ESTIMATING SURVIVAL RATES OF SNOWSHOE HARES

STAN BOUTIN, Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada
CHARLES J. KREBS, Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1W5, Canada

Abstract: Survival rates were estimated by 4 methods (minimum survival, Jolly-Seber, and 2 radio-telemetry techniques) for snowshoe hares (*Lepus americanus*) near Kluane Lake in the southern Yukon from 1978 to 1982. Jolly-Seber and minimum survival estimates from live trapping underestimated survival rates by 13 and 30%, respectively, when compared to telemetry estimates, which produced higher and nearly identical estimates of survival. Telemetry methods are recommended for estimating survival of hares.

J. WILDL. MANAGE. 50(4):592–594

Survival is an important demographic parameter, and changes in juvenile and adult survival rates are known to drive the 10-year snowshoe hare cycle (Keith and Windberg 1978). Two detailed analyses of this cycle (Keith and Windberg 1978, Krebs et al. 1986) found that survival rates tended to be underestimated (assuming census data and reproductive rates were accurate). In this paper we compare 4 methods of estimating survival rates for snowshoe hares to determine the source of this bias.

We thank B. S. Gilbert, R. A. Moses, and C. J. Krebs for their help in collecting these data and the Arct. Inst. North Am. for providing facilities at Kluane Lake. This research was supported by the Nat. Sci. and Eng. Res. Counc. Can.

METHODS

We livetrapped snowshoe hares on the 9-ha Silver Creek area (described by Boutin [1984]) near Kluane Lake in the southern Yukon from 1978 to 1982. Live trapping was carried out at 1–4-week intervals with 50–60 double- or single-door live traps. Traps were baited with alfalfa and set for 2 days during each trapping interval. Minimum trappability (Krebs and Boonstra 1984) averaged 62%.

Hares were fitted with radio transmitters weighing 30–45 g. No hares weighing <700 g were tagged. The number of hares with radios depended on the availability of transmitters. A total of 265 animals was collared during the study. Hares were located by triangulation from 2 permanent towers at least once weekly and in most cases once daily. Individuals showing no activity or changes in location over 2–3 days were located with a hand-held antenna to see if the animal was dead or if the transmitter had fallen off.

Survival rates were estimated in 4 ways:

1. Minimum survival rate—obtained from the trapping data by enumerating the marked hares:

$$\frac{N \text{ released at time } t \text{ and known alive at } t+1}{N \text{ released at time } t}.$$

A geometric mean was used to average survival rates over a time period.

2. Probability of survival—obtained from the trapping data by applying the Jolly-Seber model of estimation (Jolly 1965) and averaging the probabilities over the appropriate time period.

3. Telemetry minimum survival rate—obtained from the telemetry data by treating the telemetry data as "captures" as in (1) above.

4. Trent and Rongstad's (1974) telemetry method—obtained by calculating a daily survival rate from telemetry data by the following formula:

$$S = \frac{x - y}{x},$$

where

S = survival rate/day,
x = number of radio-hare-days (1 radio-hare-day is 1 hare with a radio in the field for 1 day) in time period t to $t + 1$, and
y = number of deaths of hares in time period t to $t + 1$.

Survival estimates were obtained for males and females for 15 time intervals, from summer 1978 to winter 1981–82, that included the latter part of the increase, peak, and start of the decline phase of the snowshoe hare population cycle. We analyzed the survival rate estimates by analysis of variance. Rates were compared using Duncan's multiple range test. Unless shown otherwise, statistical significance was accepted at $P = 0.05$.

RESULTS AND DISCUSSION

There was no difference between sexes ($P = 0.12$), but there were differences among methods ($P < 0.0001$). The telemetry minimum survival rate and Trent and Rongstad's telemetry method gave the highest survival estimates (Table 1). Jolly-Seber trapping estimates of survival were significantly lower than the telemetry estimates by an average of 13%. Minimum survival rates from trapping were significantly lower by 30% than the telemetry survival estimates and significantly lower by 19% than the Jolly-Seber estimates.

We do not know the true survival rates of hares in our study and thus can only compare among methods. All of the methods used to estimate survival were dependent on animals captured by live trapping. Consequently, all methods assume that animals were sampled randomly with respect to survival, that there was no marking or collaring effect, and that animals were independent. Keith et al. (1984) observed short-term increases in mortality of snowshoe hares caused by radio collaring during the decline phase. We did not observe any similar losses, but our animals were collared mostly during the increase and peak phase of the cycle (Boutin et al. 1986).

Minimum survival rates from trapping are biased for snowshoe hares because of low trappability (62%). Hilborn et al. (1976) showed the effect of low trappability on population estimates and Nichols and Pollock (1983) demonstrated that heterogeneity of trap response also can bias minimum trapping survival estimates.

The Jolly-Seber survival rate clearly is less than the telemetry survival rates. Carothers (1973, 1979) has shown that the assumption of equal catchability can be violated with only a very small effect on Jolly-Seber estimates of survival, if the probability of capture is >0.5 in each trapping session. Although minimum trappability was low for complete enumeration techniques, it averaged 62% during the study. Another possible reason for the lower Jolly-Seber survival rates is that the population of radio-collared hares differed from that of live-trapped hares. We could not collar hares that

Table 1. Mean survival rates/28 days for snowshoe hares in the southern Yukon. Four estimates of survival rates were obtained for 15 different time periods between 1978 and 1982, as described in the text.

Method	$\bar{x}$	SE
Trapping		
Minimum	0.604	0.030
Jolly-Seber	0.750	0.028
Telemetry		
Minimum	0.876	0.014
Trent-Rongstad	0.862	0.017

weighed <700 g, but juveniles could be trapped when they weighed as low as 250 g. Animals could have been caught at this weight between mid-June and late September only. Because Jolly-Seber survival rates were lower than telemetry rates in all time periods, it is unlikely that this bias can explain the difference in survival rates.

Forty-two percent of the hares were live-trapped a single time, whereas only 15% of the telemetry sample came from hares trapped a single time. If we omit all individuals captured only once, the mean Jolly-Seber probability of survival increases from 0.103/28 days to 0.854 and the Trent-Rongstad method increases from 0.019/28 days to 0.881.

The large fraction of snowshoe hares that were caught only once in live traps is difficult to explain. This fraction was as high during the phase of increase from 1978 to 1980 (43.6%) as during the peak phase during 1980–81 (40.5%). If these individuals are transients or dispersers, they could be under-represented in telemetry samples (Boutin et al. 1985). Hares caught only once in live traps had telemetry survival rates 0.11/28 days lower than hares caught more than once in live traps. Overall survival estimates are greatly affected by the inclusion of this class of single-capture animals.

Even if animals trapped a single time are excluded, the Jolly-Seber model produces survival rates that are lower than Trent-Rongstad estimates by an average of 0.03/28 days. Dispersal could cause underestimation in the Jolly-Seber model because dispersers are classed as mortalities in trapping data but not in telemetry data. If we treat all dispersers in the telemetry data as deaths and consider only animals caught more than once, the telemetry survival rates are reduced by 0.021/28 days to 0.860, which is similar to the Jolly-Seber estimate of 0.854 for the same class of animals.

Telemetry estimates of survival can be affected by right censoring of the data (Kalbfleisch and Prentice 1980). Right censoring occurs when a transmitter falls off before the animal dies, radio contact is lost, or the animal lives past the study period. Animals from which transmitters were lost were not included in the analysis unless they were recaptured. A very small portion of animals that were collared lived past the study period. Animals for which radio contact was lost were not included in the analysis because to do so may have biased telemetry survival estimates high. These animals were never recaptured, and consequently, either left the study area or died. Because we searched surrounding areas extensively for lost radios (Boutin et al. 1985), the latter is more likely. If all radio losses are classed as mortalities, the Trent-Rongstad survival rates are reduced from 0.019/28 days to 0.841, perhaps a lower boundary for Trent-Rongstad estimates.

We began our analysis to determine if radiocollaring reduced the survival rate of snowshoe hares. Surprisingly, survival estimates were highest for collared individuals and we found no evidence that radiocollaring snowshoe hares was detrimental. In fact, telemetry seems to be the best way of obtaining survival rates. However, the inclusion of hares captured a single time has a major influence on survival estimates obtained by both Jolly-Seber and telemetry methods.

LITERATURE CITED

BOUTIN, S. 1984. Effect of late winter food addition on numbers and movements of snowshoe hares. Oecologia 62:393–400.

———, B. S. GILBERT, C. J. KREBS, A. R. E. SINCLAIR, AND J. N. M. SMITH. 1985. The role of dispersal in the population dynamics of snowshoe hares. Can. J. Zool. 63:106–115.

———, C. J. KREBS, A. R. E. SINCLAIR, AND J. N. M. SMITH. 1986. Proximate causes of losses in a snowshoe hare population. Can. J. Zool. 64: 606–610.

CAROTHERS, A. D. 1973. The effects of unequal catchability on Jolly-Seber estimates. Biometrics 29:79–100.

———. 1979. Quantifying unequal catchability and its effect on survival estimates in an actual population. J. Anim. Ecol. 48:863–869.

HILBORN, R., J. A. REDFIELD, AND C. J. KREBS. 1976. On the reliability of enumeration for mark and recapture census of voles. Can. J. Zool. 54: 1019–1024.

JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225–247.

KALBFLEISCH, J. D., AND R. L. PRENTICE. 1980. The statistical analysis of failure time data. John Wiley & Sons, New York, N.Y. 321pp.

KEITH, L. B., J. R. CARY, O. J. RONGSTAD, AND M. C. BRITTINGHAM. 1984. Demography and ecology of a declining showshoe hare population. Wildl. Monogr. 90. 43pp.

———, AND L. A. WINDBERG. 1978. A demographic analysis of the snowshoe hare cycle. Wildl. Monogr. 58. 70pp.

KREBS, C. J., AND R. BOONSTRA. 1984. Trappability estimates for mark-recapture data. Can. J. Zool. 62:2440–2444.

———, B. S. GILBERT, S. BOUTIN, A. R. E. SINCLAIR, AND J. N. M. SMITH. 1986. Population biology of snowshoe hares I. Demography of populations in the southern Yukon, 1976–1984. J. Anim. Ecol. 55:963–982.

NICHOLS, J. D., AND K. H. POLLOCK. 1983. Estimation methodology in contemporary small mammal capture-recapture studies. J. Mammal. 64:253–260.

TRENT, T. T., AND O. J. RONGSTAD. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. J. Wildl. Manage. 38:459–472.

Received 28 June 1985.
Accepted 8 April 1986.