SURVIVAL OF GREAT HORNED OWLS IN RELATION TO THE SNOWSHOE HARE CYCLE

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ABSTRACT.—We analyzed survival and recovery rates based on 371 recoveries from 4,713 Great Horned Owls (*Bubo virginianus*) banded as nestlings or recent fledglings in Saskatchewan from 1958 through 1987. During this period, abundance of snowshoe hares (*Lepus americanus*) fluctuated over three 10-year cycles. When hares were scarce, fewer owls bred, fledging success was lower, and owls of all age classes were recovered farther from the banding sites. We estimated survival by age class and period of the hare cycle using probability models that allowed recovery rates to vary with time. These models indicated annual variation in recovery rates, with a significant long-term decline largely due to a continentwide decline in the proportion of owls shot or trapped. After allowing for variation in recovery rates, estimated survival rates were higher for all age classes in years when hares were abundant than in years when hares were scarce (58 vs. 37% for immatures, 74 vs. 59% for yearlings, and 88 vs. 81% for adults). These results, in conjunction with those of earlier studies, indicate that declines in hare densities affected Great Horned Owl populations through increased dispersal and mortality, as well as decreased fecundity. *Received 26 January 1993, accepted 19 November 1993.*

SEVERAL ASPECTS of the breeding biology of Great Horned Owls (*Bubo virginianus*) have been shown to fluctuate in close synchrony with the 10-year cycle of the snowshoe hare (*Lepus americanus*; Rusch et al. 1972, Houston 1987a). In years of high hare populations, most owls breed, and clutch and brood sizes are large. In years of low hare populations, many owls emigrate out of the area, few of the remainder attempt to breed, and relatively few young fledge per nest (Houston 1971, 1975, 1987a). In years of low hare populations and poor reproductive success, unhatched eggs are more common in owl nests (Houston et al. 1987c).

Food availability also might be expected to affect mortality of owls, both directly through starvation, and indirectly because owls may take increased risks hunting, or may disperse more, thus increasing exposure to potential hazards. Fledglings particularly might be affected at two stages: during June through September, if there is insufficient food for their parents to feed them; and after about October, when they cease re-

ceiving supplemental feeding and typically disperse from their natal territory. Thus, we would expect that, in years of low hare populations, first-year survival would be lower than near the peak of the hare cycle. If food availability also affects condition and dispersal of older owls, we also predict higher survival of adults in years of high hare abundance.

In this paper, we test for variation in survival rates of owls in relation to hares, using data from recoveries of owls banded as nestlings. Ideally, such data should be supplemented with data from birds banded or recaptured as adults to allow use of the robust statistical methods of Brownie et al. (1985). However, the value of banding adults for survival analysis was not appreciated when the study began in the 1950s. In any case, since Great Horned Owls are extremely difficult and time consuming to capture as adults, it is unlikely that sufficient numbers of owls could have been captured to justify their inclusion in the analysis.

Traditionally, survival rates for birds banded as young have been analyzed based upon life-table models (e.g. Hickey 1952). Analyses of many data sets have shown that the assumptions of these models are almost invariably vi-

olated and, hence, the conclusions are unreliable (Burnham and Anderson 1979, Anderson et al. 1981). Furthermore, the basic model is statistically flawed due to the lack of identifiability of parameters and the high sampling correlations among estimates (Lakhani and Newton 1983). Anderson et al. (1985) summarized several problems with survival analyses using life-table models and concluded that studies based only on banded young "are pointless as regards survival estimation because no valid method exists for estimating age-specific or time-specific survival rates from such data," thus reaffirming a similar statement by Brownie et al. (1985).

More recent research has shown that several of these problems can be addressed using more complex models, and that at least limited inference may be possible in many cases from such data (Rinne et al. 1987, 1990, Morgan and Freeman 1989, Freeman and Morgan 1990, 1992). In particular, if the recovery period is long in relation to the total life-span of the bird, the identifiability problems are reduced, because only a limited range of solutions produces realistic values (Rinne et al. 1987, 1990). Furthermore, models allowing recovery rates and first-year survival rates to vary with time not only increase the realism of the models (thus, addressing many of the criticisms of Anderson et al. 1985), but also reduce problems with nonidentifiability of parameters. These models still have serious limitations, particularly the assumption that recovery rates are the same for all age classes. This assumption is severely violated for some species, such as Snow Geese (*Anser caerulescens*), in which recovery rates of young birds and adults vary differently with time, preventing reliable conclusions without data from banding adults (Francis 1995). For other data sets, including examples from two duck species, age-specific differences in recovery rates are small, and simulations suggest bias from the models may be small (Freeman and Morgan 1992).

In this paper, we first use contingency-table analyses and logistic regression to examine frequencies of recoveries in relation to hare abundance and time, and to assist in designing a realistic set of models for testing variation in survival rates. We then develop a family of probabilistic survival models, and use optimality theory and likelihood-ratio tests to select the most appropriate models for estimating survival and recovery rates (Lebreton et al. 1992). We use both likelihood-ratio tests and simulations to test our original hypotheses that survival of all age classes was higher in years of high hare abundance. Finally, we examine reported causes and locations of death to evaluate some of the model assumptions and examine potential causes of the observed variation in recovery and survival rates.

METHODS

Owl banding.—Nestling owls were banded on evenings and weekends throughout May (average hatching date is last week of April) and occasionally into June. Most were banded within "aspen parkland" agricultural habitat within a 250-km radius centered 75 km east of Saskatoon, a region with relatively high owl populations (Houston 1978). The typical owl nest was 8 to 10 m above the ground, built in a previous year by a Red-tailed Hawk (*Buteo jamaicensis*) in a natural grove of aspen (*Populus tremuloides*). Most nests were reported by a network of interested farmers (Houston 1987b). A crew of volunteer climbers was always available to assist with the banding, so that young in virtually every nest found could be banded. The most productive day was experienced at the peak of the hare cycle in 1970, when one party of four climbers banded 61 nestling owls in 23 successful nests. More typically, only 10 to 15 nests were visited per day due to the long distances between nests and the time required to climb the trees.

We analyzed data from 4,713 flightless young Great Horned Owls banded by C.S.H. and his assistants between 1958 and 1987, including 36 nestlings banded by subpermittee Glen A. Fox in 1960–1961 that were omitted from earlier papers. Most owls (4,622) were banded while they were still in the nest, allowing estimates of the number of young per successful nest (Table 1). The remaining owls were banded within 400 m of their nests, after they fledged but before they could fly strongly. We have excluded from the analyses banding data from 1946 through 1957, because only 20 owls were banded (with 4 recoveries), as well as data from individuals banded as adults during the study period, because only 25 were banded (with 5 recoveries).

Selection of recoveries.—We included all recoveries up until 30 April 1990 for which the date of death could be accurately assigned to a particular recovery year, with the exception of six owls found dead in or under their nest tree shortly after banding. Recoveries were excluded if the recovery date was not known, if the owl was found long dead (i.e. as a skeleton), or if the only available information was "band found." A few owls released alive also were included if they would have died without the intervention of the band finder—a subsequent recovery

of one such owl was excluded. Three owls trapped alive and released were excluded.

To verify the accuracy of information on recoveries reported to the banding office, and to ensure the maximum number of usable recoveries, an attempt was made to contact persons reporting band recoveries (Houston and Francis 1993). More specific dates and information on the cause of death allowed 36 records to be used that otherwise would have been unsuitable for survival analysis, including three initially reported as "band only" and one as "skeleton." In all 29 instances where the original recovery indicated only the postmark date of the letter, it was possible to determine the month or exact day of recovery. Recovery locations were placed more accurately for 44 owls. Corrections or refinements in the cause of death for 54 owls revealed, for example, among owls initially reported as "found dead," that 9 had been shot, 11 killed on roads, and 8 electrocuted (Houston and Francis 1993).

Snowshoe hare abundance.—Regrettably, we do not have recent quantitative data on the annual abundance of hares in Saskatchewan. The nearly synchronous 10-year cycles of the snowshoe hare, and its main predator, the lynx (*Lynx canadensis*), were first recognized by Peter Fidler in 1820, and have been carefully plotted by Elton and Nicholson (1942), based on data from fur trapping. In good years, trapping totals for hares were 10 to 50 times higher than in poor years. More recently, hares rarely have been trapped, because their fur has lost its value, and fluctuations in lynx trapping have been more closely related to variation in market value. Nevertheless, the relative abundance of hares was easily assessed by casual observations while banding owls. In years of peak abundance, hare tracks and scats were everywhere, and many individuals were seen each day. In poor years (which began with a sudden crash in hare numbers), tracks were rarely seen, and few hares were seen over the whole season. Thus, we have split years into "high-hare years," which include those when hares were increasing in abundance and at their peak, and "low-hare years," when hares were scarce. Classified in this way, the 30-year study covered three complete 10-year cycles of hare abundance, with peaks in 1960, 1970, and 1981 (Table 1). These peaks were close to the 1961, 1970, and 1980 snowshoe hare peaks in the adjacent province of Alberta (Keith 1974, Keith et al. 1984).

As an alternative to the dichotomous classification based on hare abundance, for some analyses we also used the number of young fledged per successful nest as an indirect index of food availability (Table 1). This index was correlated with estimated hare abundance (Houston 1987a), but also may have been related to variation in other prey species.

Recovery analysis.—There is some confusion in the literature with terminology, particularly for the terms recovery and reporting rates. For most analyses, we define recovery rate (λ) as the probability a bird will be found and its band reported, given that it has died. If constant over time, the recovery rate would be equivalent to the proportion of bands that were ever recovered, provided enough time had elapsed for all birds to die. This parameter (λ) also has been called reporting rate by some authors (e.g. Lakhani and Newton 1983, Freeman and Morgan 1992), but this is misleading, because it also incorporates the probability a dead bird will be found (which may be close to 1.0 for birds that were shot, but much lower for birds dying of natural causes). Reporting rate more appropriately refers to the probability that a person who has found a band will report it (e.g. Nichols et al. 1991).

Brownie et al. (1985) defined recovery rates (f in their equations) as the probability that a bird alive at the beginning of the year will die, be found, and be reported during the year. This differs from λ by incorporating the probability that a bird will die within a particular time period. In this paper, we call f "first-year recovery rate" because it can only be estimated directly for age classes that have been banded, which in our study was only immatures. We also use the term "indirect recovery" to refer to recoveries of birds in years subsequent to the first. For some analyses, we consider only indirect recoveries two or more years after banding. The indirect recovery rate will be influenced by survival over the first year (or first two years), recovery rates (λ) of birds dying as adults, and the number of years available after banding for birds to be recovered. Because the average date of hatching is the last week of April, we define the year as starting on 1 May, and continuing to 30 April of the following year. Survival rates are defined as the probability a bird alive in a particular age class at the beginning of one year (1 May) will survive to 30 April the following year.

To explore the basic patterns of recoveries, and select an appropriate set of models for survival analysis, we used contingency tables to compare mean first-year and indirect recovery rates among time periods. Because recoveries follow a binomial distribution (i.e. bird is either recovered or it is not), we used logistic regression to test for long-term changes in first-year and indirect recovery rates, and to differentiate the effects of hare abundance from the long-term decline (this is equivalent to analysis of covariance with standard regression models). The test statistics produced by the LOGISTIC procedure (SAS Institute 1985) are distributed approximately as chi-square with the degrees of freedom equal to the number of parameters being tested.

To evaluate whether changes in recovery rate might be influenced by changes in cause of death, we grouped the codes indicating how a recovery was obtained (Canadian Wildlife Service and U.S. Fish and Wildlife Service 1991) into five categories that potentially differ in likelihood of being discovered: shot or trapped

TABLE 1. Yearly banding and recovery totals for Great Horned Owls banded in Saskatchewan between 1958 and 1987, in relation to estimated hare abundance and number of young fledged per successful nest.

Banding year	Hares[a]	Young/ banded nest	No. banded	\ Recovery year[b] 58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
58	H	2.20	22	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
59	H	2.31	70		4	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
60	H	2.31	162			9	4	4	2	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
61	L	1.94	59				4	2	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
62	L	–	–																															
63	L	–	–																															
64	L	2.00	69							8	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
65	L	1.63	13									–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
66	L	2.27	116									8	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
67	H	2.32	258										18	1	2	1	1	1	1	1	–	1	–	–	–	–	–	–	1	–	1	1	2	–	–
68	H	2.46	402											20	7	3	–	3	1	1	–	1	1	2	–	1	–	–	–	1	–	–	–	–	–
69	H	2.64	224												11	6	1	3	–	2	–	1	–	–	–	1	–	–	–	1	–	4	–	–	–
70	H	2.50	285													9	4	2	1	1	3	–	–	–	–	–	–	–	1	–	–	–	–	–	–
71	L	2.13	135														4	3	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
72	L	2.20	168															15	–	3	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
73	L	1.81	50																–	2	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–
74	L	1.71	65																	3	–	1	1	1	–	1	1	–	–	–	–	–	–	–	–
75	L	2.10	145																		2	1	2	1	1	1	2	1	–	–	–	–	–	–	–
76	L	1.98	107																			6	5	6	5	5	7	3	1	1	2	–	–	–	–
77	L	2.25	153																				1	1	1	1	3	1	1	2	1	1	–	–	–
78	H	2.35	190																					5	5	2	3	13	4	4	3	1	–	–	–
79	H	2.51	211																						1	7	3	1	9	1	5	12	18	4	3
80	H	1.78	120																																
81	H	2.53	407																																
82	L	2.04	197																																
83	L	2.06	211																																
84	L	1.91	199																																
85	L	1.93	113																																
86	L	2.43	216																																
87	L	2.30	346																																

(codes 01, 04); killed on road (14, 45); electrocuted (37, 54); found dead or injured (00, 03), and other (02, 11, 17, 21, 27, 47, 57, 96, 97). We used contingency analyses to test for differences by age and time.

We tested whether recovery locations differed with age and with hare abundance using two-way ANOVA separately on recovery latitude and longitude. Because this may be influenced by variation in banding locations over time, we also calculated distances between banding and recovery locations using the equation of Moore and Dolbeer (1989). Because distances were highly skewed, we first ranked the data before carrying out the tests. For a one-way analysis, this is approximately equivalent to the nonparametric Kruskal-Wallis test. All standard statistical analyses were implemented with the SAS statistical package (SAS Institute 1985).

Survival models.—We modeled survival rates following the procedures recommended by Lebreton et al. (1992), whereby a series of models is developed, and the one with the fewest parameters that adequately fits the data is selected. This approach leads to a compromise between increased precision (by having fewer parameters) and greater bias (by using a model that is simpler than reality). Lebreton et al. (1992) recommended initial selection of the model using the Akaike information criterion (AIC), which is a weighted sum of the log-likelihood (ln L, a measure of how well the model fits the data) and the number of parameters in the model (Akaike 1973):

$$\text{AIC} = -2 \ln L + 2(\text{no. parameters}). \quad (1)$$

The model with the lowest AIC generally is considered to be the most suitable for estimating parameters from the data. Thus, model selection is an optimization procedure, rather than a series of hypothesis tests. An alternative approach is to use likelihood-ratio tests to select between two models, provided that the models are nested (i.e. one model can be formed from the other by combining two or more parameters). In this case, the test statistic is equal to twice the difference between the log-likelihoods of the two models, and is approximately chi-square distributed, with degrees of freedom equal to the difference in the number of parameters between the models. We used likelihood-ratio tests to verify the AIC selection procedure, as well as to test specific biological hypotheses about survival rates. We also conducted a series of simulations to evaluate the validity of the likelihood-ratio tests, and to develop one-tailed tests of our original hypotheses.

For our most-general model, we followed Freeman and Morgan (1992) in choosing a model allowing recovery rates (λ) and first-year survival rates (S) to vary with time. Their models assumed that survival for subsequent age classes was constant with time, but varied with age. We had too few recoveries of adult owls to estimate age-specific mortality beyond the first two years of life, so we restricted analyses to three age classes (first year, second year, and adult). We also wished to test whether survival rates varied over time for all age classes. The most-general model allowing survival rates of all age classes to vary by year is not identifiable and, in any case, the data were too sparse to support such a model with nearly 120 parameters. However, the hare cycle divides the study into six time periods of alternating high (H) and low (L) hare abundance (Table 1). Thus, for our most general model, we allowed survival to differ among years for young owls, but to differ only among time periods for second-year and adult owls (assuming a constant rate within each period). We denote this model $S^1_Y{:}S^2_P{:}S^A_P$, where the superscripts 1, 2, and A indicate the first-year, second-year, and adult age classes, respectively, and the subscripts Y and P indicate that survival rates of each age class differ among years or periods, respectively. This model even can be used assuming that recovery rates differ every year, a condition we denote by λ_Y. Unfortunately, no models based only on birds banded as young allow recovery rates to vary with age—a serious limitation if causes of mortality differ substantially with age (C. M. Francis 1995).

This general model has 32 recovery parameters, 28 first-year survival parameters (no owls were banded in some years), and 6 survival parameters each for yearlings and adults. If some of these parameters could be combined, without significant loss of fit, the remaining parameters could be estimated with greater precision. Reduced-parameter models also can be used to test the significance of variation in survival and recovery rates. We tested models assuming recovery rates varied only among periods (λ_P), assuming they declined linearly with time (λ_D), and assuming the recovery rate was constant with time (λ_C). We also tested models assuming second-year and adult survival rates were the same ($S^1_P{:}S^A_P$) to see whether we could reduce the number of age classes. We then developed models assuming first-year survival also differed only among periods ($S^1_P{:}S^2_P{:}S^A_P$), assuming survival of all age classes differed only between years of high and low numbers of hares ($S^1_H{:}S^2_H{:}S^A_H$), and assuming that survival was constant over time ($S^1_C{:}S^2_C{:}S^A_C$). Because food availability might affect young owls most strongly, we also tested a model assuming first-year survival varied in relation to hare abundance, but survival of older age classes was constant ($S^1_H{:}S^2_C{:}S^A_C$). We tested similar models assuming survival varied linearly in relation to fledging success (subscript F). A summary of models tested and notation is given in Table 2. All models were fitted with program SURVIV (White 1983), using SAS programs to generate the required input statements.

RESULTS

Recovery rates.—First-year recovery rates (f) differed significantly for owls banded in dif-

TABLE 2.   Akaike information criterion (AIC), with number of parameters in parentheses, for various models to estimate survival rates of Great Horned Owls banded as nestlings in Saskatchewan from 1958–1987. AIC of most-parsimonious model within each column is in bold.

Survival parameters[a]	Recovery-rate parameters[a]			
	λ_Y	λ_P	λ_D	λ_C
$S^1_Y{:}S^2_P{:}S^A_P$	652.04 (72)	642.08 (46)	647.70 (42)	649.03 (41)
$S^1_P{:}S^2_P{:}S^A_P$	637.01 (50)	630.28 (24)	633.65 (20)	**638.40 (19)**
$S^1_P{:}S^A_P$	647.34 (44)	638.15 (18)	641.88 (14)	656.91 (13)
$S^1_H{:}S^2_H{:}S^A_H$	629.57 (38)	618.78 (12)	**630.68 (8)**	646.34 (7)
$S^1_H{:}S^2_C{:}S^A_C$	**629.00 (36)**	**616.58 (10)**	632.09 (6)	646.11 (5)
$S^1_C{:}S^2_C{:}S^A_C$	631.84 (35)	618.15 (9)	639.80 (5)	652.08 (4)
$S^1_F{:}S^2_C{:}S^A_C$	630.69 (36)	—	—	650.43 (5)

[a] Superscripts represent age classes: (1) first year; (2) second year; (A) adult. Subscripts: (Y) differs among all 32 years; (P) differs among six periods; (H) differs only between high- and low-hare years; (D) linear decline over time; (C) constant across all years; (F) linear relationship with fledging success.

ferent time periods (Table 3). There appeared to be more young owls recovered in periods of low hare abundance, but this effect was partly obscured by a general decline over time. To separate these effects, we used multiple logistic regression to consider simultaneously the effects of a linear change over time, and the abundance of hares, on first-year recovery rates in each year. Both the long-term decline ($X^2 = 13.9$, df = 1, $P < 0.001$) and hare abundance ($X^2 = 8.4$, df = 1, $P = 0.004$) explained significant variation in first-year recovery rates. A similar analysis based on fledging success, instead of hare abundance, suggested higher recovery rates in years when relatively few young were fledged, but the difference was not quite significant ($X^2 = 3.6$, df = 1, $P = 0.06$). Higher recovery rates in years of low hare populations could have been due to greater mortality of young birds, such that more were available to be recovered. Alternatively, they could have been due to changes in cause of death, or location of death, such that a higher proportion of birds that died were found and reported. Similarly, the long-term decline in first-year recovery rates could have been due to fewer birds dying during their first year, or to a decline in overall finding or reporting rates(λ).

If first-year mortality was higher in years of low hare populations, one would expect fewer indirect recoveries from those cohorts because fewer birds survived to be recovered in later years. To test this, we compared indirect recovery rates for cohorts banded during different time periods. To standardize the period available for recovery, we used only the first eight years after banding, and excluded cohorts banded in the last period of the hare cycle (1982 or

later), for which fewer than eight years were available for recovery. Indirect recovery rates varied significantly among the three high and three low time periods (Table 1). Logistic regression again showed a highly significant long-term decline ($X^2 = 10.7$, df = 1, $P = 0.001$), but the relationship with hares, although in the predicted direction (fewer recoveries from cohorts banded in low-hare years), was not quite significant ($X^2 = 3.7$, df = 1, $P = 0.055$). This analysis must be treated cautiously, as it does not take into account possible variation in survival or recovery rates after the first year. In particular, if yearlings continued to have higher recovery rates in low-hare years, their inclusion in the indirect recoveries would tend to obscure the expected relationship. Excluding recoveries of yearlings, the relationship with hares was more strongly significant ($X^2 = 5.8$, df = 1, $P = 0.02$), supporting the hypothesis of lower first-

TABLE 3.   Recovery rates of Great Horned Owls in relation to snowshoe hare cycle.

Time period (years)	Hares	n	Recovery rates (%)		
			First year[a]	In-direct[b]	In-direct[c]
1958–1960	High	242	6.3	8.3	4.7
1961–1966	Low	233	8.9	2.7	1.6
1967–1970	High	1,169	5.0	3.4	1.9
1971–1977	Low	823	4.4	2.2	0.8
1978–1981	High	928	2.5	2.6	2.0
1982–1987	Low	1,282	4.7	—	—

[a] Recoveries in same year as banding (test for homogeneity of rates across time periods, $X^2 = 22.1$, df = 5, $P < 0.001$).
[b] Recoveries as yearlings and adults one to eight years after banding ($X^2 = 19.5$, df = 4, $P < 0.001$).
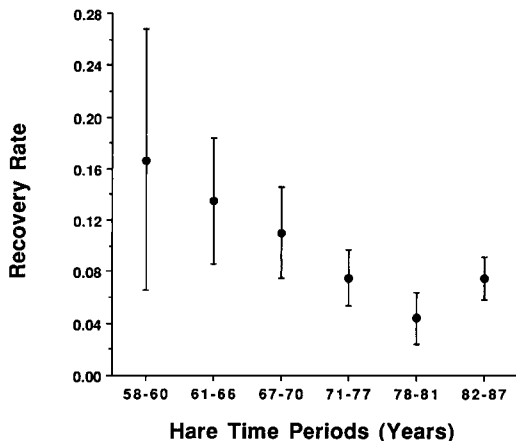[c] Recoveries as adults two to eight years after banding ($X^2 = 14.1$, df = 4, $P = 0.007$).

Fig. 1. Estimated recovery rates (λ, defined as probability a dead owl will be found and reported) with 95% confidence limits, in different time periods for Great Horned Owls banded as nestlings in Saskatchewan, 1958–1987. Estimates from model S^1_P:S^2_P:S^A_P:λ_P.

year survival rates in years of low hare populations. Similarly, there was a suggestion of lower indirect recovery rates from years when fledging success was low, although it was not quite significant statistically even when yearlings were excluded ($X^2 = 3.7$, df = 1, $P = 0.055$).

Survival models.—The preceding analyses of recovery patterns were highly suggestive of differences in immature survival rates in relation to the hare cycle, but did not allow estimating of actual survival rates, or testing of variation in survival of older birds. To estimate these rates and generate more rigorous tests of variation in survival, we used models that simultaneously incorporated variable recovery rates (λ) and survival rates. Such models also allowed us to use all data without any censorship, unlike the preceding contingency analysis of indirect recovery rates. We tested four families of models, differing in the number of recovery-rate parameters (Table 2). Because the recovery matrix (Table 1) was so sparse, with many cells containing zeros, the generalized goodness-of-fit test in SURVIV did not perform correctly (see simulations below). As a result, we had to assume that our most general model (S^1_Y:S^2_P:S^A_P:λ_Y) was an adequate fit to the data, and used that as a basis for testing various submodels.

Models assuming that recovery rates differed only among periods (λ_P) had the lowest AIC values for any given set of survival parameters

(Table 2, column 2). Estimates from these models indicated a large drop in recovery rates over the course of the study (Fig. 1). These models (λ_P) were a significantly better fit than models assuming a constant recovery rate (λ_C), even for the model with the smallest difference in AIC values (likelihood-ratio test for S^1_Y:S^2_P:S^A_P; $X^2 = 16.95$, df = 5, $P = 0.005$). The models assuming a linear decline in recovery rates (λ_D; Table 2, column 3) also had a lower AIC than models assuming constant recovery rates (λ_C; Table 2, column 4), and were a significantly better fit based on likelihood-ratio tests (e.g. for S^1_P:S^2_P:S^A_P; $X^2 = 6.75$, df = 1, $P = 0.009$). They were a worse fit than models allowing recovery rate to vary among years (λ_Y), despite a similar AIC (for S^1_P:S^2_P:S^A_P, $X^2 = 61.39$, df = 30, $P < 0.001$). This indicates that there was a significant decline in recovery rates over time, but either it was nonlinear or there was substantial additional annual variation in recovery rates not related to the decline. Despite the lower AIC for models that assumed recovery rates varied only among time periods (λ_P), these models were rejected in favor of the most general models (λ_Y) by likelihood-ratio tests (e.g. for S^1_P:S^2_P:S^A_P, $X^2 = 45.3$, df = 26, $P = 0.01$; for S^1_H:S^2_C:S^A_C, $X^2 = 39.6$, df = 26, $P = 0.04$). This suggests significant additional variation in recovery rates not explained by time periods. Thus, despite the large number of parameters and potential loss of precision, we felt it was safer to use the most-general model (λ_Y) for estimating survival rates to minimize the risk of bias.

Allowing recovery rates to differ among all years (λ_Y), the model with the lowest AIC was S^1_H:S^2_C:S^A_C (Table 2), indicating that survival rates were age-dependent until at least three years of age (i.e. differed for first-year, second-year, and adult owls) and, at least for first-year owls, were lower in years of low hare numbers (Table 4). The selection of this model was confirmed by likelihood-ratio tests. The model that assumed survival rates of second-year owls were the same as those of adults (S^1_P:S^A_P) was strongly rejected (comparison with model S^1_P:S^2_P:S^A_P; $X^2 = 22.3$, df = 6, $P = 0.001$), indicating that survival rates were significantly lower for second year than older owls. The high AIC of the model allowing survival to vary among all years for immatures (S^1_Y:S^2_P:S^A_P) indicated it was unnecessarily complex for the data. This model produced first-year survival estimates with very low precision—standard errors of these estimates

TABLE 4. Estimated survival rates (percent ± SE) by time period[a] and by stage of hare cycle[b] for Great Horned Owls banded as nestlings in Saskatchewan from 1958–1987.

Owl age class	Hare time periods (hare numbers)						Combined data on hare cycle	
	1958–1960 (High)	1961–1966 (Low)	1967–1970 (High)	1971–1977 (Low)	1978–1981 (High)	1982–1987 (Low)	High	Low
First year	58 ± 11	23 ± 9	58 ± 7	42 ± 7	54 ± 11	32 ± 6	58 ± 5	37 ± 4
Second year	34 ± 18	66 ± 12	74 ± 8	54 ± 10	89 ± 8	51 ± 10	74 ± 6	59 ± 6
Adult	—	78 ± 9	88 ± 5	86 ± 3	88 ± 5	67 ± 8	88 ± 3	81 ± 3

[a] Estimated from model $S^1_P{:}S^2_P{:}S^A_P{:}\lambda_Y$. There were no recoveries as adults during first period.

[b] Estimated from model $S^1_H{:}S^2_H{:}S^A_H{:}\lambda_Y$.

averaged 0.17, and some values were estimated at the boundaries (0 or 1). The model allowing survival to differ among all six time periods ($S^1_P{:}S^2_P{:}S^A_P$) also had a high AIC, and high standard errors of the survival estimates (Table 4). Neither of these models was a significantly better fit than the model assuming survival varied only in relation to hare abundance (model $S^1_Y{:}S^2_P{:}S^A_P$ vs. $S^1_H{:}S^2_H{:}S^A_H$, $X^2 = 49.5$, df = 36, $P = 0.07$; $S^1_P{:}S^2_P{:}S^A_P$ vs. $S^1_H{:}S^2_H{:}S^A_H$, $X^2 = 16.6$, df = 12, $P = 0.17$). The model allowing survival to differ with hare abundance for all age classes had somewhat better precision, and suggested higher survival for all ages in years of high hare abundance (Table 4). These differences were not significant for older birds, based on likelihood-ratio tests (model $S^1_H{:}S^2_H{:}S^A_H$ vs. $S^1_H{:}S^2_C{:}S^A_C$; $X^2 = 3.4$, df = 2, $P = 0.18$). However, higher survival of first-year birds in high-hare years was significant, as indicated by rejection of the constant-survival model ($S^1_H{:}S^2_C{:}S^A_C$ vs. $S^1_C{:}S^2_C{:}S^A_C$; $X^2 = 4.8$, df = 1, $P = 0.03$). The model relating first-year survival to fledging success ($S^1_F{:}S^2_C{:}S^A_C$) had a lower AIC than the constant-survival model, but the difference was not significant based on a likelihood-ratio test ($X^2 = 3.1$, df = 1, $P = 0.08$). It had a higher AIC than model $S^1_H{:}S^2_C{:}S^A_C$, suggesting that our dichotomous measure of hare abundance was a better predictor of first-year survival than fledging success.

The same survival model would have been selected, and essentially the same conclusions reached, assuming λ_P, which as noted above had the lowest AIC. However, use of models λ_D or λ_C would have been misleading in indicating significantly more variation in survival rates than supported by the data. In particular, estimates from models assuming constant recovery rates suggested that survival of all age classes differed across all time periods, with a tendency

to increase over time. This misleading result was due to the strong correlations between estimates of recovery and survival rates, so that true variation in recovery rates, which was not allowed for in model λ_C, was reflected instead in variation in estimated survival rates.

Simulations.—With a recovery matrix so sparse that the goodness-of-fit test failed, it is worth testing whether the likelihood-ratio tests are reliable. We used the simulation procedure in SURVIV to generate random recovery matrices using the actual banding totals, and the estimated recovery and survival rates from models $S^1_H{:}S^2_C{:}S^A_C{:}\lambda_Y$ and $S^1_C{:}S^2_C{:}S^A_C{:}\lambda_Y$ as the true underlying parameters. We ran 1,000 simulations for each starting model, then repeated the simulations a second time with slightly different starting values (generated by excluding a few of the original recoveries). For each simulation we estimated survival rates under both of these models, as well as for the more general model $S^1_H{:}S^2_H{:}S^A_H{:}\lambda_Y$.

The generalized goodness-of-fit test for all models, including the true models used to generate the data, always indicated an adequate fit with extremely high P-values (>0.9999). Clearly, this was not a useful test, because if the P-values were correct, the true model should have been rejected 5% of the time. SURVIV provides an algorithm to pool cells with small expected values, but these pooled chi-square tests did not perform well either. For matrices simulated using constant survival within each age class, the correct model was rejected 32% of the time (in 1,000 simulations). A more complex model, allowing survival to vary among time periods, was rejected more often (40%), despite the fact that additional parameters should always allow a slightly better fit to the data. This suggests that the pooling algorithm resulted in too few cells relative to the number of param-
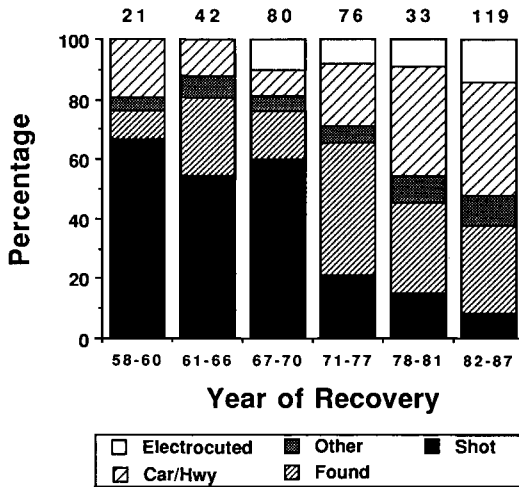
Fig. 2. Reported cause of death for Great Horned Owls banded as nestlings in Saskatchewan, 1958–1987, and recovered in each of six periods of differing hare abundance.

TABLE 5. Reported causes of death (percent) of Great Horned Owls banded in Saskatchewan from 1958–1987 in relation to age at recovery.[a]

Reported cause of death	Age at recovery		
	First year	Second year	Adult
Shot or trapped	31	41	26
Found dead or injured	29	30	27
Hit by car/dead on highway	25	20	23
Electrocuted	9	8	10
Other	6	2	15
Total	216	61	94

[a] Cause of death differed nonsignificantly with age at death (X^2 = 14.3, df = 8, P = 0.08).

eters, and incorrectly determined the degrees of freedom. Until a more appropriate test is developed, these results confirm our decision to ignore the generalized goodness-of-fit tests provided by SURVIV.

Despite the failure of the goodness-of-fit tests, the likelihood-ratio tests performed very well, at least for models differing in only a small number of parameters. On the two simulation runs in which the true survival rate was constant over time, the constant model was rejected at the 5% level in favor of $S^1_H:S^2_C:S^A_C:\lambda_Y$ in 50/1,000 and 49/1,000 simulations—nearly identical to the nominate 5% level. In comparison with the model $S^1_H:S^2_H:S^A_H:\lambda_Y$, the constant model was rejected 42/1,000 and 61/1,000 times, again very close to the nominate 5% level. This suggests the likelihood-ratio test we used to reject the constant-survival model was reliable.

These simulations also provided an opportunity for a potentially more powerful one-tailed test, corresponding to our original hypothesis that survival for all age classes would be higher in years of high hare abundance. Simulations assuming survival was constant with time only resulted in 6/1,000 cases in which the survival of immatures in high-hare years relative to low-hare years was as great as the difference observed under model $S^1_H:S^2_C:S^A_C$. When running simulations assuming that only the survival of immatures was affected by hares, only 30/1,000

simulations resulted in yearling and adult survival rates as high or higher in high-hare years as those observed under model $S^1_H:S^2_H:S^A_H:\lambda_Y$. Although the statistical basis for these one-tailed tests has not been explored in detail, the tests suggest that it was unlikely (P < 0.05) that yearling and adult survival were not also higher in years of high hare abundance.

Reported causes of death.—Changes in cause of death over time could be responsible for the observed changes in recovery rates, particularly through differences in the probability that a dead owl was found. Reported causes of mortality differed significantly among time periods (Fig. 2; X^2 = 119.1, df = 20, P < 0.001). The proportion reported shot or trapped declined very strongly, with a fairly abrupt drop between 1970 and 1972.

Differences among age classes in cause of death could lead to violation of the assumption that recovery rates were the same for all age classes. There were no significant differences among age classes in reported causes of death (Table 5).

Recovery locations.—We used a two-way ANOVA to test for differences in recovery latitude and longitude in relation to hare abundance and age class. We combined yearlings and adults for this analysis, and ranked recovery locations to minimize the influence of a few long-distance movements on the results. Controlling for differences in age, owls were recovered farther south ($\bar{x}$ = 50.2° vs. 51.3°; $F_{1,368}$ = 10.6, P = 0.001) and farther east (103.6° vs. 104.7°, $F_{1,368}$ = 4.1, P = 0.04) in low-hare years than in high-hare years. Within both high and low years, mean recovery latitudes during the first year appeared to be

A. First Year
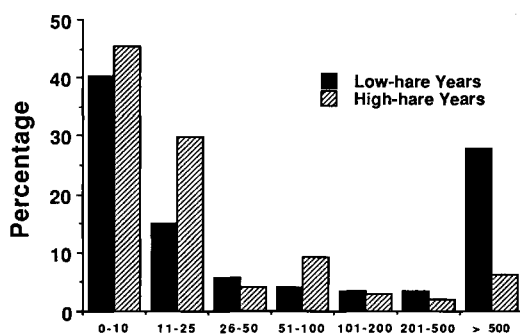
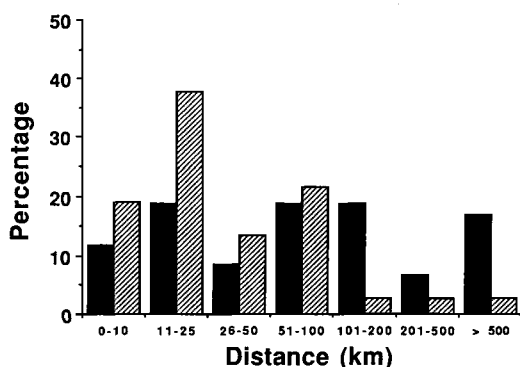## B. Subsequent Years

Distance (km)

Fig. 3. Distance between banding and recovery locations for Great Horned Owls banded as nestlings in Saskatchewan, 1958–1987, and recovered in years of high and low hare abundance in (A) first year after banding, or (B) subsequent years.

about 0.5° farther south than those of older birds, but this was not quite significant statistically ($F_{1,368} = 3.3, P = 0.07$). There were no significant age-related differences in recovery longitude ($F_{1,368} = 0.01, P = 0.9$).

We also tested for differences in the distance between banding and recovery locations. In years of low hare populations, owls were recovered significantly farther from their banding sites (first year, $\bar{x} = 281$ vs. 97 km; older birds, 226 vs. 71 km; $F_{1,368} = 18.4, P < 0.001$). Most of the difference was due to much larger numbers of recoveries more than 500 km from the banding site in years of low hare populations (Fig. 3).

Differences between first-year and older birds in the number of recoveries within 10 km of the banding site (Fig. 3) probably reflect dispersal during the first or second year to new

nesting sites. The observed differences between recovery locations of adults in high- and low-hare years potentially could also be influenced by dispersal in earlier years. If recovery locations, as adults, of owls banded only in high-hare years are compared, recovery locations were still significantly farther away in low years (175 vs. 77 km, $F_{1,98} = 9.8, P = 0.002$), suggesting that movement was related to hare numbers in the year of recovery.

Seasonal timing of mortality.—Because recoveries of owls occurred throughout the year (unlike, for example, waterfowl for which most recoveries occur in the hunting season), it was possible to look for variation in the timing of recovery within the year. Great Horned Owls remain together as family groups for several months after fledging, such that the young potentially are still receiving parental care into early October (Houston pers. obs.). During the first five months after banding (May through September), young were recovered significantly earlier in low-hare years than in high years (Fig. 4; Wilcoxon test on recovery dates, $P < 0.02$). This suggests that the parents may have been less able to care for them, leading either to higher mortality directly, or to earlier dispersal. Recovery rates for owls in low-hare years remained high throughout the following 12 months, whereas recoveries in high-hare years declined (Fig. 4).

DISCUSSION

Survival models.—Our conclusions about survival and recovery rates depend on the validity of the assumptions of the models used. Anderson et al. (1985) listed eight assumptions necessary for life-table models to hold, many of which also are relevant for the models we used. Two assumptions, common to most statistical studies, are (1) that the banded sample is representative of the population of interest, in this case Great Horned Owls nesting in southern Saskatchewan, and (2) that banding does not affect survival. We think that these assumptions were met in our study.

It is also assumed (3) that the fate of each banded bird is independent of the fate of other banded birds, and (4) that all banded birds in a particular age class have the same probabilities each year of surviving, or being reported if they die. The third assumption might be violated if birds remain together as families. Ex-
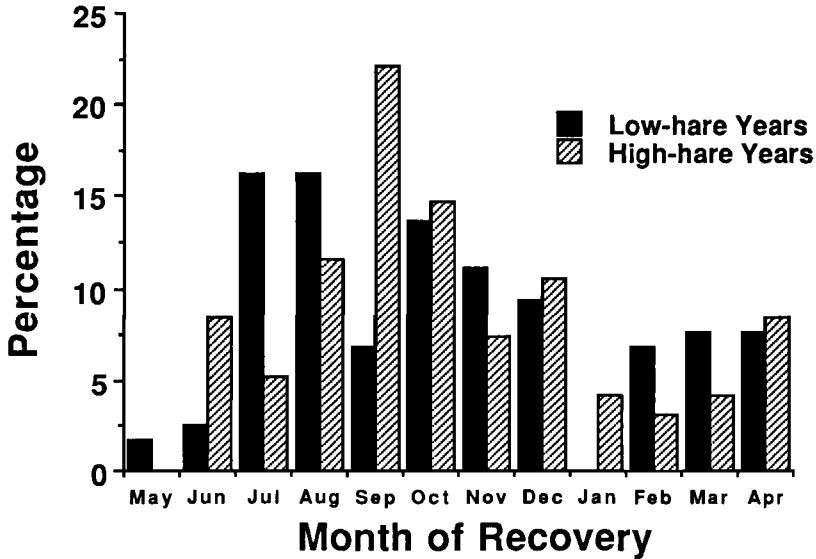
Fig. 4. Monthly distribution of recoveries of Great Horned Owls banded as nestlings in Saskatchewan, 1958–1987, during first year of life in years of high- and low-hare numbers.

cluding birds found dead under the nest, there were only two cases where two owls from the same nest were recovered together, once on the same night, and once a night apart. The fourth assumption is always an approximation, because many small factors could affect the survival or recovery of an individual owl, such as the location of its territory. In practice, unless there is very strong heterogeneity, the estimated survival rates can be considered representative of the population as a whole.

One assumption critical to these models, although less important for some others (Brownie et al. 1985), is (5) that birds do not lose their bands before they die. In many species (e.g. gulls, terns, and ducks), aluminum bands wear quite heavily and eventually fall off (Hatch and Nisbet 1983, DuWors et al. 1987). Apparently, this is not a problem with Great Horned Owls. Bands recovered from even the oldest owl in our study (at 20 years and 7 months), and on an even older owl (found injured in Manitoba 26 years after banding; Houston 1992, Nero 1992), have been well preserved. Another assumption is (6) that the year of recovery is correctly tabulated for all birds. The special effort made to contact each person reporting a dead owl (Houston and Francis 1993) has helped to ensure the accuracy of this tabulation.

The two remaining assumptions of standard

life-table methods, are (7) that annual survival rates are age-specific only, independent of year, and (8) that the recovery rate is constant over all age classes and years. In our models we relaxed these assumptions to allow survival and recovery rates to vary with time. However, the assumption that recovery rate does not vary with age is critical. Anderson et al. (1985) tabulated several examples showing how severely biased survival estimates can be, for all age classes, if recovery rates change with age.

Without banding or retrapping adults, we can test this assumption only indirectly. For Great Horned Owls, there are no significant differences among age classes in reported causes of death (Table 5). Such an analysis does not consider the possibility that birds from some age classes may be more likely to die in places where they have no chance of being found. In our study, nestlings that died in or around the nest were not represented because we excluded the six such recoveries. This exclusion seemed reasonable, because the recoveries were nonindependent (in two cases, two nest mates were recovered together), and nests were only revisited haphazardly after the young had been banded. However, if this were an important time of mortality for young (but not for adults), omitting birds found dead under nests could lead to lower recovery-rate estimates for young

than adults. Systematically checking the area around nests after fledging would have given a better estimate of mortality at the nest, but conversely would have led to increased recovery rates for young. If we assume the six owls recovered near the nest were representative of early mortality, and repeat the analyses including these birds, we get nearly identical results. None of the individual survival estimates from model $S^1_H{:}S^2_H{:}S^4_H{:}\lambda_Y$ changed by more than one percentage point, and the selection of models was unaffected.

If recovery rates for young were lower than those for adults, perhaps because of mortality near the nest, estimated first-year survival rates in Table 4 may be too high, although we doubt that the difference could be large enough to have a major impact on the estimates. Freeman and Morgan (1992) also concluded, based on simulations, that small age-specific differences in recovery rate would have little impact on survival estimates. Furthermore, unless relative recovery rates of young and adults changed in relation to the hare cycle—and a large change would have been required to generate the observed differences in survival rates—our conclusion of higher survival in years of high hare numbers remains valid.

A final assumption of our analysis was that the statistical tests, in particular the likelihood-ratio tests, were valid given the relatively sparse recovery matrix. Our simulations indicate, at least for the critical tests, that the likelihood-ratio tests were valid. However, the failure of the goodness-of-fit tests suggests a need for further statistical research, both to develop more appropriate goodness-of-fit tests, and to verify the robustness of the likelihood-ratio tests with a variety of different data matrices and models.

Variation in recovery rates.—The long-term decline in first-year recovery rates (Table 3) and at least part of the fluctuation in relation to the hare cycle appeared to be due to changes in the proportion of dead owls that were both found and reported (Fig. 1). Hickey (1952) noted that 113 of 478 nestling Great Horned Owls banded throughout North America, 1926–1941, were recovered, indicating an average recovery rate over the life-span of those cohorts of at least 23.6%—much higher than even the earliest years of our study. Similar declines in recovery rates have been observed for Great Horned Owls banded throughout North America (Houston unpubl. manuscript).

Changes in the cause of death of owls could explain much of the decline. Prior to 1970, more than 50% of owl recoveries in our study were of birds reported as shot or trapped. Similarly, 56% of the owls examined by Hickey (1952) were reported as shot, while 52% of 274 recoveries examined by Stewart (1969), which included those studied by Hickey, were reported as shot. After 1970, the proportion of birds reported as shot or trapped continued to drop in our study (Fig. 2) and across North America, contributing less than 5% of recoveries continentwide in 1981–1990 (Houston unpubl. manuscript). This change is due partly to increasing public education to counter the previous maxim, "the only good owl is a dead owl." The marked drop after 1970 coincided with the 1970 passage of legislation in Saskatchewan protecting owls year-round (Anonymous 1970). There also has been a drastic decrease in the use of muskrat and weasel traps, which accidentally caught owls; also, two game farms near Saskatoon have closed and their pole traps have been removed.

Most owls shot or trapped would have been found by the hunter/trapper and, hence, have the potential to be reported, whereas owls that died of natural causes would have been found much less often. Thus, the decline in the proportion shot could be largely responsible for the long-term decline in recovery rates. Of course, the apparent decline could have been confounded with changes in the reporting rate of bands that had already been found. Although some people believe there has been a general diminished interest in reporting bands, reward-band studies have found no evidence of changes in the proportion of Mallard (*Anas platyrhynchos*) bands reported by hunters between the early 1970s and the late 1980s (Nichols et al. 1991). For nonhunted species, such as owls, increased public awareness in natural history potentially could lead to more bands being reported. However, a marked drop in recovery rates for certain causes of mortality might have been expected if people shooting or trapping owls believed they may have done so illegally. Thus, the decline in birds reported as shot after 1970 could be due in part to a decline in the proportion reported, as well as to the evident decline in the number of birds being shot.

The proportion of owls reported electrocuted and as dead on highways or hit by cars has increased. Not until 1954 was the first Great Horned Owl anywhere in North America coded

as having been electrocuted (our first was in 1967), and not until 1957 was one coded as having been hit by a vehicle or found dead on a road (our first was in 1958), although other code numbers for cause of death were well represented, continentwide, in earlier years (Houston unpubl. manuscript). These striking changes reflect widespread rural electrification, improved roads, greater driving speeds, and increased traffic volume. The large decrease in the proportion of owls reported shot might be expected to affect their overall survival rates. There were no obvious indications of any trend for increasing survival rates over the course of our study, although the standard errors of these estimates were large (Table 4). This may indicate that other sources of mortality, such as highways, were compensating for the decline. Alternatively, survival may be regulated largely by density-dependent factors such as food supply. The reported causes do not necessarily represent the most important actual causes of mortality because of differences in finding rates for different causes of death. For example, until 1970, 61% of recovered owls were reported as shot (Fig. 2), but only about 14% of banded owls that died during that period were estimated to have been found and reported (Fig. 1). For waterfowl that have been shot, it is estimated that about one-third of bands are reported (Nichols et al. 1991). Assuming that most shot owls were found, and one-third were reported, the true proportion shot during that period would have been only 26%. This rough approximation indicates the potential biases in assessing causes of mortality from recovery data. Similarly, the importance of electrocution and highway deaths for owls is likely to be greatly overestimated by recovery data, because of the increased chance that someone will find the band. Owls electrocuted at a transformer cause a "short" that deprives that farm of its electricity supply, and owls dead on highways travelled by many people are relatively conspicuous compared to owls dead in the bush.

Hare abundance could have influenced recovery rates through affecting dispersal of owls. The increased movement of owls in years of low hare abundance (Fig. 3), mostly to the south and east, brought them through areas of lower human population density in the Dakotas into areas of higher human population density in Minnesota and Iowa, where the owls would have been more likely to be found if they died.

This may explain the slightly increased recovery rates in the most recent time period (Fig. 1), although other factors also could have been involved.

Age-specific mortality of Great Horned Owls. — Estimated survival rates were lowest in the first year of life, as has been found for most bird species, and remained significantly lower than those of older birds during the second year. Few reliable published estimates of survival rates of any species of owl are available for comparison. Anderson and Burnham (1991) estimated first-year survival rates of Northern Spotted Owls (*Strix occidentalis caurina*), based on mark-resighting data, between 20 and 30%, substantially lower than those of Great Horned Owls in our study. Their estimates may have been biased downwards by emigration from the study areas. Adult survival rates in their study appeared to decline from about 89 to 79% between 1985 and 1991, similar to the range of survival rates (81 to 88%) we observed for adult Great Horned Owls in periods of low and high hare abundance. Anderson and Burnham (1991) found no evidence for lower survival rates of second-year Spotted Owls, but they did not evaluate the power of their tests to detect such differences. In contrast, Rinne et al. (1990) found that survival rates of Tawny Owls (*Strix aluco*) did not reach adult levels until at least their fourth year; they used methods similar to ours to analyze survival rates based on recoveries of birds banded as young, but had larger samples (2,151 recoveries from 17,772 banded owls). Their estimates for average survival during the first, second, third, and subsequent years were 45, 61, 66, and 73%, respectively, lower than we observed for adult Great Horned Owls. Their estimates must be considered tentative, as their models did not consider temporal or age-specific variation in recovery rates.

Survival and dispersal in relation to snowshoe hares. —When hares were scarce, estimated survival rates were lower for all age classes (Table 4). The difference was largest during the first year, when survival in low-hare years was only two-thirds that in high-hare years. Differences for older age classes also were potentially important. Estimated mortality rates for adults (the converse of survival rates) changed from only 12% in high-hare years to 19% in low-hare years, which corresponds to a reduction of about one-third in the expected life-span as an adult. The lower statistical significance of this difference

may have been due, at least in part, to the smaller sample size of recoveries from older birds.

If greater mortality during low-hare years was due mainly to food shortage and, if food availability affected nest fledging success, we might have expected a stronger relationship between fledging success and survival. The relationship was in the predicted direction but weak. In years of low hare abundance, the estimates of mean fledging success were imprecise, because few nests were found. Furthermore, these nests may have been in atypical areas, because most owls in low-hare years failed to breed at all. Conditions during the nestling period were affected by abundance of many different prey items, while hares may have been a more critical food source during egg laying and incubation, when snow often was still deep.

Increased mortality in years of low hare abundance could have been due either to starvation, or to risks associated with dispersal from the breeding area. The tendency for early mortality during the period of dependency in low-hare years (Fig. 4) suggests that some parents had difficulty finding sufficient food for their young. Long-distance dispersal in low-hare years (Fig. 3) likely increased mortality for all age classes. Without data from multiple captures of individual birds, it was not possible to determine how many of these dispersing owls survived to breed later or, indeed, whether they returned to breed anywhere in southern Saskatchewan.

The 10-year cycle of the lynx, which has been tracked for over a century (Elton and Nicholson 1942), also depends upon or is coincident with the 10-year cycle of the snowshoe hare. In a 2.59-km² study area near Rochester, Alberta, adult hare numbers changed from 622 hares in April 1962 to 3 in the summer of 1965, due to a decrease in adult survival, a halving of the reproductive rate, and juvenile survival of only 3% (Meslow and Keith 1968). During the following cycle, the proportion of lynx kittens in the population dropped from 66% in 1971–1972 to 3% in 1973–1976 (Brand and Keith 1979), but data were not available on whether this was due to lower birth rates or decreased immature survival.

Marked population fluctuations have been documented in several other owl species, apparently in response to prey availability. In Finland, the number of breeding pairs of Tengmalm's (*Aegolius funereus*), Long-eared (*Asio otus*), and Short-eared (*A. flammeus*) owls fluctuate in relation to *Microtus* vole abundance, as do their clutch sizes and the number of young fledged (Korpimäki 1985). Decreased productivity and increased dispersal of Tengmalm's Owls during cyclical depressions in *Microtus* populations also has been documented in Norway (Sonerud et al. 1988). Fluctuations in wintering numbers of Snowy Owls (*Nyctea scandiaca*) are independently synchronous over much of eastern North America, although the relationship with microtine prey fluctuations has been challenged on the grounds that these are unlikely to be synchronous over such large areas (Kerlinger et al. 1985). Little is known about the relationship between these fluctuations and survival rates of either adults or fledged young. Higher proportions of first-time breeders in Ural Owls (*Strix uralensis*) after low-vole years (Pietiäinen 1988) may have been related to adult mortality, but direct measures of survival were not available. Higher indirect recovery rates were reported for Tengmalm's Owls raised in years of increasing vole abundance (Korpimäki and Lagerström 1988), suggesting higher survival, but the analysis did not consider the possibility of changing finding or notification rates. Also, many of the "recoveries" actually were recaptures in subsequent years in the study area, so that birds emigrating to new breeding areas, perhaps in response to low prey availability, may have been poorly represented.

The recent developments in statistical models and computer software for analyzing recapture (Lebreton et al. 1992) or recovery data (Brownie et al. 1985) provide powerful tools for testing hypotheses about changes in survival rates, while allowing for variation in capture or recovery probabilities. Our analyses demonstrate how similar models can be developed for analysis of recoveries when only young birds have been banded. Although these models have more restrictive assumptions than models including captures of adults, they provide the potential for testing hypotheses using data sets without adult banding data, which otherwise could not be analyzed.

successful nests found. The program would have been equally unattainable had it not been for an ever-changing cadre of clawed and sometimes frightened climbers, too numerous to mention, who take the most difficult trees and leave the easy climbs to C.S.H. Analyses were carried out by C.M.F. with the support of a postdoctoral fellowship from the Natural Sciences and Engineering Research Council of Canada using the computing facilities of the Zoology Department Morphometrics Laboratory at Duke University. Ian Newton, Christoph Rohner, David V. Houston, and an anonymous reviewer provided valuable comments on the manuscript.

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