundance and intruder density. *Auk* 96:551–561.
- NAMS, V. O. 1990. *Locate II*. Pacer, Truro, Nova Scotia.
- NEWTON, I. 1992. Experiments on the limitation of bird numbers by territorial behaviour. *Biological Reviews of the Cambridge Philosophical Society* 67:129–173.
- NORRDAHL, K., AND E. KORPIMÄKI. 1996. Do nomadic avian predators synchronize population fluctuations of small mammals? A field experiment. *Oecologia* 107:478–483.
- O'DONOGHUE, M., S. BOUTIN, C. J. KREBS, AND E. J. HOFER. 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. *Oikos* 80:150–162.
- O'DONOGHUE, M., AND C. J. KREBS. 1992. Effects of supplemental food on snowshoe hare reproduction and juvenile growth at a cyclic population peak. *Journal of Animal Ecology* 61:631–641.
- PITELKA, F. A., P. Q. TOMICH, AND G. W. TREICHEL. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. *Ecological Monographs* 25:85–117.
- POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* No. 107.
- PRESTON, C. J. 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. *Condor* 92:107–112.

- PULLIAM, H. R. 1974. On the theory of optimal diets. *American Naturalist* 108:59–75.
- ROHNER, C. 1995. Great Horned Owls and snowshoe hares: What causes the time lag in the numerical response of predators to cyclic prey? *Oikos* 74: 61–68.
- ROHNER, C. 1996. The numerical response of Great Horned Owls to the snowshoe hare cycle: Consequences of non-territorial “floaters” on demography. *Journal of Animal Ecology* 65: 359–370.
- ROHNER, C. 1997. Non-territorial “floaters” in Great Horned Owls: Space use during a cyclic peak of snowshoe hares. *Animal Behaviour* 53:901–912.
- ROHNER, C., AND F. I. DOYLE. 1992. Methods of locating Great Horned Owl nests in the boreal forest. *Journal of Raptor Research* 26:33–35.
- ROHNER, C., AND C. J. KREBS. 1996. Owl predation on snowshoe hares: Consequences of antipredator behaviour. *Oecologia* 108:303–310.
- ROHNER, C., AND J. N. M. SMITH. 1996. Brood size manipulations in Great Horned Owls *Bubo virginianus*: Are predators food limited at the peak of prey cycles? *Ibis* 138:236–242.
- ROSENZWEIG, M. L., AND R. H. MACARTHUR. 1963. Graphical representation and stability conditions of predator-prey interactions. *American Naturalist* 97:209–223.
- RUSCH, D. H., E. C. MESLOW, L. B. KEITH, AND P. D. DOERR. 1972. Response of Great Horned Owl populations to changing prey densities. *Journal of Wildlife Management* 36:282–296.
- SALTZ, D., AND G. C. WHITE. 1990. Comparison of different measures of telemetry error in simulated radio-telemetry locations. *Journal of Wildlife Management* 54:169–174.
- SCHOENER, T. W. 1983. Simple models of optimal feeding-territory size: A reconciliation. *American Naturalist* 121:608–629.
- SOUTHERN, H. N., AND V. P. W. LOWE. 1968. The pattern of distribution of prey and predation in Tawny Owl territories. *Journal of Animal Ecology* 37:75–97.
- STEEN, H. 1995. Untangling the causes of disappearance from a local population of root voles, *Microtus oeconomus*: A test of the regional synchrony hypothesis. *Oikos* 73:65–72.
- STEPHENS, D. W., AND J. R. KREBS. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey.
- TEMELES, E. J. 1987. The relative importance of prey availability and intruder pressure in feeding territory size regulation by harriers, *Circus cyaneus*. *Oecologia* 74:286–297.
- THOMPSON, I. D., AND P. W. COLGAN. 1987. Numerical responses of martens to a food shortage in northcentral Ontario. *Journal of Wildlife Management* 51:824–835.
- VILLAGE, A. 1982. The home range and density of Kestrels in relation to vole abundance. *Journal of Animal Ecology* 51:413–428.
- WALTERS, C. J. 1986. Adaptive management of renewable resources. Macmillan, New York.
- WARD, R. M. P., AND C. J. KREBS. 1985. Behavioural responses of lynx to declining snowshoe hare abundance. *Canadian Journal of Zoology* 63: 2817–2824.
- YDENBERG, R. C. 1987. Nomadic predators and geographical synchrony in microtine population cycles. *Oikos* 50:270–272.

Associate Editor: K. L. Bildstein