Ecology, 75(5), 1994, pp. 1512-1515
© 1994 by the Ecological Society of America

NORTHERN SPOTTED 0WLS. INFLUENCE OF PREY BASE- A COMMENT

Daniel K. Rosenberg,[1,2] Cynthia J. Zabel,[1] Barry R. Noon,[1] and E. Charles Meslow[3]

Conflicts between the needs of the Northern Spotted Owl *(Strix occidentalis caurina)* and the maintenance of a timber-based economy in the Pacific Northwest have motivated research on the habitat and area requirements of the owl. The Northern Spotted Owl has been studied extensively throughout its range and consistently has been found to select older forest stands for foraging, roosting, and nesting (reviewed in Thomas et al. [1990]). At least six hypotheses have been proposed to account for selection of older forests by Spotted Owls (Forsman et al. 1977, 1982, 1984, Carey et al. 1990, 1992, Rosenberg and Anthony 1992). Two of these relate to their prey. The prey hypotheses suggest that prey are more available to Spotted Owls by either or both of two mechanisms: (1) prey are simply more abundant in older forests (prey abundance hypothesis), and (2) prey are more efficiently hunted in older forests because of an increase in the ability of owls to forage through more open understory structure (prey availability hypothesis).

Carey et al. (1992) recently reported on associations between Spotted Owls and their prey in Oregon and Washington. They concluded that the abundance of prey across a landscape determined the carrying capacity for Spotted Owls and that within-landscape features such as stand age and forest fragmentation affected the abundance and demographic characteristics of prey. Northern flying squirrels *(Glaucomys sabrinus)* and dusky-footed and bushy-tailed woodrats *(Neotoma fuscipes* and *N. cinerea*, respectively) are the most common prey of the Northern Spotted Owl throughout its range, constituting the majority of the biomass consumed by owls (Forsman et al. 1984). Carey et al. (1992) concluded that northern flying squirrels were more abundant in older forests, populations were more stable in old than in young stands, squirrels were negatively affected by forest fragmentation, and they were isolated by intensively managed timber lands and conversion of forest to nonforest habitats. They concluded that woodrats showed similar patterns and that the home range size of Spotted Owls was related to prey abundance. These conclusions were based on comparisons of flying squirrel and woodrat abundances among forest types, seral stages, and geographic regions. These issues are critical to resource land managers who are interested in silvicultural prescriptions that might enhance prey densities for Spotted Owls and thereby increase the owls' reproductive success and reduce the amount of foraging habitat used by the owl. In our comment, we question whether the results and methods used by Carey et al. (1992) substantiate their conclusions, and cite previous studies that are not consistent with their conclusions.

Concerns Regarding Methods Used to Estimate Prey Densities

Flying squirrels were live-trapped in approximately 10 x 10 grids, with trap stations spaced 40 m apart within each grid. Trapping grids were set in 17 young and 17 old stands, for 8-10 nights. Trapping grids were placed in three forest types: western hemlock *(Tsuga heteropbylla)*, Douglas-fir *(Pseudotsuga menziesii)*, and mixed conifer. Although 17 stands of each age class were sampled, stands were not sampled consistently (Carey et al. 1992: Fig. 4). The total number of samples (i.e., number of stands x number of times sampled) is clear from only one region (southwestern Oregon; Carey et al.: Fig. 4): 43 for old stands and 18 for young stands. However, the total number of different stands sampled from this region was not mentioned. The number of stands sampled each year in this region ranged from 1 to 8 ($\bar{X} \pm 1$ SE, = 4.9 $\pm$ 0.7 stands) for old stands, and from 0 to 5 (2.0 $\pm$ 1.3 stands) for young stands. Two or more stands of each age class were sampled in only five of nine (season-year) sampling periods. However, six sampling periods were analyzed using a paired t test to compare flying squirrel density estimates between stand age classes. Each observation in the paired comparison was apparently the difference of the mean of density estimates for a given year and sampling period (spring, fall) between stand age classes within a region. The analysis (paired t test using stand means) seems inappropriate because it ignores variability within a stand age class for each sampling period, ignores the difference in sampling intensity (i.e., number of stands) between stand age classes, and does not allow for lack of independence of the repeated sampling strategy that was used (i.e., it artificially reduces variance). The rationale for using a paired test is that each estimate in the first sample is somehow related with a specific estimate from the second sample (Sne-

[1] U.S. Forest Service. Redwood Sciences Laboratory, Arcata, California 95521 USA.
[2] Address to which correspondence should be directed: Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA.
[3] US. Fish and Wildlife Service, Cooperative Wildlife Research Unit, Oregon State University, Corvallis, Oregon 97331 USA.

decor and Cochran 1967:97), and this does not seem to be the case with the samples presented in Carey et al. (1992). An analysis of variance (ANOVA) would be more appropriate to use, but must account for the repeated sampling (e.g., repeated-measures or split-plot ANOVA) and unequal sample sizes between stand age classes in each season and year.

Woodrats were live-trapped in the same 10 x 10 grids where flying squirrels were trapped. In addition, 27 stands were sampled using two parallel line transects, with 20 stations per transect spaced at 20-m intervals and two traps per station. Traps were operated for 3-4 nights.

Two types of estimators were used to assess the abundance of flying squirrels and woodrats: an enumeration method (minimum number known to be alive, MKA) and Chapman's modified Lincoln-Peterson (LP) estimator, a mark-recapture method. The estimator used was based on the number of individuals captured: MKA was used if < 10 individuals were captured, and LP if ≥ 10 individuals were caught. Density was calculated as $\hat{D} = \hat{N}/\hat{A}$, where $\hat{N}$ was computed as stated above and $\hat{A}$ was calculated using area of grid plus one-half the mean maximum distance moved within the trapping grid.

The use of two different estimators by Carey et al. (1992) was inappropriate. The MKA method yields negatively biased estimates whenever capture probabilities are < 1.0 (Hilbom et al. 1976, Nichols and Pollock 1983, Nichols 1986). MKA performed poorly as a relative measure of abundance in simulated data sets that were modeled using flying squirrel population characteristics (Rosenberg 1991). Flying squirrel capture probabilities vary temporally and spatially (Carey et al. 1991, Rosenberg 1991, Witt 199l), thus making comparisons among stands and regions using the MKA method inappropriate (Nichols 1986). Carey et al. (1992) cited a previous report (Carey et al. 1991) as an apparent justification for using the MKA method. However, in that report the number of different individuals captured was compared to results from a variety of population estimators, an inappropriate way to determine reliability of estimators (White 1992). The LP method would be expected to yield equal or higher estimates than the MKA method for a population of equal size because the objective of the LP estimator is to estimate the number of individuals present, but not captured, and to add these to the number captured (MKA). The estimator that was used on each population was not reported, making it impossible to assess the direction of the bias for flying squirrel and woodrat abundance patterns. If the MKA method was used disproportionately for young stands, and the LP method for old stands, then the reported differences in density may be artifacts.

Numbers of bushy-tailed woodrats captured were very low, and ≥ 10 individuals were captured in only 2 of 79 samples (area-season combinations) in stands sampled three or more seasons. Woodrats were not captured during most (72%, 57 of 79) samples (Carey et al. 1992: Table 5). These data make unbiased estimation of population size difficult. It is not clear which data were used to calculate woodrat densities among forest stand types. It appears that data were combined from grids and line transects. The number of stands in Table 4 (Carey et al. 1992), used to calculate woodrat densities by stand type, exceeds the number of stands in Table 5 (Carey et al. 1992), where the number of individuals captured in trapping grids was presented. Long belt transects can sample within-stand variation better than trapping grids for woodrat populations (Sakai and Noon 1993). Therefore, biases are likely when combining population size estimates from these two trapping techniques, and the comparison of results among forest stand types is suspect.

Problems with Interpretation of Data

Flying squirrels. Carey et al. (1992:233) stated "... densities in old forest were consistently higher than densities in managed, young forest . . .". Data presented by Carey et al. (1992) do not support this conclusion. During three of nine sampling periods (season-year combinations) only old-growth stands were sampled, and during one of nine sampling periods only one young stand was sampled (Carey et al. 1992: Fig. 4). Thus, ≥2 stands of each age class were sampled only during five of nine sampling periods. Among these five sampling periods when comparisons between age classes were possible, the ranges overlapped between young and old stands in four sampling periods (spring 1986-1989), and mean densities were similar (within 0.5 squirrels/ha, based on Carey et al. [1992]: Fig. 4) in at least two sampling periods. For the Olympic Peninsula, no data were presented except the overall (3-yr) mean and SE of each stand age class and the results of a paired *t* test. Again, the appropriateness of the paired *t* test is unclear. The coefficients of variation (cv = $SE/\bar{X}$) of the means were extremely high: 200% for second-growth and 40% for old-growth. cvs of this magnitude indicate low precision of estimates (Snedecor and Cochran 1967:62). The number of stands sampled each year, and the number of stands that were repeatedly sampled during the 3 yr, were not mentioned.

Carey et al. (1992:233) concluded that foraging by Spotted Owls ". . . appeared to depress flying squirrel populations . . .". Data presented in their Fig. 5 were used as supporting evidence. To test the hypothesis that Spotted Owls reduce local flying squirrel abundance, Carey et al. (1992:228) used "owl-years" as an index of foraging activity. Owl-years were calculated from the proportion of owl relocations within a stand

based on radiotelemetry data. Owl-years were divided into 3 classes: < l/3, l/3-2/3, and > 2/3. The number of stands sampled was not presented, only the mean, range, and inter-quartile range of foraging activity (Carey et al. 1992: Fig. 5). No statistical analysis of squirrel densities among the three classes of foraging activity was presented. Fig. 5 does not support the conclusion that the squirrel populations were "depressed" by owl foraging activity (Carey et al. 1992:233). Means were similar among the three classes (≈2.0, 1.3, and 1.1 squirrels/ha), and there was considerable overlap of squirrel densities among the three classes (ranges of ≈0.9–3.7, 0.5-2.8, and 0.3-3.0 squirrels/ha). Furthermore, there was no apparent adjustment for stand size when owl relocations were calculated, thus introducing another source of error in their relative estimates of foraging activity. A detection density (number of relocations per area sampled) would have been more appropriate.

The conclusions that flying squirrel abundance was more variable in young than in old stands, and that abundance in young stands increased with time (Carey et al. 1992:233), also were not supported by the data. No statistical analysis was reported to support this statement, and Fig. 7 in Carey et al. (1992) does not indicate a time trend. They suggested that effects of nearby timber harvesting, increased food supply from baited traps, and installation of nest boxes may have caused this increase in abundance. Their Fig. 7a, b, and c shows results from single young stands (a sample of three stands, described separately, with no mention of other young stands sampled) for each season and year. It is not clear how the confidence intervals were calculated from single stands. Nevertheless, means for different samples within a stand were similar, and confidence intervals overlapped, suggesting no trend. Although "stability" of abundance between age classes was not quantified, Carey et al. (1992:245) concluded that flying squirrels ". . . also seemed to maintain more constant abundance in old forest than they did in young forest, except in areas where the owls foraged intensively," Many techniques are available that would allow a quantitative assessment of constancy (e.g., Ostfeld 1988, Peltonen and Hanski 1991), but none were presented.

The results contain no analysis of forest fragmentation effects on flying squirrel populations, yet Carey et al. (1992:245) concluded that "Fragmentation of old forest does reduce overall numbers of flying squirrels. Stands intensively managed for timber, recent clear-cuttings, and conversion of forest to nonforest did isolate flying squirrel populations."

Woodrats. Carey et al. (1992:246) concluded that bushy-tailed woodrats were moderately abundant in some old-growth stands in some years, and were generally absent from pole stands. The data presented in Carey et al. do not support these conclusions. Densities of bushy-tailed woodrats were highest in "streamside sawlog" stands (Carey et al. 1992: Table 4). Such stands were not defined but were presumably young, unmanaged stands. Bushy-tailed woodrat densities in different stand types were (in decreasing order) streamside sawlog: 1.1 inds./ha; rocky areas: 0.6 inds./ha; managed pole: 0.5 inds./ha; and old growth: 0.2 inds./ha. These relative densities seem to be in direct contrast to Carey et al.'s conclusions regarding woodrat densities.

Carey et al. (1992:246) further concluded that occupancy of early seral stages was variable ". . . probably reflecting the fragmentation of old forest and the relatively short time the early seral stages are suitable for woodrats." Carey et al. (1992:246) referred to the large SE in their Table 4 to support this conclusion. Data presented do not support this interpretation. On the contrary, the cvs (i.e., the SE relative to the mean) that we calculated from their estimated densities of bushy-tailed woodrats in mixed-conifer forest (Carey et al. 1992: Table 4) were highest in old-growth stands (400%), followed by clearcuts (100%); the cv of managed pole stands was 43%. Reported dusky-footed woodrat densities varied less among seral stages, but streamside sawlogs had the highest cv (100%), followed by managed pole (45%) and old-growth (30%) stands. Although these might not be appropriate data to test variability of occupancy, they are what Carey et al. used in support of the above conclusions. Other data would have been more appropriate to test variability of occupancy, such as the proportion of trapping grids with or without presence of woodrats over time (temporal variability) or among grids (spatial variability).

Carey et al. (1992:246) concluded that the trapping data from old growth stands suggest regular local extinctions of woodrat populations, and that fragmentation of old Douglas-fir forest isolated bushy-tailed woodrat populations: "The large areas of early to mid-seral stages . . . had few bushy-tailed woodrats and certainly contributed to the isolation of woodrat populations in old growth and along streams." These conclusions were presumably based on trapping results from some grids (e.g., Carey et al. 1992: Table 5: "Miner," "Cherry4") where l-3 woodrats were captured on at least one occasion, but where no individuals were captured in a subsequent season. Carey et al. did not present data on movements or survival to support these conclusions. No data were presented concerning forest fragmentation effects on woodrats.

Prey biomass and owl home-range size. The conclusion that the "Area of old forest used by Spotted Owls decreased with increasing biomass of prey" (Carey et al. 1992:235) was unfounded based on the data presented. Problems associated with using different techniques (grid vs. line transect) to compare abundance among regions and species, coupled with the

problems of using two estimators, makes reliable estimation of prey biomass across regions difficult. Finally, not only was a relationship stated, but it was described based on only three data points (Carey et al. 1992: Fig. 8); no statistical analysis was attempted. As a result of the omission of the level of variance within and among plots (i.e., grids or stands), the relationship of old forest used by Spotted Owls and prey biomass is much less certain than shown in Fig. 8 of Carey et al. (1992). Rather than simply proposing a hypothesis with these data, an "effect" was stated (Carey et al. 1992: Fig. 8). Presentation and analyses of these data could have been improved by including the variation in owl home-range sizes and prey biomass within regions, as well as providing estimates of the error involved in estimation of these parameters.

Conclusions

The ability of specific silvicultural prescriptions to increase prey densities for Spotted Owls, and thereby to reduce the amount of foraging habitat used by Spotted Owls, is currently unknown. Furthermore, simply increasing prey densities within a stand may not result in an increase in prey available to Spotted Owls if their foraging efficiency is low in these stands. The hypothesis that higher prey abundance is responsible for the selection of older forests by Spotted Owls for foraging (Forsman et al. 1977, 1982, 1984, Carey et al. 1990, 1992) is not supported by data presented by Carey et al. (1992) or by data from other parts of the Northern Spotted Owls' range. Within the range of the Northern Spotted Owl, flying squirrel densities were found to be similar between young and old-growth stands in the Oregon Cascades (Rosenberg and Anthony 1992), and higher densities of woodrats were found in early seral stages than in older forests in northern California (Sakai and Noon 1993). Results from radiotelemetry studies consistently indicated that Spotted Owls selected older stands for foraging (reviewed in Thomas et al. [1990]), yet prey abundance did not appear to be consistently higher in old than in young forests. This does not falsify the prey abundance hypothesis, but suggests that differences in stand structure, or other factors that affect prey availability, may be responsible for selection of older forests for foraging (Carey et al. 1992, Rosenberg and Anthony 1992). This hypothesis could be tested in a semi-captive environment where owl foraging efficiency is compared among different stand structures. Creative experimental work needs to be conducted to determine what factors lead to the selection of old forests by Northern Spotted Owls.

Acknowledgments: We thank S. DeStefano, R. L. Hutto, W. C. McComb, and J. D. Nichols for their constructive criticisms of earlier drafts of this manuscript. Publication of this paper was supported, in part, by the Thomas G. Scott Achievement Fund.

Literature Cited

Carey, A. B., B. L. Biswell, and J. W. Witt. 1991. Methods for measuring populations of arboreal rodents. USDA Forest Service General Technical Report PNW-GTR-273.

Carey, A. B., S. P. Horton, and B. L. Biswell. 1992. Northern Spotted Owls: influence of prey base and landscape character. Ecological Monographs 62:223-250.

Carey, A. B., J. A. Reid, and S. P. Horton. 1990. Spotted Owl home range and habitat use in southern Oregon Coast Ranges. Journal of Wildlife Management 54:1l-l7.

Forsman, E. D., K. M. Horn, and W. Neitro. 1982. Spotted Owl research and management in the Pacific Northwest. Transactions of the North American Wildlife and Natural Resources Conference 47:323-331.

Forsman, E. D., E. C. Meslow, and M. J. Straub. 1977. Spotted owl abundance in young versus old-growth forests, Oregon. Wildlife Society Bulletin 5:43-47.

Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildlife Monographs 87.

Hilbom, R., J. A. Redfield, and C. J. Krebs. 1976. On the reliability of enumeration for mark and recapture census of voles. Canadian Journal of Zoology 54:1019-1024.

Nichols, J. D. 1986. On the use of enumeration estimators for interspecific comparisons, with comments on a "trappability" estimator. Journal of Mammalogy 67:590-593.

Nichols, J. D., and K. H. Pollock. 1983. Estimation methodology in contemporary small mammal capture-recapture studies. Journal of Mammalogy 64:253-260.

Ostfeld, R. S. 1988. Fluctuations and constancy in populations of small rodents. American Naturalist l31:445-452.

Peltonen, A., and I. Hanski. 1991. Patterns of island occupancy explained by colonization and extinction rates in shrews. Ecology 72:1698-l708.

Rosenberg, D. K. 1991. Population characteristics of northem flying squirrels and Townsend's chipmunks in second- and old-growth forests. Thesis. Oregon State University, Corvallis, Oregon, USA.

Rosenberg, D. K., and R. G. Anthony. 1992. Characteristics of northern flying squirrel populations in second- and old-growth forests in-western Oregon. Canadian Journal of Zoology 70:161-166.

Sakai, H. F., and B. R. Noon. 1993. Dusky-footed woodrat abundance in different-aged forests in northwestern California. Journal of Wildlife Management 57:373-382.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. Iowa State University Press, Ames, Iowa, USA.

Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Vemer. 1990. A conservation strategy for the Northern Spotted Owl. Interagency Scientific Committee to Address the conservation of the Northern Spotted Owl. (USDA: Forest Service, USDI: Bureau of Land Management, Fish and Wildlife Service, and National Park Service). 1990-791-171/120026. United States Government Printing Office, Washington, DC., USA.

White, G. C. 1992. Do pellet counts index white-tailed deer numbers and population change?: a comment. Journal of Wildlife Management 56:611-612.

Witt, J. W. 1991. Fluctuations in the weight and trapping response for *Glaucomys sabrinus* in western Oregon. Journal of Mammalogy 72:612-615.

Manuscript received 8 March 1993;
revised 30 June 1993;
accepted 5 August 1993.