

# Influence of prey abundance on northern spotted owl reproductive success in western Oregon

Daniel K. Rosenberg, Keith A. Swindle, and Robert G. Anthony

**Abstract:** The hypothesis that high temporal variability of northern spotted owl (*Strix occidentalis caurina*) reproductive success is a response to prey abundance remains largely untested. We evaluated this relationship in the Oregon Cascade Mountains. Despite similar biomass of northern flying squirrels (*Glaucomys sabrinus*) ( $169 \pm 13.9$  g/ha) and deer mice (*Peromyscus maniculatus*) ( $160 \pm 18.8$  g/ha), flying squirrels dominated the breeding season diet based on both biomass (49%) and numbers (40%). Abundance of flying squirrels and western red-backed voles (*Clethrionomys californicus*) was more variable spatially ( $\geq 38\%$  of process variation) than temporally (15%–24%), whereas abundance of deer mice was more similar across stands (12% spatial variation) than among years (68% temporal variation). Spotted owl reproductive success was statistically associated only with the abundance of deer mice (number of young per territory:  $r^2 = 0.68$ ). However, deer mice comprised only  $1.6 \pm 0.5\%$  of the biomass consumed. The low temporal variability of the dominant prey species provided evidence that simple prey relationship models were not likely to explain the highly synchronous and temporally dynamic patterns of spotted owl reproductive performance. Reproductive success was likely a result of the interaction of both weather and prey and the life history strategy of this long-lived owl.

**Résumé :** L'hypothèse qui veut que l'importante variabilité temporelle du succès reproducteur de la chouette tachetée du nord (*Strix occidentalis caurina*) s'explique par les variations d'abondance des proies reste à vérifier. Nous avons évalué cette relation dans les monts Cascades de l'Oregon. Bien que les grands polatouches (*Glaucomys sabrinus*) ( $169 \pm 13,9$  g/ha) et les souris sylvestres (*Peromyscus maniculatus*) ( $160 \pm 18,8$  g/ha) aient des biomasses semblables, les polatouches prédominent dans le régime alimentaire de la chouette durant la saison de reproduction, tant par la biomasse (49 %) que par la densité (40 %). L'abondance des grands polatouches et celle des campagnols-à-dos-roux de l'Ouest (*Clethrionomys californicus*) varient plus dans l'espace ( $\geq 38$  % de la variation de processus) que dans le temps (15 % – 24 %), alors que celle des souris sylvestres est plus semblable d'une parcelle à l'autre (12 % de variation spatiale) que d'une année à l'autre (68 % de variation temporelle). Le succès de la reproduction de la chouette tachetée est en corrélation statistiquement significative seulement avec l'abondance des souris sylvestres (nombre de petits pour territoire:  $r^2 = 0,68$ ). Cependant, les souris sylvestres ne représentent que  $1,6 \pm 0,5$  % de la biomasse ingérée. La faible variabilité temporelle de l'espèce prédominante de proies indique que des modèles simples de prédation sont peu susceptibles d'expliquer les patterns très synchronisés et la dynamique temporelle de la performance reproductive de la chouette tachetée. Le succès de la reproduction s'explique probablement par l'interaction du climat et des proies, ainsi que par la stratégie démographique de cette chouette à grande longévité.

[Traduit par la Rédaction]

## Introduction

An important issue in the management of northern spotted owl (*Strix occidentalis caurina*) populations concerns the amount and distribution of older forests in the landscape to support sustainable populations. Older forests provide the highest quality foraging habitat for spotted owls in the western Oregon Coast Ranges and Cascades (Forsman et al. 1984; Carey et al. 1992). Successful reproduction by north-

ern spotted owls depends, in part, on patterns of prey abundance. An understanding of the influence of prey abundance on spotted owl reproductive success is integral to interpreting their population dynamics and important for successfully implementing guidelines to manage the landscape for spotted owls, their prey, and lumber production.

Reduction in prey abundance affects the demography of populations of territorial raptor species through mechanisms affecting reproduction and survival (Southern 1970; Newton

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1979; Wendland 1984; Steenhof et al. 1997; Brommer et al. 1998). Few studies, however, have quantified the magnitude of change in the reproductive success of spotted owls attributable to prey abundance. Ward et al. (1998) evaluated the relationship of northern spotted owl reproduction with the abundance of prey at the level of the individual territory and found that because of the high spatial variability of prey abundance, they could not reliably estimate the abundance of prey at the scale of the individual owl. Most of the studies conducted on northern spotted owls either have investigated prey abundance in different forest age classes (Carey et al. 1992; Rosenberg and Anthony 1992; Rosenberg et al. 1994b; Waters and Zabel 1995) or have used habitat composition surrounding nest sites as an assumed surrogate to prey abundance (Ripple et al. 1997; Meyer et al. 1998; Swindle et al. 1999; Franklin et al. 2000). These types of studies do not directly address the relationship of prey abundance to owl reproductive success. Several studies that have examined the relationship of diet and reproductive success of spotted owls found a positive relationship of success with the proportion of large prey (e.g., northern flying squirrels, *Glaucomys sabrinus* (hereinafter, flying squirrels), and wood rats *Neotoma* spp.) in pellets (Barrows 1987; Laymon 1988; Thrailkill and Bias 1989; White 1996). Despite the apparent selection for larger prey species, Ward (2001) found that reproductive success of Mexican spotted owls (*Strix occidentalis lucida*) was most highly correlated with abundance of the smaller prey species and concluded that the broad assemblage of prey species is key to reproductive performance of the Mexican spotted owl through mechanisms of prey switching and increased prey biomass during years of high density of the smaller prey species.

If spotted owls are food limited, reproductive performance should increase with higher densities of prey up to a satiation threshold. Changes in reproduction should be most apparent in the proportion of females that attempt to breed (breeding probability) and the number of young that successfully fledge, as these parameters are most sensitive to short-term fluctuations in food supply in raptor populations (Southern 1970; Rusch et al. 1972; Newton 1979:128; Wendland 1984; Ward and Kennedy 1996; Steenhof et al. 1997). The highly synchronous pattern of reproductive success of northern spotted owls across large regions (Burnham et al. 1996) suggests that their reproductive success would be most strongly associated with prey species whose abundance fluctuates more through time than through space. If so, we hypothesized that there would be a similar pattern at smaller spatial scales because the high temporal variation of owl reproduction has been noted within as well as among regions (Forsman et al. 1996). We evaluated this hypothesis with data on spotted owl diet, prey abundance, and owl reproductive success in the western Cascade Mountains of Oregon.

### Study areas

The study area was located on the western slope of the Cascade Mountain Range in Lane County, Oregon. It included portions of the Blue River, McKenzie Bridge, and Sweet Home Ranger Districts of the Willamette National Forest as well as some interspersed private holdings, comprising approximately 31 700 ha (Miller et al. 1996). Eleva-

tions ranged from 375 to 1500 m. The climate was maritime with wet, mild winters and dry, warm summers. The study area was located within the Western Hemlock Zone (Franklin and Dyrness 1973), which was dominated by subclimax forests of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red-cedar (*Thuja plicata*). Although 49% of the area had been converted to young conifer plantations through timber harvest or was otherwise not suitable as spotted owl nesting habitat, the remainder comprised older forests (Cohen et al. 1995; Swindle et al. 1999) in which northern spotted owls concentrated their foraging (Forsman et al. 1984).

Within the larger study area described above, we estimated small-mammal abundance within five old-growth stands, all of which were typical of the primary nesting and foraging habitats of the spotted owl in our study area (Forsman et al. 1984; Ripple et al. 1991; Swindle et al. 1999). We selected old-growth stands that were dominated by Douglas-fir with a stand age of  $\geq 400$  years old, large enough to accommodate a 13-ha grid with a 50-m buffer and accessible by road (Rosenberg and Anthony 1992). We assumed that the trapping grids were representative of the type of primary foraging habitat of the spotted owl in the study area, primarily older growth Douglas-fir and western hemlock forests (Forsman et al. 1984). This assumption was reasonable for evaluating our hypotheses on temporal and spatial variation of owl reproductive success and population dynamics of small mammals but precluded evaluation of the association of prey and reproductive success at the scale of the individual territory.

## Methods

### Diet

Diet composition was estimated from prey remains in regurgitated pellets that were collected during 1987–1996 within the breeding season (1 March through 31 August). We considered an individual territory in a given year the sample unit, so we pooled all pellets within a territory and year for analysis. In 1993, pellet samples were collected from only two territories and were few in number, so we omitted these data from analyses. Pellets included in analyses were collected from four or more ( $16.6 \pm 2.5$ , mean  $\pm 1$  SE) owl territories each year. Estimation of the numbers and biomass of prey consumed followed methods described in Forsman et al. (2001). Because remains of brush rabbits (*Sylvilagus bachmani*) and snowshoe hare (*Lepus americanus*) were not identified separately, we pooled these as a single class, leporids.

### Prey abundance

We used estimates of small-mammal abundance from the five old-growth stands studied by Rosenberg and Anthony (1992). We livetrapped small mammals during spring or late fall, depending on the ability to capture each species. We assumed that the estimates during late fall were correlated equally among years with prey abundance during the breeding season of spotted owls; estimates of prey abundance during spring corresponded to the breeding season, including incubation.

**Table 1.** Composition of diets of northern spotted owls (*Strix occidentalis caurina*) on the west slope of the Cascade Mountains, Blue River, and McKenzie Ranger Districts, Oregon, 1987–1996.

| Species   | Prey biomass (%) |     |           | Prey number (%) |     |           |
|---|------------------|-----|-----------|-----------------|-----|-----------|
|   | Mean             | SE  | Range     | Mean            | SE  | Range     |
| Northern flying squirrel ( <i>Glaucomys sabrinus</i> )        | 48.8             | 3.9 | 27.3–62.2 | 48.7            | 3.1 | 24.1–53.5 |
| Leporids <sup>a</sup>   | 10.7             | 3.5 | 2.3–31.0  | 5.7             | 1.9 | 0.9–18.8  |
| Bushy-tailed wood rat ( <i>Neotoma cinerea</i> )              | 10.5             | 2.4 | 0–23.4    | 5.1             | 1.2 | 0–11.6    |
| Mazama pocket gopher ( <i>Thomomys mazama</i> )               | 7.3              | 1.8 | 0.8–17.2  | 7.3             | 1.6 | 1.0–15.9  |
| Western red-backed vole ( <i>Clethrionomys californicus</i> ) | 5.5              | 1.5 | 0.6–13.7  | 12.8            | 3.3 | 3.1–33.4  |
| Red tree vole ( <i>Phenacomys longicaudus</i> )               | 3.7              | 0.8 | 0.2–8.6   | 6.7             | 1.2 | 0.5–13.1  |
| Deer mouse ( <i>Peromyscus maniculatus</i> )                  | 1.6              | 0.5 | 0–4.3     | 4.9             | 1.4 | 0–12.4    |
| Douglas squirrel ( <i>Tamiasciurus douglasii</i> )            | 1.1              | 0.6 | 0–5.5     | 0.6             | 0.4 | 0–5.6     |
| Coast mole ( <i>Scapanus orarius</i> )                        | 1.2              | 0.7 | 0–6.4     | 1.4             | 0.8 | 0–5.9     |

**Note:** Only prey species that contributed  $\geq 5\%$  biomass in any given year or for which we estimated abundance are shown; data from 1993 was excluded because the samples were from only two territories. Individual owl territories each year were considered the sample, and SE was based on yearly variation in mean estimates among territories. Sample size of number of owl territories where pellets were collected ranged from 4 to 27 ( $16.6 \pm 2.5$ , mean  $\pm 1$  SE) among years. Estimation of prey biomass and numbers of prey consumed followed methods described in Forsman et al. (2001).

<sup>a</sup>Includes brush rabbit (*Sylvilagus bachmani*) and snowshoe hare (*Lepus americanus*).

Estimates of flying squirrel abundance were based on livetrapping during October–December. Livetrapping for flying squirrels was conducted for eight consecutive nights in 1987 and 16–23 consecutive nights in 1988–1992. Trap grids covered approximately 13 ha and consisted of 96–100 trap stations spaced at 40-m intervals with two Tomahawk No. 201 (41 cm  $\times$  13 cm  $\times$  13 cm) live traps per station (Rosenberg and Anthony 1992). We estimated abundance of deer mice (*Peromyscus maniculatus*) and western red-backed voles (*Clethrionomys californicus*) (hereinafter, voles) from livetrapping for eight consecutive nights during April–June 1988–1996. Trap grids covered 3.2 ha and consisted of 100 Sherman live traps (7.6 cm  $\times$  7.6 cm  $\times$  25.4 cm) spaced at 20-m intervals (Rosenberg et al. 1994a; D.K. Rosenberg, unpublished data).

We estimated population size of flying squirrels, deer mice, and voles in each stand each year. On average, these three species comprised 56% of the biomass consumed by spotted owls on the study area (Table 1). Although a number of other mammals were common prey of spotted owls in the study area, we did not have the resources to sample them. These included red tree voles (*Phenacomys longicaudus*), bushy-tailed wood rats (*Neotoma cinerea*), Mazama pocket gophers (*Thomomys mazama*), snowshoe hare, and brush rabbits (Table 1). We used the program CAPTURE (Otis et al. 1978) to evaluate sources of variation in capture probabilities. Capture probabilities were most affected by heterogeneity (Otis et al. 1978, p. 33), so we used the jackknife estimator (Burnham and Overton 1979) to estimate population size. For flying squirrels, we used the first-order jackknife estimator and a modified variance estimator because capture probabilities were low and these estimators performed best (Rosenberg et al. 1995). We estimated population size of deer mice, which had relatively high capture probabilities ( $>0.2$ ), with the selected order of the jackknife estimator in the program CAPTURE (Otis et al. 1978).

We captured few or no voles in most stands and years, thus making estimation of stand- and year-specific capture probabilities impossible for some stands. Therefore, we used the number of individuals captured as an estimate of relative abundance, although the implicit assumption that capture probabilities were constant across stands and years was

likely incorrect. To allow estimation of vole density that accounted at least partially for capture probabilities  $<1.0$ , we used data from several grids that had sufficient data ( $\geq 10$  individuals) to estimate population size. There were typically one or two grids per year that met this criterion. We used data from these grids to estimate the mean proportion captured as

$$\bar{f} = \sum_{i=1}^n (S_i / \hat{N}_i)$$

where  $\bar{f}$  is the estimated mean proportion captured,  $S_i$  is the number of individuals captured,  $\hat{N}_i$  is the estimated population size with the first-order jackknife estimator for the  $i$ th stand and year combination, and  $n$  is the number of these combinations for which we estimated population size. We used  $\bar{f}$  to estimate the population size for each grid as

$$\hat{N}_{i(f)} = S_i / \bar{f}$$

which allowed estimation of vole density.

We used the distance between successive locations of captures of individuals to estimate the effective area trapped, which we then used to estimate standing biomass (grams per hectare) of each species. Estimation of biomass consumed and standing allowed us to evaluate the importance of particular prey species to spotted owls. We estimated an effective trapping area around the trapping grids by using one half of the mean maximum distance moved (MMDM) (Wilson and Anderson 1985). Because of the large variation in MMDM, there were no clear year or grid effects (D.K. Rosenberg, unpublished data). Therefore, we estimated MMDM with all grids and years pooled to provide a more precise estimate for each species. To estimate density of voles, we used the average MMDM from the year–grid combinations that met the minimum data requirements described above. We computed biomass of each species by multiplying its mean mass (based on Forsman et al. 1984) by its estimated density in each stand and year.

To estimate the relationship between owl reproductive parameters and prey abundance and to evaluate the relative role of spatial and temporal variation of prey abundance, we used an empirical Bayes approach to estimate  $\hat{N}$ , the “shrunk” es-

timator of  $\hat{N}$  (White et al. 2001). Such an approach attempts to remove sampling error and is important when evaluating biological (process) sources of variation (Burnham et al. 1987; Johnson 1989; Skalski and Robson 1992, p. 27; Link and Nichols 1994). Total variation included both sampling and process variation and was computed from  $\hat{N}$  or  $S$  (voles) using the empirical variance estimator

$$\widehat{\text{Var}}(\hat{N}) = 1/(n-1) \sum_{i=1}^n (\hat{N}_i - \bar{\hat{N}})^2$$

We estimated process variation as

$$\widehat{\text{Var}}(\tilde{N}) = 1/(n-1) \sum_{i=1}^n (\tilde{N}_i - \bar{\tilde{N}})^2$$

This allowed us to estimate percent average sampling variation as (total variation – process variation)/total variation  $\times$  100. We estimated separate components of process variation of  $\tilde{N}$  as spatial (stand), temporal (years), and residual (unexplained) variance using analysis of variance. For example, the abundance of populations may vary from year to year (temporal variation) but remain similar from one location to another (spatial variation). Prior to analyses,  $\tilde{N}$  were square-root transformed to improve homogeneity of variances.

### Spotted owl reproductive success

We used three measures of reproductive success in our analyses: (1) the proportion of territorial females that attempted to nest each year, (2) mean number of young produced per territorial female each year whether or not they nested (Franklin et al. 1996), and (3) mean number of young produced per nesting attempt. The number of territorial females that attempted to nest and the number of young per nesting attempt were estimated using methods described in Franklin et al. (1996) and Miller et al. (1996). We located nesting pairs using call surveys conducted during both day and night. Nesting status surveys were conducted from 1 April to 1 June. The number of young were counted during two or more visits during late May to mid-June. Mice were offered to the adults to facilitate determining reproductive status and locating young. We assumed that the detection probability for fledged young was equal among pairs and years.

We used simple linear regression to evaluate the association between owl reproductive success and mean annual prey abundance. We evaluated each reproductive parameter (proportion of spotted owl pairs that attempted to nest each year, mean number of young per territory per year, and mean number of young per nesting attempt per year) separately as the response variable. Because the mean number of young per territory per year was approximately normally distributed and there was no evidence that the variance was related to the mean, we used linear regression rather than alternative approaches (e.g., White and Bennetts 1996). We arcsine square-root transformed the proportion of pairs that attempted to nest in the analysis of variance models. The explanatory variable in the regression models was the mean annual population estimate ( $\tilde{N}$ ) of a given prey species among the five stands.

Because the approach of our analysis was an exploration of statistical associations rather than experimental confirmation, we evaluated the potential importance of a prey species by estimating the degree to which the proportional consumption of a prey species was positively related to its abundance (functional response; Solomon 1949). We reasoned that the stronger the response, as estimated by the regression coefficient,  $\beta$ , the greater the potential for a particular prey species to affect reproductive performance. We estimated this relationship with only simple linear regression rather than more complex nonlinear relationships because of small sample size. We used the estimated mean proportion of biomass consumed (from pellet analyses) as the response variable and standing biomass (from small-mammal trapping) as the explanatory variable for each species. We used the arcsine square-root transformation of the proportion of biomass consumed in analyses. Because we assumed that reproductive performance and diet are dependent on prey resources, we used regression analyses to estimate the degree of the relationship rather than to test hypotheses (e.g., Johnson 1999). Therefore, we only report the estimate and SE of  $\beta$ , the slope of the relationship of prey abundance to owl reproductive performance or to diet. All regression analyses were conducted with SAS using PROC GLM (SAS Institute Inc. 1994). We report data as means  $\pm$  1 SE.

## Results

### Diet

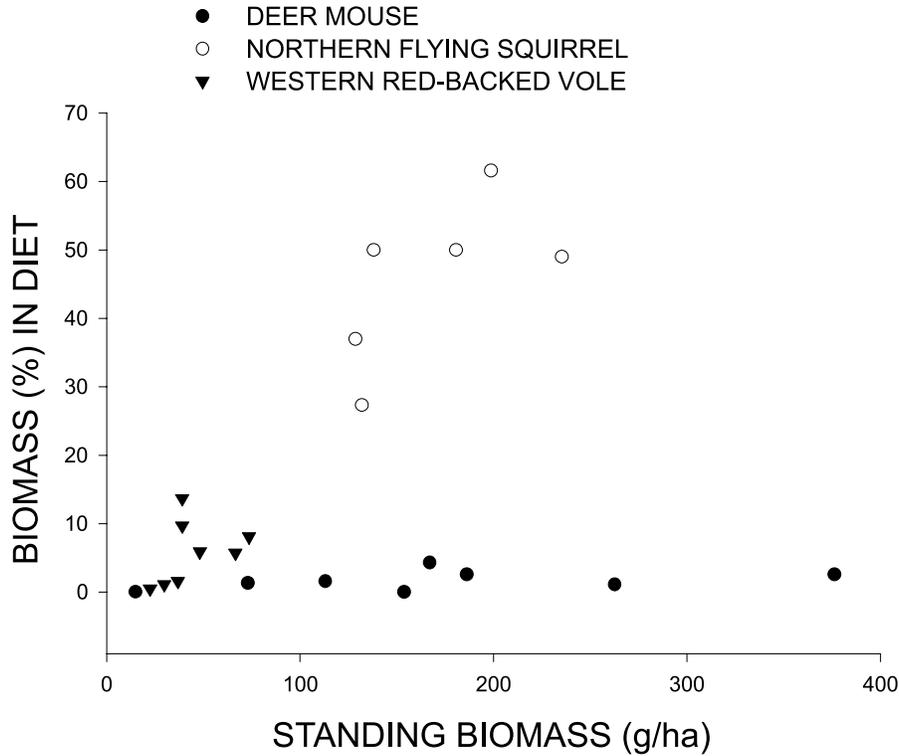
Patterns of diet composition were similar between analyses of pellets based on prey biomass and numbers consumed. There was high annual variability in the percentage of each prey species consumed, although flying squirrels, leporids, and bushy-tailed wood rats were typically the most common species in the diet (Table 1). Other species, including voles, were occasionally common in the diet, whereas deer mice were relatively uncommon. We found some evidence that composition of the diet was related to the density of each prey species, particularly for flying squirrels, but the effects were imprecise and generally weak (flying squirrels:  $0.002 \pm 0.001$ ,  $r^2 = 0.40$ ,  $n = 6$  years; deer mice:  $0.0003 \pm 0.0002$ ,  $r^2 = 0.20$ ,  $n = 8$  years; voles:  $0.003 \pm 0.002$ ,  $r^2 = 0.25$ ,  $n = 8$  years) (Fig. 1).

### Prey abundance

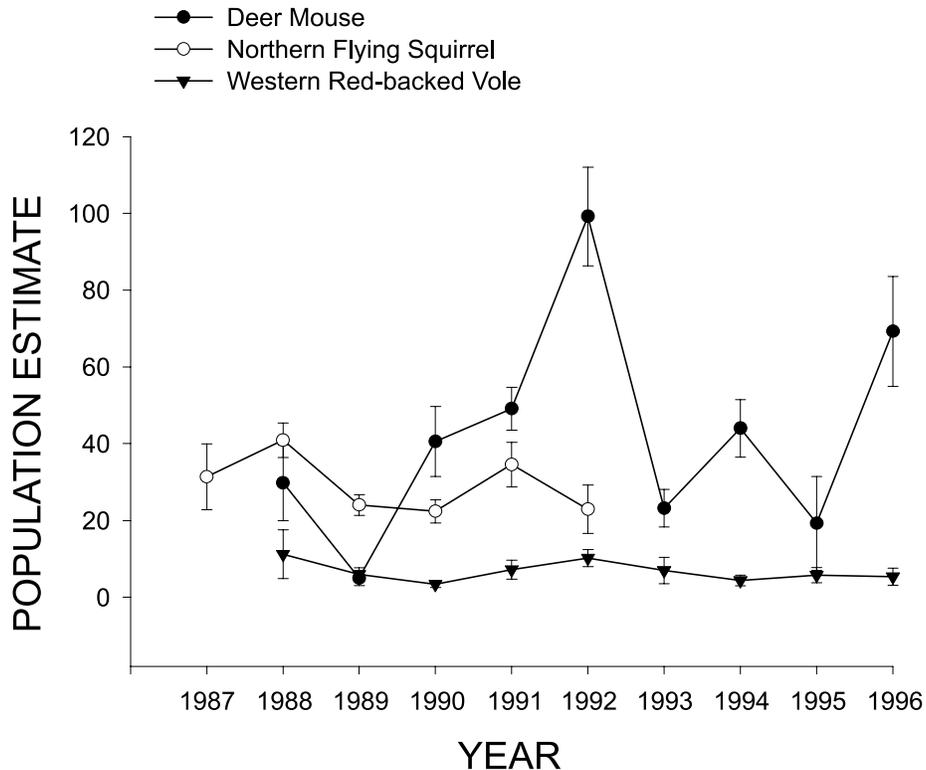
Flying squirrels were abundant but varied among years and stands. We captured 610 flying squirrels during 1987–1992. Estimated population size averaged  $29.4 \pm 2.4$  squirrels/grid and varied among stands and years (Fig. 2). There was greater spatial (37.8%) than temporal (24.2%) variance (Table 2). Spatial variation was year dependent, with the lowest variation during 1989 and 1990 when mean population size was low (Fig. 2). The mean maximum distance moved averaged  $88 \pm 4.0$  m, which increased the effective trap area from a grid size of 13 ha to one of 20 ha. This resulted in an average density of  $1.5 \pm 0.1$  squirrels/ha and an average flying squirrel biomass of  $169 \pm 13.9$  g/ha.

Of the prey species, abundance of deer mice varied least among stands but most among years. We captured 1501 deer mice during 1988–1996. Estimated population size averaged  $42.2 \pm 5.0$  deer mice/grid. The high daily capture probability

**Fig. 1.** Relationship between northern spotted owl (*Strix occidentalis caurina*) diet and biomass of northern flying squirrels (*Glaucomys sabrinus*) (1987–1992), deer mice (*Peromyscus maniculatus*) (1988–1996), and western red-backed voles (*Clethrionomys californicus*) (1988–1996) in the central Oregon Cascade Mountains. Percent biomass in the diet was estimated from analyses of regurgitated pellets following methods in Forsman et al. (2001). Prey biomass was estimated from the mean estimated densities in five old-growth stands in the study area. Data from 1993 were excluded because pellets were collected from only two territories.



**Fig. 2.** Patterns of abundance of three prey species of northern spotted owls in five old-growth stands in the central Oregon Cascade Mountains, 1987–1996. Estimates indicate the mean ( $\pm$ SE) number of individuals captured (western red-backed voles) or estimates ( $\tilde{N}$ ) of population size (northern flying squirrels and deer mice); the SE displays the extent of spatial variation.



**Table 2.** Sources of variance in population size for northern flying squirrel, deer mouse, and western red-backed vole populations in five old-growth Douglas-fir (*Pseudotsuga menziesii*) stands, central Oregon Cascades, during autumn 1987–1992 (northern flying squirrels) and spring 1988–1996 (deer mice and western red-backed voles).

| Species                  | CV( <i>S</i> ) <sup>a</sup> | CV( $\tilde{N}$ ) <sup>b</sup> | Total variation <sup>c</sup> | Percent sampling variation <sup>d</sup> | Process variation <sup>e</sup> |                  |                 |                  |
|--------------------------|-----------------------------|--------------------------------|------------------------------|---|--------------------------------|------------------|-----------------|------------------|
|                          |                             |                                |                              |   | Percent total                  | Percent temporal | Percent spatial | Percent residual |
| Northern flying squirrel | 9.4                         | 8.2                            | 243.6                        | 30.0                                    | 70.0                           | 24.2             | 37.8            | 38.1             |
| Deer mouse               | 12.0                        | 11.8                           | 1196.0                       | 7.6                                     | 92.4                           | 67.6             | 12.1            | 20.3             |
| Western red-backed vole  | 14.2                        |                                | 41.1                         |   |                                | 15.0             | 38.6            | 46.4             |

<sup>a</sup>Coefficient of variation (CV) of the number of individuals captured among years and stands.

<sup>b</sup>CV of the estimated population size using the shrinkage estimator,  $\tilde{N}$  (White et al. 2001), among years and stands.

<sup>c</sup>Total variation included both sampling and process variation and was computed from  $\tilde{N}$  or *S* (voles) using the empirical variance estimator  $\widehat{\text{Var}} = 1/(n-1) \sum_{i=1}^n (\hat{N}_i - \tilde{N})^2$ , replacing *N* with *S* in the case of voles.

<sup>d</sup>We estimated percent average sampling variation as (total variation – process variation)/total variation × 100, where process variation was estimated by the variance of  $\tilde{N}$ ,  $\widehat{\text{Var}}(\tilde{N}) = 1/(n-1) \sum_{i=1}^n (\tilde{N}_i - \tilde{N})^2$ .

<sup>e</sup>We estimated the components of the process variation (temporal, spatial, and unexplained) with analysis of variance on the square-root-transformed  $\tilde{N}$  (flying squirrels and deer mice) or *S* (voles).

resulted in a small percentage of total variance attributed to sampling (7.6%) (Table 2). This resulted in little difference between  $\hat{N}$  and  $\tilde{N}$ . Variation in population size among stands for any given year was moderate except during 1989 when all population estimates were low (Fig. 2). Abundance of deer mice fluctuated widely among years, with greater than a 20-fold difference (Fig. 2). Temporal effects explained most (67.6%) of the process variation, whereas spatial effects explained much less (12.1%) (Table 2). Mean maximum distance moved averaged  $60.6 \pm 3.4$  m, which increased the effective trap area from 3.2 to 5.8 ha. This resulted in an average density estimate of  $7.3 \pm 0.9$  deer mice/ha and a biomass of  $160 \pm 18.8$  g/ha.

Vole populations varied widely among years and stands. We captured 303 voles ( $6.7 \pm 1.0$  voles/grid). Large variation in the number of voles captured among stands and years (Fig. 2) resulted in the highest coefficient of variation (CV) among the three species (Table 2). The difference in CV between voles and the other species could have been due to using the index of abundance, *S*, rather than  $\tilde{N}$ , which was not estimable. However, we obtained similar results when comparing CV(*S*) among all three species (Table 2). Most of the variation in *S* was not due to spatial or temporal variance but remained unexplained in our model (Table 2). Voles had the lowest temporal variance (15.0%) relative to spatial variance (38.6%) of all three species (Table 2). We did not observe any distinctly high or low years of abundance and there was less than a fourfold difference in mean annual abundance during the study (Fig. 2). Mean maximum distance moved averaged  $41.6 \pm 5.6$  m, which increased the effective trap area from 3.2 to 4.9 ha. We estimated an average density of  $1.9 \pm 0.3$  voles/ha, resulting in an average biomass of  $44.5 \pm 6.3$  g/ha.

### Spotted owl reproductive success

Reproductive success of spotted owls fluctuated annually with a marked biannual pattern. We sampled 45–83 owl territories/year. The proportion of owls that attempted to nest was the most dynamic reproductive parameter, ranging from only 2 of 33 owl pairs (6.1%) in 1993 to 46 of 53 pairs

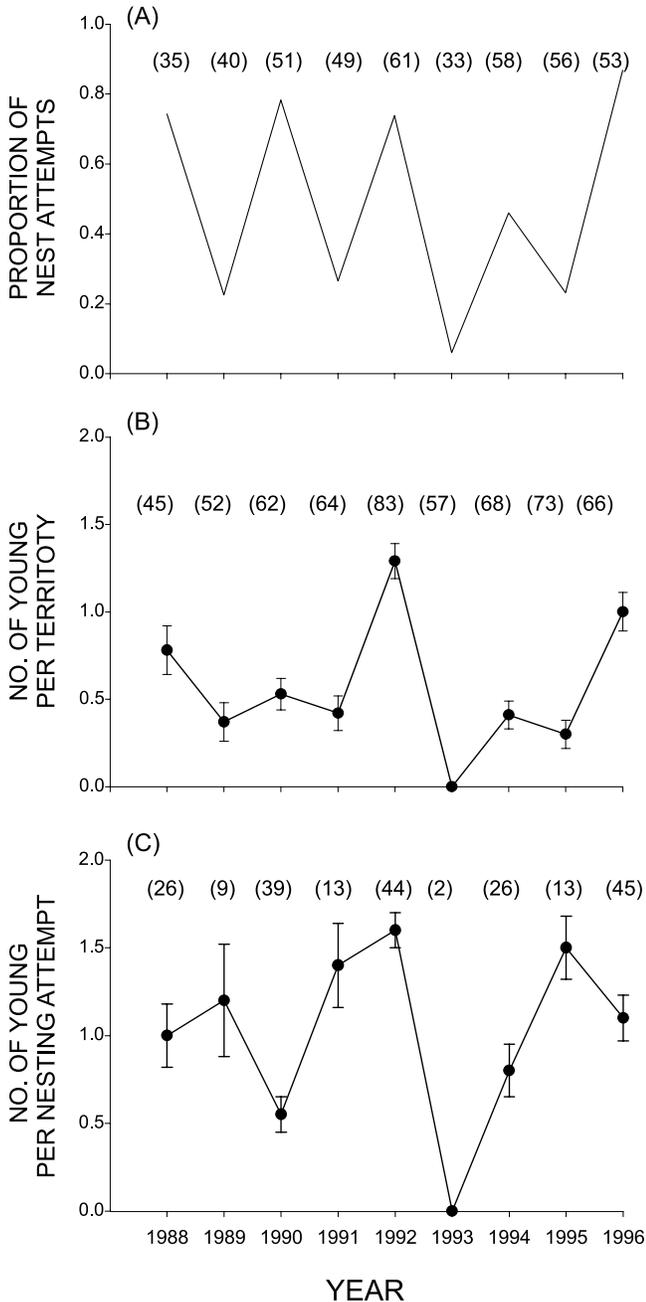
(86.8%) in 1996 (Fig. 3A). Owls in occupied territories produced an average of  $0.57 \pm 0.14$  young/year (Fig. 3B), with most pairs either failing to fledge young or producing two (Fig. 4). Temporal variation in the number of young per territory was high, although a biannual pattern was most pronounced in the proportion of pairs that attempted to nest (Fig. 3). There was no evidence of a relationship ( $0.003 \pm 0.006$ ,  $r^2 = 0.03$ ) between the number of young per nesting attempt and the proportion of nest attempts, indicating that owls that bred in years that most did not (odd-numbered years) (Fig. 3) reproduced as well as during years when most owls attempted to nest, averaging 1.0 young per nest attempt. This demonstrates the considerable individual variability in owl reproduction despite the predominate temporal variability.

Although flying squirrels were a primary prey of spotted owls, we found only a weak relationship between flying squirrel abundance during fall and reproductive success of spotted owls the following spring. There was no evidence of an increase in the proportion of owls that nested ( $0.007 \pm 0.02$ ,  $r^2 = 0.02$ ), overall number of young produced ( $0.024 \pm 0.027$ ,  $r^2 = 0.17$ ), or number of young per nest attempt ( $0.04 \pm 0.03$ ,  $r^2 = 0.26$ ) with changes in flying squirrel abundance. Similarly, owl reproductive parameters were only weakly associated with the proportion of flying squirrels in the diet ( $r^2 \leq 0.19$ ).

Despite the relatively small contribution of deer mice to the diet of northern spotted owls, reproductive success of owls was positively associated with deer mouse abundance (Fig. 5). The number of young per territory was the reproductive parameter most closely associated with deer mouse abundance ( $0.01 \pm 0.003$ ,  $r^2 = 0.68$ ) relative to the proportion of pairs that attempted to nest ( $0.007 \pm 0.003$ ,  $r^2 = 0.39$ ) and the number of young per attempt ( $0.006 \pm 0.006$ ,  $r^2 = 0.12$ ) (Fig. 5). There was no evidence of an association between owl reproductive parameters and proportion of deer mice in the diet ( $r^2 \leq 0.12$ ).

Of the three prey species, the relationship between owl reproductive success and vole abundance was weakest. There was no evidence that the proportion of owls that attempted

**Fig. 3.** Annual variation in northern spotted owl reproductive rates in the central Oregon Cascades. (A) Proportion of owl pairs that attempted to nest. (B) Number (mean  $\pm$  SE) of young per territory. (C) Number (mean  $\pm$  SE) of young per nest attempt. Total number of spotted owl territories (A and B) and number of pairs that attempted to nest (C) are shown in parentheses.



to nest ( $0.014 \pm 0.05$ ,  $r^2 = 0.10$ ), the mean number of young per territory ( $0.07 \pm 0.05$ ,  $r^2 = 0.20$ ), or the number young per nest attempt ( $0.06 \pm 0.07$ ,  $r^2 = 0.10$ ) was related to vole abundance. This finding was consistent with the low temporal variation in vole abundance but relatively high levels of temporal variation in reproductive success of spotted owls. Despite the lack of evidence of effects of prey abundance on owl reproductive success, an increase in the proportion of voles in the diet was associated with a greater number of

young per attempt ( $\beta = 2.2 \pm 1.0$ ,  $r^2 = 0.44$ ) with some evidence of a higher proportion of owls that attempted to nest ( $\beta = 1.6 \pm 0.9$ ,  $r^2 = 0.37$ ). There was no evidence of an association, however, between the proportion of voles in the diet and the number of young per territory ( $\beta = 0.6 \pm 1.3$ ,  $r^2 = 0.03$ ).

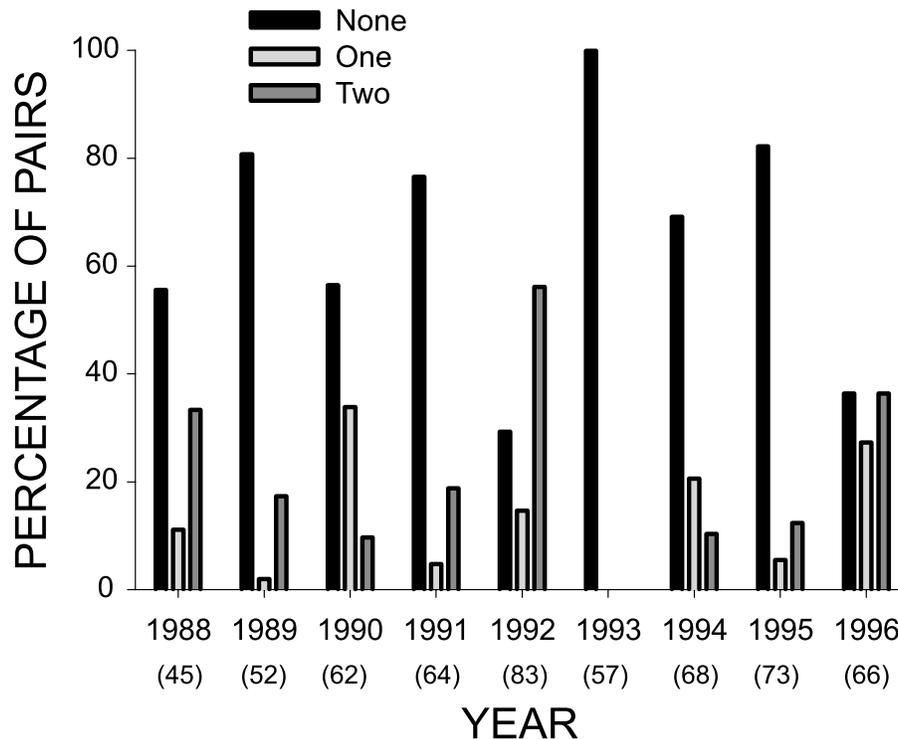
### Discussion

One of the most interesting aspects of reproduction by northern spotted owls is the biannual pattern of reproductive success (Burnham et al. 1996). This pattern was evident with the population that we studied (Miller et al. 1996) and was strongest for the proportion of pairs that attempted to nest. During odd-numbered years, less than 30% of the owl pairs attempted to nest, whereas on even-numbered years, approximately 70% nested. Interestingly, the reproductive success of owls that nested during otherwise poor reproductive years was similar to that of owls that bred during good years, providing some evidence that owls were able to gauge resources for successful reproduction. This demonstrated the variation in nest success, which may be due to characteristics of the individual, such as age (Burnham et al. 1996), or territory quality (Franklin et al. 2000), similar to findings for other owl species (Newton 1979; Pietiäinen 1989; Brommer et al. 1998). The high spatial variability of prey abundance likely contributes to the spatial variation in reproductive success of spotted owls (Ward et al. 1998) and raptors in general (Newton 1979).

Temporal fluctuations in flying squirrel abundance, the primary prey of spotted owls in our study area, were insufficient to account for the biannual variability of owl reproductive success. It is possible that our estimates of flying squirrel abundance during the fall minimized temporal variation that spotted owls may respond to reproductively; however, the weak relationship of the proportion of flying squirrels in the diet and owl reproduction supports our findings that annual fluctuations in the density of flying squirrels did not account for the temporal patterns of spotted owl reproductive parameters despite their dominance in their diet, consistent with Ward's (2001) findings with Mexican spotted owls and wood rats (*Neotoma mexicana*).

Previous findings, if real (see Forsman et al. 2001), that larger prey may be related to higher reproductive rates of spotted owls (Barrows 1987; Laymon 1988; Thrailkill and Bias 1989; White 1996) suggest that reproductive success of northern spotted owls should be influenced by flying squirrel abundance. The high proportion of the diet comprising flying squirrels demonstrated that they were an important prey species for northern spotted owls in our study area. However, reproductive performance of spotted owls in our study area may not have been sensitive to the changes in squirrel abundance that occurred during the study if owls switched to more common prey during years of low squirrel abundance. This is more likely if prey have species-specific responses to temporal changes in their environment. Indeed, the species that we investigated varied independently, suggesting that these mammals responded to different environmental factors. The ecology of these species are very different and may explain the lack of similar dynamics. Prey switching may be common with owls in response to lower abundance of pri-

**Fig. 4.** Frequency distribution of the number of northern spotted owl young per territory in the central Oregon Cascades, 1988–1996. Not shown is a single nest that produced three young in 1992. Total number of territories included in the histogram is shown in parentheses.



mary prey (Wendland 1984; Petty 1999) or alternatively when secondary prey irrupt (Ward 2001). Bushy-tailed wood rats, leporids, pocket gophers, and red tree voles were common prey of spotted owls in our study area. However, we did not estimate their abundance, so we were unable to test the hypothesis that reproductive performance was related to total prey biomass. Our methods did allow us to capture bushy-tailed wood rats, apparently with a high capture probability (D.K. Rosenberg, unpublished data). However, few were captured, suggesting sparse populations in the forests that we examined. Unfortunately, the role of leporids and pocket gophers has been largely ignored in studies of spotted owl prey (summarized in Thomas et al. 1990) in areas where the flying squirrel dominates the owls' diet.

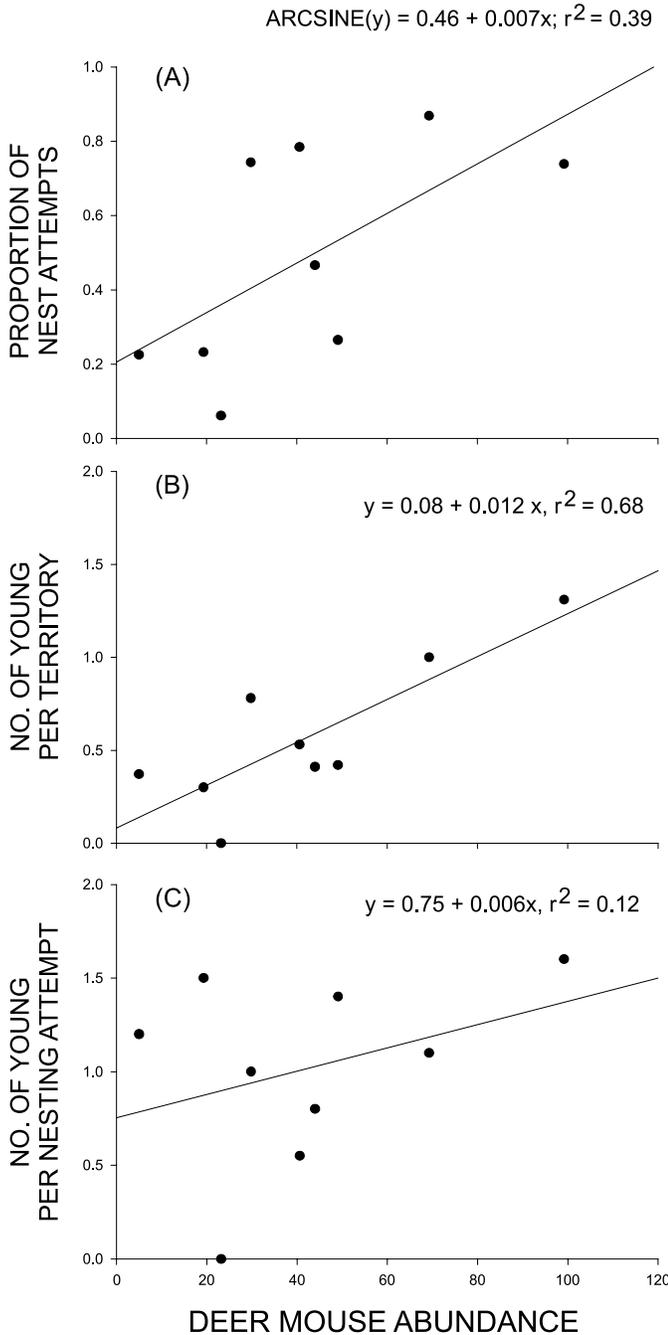
Given the low density of wood rats in mesic western hemlock forests (Carey et al. 1999) and their contribution to the diet of spotted owls in our study area, northern spotted owls may select wood rats as prey even when flying squirrels predominate in the diet. For example, Forsman et al. (1984) found that some spotted owls foraged selectively in talus outcrops, and Glenn et al. (2004) reported selection for proximity to riparian habitats. Bushy-tailed wood rats are often associated with both of these habitat types (Verts and Carraway 1998; Carey et al. 1999). Wood rats may be more abundant in our study area than previously believed. The relatively large component of wood rats in the diet of spotted owls in the western Oregon Cascades despite their apparently low densities warrants further research.

The biology of northern spotted owls suggests that there should be strong reproductive responses to variation in food resources. Characteristics of spotted owl foraging behavior

and densities of their prey suggest that their populations are limited by prey (Forsman et al. 1984; Thomas et al. 1990; Carey et al. 1992). Despite the owl's selection of older forests, prey density is low. For example, flying squirrel densities are typically about 2 individuals/ha in old forests in western Oregon and northern California (Carey et al. 1992; Rosenberg and Anthony 1992; Waters and Zabel 1995). Molt, which is energetically demanding, requires 2 years to complete (Forsman 1981). Further, spotted owls have small clutches and do not regularly attempt to nest each year (Forsman et al. 1984; Burnham et al. 1996). Newton's (1979, p. 63) model of the relationship of home range size to body mass of raptors predicts a home range of approximately 200 ha for spotted owls. However, spotted owl home ranges typically exceed this by an order of magnitude (Forsman et al. 1984, Carey et al. 1990; Thomas et al. 1990). These very large home ranges, particularly in the northern part of the geographic range, further suggest that density of available prey must be low (Carey et al. 1992; Zabel et al. 1995; Perry 2000). These characteristics suggest that the reproductive rate of spotted owls is limited by prey resources, consistent with the findings from studies of other raptors (Newton 1979; Ward and Kennedy 1996; Steenhof et al. 1997; Wiehn and Korpimäki 1997).

The association between reproductive performance of spotted owls and abundance of deer mice (*Peromyscus* spp.) that we observed, and that Ward and Block (1995) and Ward (2001) noted for Mexican spotted owls, may be a response to prey abundance, although the mechanisms have not been elucidated. Indeed, deer mice had the greatest temporal variation among prey in both our study and Ward's (2001), thus

**Fig. 5.** Association of mean deer mouse abundance in five old-growth stands with the reproductive rate of northern spotted owls in the central Oregon Cascade Mountains, 1988–1996. (A) Proportion of owls that cascaded to nest. (B) Mean number of young per territory. (C) Number of young per nest attempt. Although the nontransformed data are shown for the proportion of nest attempts (A), the regression equation represents the arcsine-transformed data.



allowing periodic inputs of high prey biomass. The numeric abundance of deer mice in the diet may provide critical levels of nutrients and energy required for successful reproduction, or alternatively, the density of deer mice may act as a physiological cue to stimulate courtship. Experimental re-

search on the physiological response of spotted owls to supplemental food prior to egg-laying is needed to elucidate the possible causal association of deer mouse abundance and northern spotted owl reproduction. In addition, unbiased estimates of the contribution of smaller rodents in the diet of spotted owls (see Forsman et al. 2001) and a better understanding of their role in the maintenance of young are needed.

An alternative explanation of the causal relationship of deer mouse abundance and owl reproductive success is that both owls and deer mice respond similarly to weather patterns. Cold, wet weather could lower reproductive success by affecting the owl's ability to hunt effectively as well as by directly increasing the mortality of young (Franklin et al. 2000). Deer mice may be similarly affected by these conditions (Sadleir 1974; Myers et al. 1985). If prey and predator respond to similar environmental conditions, a synergistic effect could result such that lower prey abundance may occur when weather conditions result in greater daily energy expenditures. Steenhof et al. (1997) found such a synergism with golden eagles (*Aquila chrysaetos*) and jack rabbits (*Lepus californicus*), although jack rabbit numbers were apparently unrelated to weather conditions. Steenhof et al. (1997) found that prey and weather interacted so that weather was more likely to negatively affect reproductive success when prey numbers were low. How weather affects spotted owl reproductive success is not well understood. Evidence suggests that inclement weather during the late breeding season when owls have their highest energetic demand (Wijnandts 1984) and the young are vulnerable to hypothermia may be detrimental (Franklin et al. 2000). If so, then the most likely model that explains temporal variability in reproductive success of spotted owls includes the interaction of weather and prey abundance, similar to the findings of Steenhof et al. (1997). Many factors affect avian reproductive success. The difficulty of identifying causative factors for spotted owls is likely due to the high temporal and individual variability in reproductive success, the difficulty of estimating prey resources at the scale of the home range (e.g., Ward et al. 1998), and the lack of experimental research (Noon and Franklin 2002). The latter will allow a more precise understanding of factors affecting annual variation in reproductive success of northern spotted owls.

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