

CLIMATE, HABITAT QUALITY, AND FITNESS IN NORTHERN SPOTTED OWL POPULATIONS IN NORTHWESTERN CALIFORNIA

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Abstract. A controversy exists in the Pacific Northwest of the United States between logging of old-growth coniferous forests and conservation of Northern Spotted Owl (*Strix occidentalis caurina*) populations. This species has a strong association with old-growth forests that also have economic value as timber. Research questions relevant to conservation of this species include how temporal trends in Northern Spotted Owl populations are influenced and how spatial configuration of old-growth forests affects these populations. To address these questions, we studied a population of marked Northern Spotted Owls on 95 territories in northwestern California from 1985 through 1994. We examined the magnitude of temporal and spatial variation in life history traits (survival, reproductive output, and recruitment), the effects of climate and landscape characteristics on temporal and spatial variation in these traits, respectively, and how this variation affected aspects of population dynamics. We used a components-of-variation analysis to partition sampling from process variation, and a model selection approach to estimate life history traits using capture–recapture and random-effects models. Climate explained most of the temporal variation in life history traits. Annual survival varied the least over time, whereas recruitment rate varied the most, suggesting a “bet-hedging” life history strategy for the owl. A forecast of annual rates of population change (λ), estimated from life history traits, suggested that Northern Spotted Owl populations may change solely due to climate influences, even with unchanging habitat conditions. In terms of spatial variation, annual survival on territories was positively associated both with amounts of interior old-growth forest and with length of edge between those forests and other vegetation types. Reproductive output was negatively associated with interior forest, but positively associated with edge between mature and old-growth conifer forest and other vegetation types. A gradient existed in territory-specific estimates of fitness derived from these life history estimates. This gradient suggested that a mosaic of older forest interspersed with other vegetation types promoted high fitness in Northern Spotted Owls. Habitat quality, as defined by fitness, appeared to buffer variation in annual survival but did not buffer reproductive output. We postulated that the magnitude of λ was determined by habitat quality, whereas variation of λ was influenced by recruitment and reproductive output. As habitat quality declines, variation in λ should become more pronounced.

Key words: California; climate effects; components of variation; environmental stochasticity; fitness; fragmentation; habitat effects; habitat mosaics; model selection; Northern Spotted Owl; population rates of change; *Strix occidentalis caurina*.

INTRODUCTION

The Northern Spotted Owl (*Strix occidentalis caurina*) is a medium-sized owl that inhabits conifer forests of the Pacific Northwest, including northwestern California, USA (Forsman et al. 1984, Gutiérrez et al. 1995). Pairs of Northern Spotted Owls occupy large home ranges (≥ 1200 ha), portions of which are actively defended against conspecifics (see review in Thomas et al. 1990). This species exhibits strong affinities for mature and old-growth forests (reviewed in Thomas et al. 1990), and may incorporate large tracts (≥ 400 ha) of these forests into its home range (Forsman et al.

1984, Carey et al. 1990, Solis and Gutiérrez 1990). Thus, mature and old-growth coniferous forest has been considered equivalent to Northern Spotted Owl habitat (see Thomas et al. 1990). Forests potentially suitable for spotted owls in the Pacific Northwest have declined by 61% since the 18th century because of logging; most of this decline has occurred in the last 60 yr (U.S. Forest Service 1992). In addition to reduction in size, once-contiguous blocks of mature and old-growth forests have become increasingly fragmented into mosaics of different seral stages.

A major conflict developed in managing spotted owl populations because of the high economic value of the remaining timber present within spotted owl habitat (Dixon and Juelson 1987). This conflict escalated when the Northern Spotted Owl was federally listed as a threatened subspecies in 1990 (U.S. Fish and Wildlife

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Service 1990). Various assessments predicted declines among females in Northern Spotted Owl populations (Marcot and Holthausen 1987, Lande 1988, Noon and Biles 1990, Franklin 1992). Compelling evidence indicated that population declines were a function of loss of mature and old-growth forests (U.S. Fish and Wildlife Service 1990).

Long-term research questions regarding Northern Spotted Owls have been based primarily on conservation agendas. Such questions include: "What influences population trends in Northern Spotted Owls over time?" and "How does the spatial distribution and extent of mature and old-growth forests affect Northern Spotted Owl populations?" (after Noon and McKelvey 1996). These and other questions regarding Northern Spotted Owl populations can be addressed with empirical data because demographic parameters for this species are relatively easy to estimate from field data, compared with most avian predators (see Franklin et al. 1996a). In this paper, we attempted to address these questions by examining (1) the magnitude of variation in life history traits, (2) the factors that may influence variation in life history traits, and (3) how this variation might affect population dynamics.

The role of variation in population dynamics

Populations of organisms, and the life history traits that characterize them, vary over space and time. Understanding this variation is necessary for understanding life history strategies and population dynamics, as well as for developing conservation strategies (Rhodes and Odum 1996). In addition to spatial and temporal variation, individuals within populations also vary in their abilities to cope with their environment (Łomnicki 1988). Thus, three sources of variation—temporal, spatial, and individual—affect population dynamics and the life history traits (e.g., survival, reproductive output, and recruitment) that define those dynamics. These sources of variation are also important for determining population persistence over time and space (White 2000). In this paper, we concentrate only on temporal and spatial variation. Although we consider individual attributes, such as age and sex, we do not incorporate individual variation resulting from phenotypic and genetic variation.

There are important considerations regarding spatial and temporal variation in biological systems. First, a distinction must be made between *process variation* ($\sigma_{\text{process}}^2$), the variation in a given parameter ($\hat{\theta}$) over time and space, and *sampling variation* ($\text{var}(\hat{\theta}|\theta)$), the variation attributable to estimating a parameter from sample data (Box et al. 1978, White 2000). Here, we are interested in the natural variability, estimated as process variation, of life history traits and measures of fitness. Sampling variation is of little interest, except that it must be properly dealt with to estimate process variation.

If no sampling variation is associated with parameter

values measured over time or space, then process variation can be estimated as follows:

$$\hat{\sigma}_{\text{process}}^2 = \frac{1}{n} \sum_{i=1}^n (\theta_i - \bar{\theta})^2 \quad (1)$$

(Burnham et al. 1987). However, parameters such as life history traits are never measured without sampling variance, although sampling variance is often ignored. Therefore, the total variation (σ_{total}^2) estimated in a set of parameter estimates over time or space is a combination of process and sampling variation, which can be generally viewed as follows (Skalski and Robson 1992):

$$\hat{\sigma}_{\text{total}}^2 = \hat{\sigma}_{\text{process}}^2 + \widehat{\text{var}}(\hat{\theta}|\theta). \quad (2)$$

Typically, the relationship in Eq. 2 becomes more complex as process or sampling variation is temporal, spatial, or both (see Burnham et al. 1987). Process variation in population parameters can be further decomposed into additional components of interest, such as temporal and spatial process variation, where

$$\sigma_{\text{process}}^2 = \sigma_{\text{temporal}}^2 + \sigma_{\text{spatial}}^2. \quad (3)$$

Such decomposition of variance components is termed components of variance analysis (Box et al. 1978, Searle et al. 1992). Although knowing the relative magnitude of temporal and spatial variance components is necessary to understand population dynamics, the factors that cause temporal and spatial variation are also important, especially for understanding ecological relationships and developing conservation strategies. If climate and habitat quality are considered to be useful starting points for examining the determinants of temporal and spatial variation, respectively (see *Climate and temporal variation* and *Habitat quality and spatial variation*), a sound, statistically based model can be developed that relates these factors to life history traits using meaningful covariates. Once such models are developed, process variation can be partitioned as

$$\sigma_{\text{process}}^2 = \sigma_{\text{model}}^2 + \sigma_{\text{residual}}^2 \quad (4)$$

where $\sigma_{\text{process}}^2$ is either temporal or spatial process variation in a life history trait; σ_{model}^2 is the amount of that process variation theoretically explainable by some model incorporating the factors thought to be responsible for that variation; and $\sigma_{\text{residual}}^2$ is the amount of $\sigma_{\text{process}}^2$ not explained by the model. For example, explainable variation in temporal process variation due to climatic factors can be viewed as $\sigma_{\text{temporal}}^2 = \sigma_{\text{climate}}^2 + \sigma_{\text{residual}}^2$, where $\sigma_{\text{residual}}^2$ is the amount of temporal variation not explained by climatic factors in the model.

Once an understanding of the magnitude of process variation in life history traits and the factors that affect it has been achieved, an approach relating this process variation to overall population dynamics is needed. We chose the finite rate of population change (λ) as the common currency to relate temporal variation to pop-

ulation growth rates (Caswell 1989a) and spatial variation to fitness (Caswell 1989b, McGraw and Caswell 1996). Ricklefs (1983) and Nur (1987) suggest that the finite rate of population change (λ) is a good estimate of fitness because it explicitly incorporates age-specific survival and fecundity. Although interpretations of λ may differ slightly when it is used as a measure of population growth rate or as fitness, at least the effects of temporal and spatial variation can be compared using the same metric. For example, the finite rate of population change can be viewed as the average fitness across individuals within a year, as well as the growth rate of the population (Danchin et al. 1995).

Climate and temporal variation

Temporal variation is important in defining life history tactics and understanding the evolutionary processes that may shape life history traits. Much of life history theory ignores the influence of temporal variation when, in fact, the influence of temporal variability on life history traits, such as survival and recruitment, can have different consequences for life history tactics (Stearns 1976, 1992). The effect of temporal variation on life history tactics depends on several factors such as the amount of variation, the covariation among life history traits, the life history being considered, and factors that also affect long-term rates of population change (Tuljapurkar 1989, Benton and Grant 1996).

Temporal variation in population dynamics is often represented as environmental stochasticity, a nearly continuous series of perturbations over time that simultaneously affect birth and death rates of all individuals in a population (Shaffer 1987, Lande 1993). Extremes in environmental stochasticity are viewed as random catastrophic events when they produce sudden and large reductions in population size (Mangel and Tier 1993). Environmental stochasticity can accelerate the risk of extinction even in large populations (Goodman 1987, Shaffer 1987), especially in populations whose long-term growth rate is near zero (Lande 1993). However, understanding how environmental stochasticity affects population processes and extinction probabilities requires an understanding of the effects of environmental stochasticity on organisms (Boyce 1992). Models attempting to approximate population processes have progressed from simple, deterministic forms to increasingly complex, stochastic forms that induce random temporal variation on model parameters. Population viability analyses, in particular, incorporate forms of environmental stochasticity when predicting the probability of persistence of a given population. However, Boyce (1992) points out that environmental stochasticity is usually approximated poorly in such models because it is represented as unstructured, random noise rather than as a structured temporal process. If environmental stochasticity is, in reality, a structured process, then it becomes predictable to some degree and should no longer be represented as random noise.

This implies that changes in temporal conditions can be explained in some manner. Thus, there is a real need for empirical understanding of whether environmental stochasticity can be represented as structured variation, and how this variation affects populations, especially through its influence on life history traits.

Climatic variation is one structured source of temporal variation that may affect avian populations through its influence on life history traits, largely in a density-independent manner (Boyce 1984). Extremes in climatic variation also can function as catastrophic events and have been associated with sudden large-scale mortality in avian populations (Tompa 1971, Johnson et al. 1991, Rogers et al. 1991, Smith et al. 1991). Most studies have focused on the effect of climatic variation on reproductive output (Kostrzewa and Kostrzewa 1990, 1991, Rotenberry and Wiens 1991, Cooper and Lutjeharms 1992, Dykstra and Karasov 1993, Neal et al. 1993, Swenson et al. 1994), with less emphasis on the effect of this variation on survival (e.g., Martinson and Grondahl 1966, Peach et al. 1994, Cézilly et al. 1996). Few studies empirically examine the effects of climate, as a source of temporal variation, on the collective suite of life history traits of a single avian species (but see Grant and Grant 1989, Jouventin and Weimerskirch 1991), and the overall influence of such variation on population growth rates.

Rotenberry and Wiens (1991) identify two major scales over which climatic variation could affect life history traits: within-year effects reflecting day-to-day variation, and among-year effects attributed to variation over larger temporal and spatial scales. In this study, we deal solely with among-year effects as a measure of temporal variation. When considering annual temporal variation, one can express the total variation (σ^2) in an *estimated* life history trait ($\hat{\theta}$) as $\sigma_{\text{temporal}}^2 + \text{var}(\hat{\theta}|\theta)$ in its simplest form, where $\sigma_{\text{temporal}}^2$ is temporal process variation (the variance of the parameter θ among years) and $\text{var}(\hat{\theta}|\theta)$ is the mean sampling variation due to estimation of θ within years. Temporal process variation can be partitioned further into variation due to climate ($\sigma_{\text{climate}}^2$) and residual, unexplained variation ($\sigma_{\text{residual}}^2$) such that

$$\sigma_{\text{temporal}}^2 = \sigma_{\text{climate}}^2 + \sigma_{\text{residual}}^2. \quad (5)$$

If climate is a primary mechanism governing temporal variation, then $\sigma_{\text{climate}}^2$ should be large relative to $\sigma_{\text{residual}}^2$; the reverse suggests that other influences are responsible for temporal variation.

When estimating the effects of climatic variation on Northern Spotted Owl populations, we addressed three questions in a step-wise fashion, using 10 yr of data on marked spotted owls in northwestern California. First, we asked: *What is the magnitude of temporal process variation in key life history traits of Northern Spotted Owls?* We approached this question by estimating $\sigma_{\text{temporal}}^2$ in capture-recapture estimates of survival, recruitment (the number of new individuals in

the population per individual from the previous year), and reproductive output (the number of young fledged per pair), using components of variance analysis that accounted for sampling variance in the parameter estimates. Second, we asked: *Is temporal process variation explained primarily by climatic variation?* That is, does $\hat{\sigma}_{\text{climate}}^2$ explain a large portion of $\hat{\sigma}_{\text{temporal}}^2$. Finally, we asked: *What are the long-term consequences of climatic variation on population growth and stability if climatic variation strongly influences life history traits?* We evaluated this last question by applying climate models describing variation in life history traits and rates of population change to a 30-yr climate trace. In this way, we attempted to assess the probable behavior of these climate models in describing temporal variation, given that selected climate models were reasonable approximations of nature.

Habitat quality and spatial variation

Habitat for a particular organism can be defined as an area with the combination of resources and environmental conditions necessary to allow occupancy, survival, and reproduction of individuals (Morrison et al. 1992). Habitat use by an organism can be described at four nested scales (Johnson 1980): the overall geographic range of the species, the home range or territory within the geographic range, various habitat components within the territory, and specific foraging locations within those habitat components. This study focuses on the territory scale, specifically in terms of macrohabitat (Block and Brennan 1993): the extent and configuration of vegetation stands within territories.

Habitat occupied by a particular species often spans a gradient from low to high quality, in which quality can be defined based on the habitat's effect on the survival and reproductive performance of individuals occupying particular grades of habitat. High-quality habitat promotes some combination of survival and reproductive performance that increases an individual's contribution to future generations (Van Horne 1983). As such, habitat is a key component in shaping an individual's fitness. Individual fitness can be loosely defined as a composite measure of reproduction and survival (Stearns 1992): a measure of the relative genetic contribution by an individual to the next generation (Charlesworth 1970, Nur 1987). Fitness is generally considered to be an individual measure; as an individual's probability of survival and offspring production increases, so does its fitness. However, Fretwell and Lucas (1970) combined the concepts of habitat and individual fitness into the idea that habitat quality confers fitness on individuals where the quality of habitat occupied by individuals of a given species is related to the average potential contribution from that habitat to the gene pool of succeeding generations. According to density-dependent habitat selection, individuals should occupy only habitats that maximize their fitness (Morris 1989). Wiens (1989a:301) referred to this ef-

fect of habitat quality on an individual as the *fitness potential* of habitat, denoted here as λ_H . However, λ_H can be a reflection of either habitat quality or some interaction between the individual and the habitat it occupies (Newton 1989a). At two extremes, individual fitness and fitness realized only when an individual occupies a certain habitat can be either additive or compensatory. If additive, λ_H is a combination of individual fitness and realized fitness that may also include interactions. If compensatory, then individual fitness is only realized when some optimal habitat is occupied; λ_H is then a direct measure of individual fitness. In either case, habitat fitness potential is a useful measure for both defining the quality of an animal's habitat and determining the relative contributions to the overall population of individuals occupying those habitats.

For territorial species, two competing theories of habitat selection have been proposed to explain how habitat quality affects habitat fitness potential in territorial species: the ideal-free distribution and the ideal-despotic distribution (Fretwell and Lucas 1970). Under the ideal-free distribution, high-quality habitats are occupied first. As the density of individuals increases, the fitness potential of high-quality habitats declines because of density-dependent influences and habitats of lesser quality are occupied. Habitat fitness potential in lower quality habitat now becomes equivalent to that of the high-quality habitat. When the entire habitat quality gradient is occupied, habitat fitness potential becomes similar across the whole gradient. Under the ideal-despotic distribution, habitat selection is constrained by the activities of dominant individuals. Dominant individuals achieve higher habitat fitness potential by occupying higher quality habitats, whereas less dominant individuals are relegated to lower quality habitat. In both distributions, "ideal" refers to the assumption that individuals have the dispersal and cognitive abilities to locate the best available territory (Pulliam and Danielson 1991).

If the gradient of all potentially suitable habitats for a species is assumed to be fully occupied, then a prediction from the ideal-free distribution is that habitat fitness potential among territories exhibiting different habitat characteristics should be relatively uniform (Morris 1989); spatial process variation (the variation among territories) in habitat fitness potential should be essentially zero. Under the ideal-despotic distribution, habitat fitness potential should be unequal among territories of differing habitat configurations; spatial process variation should be greater than zero. Whether a species follows the ideal-free or ideal-despotic model has important implications for population dynamics. Under the ideal-free distribution, individuals are assumed to have similar individual fitness (Fretwell and Lucas 1970); fitness is a function of habitat and density. However, under the ideal-despotic distribution, individuals in high-quality habitat are inherently more fit;

fitness is a function of both the individual and the habitat it occupies.

In field studies, fitness, whether individual or habitat-realized, is often poorly defined using either surrogate indices (such as behavioral responses) or only a single component (such as survival, reproduction, or some index of either) to represent fitness (Nur and Clobert 1988). However, fitness is a function of both survival and reproduction. Variation in external factors (such as habitat) can affect each of these components differently, with different combinations yielding different fitness values.

Here, we attempt to address a series of questions relating landscape habitat configuration in spotted Owl territories to survival, reproduction, and, ultimately, fitness. We examine spatial process variation in terms of habitat quality, ignoring the influence of temporal variation discussed previously. First, we address *whether Northern Spotted Owl survival and reproductive output vary with respect to landscape habitat covariates at the individual territory scale*. Noon and McKelvey (1996) considered that a within-population scale, with reproductive pairs as the sampling unit, was more relevant than a between-subpopulations scale for assessing relationships between demography and habitat in Northern Spotted Owls. Here, we are particularly interested in the effects of fragmentation of mature and old-growth forest on life history traits and fitness of Northern Spotted Owls. We define fragmentation as the conversion of continuous patches into smaller patches surrounded by a matrix of other vegetation types (after Wiens 1989b). Second, we ask *whether a compromise exists in these components of fitness*. Does one habitat element favor survival and another favor reproductive output, or is there a unifying habitat element that favors both? Third, *is there spatial process variation in fitness, or is fitness relatively uniform across territories?* In other words, does spatial variation in fitness among Northern Spotted Owl territories follow an ideal-free or an ideal-despotic distribution?

When considering only spatial variation, estimated variation ($\hat{\sigma}^2$) in estimates of fitness can be approximated as $\hat{\sigma}^2 = \hat{\sigma}_{\text{spatial}}^2 + \widehat{\text{var}}(\hat{\lambda}_H | \lambda_H)$, where $\hat{\sigma}_{\text{spatial}}^2$ is the estimated spatial process variation of fitness among territories, and $\widehat{\text{var}}(\hat{\lambda}_H | \lambda_H)$ is average estimated sampling variation due to estimating fitness. Given some model and measures of habitat, spatial process variation can be further expressed as

$$\sigma_{\text{spatial}}^2 = \sigma_{\text{habitat}}^2 + \sigma_{\text{residual}}^2 \quad (6)$$

where $\sigma_{\text{habitat}}^2$ is the spatial process variation of fitness attributed to habitat differences among territories; and $\sigma_{\text{residual}}^2$ is residual variation attributed to other factors, such as individual variation. Similarly, variation in survival and reproductive output, the components of fitness, can be estimated. Understanding variation in fitness among spotted owl territories provides insights into how differences in habitat quality influence spotted

owl populations, and into conservation strategies to manage those populations.

Influences of climate and habitat on population dynamics

Blondel (1991) suggests that effects of extreme climatic events may be overcome by habitat heterogeneity, in which high-quality habitat buffers some individuals from such extreme events. This concept of buffering by high-quality habitats has little empirical support except for Van Horne et al. (1997), who found differential demographic responses to a drought and a prolonged winter by Townsend's ground squirrels (*Spermophilus townsendii*) in two different habitats.

Strategies proposed for organisms dealing with both climatic and habitat variation include short-term responses, such as large-scale spatial shifting of populations within a landscape in response to temporal shifts in climate (Karr and Freemark 1983, Kindvall 1995), and long-term, adaptive responses, such as increasing longevity of individuals to encompass as much temporal variation as possible, thus ensuring that a number of "good" years will be included in an individual's life-span (Newton 1989b). In the first strategy, population responses are based on changes in habitat quality for a given species in relation to climate; changes in climate alter habitat quality and individuals move in response to those changes. The second strategy assumes that habitat quality is more stable over time and that organisms are responding to this habitat stability in the face of temporal variation. Although the first strategy is probably irrelevant for nonmigratory, territorial species such as the Northern Spotted Owl, the second strategy is relevant for territorial species. A third strategy is that individuals should compete for habitats that dampen climatic variation, if climatic variation is important in determining variation in life history traits. This latter hypothesis is particularly relevant to territorial species and incorporates protection from extremes in climatic variation as a component of habitat quality.

Regarding effects of climate and habitat in population dynamics, we first asked the question: *What proportion of the total process variation in life history traits is explained by variation in climate, habitat, and other unknown factors?* For example, does climate account for only a minor proportion of the variation in survival and reproductive output, or does it contribute a proportion similar to that contributed by habitat? In addition, we examined whether there was sufficient residual process variation not accounted for by either habitat or climate that may be caused by other factors not examined in this study. We then asked the question: *Are survival and reproductive output impacted by an interaction between climate and habitat variation?* This can be rephrased as: *Do territories containing habitat that promotes high survival and reproduction buffer the occupants of those habitats from extremes*

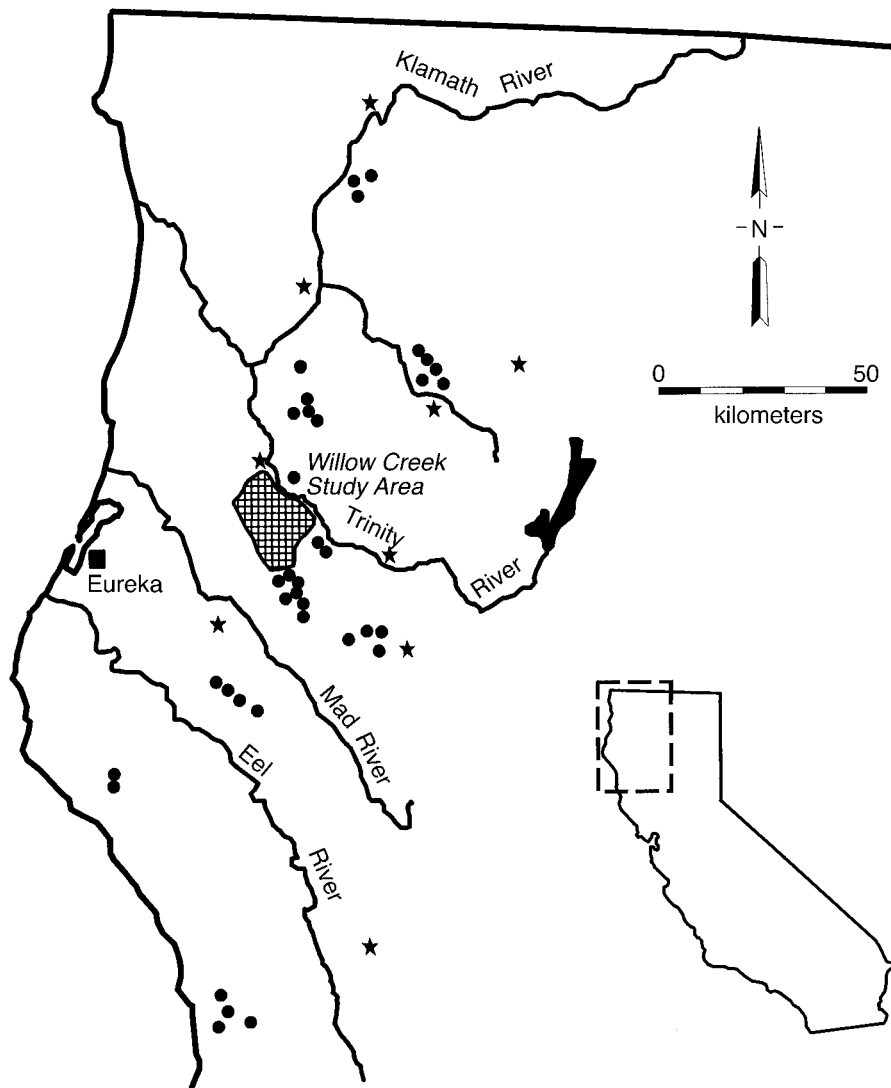


FIG. 1. Location of the Willow Creek study area (hatched area), satellite Northern Spotted Owl sites (dots), and weather stations (stars) in northwestern California.

in climatic variation? An interaction between habitat and climate would be expressed in which individuals occupying territories with "good" habitat quality maintain higher survival and reproduction during periods of "bad" climatic extremes than do those individuals occupying territories of "inferior" habitat quality. Both of these questions are relevant to conservation strategies because habitat variation can, theoretically, be controlled and predicted to some extent, whereas climate variation cannot. In addition, we evaluated what roles climatic and habitat variation may play in the population dynamics of Northern Spotted Owls.

STUDY AREA

We studied Northern Spotted Owls within a 10 000-km² area in the North Coast Range and Klamath Mountains of northwestern California, USA (Fig. 1) that in-

cluded portions of three National Forests and isolated parcels administered by the Bureau of Land Management. Within this area, a 292-km² study area, near Willow Creek, Humboldt County, California, was established and was systematically surveyed each year from 1985 through 1994 to estimate density of Northern Spotted Owls (Franklin et al. 1990). The Willow Creek study area contained 49 Northern Spotted Owl sites (areas where owls exhibited territorial behavior sensu Franklin et al. 1996a). Twelve 10–30 km² satellite survey areas were also used, containing an additional 41 owl sites. These satellite areas were selected to increase sample size over a wider geographic area, and were surveyed from 1987 through 1994.

Elevations in the study area ranged from 200 to 1700 m. The study area was located within the Klamath physiographic province (Küchler 1977), which has

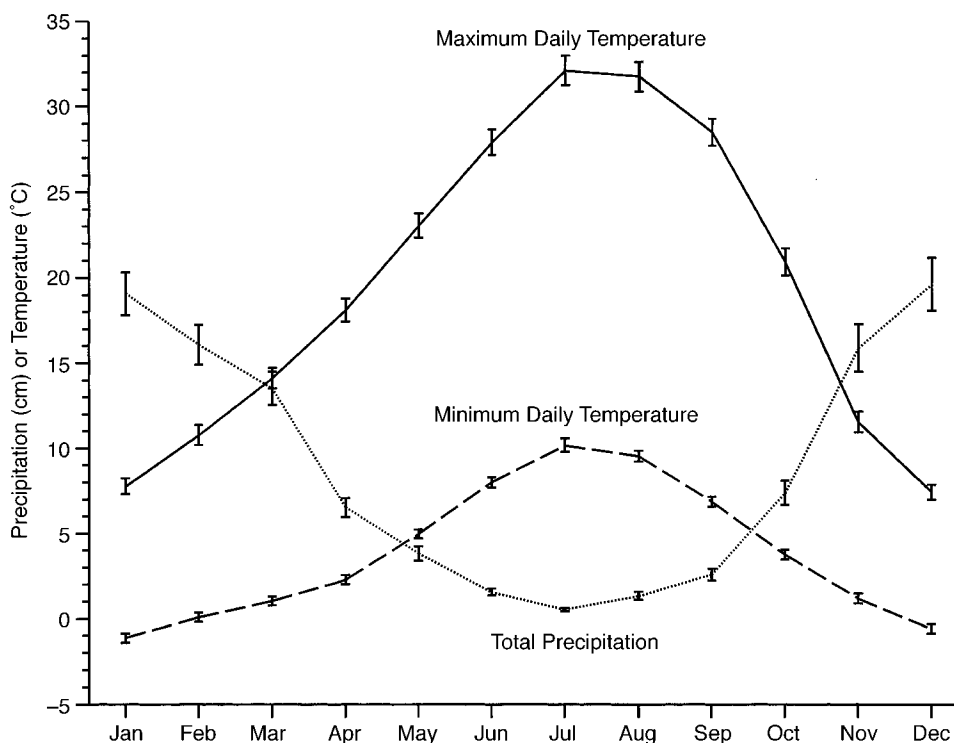


FIG. 2. Seasonal variation in climate in northwestern California. Data are means with 95% confidence intervals for nine weather stations distributed within the study area (see Fig. 1) from April 1954 through April 1994.

unique characteristics not found in other parts of the Northern Spotted Owl's range. This physiographic province encompassed southern Oregon and northern California, where forests were generally characterized by 3–5 major conifer species, often mixed with several hardwood species. Early-seral stages were often dominated by hardwoods, whereas older seral stages were dominated by a conifer overstory, a midstory of hardwood trees, and an understory of hardwood shrubs. As elevations increased, forested stands tended to be dominated solely by conifers. Below 1200 m, forests were dominated by a Douglas-fir (*Pseudotsuga menziesii*) overstory and a hardwood subcanopy dominated by madrone (*Arbutus menziesii*), tanoak (*Lithocarpus densiflora*), and canyon live oak (*Quercus chrysolepis*). Above 1200 m, forests were dominated by white fir (*Abies concolor*) associated with pines (*Pinus* spp.). Because of differing site qualities, pure hardwood stands also occurred, dominated by Oregon white oak (*Quercus garryana*), tanoak, or canyon live oak. Whitaker (1960) considered this forest region to be one of the most complex and diverse in the western United States, because of this blend of conifer and hardwood species.

The climate was mediterranean (Major 1977), characterized by cool, wet winters and hot, dry summers (Fig. 2). The growing season for vegetation was limited by the cool temperatures in winter and lack of precipitation during the summer. This climate was subject to

periodic droughts at 10–15 yr intervals (Major 1977). The Klamath physiographic province has the highest patterns of lightning strikes in the Pacific Northwest; and pre-settlement fire-return rates averaged 11–20 yr at lower elevations and 37 yr at higher elevations (Agee 1993). Most pre-settlement fire appeared to be of low-to-moderate severity, resulting in hardwood understory removal, but retention of large overstory trees. High-severity fires, resulting in removal of most overstory trees, occurred infrequently (Agee 1993). Hardwood brush often became established first after severe fires, and could persist for decades before conifers eventually dominated (Thornburgh 1982).

Since the exclusion of fire by intentional suppression, logging has had the greatest influence on forests in this region (Beardsley and Warbington 1996). Logging patterns of mature and old-growth coniferous forests are similar to those in Oregon, which Spies et al. (1994) described as follows. Dominant silvicultural practices are to develop even-aged plantations, primarily of Douglas-fir (*Pseudotsuga menziesii*), in a dispersed fashion. This is achieved primarily through clear-cutting in regularly shaped blocks of ~16 ha, although earlier clear-cutting practices led to clearcuts of 32–41 ha. Hardwood species that become established after clear-cutting are usually removed through thinning. Logging on public lands began in the 1960s in our study area. In the 1930s and 1940s, $\geq 56\%$ of productive coniferous forest land in California was

considered to be old growth prior to commercial logging on public lands (Bolsinger and Waddell 1993). Approximately 31% of the four National Forests in northwestern California is now covered by mature and old-growth conifer forests, defined as having trees >53 cm diameter at breast height (Beardsley and Warbington 1996). Much of the remaining old-growth in the Pacific Northwest is on National Forests within the Klamath Mountains province in southern Oregon and northwestern California, USA (Bolsinger and Waddell 1993).

STUDY SPECIES

Previous studies in our study area have demonstrated a strong association between Northern Spotted Owls and mature and old-growth forests at the scales of (1) home ranges within the geographical distribution (Blakesley et al. 1992, Hunter et al. 1995), and (2) habitat components within home ranges (Lahaye 1988, Solis and Gutiérrez 1990).

The primary prey of spotted owls in the study area are, in decreasing importance: dusky-footed woodrat (*Neotoma fuscipes*), northern flying squirrel (*Glaucomys sabrinus*), red tree vole (*Phenacomys longicaudus*), and deer mice (primarily *Peromyscus maniculatus*) (see Franklin 1997). *Neotoma* and *Glaucomys* are the most important prey taken, in terms of both frequency and biomass. Based on a number of studies with similar climatic regimes (Howell 1926, Linsdale and Tevis 1951, Tevis 1956, Sadleir 1974, Van Horne 1981, Wells-Gosling and Heaney 1984, Carey 1991, Witt 1991), these four prey species reproduce primarily in the spring and early summer. Breeding seasons of prey are probably determined by availability of high-quality forage during the spring. The primary plant species providing forage for Northern Spotted Owl prey in the spring are oaks, conifers, and hypogeous fungi. *Neotoma* forages heavily on evergreen sclerophyll vegetation, such as tanoak and *Quercus* species in northern California (Linsdale and Tevis 1951, Atsatt and Ingram 1983). In southwestern Oregon, *Glaucomys* eats almost exclusively hypogeous fungi (Maser et al. 1986), whereas *Phenacomys* feeds exclusively on conifer needles, principally from Douglas-fir (Howell 1926, Carey 1991). *Peromyscus* consumes primarily conifer seeds in spring (Jameson 1952, Tevis 1956). In general, phenology of important plant species coincides with the breeding seasons of spotted owl prey. Leaf production for oaks and conifers (Douglas-fir) begins in early spring (Burns and Honkala 1990). Flower production for oaks and other hardwoods extends from May through August, whereas seed production occurs between August and November (Burns and Honkala 1990), providing important food sources for overwintering *Neotoma* and *Peromyscus*. Sporocarp biomass of hypogeous fungi used by *Glaucomys* is highest in March–September (Luoma et al. 1991).

There is conflicting evidence as to whether Northern

Spotted Owls are dependent primarily on interior mature and old-growth coniferous forest, are edge dependent, or are dependent on a mixture of interior habitat and edge. *Neotoma* attains its highest densities in early-seral stages where dense hardwood brush is abundant, and achieves low densities in mature and old-growth forests (Sakai and Noon 1993). Other small mammals important in the diet of Northern Spotted Owls are also found in higher densities in early- to mid-seral stages (Raphael 1988). For this reason, Carey and Peeler (1995) suggest that the mixed-conifer forests of the Klamath Mountains have the greatest diversity and biomass of prey for Northern Spotted Owls. In northern California, Zabel et al. (1995) found spotted owls foraging near edges of late- and early-seral stage forests more often than expected. Ward et al. (1998) reported that woodrat abundance was greatest at spotted owl foraging sites at the ecotone between late- and early-seral stages. Thus, there is a dichotomy between the strong association for spotted owls with late-seral stage forests and the primary prey source for owls that are associated with early-seral stages.

The link between older forests and life history traits, such as survival and reproductive output, is currently tenuous in Northern Spotted Owls. Using turnover rates as an index of survival, Bart and Earnst (1992) found that persistence of adults was significantly correlated with the proportion of mature and old-growth forest within Northern Spotted Owl territories. Bart and Forsman (1992) and Ripple et al. (1997) found similar positive correlations between amounts of mature and old-growth forest and reproductive output in Northern Spotted Owls, on the scale of aggregations of territories and individual territories, respectively. However, in all cases, relationships with other habitat configurations were not considered, and Bart and Earnst (1992) and Ripple et al. (1997) used indices of life history traits, rather than direct parameter estimates. In addition, the link between habitat and fitness is still lacking. The problem with studies that examine only the components of fitness (survival and fecundity) is that potential trade-offs maximizing long-term survival and fecundity are often ignored. In other words, factors that maximize either survival and fecundity may be different, and neither component by itself may reflect fitness.

METHODS

We used the following general analytical approach in assessing the effects of variation in climate covariates on the three life history traits of Northern Spotted Owls. After developing the biological background for potential effects of climate on Northern Spotted Owls, we divided the annual cycle into specific life history periods to identify when climatic stresses may affect spotted owls. We relied on existing biological information to identify these periods. In dividing the annual cycle into specific periods, we reduced the number of climatic covariates from arbitrary weekly or monthly

intervals to those included in fewer, more biologically meaningful, intervals (Appendix A). We used these steps to develop a priori verbal hypotheses, which we then expressed as models that could be fit to the available data. In these models, the response variables were life history traits (survival, reproductive output, and recruitment) and the explanatory variables were climate covariates (temperature and precipitation during life history periods) and individual covariates (age and sex). Thus, we had suites of candidate statistical models for each life history trait that were developed prior to analyzing the empirical data and that related the respective life history trait to climatic covariates. These suites of candidate models were analogous to the 26 predator-prey models suggested by Berryman et al. (1995), some of which represented competing theories. The importance of a priori model development in data analysis, as opposed to analyzing data by iteratively searching the data for relationships (i.e., data dredging), has been alluded to by Hofacker (1983) and Chatfield (1995), and more recently has been formalized by Burnham and Anderson (1998).

After a priori hypothesized models were developed, we used an objective model selection criterion (AICc; see *Selection of hypothesized models*) to rank and calibrate the candidate hypothesized models in terms of their ability to explain the empirical data. In this way, a "best approximating" model was selected from each suite of candidate models as the most parsimonious explanation of the data. Other candidate models were then ranked below in terms of their plausibility to explain the same data. Model selection based on AIC has an advantage in that multiple hypotheses can be ranked according to their importance in explaining the data; a hypothesis-testing approach only allows for rejection or failure to reject two models at a time (Akaike 1974). Burnham and Anderson (1998) present other, numerous reasons for using AIC-based model selection rather than hypothesis testing when dealing with data collected in an observational study such as this one. Model selection, based on AIC, has been used extensively in capture-recapture studies (see Lebreton et al. 1992).

The analytical strategy that we outline here avoids models with more covariates than can be supported by the data, which often results in imprecise parameter estimates, and excessive data dredging, which can result in spurious explanatory models (Freedman 1983). Thus, the strategy that we use here balances precision and bias when selecting an appropriate model to relate variation in life history traits to climatic covariates (Burnham and Anderson 1992).

Data collection

Life history traits.—The general design for collection of field data to estimate survival, reproductive output, and recruitment was to monitor marked individuals over time. Each year, we attempted to locate and individually identify all spotted owls in the Willow Creek

and satellite study areas. Territorial spotted owls were located with multiple surveys, using vocal imitations of their calls to elicit responses (Forsman 1983, Franklin et al. 1996a), from April through August of each year. Surveys were not conducted on days when precipitation occurred. Northern Spotted Owls were aged by plumage characteristics as fledged young of the year, 1-, 2-, or ≥ 3 -yr old (Moen et al. 1991); sexes were distinguished by vocalizations (Forsman et al. 1984). Once located, owls ≥ 1 yr old were checked for reproductive output. Using specific criteria outlined in Franklin et al. (1996a), each pair of owls visited was categorized as having 0, 1, 2, or (rarely) 3 fledged young. Individuals were uniquely identified through capture, recapture, or resighting of colored leg bands using several techniques (see Forsman 1983, Franklin et al. 1996a). Locking numbered aluminum bands were placed on one leg of each captured owl, and a colored plastic leg band with colored vinyl tabs (Forsman et al. 1996) was placed on the opposing leg to identify individuals without recapturing in subsequent years. If identification of color marks was ambiguous, birds were recaptured and the numbered band was read. We used the term "recapture" to describe physical recapture of marked individuals or resighting of previously color-marked individuals. Although juveniles were recaptured as ≥ 1 -yr olds, these data were not used to estimate juvenile survival because of potential biases (see Franklin et al. 1996a).

Climate covariates.—To estimate climatic covariates, we first divided the annual cycle experienced by spotted owls into critical periods based on weather conditions and specific life history stages (see Appendix A for details). These critical periods were the *winter stress period* (November–February), the *early nesting period* (March–April), the *late nesting period* (May), the *heat stress period* (July–August), and the *dispersal period* (September–October).

Within each defined life history period, we obtained daily measurements for amounts of precipitation and minimum and maximum temperatures from nine weather stations operated by the U.S. Weather Service (Fig. 1). These stations were selected because they provided adequate spatial coverage of the study areas and had complete records both during and before the study. The range of weather station elevations included 83% of the elevational distribution for owl capture locations. Therefore, we assumed that data from the weather stations were representative of conditions experienced by spotted owls in the study area. We also assumed that changes between years adequately represented real changes as long as climate conditions within years were reasonably represented, because the relationship of interest was year-to-year variation.

Climate covariates had to be biologically meaningful in their effects on owls, and had to be precisely estimated ($CV < 10\%$) when averaged across stations within years, because we did not incorporate sampling var-

iances of covariates into statistical analyses. For precipitation, we used the number of days of measurable precipitation (≥ 0.03 cm) within each life history period because we felt that the duration of precipitation was more important in its effects than the absolute amount. Regardless, the annual number of days of precipitation was highly correlated with annual precipitation amount within the life history periods ($r = 0.87\text{--}0.94$, $df = 8$, $P < 0.001$). The number of days with precipitation averaged across stations within years was precise ($cv = 2.5\text{--}7.1\%$).

Estimating daily temperature only from daily maximum and minimum temperatures can be problematic. Means of maximum and minimum temperature in a given day fail to account for the duration of temperatures, and typically underestimate the actual mean daily temperature, based on hourly data (Lindsey and Newman 1956). Therefore, we estimated degree-hours (the product of temperature and the time over which temperatures occur; Lindsey and Newman 1956, Tuhtanen 1980) by modeling hourly temperature over the course of a 24-h day using a cosine model (from Allen 1976):

Hourly temperature

$$= T_{\min} + \left(\frac{T_{\max} - T_{\min}}{2} \right) \left[1 - \cos \left(\frac{\gamma \pi}{24} h - \frac{\delta \pi}{24} \right) \right] \quad (7)$$

where T_{\max} and T_{\min} were daily maximum and minimum temperatures, respectively; h was the hour of the day; and γ and δ were parameters controlling phase angle and width, respectively. Daily degree-hours were estimated by integrating Eq. 7 from $h = 0$ to 24. Parameters γ and δ were estimated for life history periods using Eq. 7 in nonlinear regression (Proc NLIN; SAS Institute 1990) with hourly data available from two weather stations. Degree-hours were estimated for each day and were then averaged within the life history periods for each year. Daily temperature models explained a high proportion of the variation in hourly temperature over the course of a day ($R^2 = 0.912\text{--}0.995$) within the life history periods. Estimates of γ ($cv = 1.4\text{--}5.0\%$) and δ ($cv = 5.2\text{--}11.2\%$) from Eq. 7 were precise. Degree-hours averaged across stations within years were precise ($cv = 1.2\text{--}3.6\%$). As an additional covariate during the heat stress period, we estimated surplus stress units, in terms of increased oxygen consumption by the owls ($\text{mL O}_2/\text{g/h}$), attributed to daily temperatures, and the length of time that they were maintained, according to:

$$\text{cc O}_2 \text{ g}^{-1} \text{ h}^{-1} \\ = \int_{h_a}^{h_b} [0.649 + 0.008(f(H)) - 0.905] dt \quad (8)$$

where $f(H)$ was Eq. 7, h_a was the hour when temperatures began exceeding the 32°C threshold temperature when owls exhibited heat stress, and h_b was the hour

when temperatures decreased below the 32°C threshold temperature. The linear equation in Eq. 8 is the regression equation estimated by Ganey et al. (1993) for oxygen consumption in Mexican Spotted Owls (*Strix occidentalis lucida*) above their thermal neutral zone. In using the equation from Ganey et al. (1993), we assumed that Northern Spotted Owls had a physiological response to temperature similar to that of Mexican Spotted Owls.

Landscape habitat covariates.—We used a digital vegetation map, developed by the California Timberland Task Force (TTF), that covered both private and public lands over the extent of our entire study area (Geographic Resource Solutions 1996). This map was developed from 1990 Landsat Thematic Mapper imagery that was resampled to a pixel size of 25×25 m. Pixels were aggregated into polygons with a minimum polygon size of 2 ha. Polygon attributes pertinent to this study were (1) average quadratic mean diameter (Husch et al. 1982) at breast height of all conifer trees in the polygon, (2) average quadratic mean diameter at breast height of all hardwood trees in the polygon, (3) canopy closure of all trees in the polygon, and (4) percentage of conifers in the total canopy closure. This vegetation map was chosen because it covered all lands regardless of ownership, it covered the entire study area, and it contained polygon attributes classifiable into vegetation types relevant to spotted owls. Although other vegetation maps existed, they lacked one or more of these attributes.

We initially defined two habitats: spotted owl habitat and high-density dusky-footed woodrat habitat. Based on previous experience with Landsat coverages that were used to define habitats on the Willow Creek study area (Hunter et al. 1995), these were the only two habitats that we felt could be reliably estimated. Spotted owl habitat was based on the strong association of the owl with mature and old-growth forests for nesting, roosting, and foraging on the study area (Solis and Gutiérrez 1990, Blakesley et al. 1992, Hunter et al. 1995). Woodrat habitat was based on vegetation characteristics associated with high densities of dusky-footed woodrats (Sakai and Noon 1993). However, Northern Spotted Owls were not known to forage within this habitat (Solis and Gutiérrez 1990), but possibly along its edges (Zabel et al. 1995). Therefore, we initially distinguished woodrat habitat from spotted owl habitat based on the definition of habitat used here (Morrison et al. 1992). Both habitats were defined using the polygon attributes in the TTF vegetation map. Two phases of field verification were used to iteratively assess the accuracy of our definitions for the two habitats (Franklin 1997). However, woodrat habitat was poorly classified (68.6% probability that stands on the ground were correctly classified in the TTF coverage). In addition, analyses including this habitat did not suggest that woodrat habitat was important in explaining spatial variation in spotted owl survival and reproductive out-

put. Therefore, we did not consider this habitat further. In the end, we used two habitats: spotted owl habitat vs. other vegetation types. Spotted owl habitat was mature and old-growth forest with a quadratic mean diameter of conifers ≥ 53 cm, quadratic mean diameter of hardwoods ≥ 15 cm, percentage of conifers $\geq 40\%$, and overstory canopy coverage $\geq 70\%$. This definition corresponded to other classifications used to define spotted owl habitat (Solis and Gutiérrez 1990) and to definitions used in other studies in this area (Blakesley et al. 1992, Hunter et al. 1995). By including hardwood tree species, our definition of spotted owl habitat indirectly reflected multiple canopy layers, an important component identified in previous studies (Solis and Gutiérrez 1990). Based on both phases of field verification (Franklin 1997), spotted owl habitat was correctly classified 89.0% of the time using the TTF vegetation coverage.

We used a 0.71 km radius circle around territory centers to represent spotted owl territories. Landscape habitat characteristics were then measured within these circles as covariates, when estimating survival and reproductive output of individual spotted owls occupying territories represented by the circles. Rationales and methods used to derive the 0.71 km radius circles as sampling units are described as follows. First, territory centers were estimated for all territories by averaging the UTM (Universal Transverse Mercator) coordinates representing roost and nest locations at each site. Multiple roosts at the same territory within the same year were included only once when averaging. However, if individuals roosted or nested at the same location in different years, those locations were included because they represented choices by individuals between years. In general, roost and nest locations at individual territories were tightly clustered; coefficients of variation for mean Easting and Northing UTM coordinates were ≤ 0.1 for 90% of the territories. Second, the radius of the circle was estimated as one-half of the median nearest neighbor distance (Hunter et al. 1995) between 37 territory centers in the Willow Creek Study area only. We assumed that the locations of almost all territories were known in the Willow Creek study area, to provide an adequate measure of territory adjacency. This median measure (0.71 km) was similar to the mean (0.75 km), with a range of 0.21–1.21 km.

We considered the 0.71 km radius circles as territory core areas for spotted owls in this study because of the small area (1.58 km²) relative to expected home range size in northwestern California (4.2–5.9 km²; Zabel et al. 1995). Hunter et al. (1995) and Meyer et al. (1998) found that landscape characteristics had the highest levels of significance between random sites and sites used by Northern Spotted Owls in the Klamath province when 0.8-km circles were used as a sampling unit, as opposed to larger diameter circles centered around the same sites. Meyer et al. (1998) suggested that characteristics of the inner core represented by these size

circles may be most influential in determining territory locations for Northern Spotted Owls.

In describing landscape characteristics within territories, we chose not to use indices such as fractal dimension, contagion, evenness, and the variety of patch indices commonly used in landscape ecology to describe fragmentation and landscape pattern. Often these indices do not capture obvious differences in landscape pattern (Ripple et al. 1991, Groom and Schumaker 1993, Li and Reynolds 1994), are ad hoc (thus lacking an appropriate theoretical basis as meaningful measures), and are highly correlated with each other (Li and Reynolds 1994). In addition, we did not use metrics that included area in the denominator, such as patch density, because all territory circles were the same size. The metrics that we chose to describe landscape characteristics within spotted owl territories were those that we considered to be the fundamental characteristics describing habitat amounts, patch size, patch abundance, patch shape, and patch spacing. Together, the patch characteristics accounted for varying degrees of fragmentation.

Within the 0.71 km radius circles around territory centers, we chose nine habitat covariates and one topographic covariate (elevation) to examine with respect to spotted owl survival and reproduction (Table 1). We estimated mean elevation (ELEV) for each spotted owl territory by averaging the elevations of each roost and nest site used to estimate the centers of each territory. SOHAB and SOMP were estimates of amounts of spotted owl habitat, whereas SODIS was an estimate of the spatial distribution of patches of owl habitat (Ripple et al. 1991, Groom and Schumaker 1993). SOEDG, in conjunction with SOCOR, was a measure of patch shape (Groom and Schumaker 1993). For example, patches with little SOCOR and high SOEDG indicated linear patch shapes. The core habitat covariates, SOCOR and SONCA, are additional measures of general patch shape because they account for relative amounts of interior habitat vs. edge (Groom and Schumaker 1993). The combination of SOCOR and SONCA also measures fragmentation (Temple 1986) by measuring the amount and distribution of interior habitat; many small patches will have little or no core habitat. We used a 100-m distance from the edge to define core habitat area, because ecological characteristics of old-growth coniferous forests begin to stabilize beyond this distance (Spies et al. 1994, Chen et al. 1995), and the negative edge-associated impacts on forested habitats, in general, have been ameliorated after this distance (Temple 1986).

We estimated covariates for each spotted owl territory using operations in the ARC/INFO geographic information system (ESRI 1987). We first made a new coverage from the TTF vegetation map, which only included polygons of either spotted owl habitat or other vegetation types. Territory centers were circumscribed by the 0.71-km sampling radius and coverages for each

TABLE 1. Age and landscape habitat covariates used in models to estimate survival and reproductive output for Northern Spotted Owls in northwestern California.

Variable	Definition	Original metric†	Rescaled metric‡
a_2	Dummy variable with 1-yr-old age class vs. ≥ 2 -yr-old age class		
a_2'	Dummy variable with 1- and 2-yr-old age class vs. ≥ 3 -yr-old age class		
a_3	Dummy variables with 1-yr-old age class vs. 2-yr-old age class vs. ≥ 3 -yr-old age class		
SOHAB	Total amount of Northern Spotted Owl habitat	ha	ha \div 10
SONP	No. discrete patches of spotted owl habitat	n	n
SOMP	Maximum patch size of spotted owl habitat	ha	ha \div 10
SOEDG	Total amount of edge between spotted owl habitat and all other vegetation types	m	km
SODIS	Mean nearest neighbor distance between patches of spotted owl habitat measured from edge to edge of patches	m	m \div 10
SOCOR	Total amount of spotted owl core habitat, defined as the amount of spotted owl habitat ≥ 100 m from an edge	ha	ha
SONCA	No. patches of spotted owl core habitat	n	n
ELEV	Mean elevation of spotted owl territory	m	m \div 100

† Original scale on which the covariate was measured.

‡ Rescaling factor used for analyses with covariates.

territory were then developed, containing the two categories within each circle. We used program FRAGSTATS (McGarigal and Marks 1995) to estimate each of the habitat covariates for each spotted owl territory. We manually checked measurements of a subsample ($n = 15$) of the territories to ensure that FRAGSTATS was correctly estimating the habitat covariates. Prior to analyses, covariates were rescaled in order to avoid large values in quadratic terms and interactions (Table 1).

Logging occurred within the sampling circle on nine territories over the course of the study. We adjusted polygons for loss of habitat due to timber harvest, based on U.S. Forest Service timber harvest records and aerial photographs, made new coverages of these territories, and estimated habitat covariates for both before and after logging.

Formulation of hypothesized models

Model development.—Prior to analyzing the empirical data, we explored ways in which climate and habitat configuration might affect spotted owls, based on the existing literature. We used this information to develop qualitative, potential effects of climate and habitat conditions on the owls, and incorporated these into statistical models as a priori hypotheses for analyzing the empirical data on the three life history traits. We used three forms of models when translating ideas into statistical models: a linear, a pseudothreshold, and a quadratic form (Fig. 3). For survival analyses, these

model forms were incorporated using a logit link function (see *Modeling survival*).

The linear form of models could be written as

$$\theta = \beta_0 + \beta_1(x_1) + \dots + \beta_n(x_n) \quad (9)$$

and the quadratic form as

$$\theta = \beta_0 + \beta_1(x_1) + \beta_2(x_1^2) + \dots + \beta_{2n-1}(x_n) + \beta_{2n}(x_n^2) \quad (10)$$

where θ was the life history trait and x_i was the i th covariate. For the sake of parsimony in quadratic forms of the models, we used the squared differences of covariate values from their mean (denoted by preceding the covariate name with a D), which were calculated as

$$Dx_{ij} = (x_{ij} - \bar{x}_i)^2 \quad (11)$$

where x_{ij} was the j th value of the i th covariate. By using the squared differences, we could rewrite Eq. 10 as

$$\theta = \beta_0 + \beta_1(Dx_1) + \dots + \beta_n(Dx_n). \quad (12)$$

This saved an extra parameter for each covariate used in the quadratic form of the models. However, the form in Eq. 12 was a restricted quadratic because it assumed that the curve was centered on the covariate mean. Therefore, quadratic models using the squared differences were also examined with the full quadratic terms ($x_i + x_i^2$) as a check.

The pseudothreshold form of models was

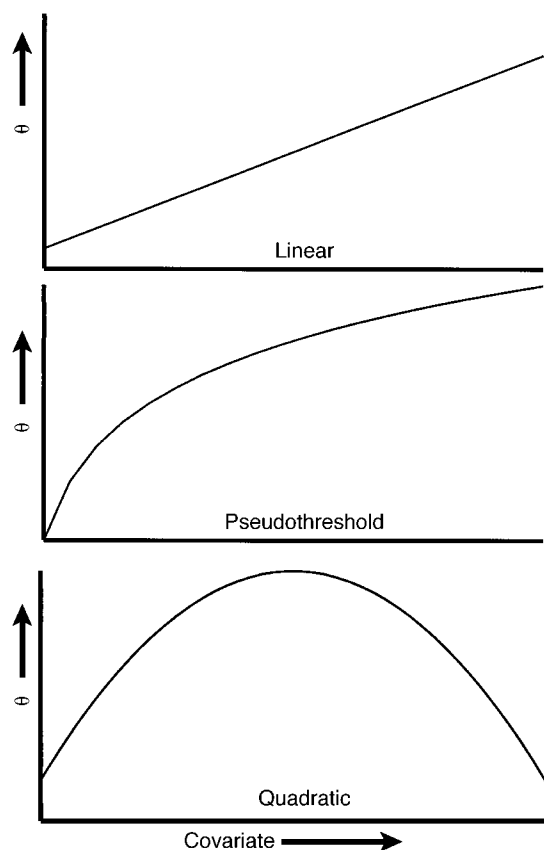


FIG. 3. Model forms used in hypothesized models relating landscape habitat covariates to life history traits (θ).

$$\theta = \beta_0 + \beta_1 \log_e(x_1 + 0.5) + \dots + \beta_n \log_e(x_n + 0.5). \quad (13)$$

Covariate names in these models were preceded by an L (e.g., LSOCOR). In using log transforms, we added 0.5 to covariate values to account for values of zero. This was considered a pseudothreshold because an asymptote (threshold) was approached, but never reached, using the log transform. However, we considered this a parsimonious approximation to a true threshold model.

Each model structure indicated different predictions for each of the hypothesized models. A linear structure predicted that effects of the covariates changed at some constant rate; a pseudothreshold structure predicted that effects changed at a constant rate to some point and then approached (but did not reach) an asymptote; and a quadratic structure predicted some optimal maximum at intermediate effects, and lower effects at the extremes (Fig. 3). In denoting combinations of effects in models, we used “+” to denote an additive effect, where no interactions were considered, and used “*” to denote inclusion of interactions (Lebreton et al. 1992).

Climate models.—We hypothesized that variation in precipitation and ambient temperature can affect spotted

owls directly through energetic constraints, and indirectly through the population dynamics and activity patterns of their prey, and the food resources required by those prey. Collectively, we referred to models examining the relationship between the life history traits and climate covariates as climate models. The underlying biological rationale for developing the following hypothesized climate models is detailed in Appendix A.

Prior to data analysis, we developed eight hypothetical climate models for survival (Table 2). The late nesting period was not included in survival models because of overlap with sampling periods when owls were captured. Models 1–6 in Table 2 examined climate effects within each period based on biological characteristics outlined previously, but with no drought effects. Longer term drought effects were considered in model 7, using a quadratic model in which survival could be negatively affected at either end of the drought–mesic continuum. Model 8 in Table 2 hypothesized that optimal growing conditions (e.g., wet winters followed by warm springs) in one year can positively influence prey populations in the following year and, hence, may increase spotted owl survival over the winter stress period. Additional variations of the hypothesized models included quadratic forms of the covariates and inclusion of age and sex effects.

We proposed 11 a priori climate models for reproductive output (Table 2) in which only the winter stress, early nesting, and late nesting periods were considered relevant. The complexity of hypothesized models for reproductive output was constrained by the existing sample of 10 yr, because annual means were used as the response. In Northern Spotted Owls, we presumed that food during the winter stress, early nesting, and late nesting periods was crucial for determining reproductive success, based on food supplementation experiments with other raptor species (Ward and Kennedy 1994, 1996, Wiehn and Korpimäki 1997). Models 1–3 in Table 2 reflected the effects of high precipitation alone on the ability of males to provide adequate food for incubating females or nestlings. Model 4 hypothesized that cold, wet winters negatively affected a female’s ability to attain adequate body condition for reproduction, whereas models 5 and 6 examined the effects of both temperature and precipitation on hunting success of males and their ability to provide females with sufficient food during the early and late nesting periods. Lacking sufficient food, we surmised that females would leave nests for extended periods to forage, exposing eggs and young to the chilling effects of cold, wet weather. Models 7 and 8 examined the combined effects of wet and cold on the postulated effects from models 4–6. Models 9–11 hypothesized that optimal climatic conditions promoting the production of plant forage for prey led to increased reproductive output by the owls (see Appendix A).

We hypothesized six additional models to explain the effects of climate on recruitment (Table 2). Model

TABLE 2. Description and representation of a priori models concerning the effects of precipitation and ambient temperature on survival, reproductive output, and recruitment rates of Northern Spotted Owls in northwestern California.

Hypothesis	Model	Model structure	Expected result†
Survival (logit ϕ)			
1) Negative effects of high temperatures in H.	ϕ_{T_H}	$\beta_0 + \beta_1(T_H)$	$\beta_1 < 0$
2) Negative effects of high precipitation and cold temperatures in W (no drought effect).	$\phi_{P_W+T_W}$	$\beta_0 + \beta_1(P_W) + \beta_2(T_W)$	$\beta_1 < 0, \beta_2 > 0$
3) Negative effects of high precipitation and cold temperatures in E (no drought effect).	$\phi_{P_E+T_E}$	$\beta_0 + \beta_1(P_E) + \beta_2(T_E)$	$\beta_1 < 0, \beta_2 > 0$
4) Negative effects of combined precipitation in both W and E.	$\phi_{P_W+P_E}$	$\beta_0 + \beta_1(P_W) + \beta_2(P_E)$	$\beta_1 < 0, \beta_2 < 0$
5) Positive effects of high precipitation in W followed by warm temperatures in E.	$\phi_{P_W+T_E}$	$\beta_0 + \beta_1(P_W) + \beta_2(T_E)$	$\beta_1 > 0, \beta_2 > 0$
6) Negative effects of high precipitation and cold temperatures in both W and E (no drought effect).	$\phi_{P_W+T_W+P_E+T_E}$	$\beta_0 + \beta_1(P_W) + \beta_2(T_W) + \beta_3(P_E) + \beta_4(T_E)$	$\beta_1 < 0, \beta_2 > 0$ $\beta_3 < 0, \beta_4 > 0$
7) Negative effects of high precipitation or drought, both combined with temperatures, in both W and E.	$\phi_{P_W+P_W^2+P_E+P_E^2+T_W+T_E}$	$\beta_0 + \beta_1(P_W) + \beta_2(P_W)^2 + \beta_3(P_E) + \beta_4(P_E)^2 + \beta_5(T_W) + \beta_6(T_E)$	$\beta_1 > 0, \beta_2 < 0$ $\beta_3 > 0, \beta_4 < 0$ $\beta_5 > 0, \beta_6 > 0$
8) Lagged positive effect of high precipitation in W and warm temperatures in E in time t on survival in $t + 1$.	$\phi_{P'_W+T'_E}$	$\beta_0 + \beta_1(P'_W) + \beta_2(T'_E)$	$\beta_1 > 0, \beta_2 > 0$
Reproductive output (R)			
1) Negative effects of high precipitation in E.	R_{P_E}	$\beta_0 + \beta_1(P_E)$	$\beta_1 < 0$
2) Negative effects of high precipitation in L.	R_{P_L}	$\beta_0 + \beta_1(P_L)$	$\beta_1 < 0$
3) Negative effects of high precipitation in both E and L.	$R_{P_E+P_L}$	$\beta_0 + \beta_1(P_E) + \beta_2(P_L)$	$\beta_1 < 0, \beta_2 < 0$
4) Negative effects of high precipitation and cold temperatures in W (no drought effect).	$R_{P_W+T_W}$	$\beta_0 + \beta_1(P_W) + \beta_2(T_W)$	$\beta_1 < 0, \beta_2 > 0$
5) Negative effects of high precipitation and cold temperatures in E.	$R_{P_E+T_E}$	$\beta_0 + \beta_1(P_E) + \beta_2(T_E)$	$\beta_1 < 0, \beta_2 > 0$
6) Negative effects of high precipitation and cold temperatures in L.	$R_{P_L+T_L}$	$\beta_0 + \beta_1(P_L) + \beta_2(T_L)$	$\beta_1 < 0, \beta_2 > 0$
7) Negative effects of high precipitation and cold temperatures in both E and L.	$R_{P_E+T_E+P_L+T_L}$	$\beta_0 + \beta_1(P_E) + \beta_2(T_E) + \beta_3(P_L) + \beta_4(T_L)$	$\beta_1 < 0, \beta_2 > 0$ $\beta_3 < 0, \beta_4 > 0$
8) Negative effects of high precipitation and cold temperatures in both W and E.	$R_{P_W+T_W+P_E+T_E}$	$\beta_0 + \beta_1(P_W) + \beta_2(T_W) + \beta_3(P_E) + \beta_4(T_E)$	$\beta_1 < 0, \beta_2 > 0$ $\beta_3 < 0, \beta_4 > 0$
9) Positive effects of high precipitation in W followed by warm temperatures in E.	$R_{P_W+T_E}$	$\beta_0 + \beta_1(P_W) + \beta_2(T_E)$	$\beta_1 > 0, \beta_2 > 0$
10) Positive effects of high precipitation in W followed by warm temperatures in L.	$R_{P_W+T_L}$	$\beta_0 + \beta_1(P_W) + \beta_2(T_L)$	$\beta_1 > 0, \beta_2 > 0$
11) Positive effects of high precipitation in W followed by warm temperatures in E and L.	$R_{P_W+T_E+T_L}$	$\beta_0 + \beta_1(P_W) + \beta_2(T_E) + \beta_3(T_L)$	$\beta_1 > 0, \beta_2 > 0$ $\beta_3 > 0$
Recruitment rate (b)			
1) Negative effects of high precipitation in D.	b_{P_D}	$\beta_0 + \beta_1(P_D)$	$\beta_1 < 0$
2) Negative effects of high precipitation in both D and W.	$b_{P_D+P_W}$	$\beta_0 + \beta_1(P_D) + \beta_2(P_W)$	$\beta_1 < 0, \beta_2 < 0$
3) Negative effects of high precipitation and cold temperatures in D.	$b_{P_D+T_D}$	$\beta_0 + \beta_1(P_D) + \beta_2(T_D)$	$\beta_1 < 0, \beta_2 > 0$
4) Negative effects of high precipitation in D, W, and E.	$b_{P_D+P_W+P_E}$	$\beta_0 + \beta_1(P_D) + \beta_2(P_W) + \beta_3(P_E)$	$\beta_1 < 0, \beta_2 < 0$ $\beta_3 < 0$
5) Negative effects of high precipitation and cold temperatures in D with high precipitation in W.	$b_{P_D+T_D+P_W}$	$\beta_0 + \beta_1(P_D) + \beta_2(T_D) + \beta_3(P_W)$	$\beta_1 < 0, \beta_2 > 0$ $\beta_3 < 0$
6) Negative effects of high precipitation and cold temperatures in both D and W.	$b_{P_D+T_D+P_W+T_W}$	$\beta_0 + \beta_1(P_D) + \beta_2(T_D) + \beta_3(P_W) + \beta_4(T_W)$	$\beta_1 < 0, \beta_2 > 0$ $\beta_3 < 0, \beta_4 > 0$

Notes: P and T indicate precipitation and temperature covariates, respectively. Abbreviations for life history periods where covariates apply are: W, winter stress; E, early nesting; L, late nesting; D, dispersal; and H, heat stress period.

† Expected direction in regression coefficients, given that the hypothesized model is correct to use.

1 was a hypothesis that high precipitation would negatively affect recruitment by negatively affecting the hunting success of juveniles when they first disperse. We based models 2 and 4 on a similar supposition, but over the longer period of time when young owls must first fend for themselves during dispersal. In models 3, 5, and 6, we considered the effects of temperature in

addition to precipitation. Because recruitment is a function of survival and reproduction, we tested all of the Table 2 hypothesized models related to those parameters. We made an additional prediction based on potential population dynamics: if floaters were present in sufficient numbers, then climate covariates that negatively affect the survival of territory holders should

TABLE 3. A priori hypothesized models used to relate the effects of landscape habitat characteristics with survival and reproduction of Northern Spotted Owls in northwestern California; θ represents either apparent survival or reproductive output.

Hypothesized model	Predicted effects		
	Linear structure	Pseudothreshold structure	Quadratic structure [†]
1) θ_{SOHAB}	$\beta_{\text{SOHAB}} > 0$	$\beta_{\text{ln(SOHAB)}} > 0$	$\beta_{\text{SOHAB}} > 0, \beta_{(\text{SOHAB})^2} < 0$
2) θ_{SOMP}	$\beta_{\text{SOMP}} > 0$	$\beta_{\text{ln(SOMP)}} > 0$	$\beta_{\text{SOMP}} > 0, \beta_{(\text{SOMP})^2} < 0$
3) $\theta_{\text{SOMP+SONP}}$	$\beta_{\text{SOMP}} > 0, \beta_{\text{SONP}} < 0$	$\beta_{\text{ln(SOMP)}} > 0, \beta_{\text{ln(SONP)}} < 0$	$\beta_{\text{SOMP}} > 0, \beta_{(\text{SOMP})^2} < 0$ $\beta_{\text{SONP}} > 0, \beta_{(\text{SONP})^2} < 0$
4) $\theta_{\text{SOMP+SODIS}}$	$\beta_{\text{SOMP}} > 0, \beta_{\text{SODIS}} < 0$	$\beta_{\text{ln(SOMP)}} > 0, \beta_{\text{ln(SODIS)}} < 0$	$\beta_{\text{SOMP}} > 0, \beta_{(\text{SOMP})^2} < 0$ $\beta_{\text{SODIS}} > 0, \beta_{(\text{SODIS})^2} < 0$
5) $\theta_{\text{SOMP+SONP+SODIS}}$	$\beta_{\text{SOMP}} > 0, \beta_{\text{SONP}} < 0,$ $\beta_{\text{SODIS}} < 0$	$\beta_{\text{ln(SOMP)}} > 0, \beta_{\text{ln(SONP)}} < 0,$ $\beta_{\text{ln(SODIS)}} < 0$	$\beta_{\text{SOMP}} > 0, \beta_{(\text{SOMP})^2} < 0$ $\beta_{\text{SONP}} > 0, \beta_{(\text{SONP})^2} < 0$ $\beta_{\text{SODIS}} > 0, \beta_{(\text{SODIS})^2} < 0$
6) $\theta_{\text{SOMP+SOEDG}}$	$\beta_{\text{SOMP}} > 0, \beta_{\text{SOEDG}} < 0$	$\beta_{\text{ln(SOMP)}} > 0, \beta_{\text{ln(SOEDG)}} < 0$	$\beta_{\text{SOMP}} > 0, \beta_{(\text{SOMP})^2} < 0$ $\beta_{\text{SOEDG}} > 0, \beta_{(\text{SOEDG})^2} < 0$
7) θ_{SOCOR}	$\beta_{\text{SOCOR}} > 0$	$\beta_{\text{ln(SOCOR)}} > 0$	$\beta_{\text{SOCOR}} > 0, \beta_{(\text{SOCOR})^2} < 0$
8) $\theta_{\text{SOCOR+SONCA}}$	$\beta_{\text{SOCOR}} > 0, \beta_{\text{SONCA}} < 0$	$\beta_{\text{ln(SOCOR)}} > 0, \beta_{\text{ln(SONCA)}} < 0$	$\beta_{\text{SOCOR}} > 0, \beta_{(\text{SOCOR})^2} < 0$ $\beta_{\text{SONCA}} > 0, \beta_{(\text{SONCA})^2} < 0$
9) $\theta_{\text{SOCOR+SODIS}}$	$\beta_{\text{SOCOR}} > 0, \beta_{\text{SODIS}} < 0$	$\beta_{\text{ln(SOCOR)}} > 0, \beta_{\text{ln(SODIS)}} < 0$	$\beta_{\text{SOCOR}} > 0, \beta_{(\text{SOCOR})^2} < 0$ $\beta_{\text{SODIS}} > 0, \beta_{(\text{SODIS})^2} < 0$
10) $\theta_{\text{SOCOR+SONCA+SODIS}}$	$\beta_{\text{SOCOR}} > 0, \beta_{\text{SONCA}} < 0,$ $\beta_{\text{SODIS}} < 0$	$\beta_{\text{ln(SOCOR)}} > 0, \beta_{\text{ln(SONCA)}} < 0,$ $\beta_{\text{ln(SODIS)}} < 0$	$\beta_{\text{SOCOR}} > 0, \beta_{(\text{SOCOR})^2} < 0$ $\beta_{\text{SONCA}} > 0, \beta_{(\text{SONCA})^2} < 0$ $\beta_{\text{SODIS}} > 0, \beta_{(\text{SODIS})^2} < 0$
11) $\theta_{\text{SOCOR+SOMP}}$	$\beta_{\text{SOCOR}} > 0, \beta_{\text{SOMP}} > 0$	$\beta_{\text{ln(SOCOR)}} > 0, \beta_{\text{ln(SOMP)}} > 0$	$\beta_{\text{SOCOR}} > 0, \beta_{(\text{SOCOR})^2} < 0$ $\beta_{\text{SOMP}} > 0, \beta_{(\text{SOMP})^2} < 0$
12) $\theta_{\text{SOCOR+SOEDG}}$	$\beta_{\text{SOCOR}} > 0, \beta_{\text{SOEDG}} < 0$	$\beta_{\text{ln(SOCOR)}} > 0, \beta_{\text{ln(SOEDG)}} < 0$	$\beta_{\text{SOCOR}} > 0, \beta_{(\text{SOCOR})^2} < 0$ $\beta_{\text{SOEDG}} > 0, \beta_{(\text{SOEDG})^2} < 0$
13) $\theta_{\text{SOCOR+SOMP+SOEDG}}$	$\beta_{\text{SOCOR}} > 0, \beta_{\text{SOMP}} > 0,$ $\beta_{\text{SOEDG}} < 0$	$\beta_{\text{ln(SOCOR)}} > 0, \beta_{\text{ln(SOMP)}} > 0,$ $\beta_{\text{ln(SOEDG)}} < 0$	$\beta_{\text{SOCOR}} > 0, \beta_{(\text{SOCOR})^2} < 0$ $\beta_{\text{SOMP}} > 0, \beta_{(\text{SOMP})^2} < 0$ $\beta_{\text{SOEDG}} > 0, \beta_{(\text{SOEDG})^2} < 0$

Note: Subscripted covariates represent the structure of the model, and covariates are described in Table 1.

[†] Represented as $\beta_0 + \beta_1x + (-\beta_2x^2)$.

positively affect recruitment; otherwise, covariates negatively affecting survival also should negatively affect recruitment. This prediction applied to all of the Table 2 hypothesized models for survival and recruitment.

Habitat models.—We developed 13 base hypothesized models to examine the effects of the 10 covariates on Northern Spotted Owl survival and reproduction (Table 3). The response variable (θ) was either apparent survival or reproductive output, and the independent variables were combinations of the nine habitat covariates, age, and elevation effects. These models were centered around three basic themes: habitat amounts only, distribution of habitat patches, and shape of habitat patches (i.e., edge effects). In addition, there were two general effects, which we felt could influence all of the base hypothesized models. The first was age: we predicted that 1–2 yr old owls would have lower apparent survival and lower reproductive output than owls ≥ 3 yr old. Based on a limited sample, Carey et al. (1992) found that radio-tagged 1-yr-old Northern Spotted Owls suffered high mortality in highly fragmented landscapes. Therefore, the initial age effect in survival analyses included a 1-yr-old class vs. a class with owls ≥ 2 yr old (denoted as a_2 in models; Table 1). Franklin et al. (1996b) found that 1- and 2-yr-old owls fledged fewer young, on average, than did owls ≥ 3 yr old on this study area. Therefore, the initial age effect in reproductive output analyses included a class

with 1- and 2-yr old owls vs. a class with owls ≥ 3 yr old (denoted as a_2' in models). During modeling procedures, we also examined the age effect by separating owls into 1-, 2-, and ≥ 3 -yr-old classes (denoted as a_3 ; see Table 1). The second general effect was ELEV: we predicted that both survival and reproductive output would be negatively affected as elevation increased, because of harsher climatic conditions at higher elevations, and a shift from Douglas-fir/hardwood forests at lower elevations to more pure fir stands at higher elevations, which were less productive in terms of prey biomass (Carey et al. 1992).

Alternate forms (Eqs. 9, 10, and 13) of the same model represented alternate hypotheses as to whether the Northern Spotted Owl is primarily an interior, edge, or mixed interior–edge species. For example, a life history trait positively associated with SOCOR and negatively associated with SOEDG in a linear or pseudothreshold relationship suggests an interior species; the opposite trend would indicate an edge species; and a quadratic relationship would indicate a mixed interior–edge species.

Model 1 in Table 3 was based on the hypothesis that survival and reproductive output increase as the amount of spotted owl habitat increases, as suggested by Bart and Earnst (1992) and Bart and Forsman (1992). The quadratic form of this model suggested some optimal amount of vegetation type (such as mature and old-growth forest) that promotes high survival

or reproductive output, with too much or too little of the vegetation type being suboptimal. Hypothesized models 2–5 incorporated patch dynamics in which a single large patch promotes higher survival or reproductive output than do many small, distantly spaced patches under the linear and pseudothreshold forms, and some optimal maximum under the quadratic forms. Hypothesized models 6–13 incorporated amounts of habitat, patch distribution, and patch shape to varying degrees, and included the possibility of alternate hypotheses concerning the juxtaposition of edge and interior spotted owl habitats and their distribution within the territory.

Estimation of life history traits

Modeling survival.—Capture–recapture models were used to estimate conditional survival probabilities (ϕ) for Northern Spotted Owls from the banding data (Franklin et al. 1996a). Capture–recapture estimates of juvenile survival (probability of fledged young surviving their first year) are not considered here because of likely biases due to permanent emigration from study areas (Franklin et al. 1996b). Instead, recruitment was estimated with the climate covariates (see *Modeling recruitment*).

We examined capture–recapture data for goodness-of-fit to a global model, using tests in program RELEASE (Burnham et al. 1987:71–77). Goodness-of-fit for reduced models was assessed by computing likelihood ratio tests between global and reduced models, and then adding the χ^2 values and degrees of freedom from these tests to global model values (Lebreton et al. 1992). The requisite assumptions of capture–recapture models are outlined in Burnham et al. (1987), most of which can be tested in program RELEASE. No loss of bands was observed through double banding of owls with both color and U.S. Fish and Wildlife Service (USFWS) bands. Permanent emigration probably was negligible for owls ≥ 1 yr old (Franklin et al. 1996b). We used program MARK (White and Burnham 1999) for analysis of capture–recapture data. We used 95% confidence intervals to assess the degree to which the signs of estimated slope parameters (β_i) in models were reliably estimated (Graybill and Iyer 1994).

In climate models, estimates of ϕ represent apparent survival, defined as the probability that an owl survives and remains within the study area to year $t + 1$, given that it was alive at the start of year t . Recapture probabilities (p) must also be modeled and are the probability that an animal alive in year t is captured in year t . Recapture probabilities are nuisance parameters, but must be properly treated; otherwise, estimators of survival probabilities will be biased or imprecise (Lebreton et al. 1992). Parameter estimation was based on Fisher's method of maximum likelihood (Lebreton et al. 1992). Relationships of estimated survival probabilities to climatic covariates were modeled using the logit transformation, which constrains $0 \leq \theta \leq 1$, where

θ represents either ϕ or p (Lebreton et al. 1992). These parameters could then be modeled as a linear logistic function, e.g., $\text{logit}(\theta_w) = \beta_0 + \beta_1(w)$, where w is a categorical (e.g., age class) or a continuous (e.g., precipitation) covariate. In addition to climate covariates, we included age (a), sex (s), and time effects in the models. Time was modeled both as a categorical (t) and linear ($1t$) effect without any climate covariates. In addition to modeling the same effects on p , we also modeled the structure of p constrained by different capture methods used during the study, denoted as p_c . During 1985–1987, birds were physically recaptured each year to read their USFWS bands, whereas from 1988 through 1994, owls were primarily resighted using color bands. Models with p_c represented a single estimate of p for 1986–1987 and a single estimate of p for 1988–1994.

In climate models, precipitation was denoted as P and temperature degree-hours as T . Life history periods were denoted with subscripts; W for the winter stress period, E for the early nesting period, L for the late nesting period, H for the heat stress period, and D for the dispersal period. This notation was also used for models of recruitment and reproductive output.

In terms of habitat covariates, we estimated apparent survival (ϕ), defined as the probability that an owl on territory i survives and remains on territory i to year $t + 1$, given that it was alive at the start of year t . We used the same capture history matrix used with the climate models, except for two adjustments. These adjustments were necessary because we examined effects on individuals rather than on annual cohorts of individuals (as with the climate models). First, “losses on capture” (Jolly 1965) were used to account for movements of individuals between territories. For example, a capture history for individual 1 that occupied territory A for the first five years and territory B for the second five years might appear as follows:

Capture occasion:	1	2	3	4	5	6	7	8	9	10	Frequency
Territory:	A	A	A	A	A	B	B	B	B	B	
Capture history:	1	1	1	0	1	1	1	1	0	1	1

where frequency is the number of capture histories. However, using “losses on capture,” the capture history for this individual was rewritten as two capture histories, one for territory A and one for territory B:

Capture occasion:	1	2	3	4	5	6	7	8	9	10	Frequency
Territory:	A	A	A	A	A	B	B	B	B	B	
Capture history 1:	1	1	1	0	1	0	0	0	0	0	–1
Capture history 2:	0	0	0	0	0	1	1	1	0	1	1

Second, territories in which timber harvest had occurred during the study were considered to be a movement from the pre-harvest territory to the post-harvest territory after the year when harvest had occurred. Capture histories on these territories were dealt with in the same manner, using “losses on capture” as movements

of individuals between territories. Use of losses on capture resulted in the loss of information on survival between the occasions when movements or timber harvest occurred. However, in losing this information, no assumption was required as to which territory affected survival during these intervening periods. For each individual capture history, we attached landscape covariates associated with the territory occupied by that individual. Thus, the sampling unit to which inferences were made was individuals on territories.

Modeling reproductive output.—In counting the number of fledged young within each year, we assumed detection probabilities of fledged young equal to 1.0 after two visits to a site. There are numerous biases that may affect estimation of reproductive output (see Franklin et al. 1996a). As long as biases were unaffected by climate and did not vary from year to year, our estimates of reproductive output provided a reasonable approximation as a basis for examining temporal effects.

Data analysis for climate models was performed on mean annual reproductive output, R_t ($t = 1, 2, \dots, 10$ yr), which was defined as the mean annual number of young fledged per pair and which was estimated from the number of owl pairs assessed for reproductive output each year ($n = 38\text{--}74$). To examine the effects of climate covariates, we used linear regression models with expected annual reproductive output (R) as the response. The use of linear regression assumed normally distributed subpopulations within years and similar subpopulation variances across years (Graybill and Iyer 1994:110). Our data probably met the first assumption because means, in general, are normally distributed under the Central Limit Theorem, regardless of the underlying distribution (Johnson 1995). The second assumption could not be met. Annual sampling variances were proportional to their means, but were not distributed as Poisson ($P < 0.01$) because fewer broods of one young were observed relative to broods of zero and two young. To deal properly with the lack of homogeneity of variances in estimating $\sigma_{\text{residual}}^2$, we used a maximum likelihood equivalent of least squares regression (Sakamoto et al. 1986:181), which accounted for separate variance components. The generalized linear model we used was $\hat{R}_i = \mathbf{X}\boldsymbol{\beta} + \varepsilon_i + \gamma_i$, where \mathbf{X} was the design matrix, $\boldsymbol{\beta}$ was the vector of parameters, $\varepsilon_i \sim \mathcal{N}(0, \sigma_{\text{residual}}^2)$ that incorporated residual variation unexplained by the model, and $\gamma_i \sim \mathcal{N}(0, \text{var}(\hat{R}_i | R_i))$ that incorporated sampling variation around the R_i . Solution of this model was expressed as the likelihood to be maximized (McCullagh and Nelder 1989:24, 254):

$$\begin{aligned} \ln \mathcal{L}(\boldsymbol{\beta}, \sigma_{\text{residual}}^2) &= -\frac{1}{2} \ln |\mathbf{D}| \\ &\quad - \frac{1}{2} \mathbf{Y}' [\mathbf{D}^{-1} - (\mathbf{D}^{-1} \mathbf{X})(\mathbf{X}' \mathbf{D}^{-1} \mathbf{X})^{-1} (\mathbf{D}^{-1} \mathbf{X})'] \mathbf{Y} \quad (14) \end{aligned}$$

where \mathbf{D} was the dispersion matrix with $\sigma_{\text{residual}}^2 + \widehat{\text{var}}(\hat{R}_i | R_i)$ as the diagonal elements and $\sigma_{\text{residual}}^2 + \widehat{\text{covar}}(\hat{R}_i, \hat{R}_j | R_i, R_j)$ as the off-diagonal elements, and $|\mathbf{D}|$ was the determinant of \mathbf{D} . Eq. 14 was solved numerically for $\sigma_{\text{residual}}^2$ at the maximum log likelihood, which was equivalent to minimizing the sum of the squared ε_i under least squares estimation procedures (Draper and Smith 1981:88). The β_i were estimated as $\hat{\boldsymbol{\beta}} = \mathbf{X}' \mathbf{D}^{-1} \mathbf{X})^{-1} \mathbf{X}' \mathbf{D}^{-1} \mathbf{Y}$, with the corresponding variance-covariance matrix as $\hat{\mathbf{V}} = (\mathbf{X}' \mathbf{D}^{-1} \mathbf{X})^{-1}$. This procedure was a regression model that included random measurement error and allowed for direct estimation of $\sigma_{\text{residual}}^2$.

In addition to the climate covariates included in the hypothesized reproduction models (Table 2), we included age and sex effects in models as the proportion of the pairs checked each year that had males (m) and females (f) ≥ 3 yr old. We evaluated the goodness-of-fit of models to the data, based on deviance estimates and examination of residual plots. Deviance was estimated as $2(\ln \mathcal{L}_{\text{max}} - \ln \mathcal{L}_{\text{model}})$, where $\ln \mathcal{L}_{\text{max}}$ is the maximum achievable log likelihood, given the data, and $\ln \mathcal{L}_{\text{model}}$ is the log likelihood for the model of interest (McCullagh and Nelder 1989:33). We used deviance to test whether a given model adequately fits the data relative to the saturated model (in which the number of parameters equals the number of data points), which is asymptotically distributed as χ^2 with $n - K$ degrees of freedom. We also visually examined plots of standardized residuals against time, the predictors, and \hat{R} for indications of lack of normality or heteroscedasticity (Graybill and Iyer 1994:251).

To examine the effects of landscape habitat covariates, we estimated reproductive output (mean annual number of young fledged per territory, again denoted as R) using general linear mixed models. Mixed models were used to appropriately estimate the standard error of the sex, age, and landscape covariates that were considered fixed effects. Territory was considered a random effect, such that standard errors of the fixed effects were estimated using the number of territories ($n = 95$) rather than the total number of reproductive outcomes occurring over all territories ($n = 598$). In addition, mixed models allowed for direct estimation of variance components, notably the spatial process variation in reproductive output among owl territories. Ideally, territories should have been randomly sampled from a larger population in order to be considered random effects, but they were not. However, the focus of the analysis was on habitat effects, where the territories acted as blocks, and not on territory effects. Therefore, we considered territories to be a random effect, recognizing that they were not randomly drawn from a larger population.

The form of the general linear mixed model we used was

$$\mathbf{Y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e} \quad (15)$$

where \mathbf{Y} is an n -vector of observed reproductive output over t years and s territories; \mathbf{X} was an n by p known design matrix representing p effects; $\boldsymbol{\beta}$ was a p -vector of unknown fixed-effect regression parameters; \mathbf{Z} was an n by q known design matrix for the random-effects portion of the model; \mathbf{u} was the q -vector of unknown random coefficient parameters; and \mathbf{e} was the n -vector of random (often measurement) errors whose elements were not required to be independent (Wolfinger 1993, Littell et al. 1996). The variance of y is $\sigma_{\text{spatial}}^2 + \sigma_{\epsilon}^2$, where $\sigma_{\text{spatial}}^2$ is the spatial process variance component among spotted owl territories, and σ_{ϵ}^2 is the variance due to random errors. The covariance matrix of \mathbf{Y} is denoted as: $\mathbf{V}(\mathbf{Y}) = \mathbf{Z}\mathbf{G}\mathbf{Z}' + \mathbf{E}$, where \mathbf{G} is the diagonal matrix containing variance components (i.e., $\sigma_{\text{spatial}}^2$), and \mathbf{E} contains the error variances, i.e., σ_{ϵ}^2 (Jennrich and Schluchter 1986, Wolfinger 1993). The random variable \mathbf{u} and error vector \mathbf{e} are assumed to be distributed as multivariate normal with a mean vector of zero and covariance matrix \mathbf{E} . Thus, \mathbf{Y} is assumed to be distributed as multivariate normal with mean $\mathbf{X}\boldsymbol{\beta}$ and variance $\mathbf{Z}\mathbf{G}\mathbf{Z}' + \mathbf{E}$. Several lines of evidence support the use of a normal-based approach in analyzing these data. ANOVA methods are robust to fairly severe departures from normality and heterogeneity in sampling variances, even with data distributed as a negative binomial (Mitchell 1977, White and Bennetts 1996). Although Poisson regression in a generalized linear model may adequately deal with overdispersion in count data, such as that used in estimating reproductive output, ANOVA is more robust to considerable departures from non-normality and heterogeneity of sampling variances than is Poisson regression when count data are not distributed as Poisson (White and Bennetts 1996).

The error variance matrix \mathbf{E} can be structured to account for heterogeneous sampling variance structures using maximum likelihood approaches (Littell et al. 1996), which are analogous to a weighted regression (Draper and Smith 1981:108). Thus, the problem of heterogeneous sampling variances discussed previously can be dealt with adequately. We used a maximum likelihood-based approach in PROC MIXED of program SAS (SAS Institute 1997) to model first the covariance structure of \mathbf{E} and then to examine the fixed effects in the hypothesized models and their variants. Following Diggle (1988) and Wolfinger (1993), we used restricted maximum likelihood estimation in an over-fitted model that included all of the fixed effects to explore various covariance structures in \mathbf{E} to model annual sampling variances. Selection of an appropriate covariance structure was based on AICc (see *Model selection*) using the number of estimated covariance parameters, but not the number of estimated fixed effects, because restricted maximum likelihood estimation is based solely on the covariance parameters. Once an appropriate covariance structure was achieved for properly weighting the years, full maximum likelihood

estimation, rather than restricted maximum likelihood estimation, was used as the basis for examining hypothesized models because the latter eliminates the fixed effects (Wolfinger 1993).

We modified the data slightly to estimate reproductive output with the landscape habitat covariates. First, we excluded eight Northern Spotted Owl territories in which reproductive output had not been adequately estimated for at least three years. This reduced the number of territories included in the analysis to 87. In addition, we included only reproductive outcomes in which the female age was known (to allow for adequate modeling of female age effects). Female age has a strong effect on reproductive output (Franklin et al. 1996b), whereas male age seems to have little effect (Franklin 1992). Thus, reproductive output was redefined as the mean annual number of young fledged per female of known age.

Modeling recruitment.—Recruitment is a function of survival of young through their first year, reproductive output, and immigration. Immigration in Northern Spotted Owls may be from interterritorial movements or from a surplus population of nonterritorial birds, i.e., floaters (Franklin 1992). Spotted owls are highly territorial and tend to exhibit high site and mate fidelity (Forsman et al. 1984, Gutiérrez et al. 1995), suggesting that spacing behavior may limit the number of individuals that are able to breed. Thus, recruitment is an important parameter because it represents the successful integration of young into the breeding population, even when that entry is delayed by several years (young may enter a floating, surplus population before attaining a territory; Franklin 1992). Recent developments in capture–recapture theory (e.g., Schwarz and Arnason 1996) allowed recruitment to be modeled using the approach previously outlined.

Recruitment was estimated from a subset of the capture–recapture data using modeling procedures in program POPAN-4 (Arnason et al. 1995). This subset included data from the Willow Creek study area and 12 sites from satellite areas that had been consistently surveyed since 1985. Recruitment was modeled with the climate covariates under a framework similar to that for survival probabilities, with some exceptions. In the most general model under POPAN-4, maximum likelihood estimates are computed simultaneously for ϕ , p , and two new parameters: ψ , the fraction of total net births that enter the system between t and $t + 1$ (called entry probabilities), and N_{tot} , the total number of animals that enter the system and survive until the next sample time (Schwarz and Arnason 1996) during the 10-yr study period. Population size, N , is then estimated from these parameters. Parameter estimates of ϕ , p , and ψ can be constrained by external covariates. Model selection procedures followed those described in *Modeling survival*. However, POPAN-4 does not allow the inclusion of group effects, such as sex, so we

were unable to estimate recruitment separately for males and females.

In all recruitment models, ϕ and p were structured based on the best climate model selected from the survival analysis. Hypothesized models were first analyzed in terms of ψ . After selection of the “best” model in terms of ψ , we estimated recruitment rate (b) as

$$\hat{b}_t = \frac{\hat{\psi}_t \hat{N}_{\text{tot}}}{\hat{N}_{t-1}} \quad (16)$$

where \hat{N}_{t-1} was the estimated territorial population size from the previous year, and $\hat{\psi}_t \hat{N}_{\text{tot}}$ represented the number of new recruits into the territorial population at time t . Thus, b was the number of new recruits in the territorial population at time $t + 1$ per territory holder in time t . The variance–covariance matrix for \hat{b} was estimated using the delta method (Bajpai et al. 1978: 146). The estimates of b and their sampling variance–covariance matrix were used in Eq. 14 with the climatic covariates from the selected model to obtain regression coefficients, and their standard errors, in terms of b rather than ψ .

Selection of hypothesized models for life history traits

The most critical problem in analyzing empirical data is selecting an appropriate model that is supported by the science of the situation, by the data, and that has enough parameters to avoid bias, but not so many that precision is lost (Burnham and Anderson 1992). We used a bias-corrected version of Akaike’s Information Criterion, AICc (Akaike 1973, Hurvich and Tsai 1989, Burnham et al. 1995) as the basis for objectively ranking models and selecting an appropriate “best approximating” model. AICc was defined as

$$\text{AICc} = -2(\ln \mathcal{L}) + 2K + \frac{2K(K+1)}{n-K-1} \quad (17)$$

where $\ln(\mathcal{L})$ is the natural logarithm of the likelihood function evaluated at the maximum likelihood estimates for a given model; K is the number of estimable parameters from that model; and n is sample size. In the capture–recapture models, n was the sum of the total number of animals captured and released in each year. The “best approximating” model for each life history trait was selected based on minimum AICc.

Models were ranked and compared using ΔAICc (Lebreton et al. 1992, Burnham and Anderson 1998) and Akaike weights (Buckland et al. 1997). ΔAICc was computed as

$$\Delta\text{AICc}_i = \text{AICc}_i - \text{AICc}_{\min} \quad (18)$$

where AICc_i was the AICc value for the i th model in a suite of models being compared, and AICc_{\min} was the minimum AICc value among those models. In short, ΔAICc_i is an estimate of the relative distance between the best approximating model and model i . Akaike weights (w_i) were computed for each i th model as follows:

$$w_i = \frac{\exp\left[-\left(\frac{\Delta\text{AICc}_i}{2}\right)\right]}{\sum \exp\left[-\left(\frac{\Delta\text{AICc}_i}{2}\right)\right]} \quad (19)$$

ΔAICc and Akaike weights were used to address model selection uncertainty. In general, models within 1–2 AICc units of the selected model were considered competing models. Because standard errors estimated for the life history traits are conditional on the selected model, there was another element of uncertainty in selecting an appropriate model when evaluating estimates of precision (Buckland et al. 1997). Therefore, estimates of precision in the parameters may have been somewhat optimistic. We were unable to account for this uncertainty due to model selection using current methods (Buckland et al. 1997), because we were interested in $\hat{\beta}_i$ and $\widehat{\text{SE}}(\hat{\beta}_i)$, which corresponded to different effects among models.

We had a number of variations that represented the specified effects of the base hypothetical models in Tables 2 and 3; of these variations on the same model, we selected the best approximating model based on minimum AICc. Thus, each hypothesized model was represented by a suite of models that included age and elevation effects, interactions between effects, and different forms (i.e., linear, pseudothreshold, and quadratic) of the covariates. We then used the model with minimum AICc from each suite to represent each of the hypothesized models. After model selection, the influence of additional effects, such as sex, on the “best” model selected was assessed by examining Akaike weights for the best approximating model, using models that included or excluded pertinent effects of interest. The utility of slope parameters (β_i) in models was assessed based on the degree to which 95% confidence intervals overlapped zero (Graybill and Iyer 1994).

We examined potential correlations between covariates after the analysis of hypothesized models to avoid subjective biases in formulation of the models. Information on correlations between covariates was then used to explore better models for the data than those initially hypothesized. Sensitivity of either $\hat{\phi}$ or \hat{R} to changes in covariates in the best approximating models was assessed by (1) setting covariate values to their mean, (2) changing the covariate of interest by 25% of its mean value, (3) estimating percentage change in $\hat{\phi}$ or \hat{R} due to the 25% change in the covariate of interest, and (4) ranking covariates based on the percentage change in $\hat{\phi}$ or \hat{R} . Sensitivities were expressed as percentage change in the parameter.

Estimation of fitness

Rates of population change.—We estimated annual rates of population change (λ) as a function of both recruitment rate and apparent survival. Population size

can be expressed in terms of the difference equation:

$$N_{t+1} = (\beta + i)N_t + (1 - d - e)N_t \quad (20)$$

where, β , d , i , and e are rates of birth, death, immigration, and emigration, respectively. Because our estimates of recruitment rate and apparent survival can be expressed as $\hat{b} = \hat{\beta} + \hat{i}$ and $\hat{\phi} = 1 - \hat{d} - \hat{e}$, Eq. 20 can be rewritten as $\hat{N}_{t+1} = \hat{b}\hat{N}_t + \hat{\phi}\hat{N}_t$. By definition, annual estimates of λ can be expressed as $\hat{\lambda}_t = \hat{N}_{t+1}/\hat{N}_t$, which can then be rewritten, in terms of recruitment rates and apparent survival, as

$$\hat{\lambda}_t = \hat{b}_t + \hat{\phi}_t \quad (21)$$

Sampling variances for $\hat{\lambda}_t$ were estimated as $\widehat{\text{var}}(\hat{\lambda}_t) = \widehat{\text{var}}(\hat{b}_t) + \widehat{\text{var}}(\hat{\phi}_t) + 2\widehat{\text{cov}}(\hat{b}_t, \hat{\phi}_t)$ (Bajpai et al. 1978).

To evaluate potential long-term consequences of climate variation on life history traits and rates of population change, we examined the behavior of climate models for each life history trait using a long-term record of climatic observations from 1955 through 1984 obtained from the same weather stations used to develop the climate models. We examined model behavior using a forecasting philosophy (what could happen, given that a particular empirical model is correct and underlying conditions remain similar) rather than as prediction (what will happen) (Caswell 1989a:20). We also used the same covariates as those used to develop the models, and that appeared in the final selected climate models. Sampling variances of estimates from before the study period were estimated using the delta method (Bajpai et al. 1978).

Habitat fitness potential.—To estimate fitness, we used the Leslie matrix approach outlined by McGraw and Caswell (1996), but with some modifications. We estimated the necessary components of fitness (survival and reproductive output) based on landscape habitat characteristics, not on individual attributes. Therefore, we defined *habitat fitness potential* (λ_H) as the fitness conferred on an individual occupying a territory of certain habitat characteristics. This definition does not imply that territories have fitness themselves, because territories with high habitat fitness potential may not always be occupied; occupancy was not included in the estimation of fitness. Rather, λ_H can be viewed as the potential fitness that an individual can achieve if it occupies a particular territory with certain habitat characteristics.

To estimate λ_H , we used the best approximating models for survival and reproductive output to estimate survival, fecundity, and their sampling variances for each of the 95 Northern Spotted Owl territories. Sampling variances were estimated using the delta method (Bajpai et al. 1978), which incorporated the covariance matrix from the best approximating model. Fecundity (the mean number of female young fledged per female) was estimated by dividing estimates of reproductive output by two; the sampling variances for fecundity

were calculated by dividing the sampling variances for reproductive output by 4 (see Franklin et al. 1996a). Because fecundity was female based, λ_H was applicable to female fitness only.

Once survival and fecundity had been estimated for each of the 95 territories, λ_H was estimated for each territory as the dominant, real eigenvalue of an estimated stage-based Leslie matrix. This matrix took the following form:

$$\begin{bmatrix} \hat{\phi}_{1,2}\hat{m}_{1,2} & \hat{\phi}_{1,2}\hat{m}_3 & \hat{\phi}_3\hat{m}_3 \\ \hat{\phi}_{1,2} & 0 & 0 \\ 0 & \hat{\phi}_{1,2} & \hat{\phi}_3 \end{bmatrix} \quad (22)$$

where $\hat{\phi}$ was apparent survival; and \hat{m} was fecundity, with subscripts “1, 2” representing parameter estimates for 1- and 2-yr-old owls, and subscript “3” representing estimates for owls >3 yr old. The form of the matrix was based on the age effects found in the best models for survival and reproductive output (see *Results*). For example, estimates of ϕ and reproductive output for territory A were obtained from the best models for survival and reproductive output, respectively, using the habitat covariates from territory A. After transforming reproductive output to fecundity, we then used these estimates in matrix 22 to estimate λ_H for territory A.

The final form of the matrix depended on the age structure in the best approximating models for survival and reproductive output. Standard errors of territory-specific estimates of λ_H were estimated using the delta method, which incorporated the standard errors for territory-specific estimates of the survival and fecundity estimates. Incorporation of age structure into the estimates of λ_H further complicated its interpretation. If age structure was incorporated into the best approximating models for either survival or reproductive output, then λ_H was based on a female first colonizing a territory as a 1- or 2-yr-old.

Components of variation analysis

We used the annual means estimated directly from the data as a basis for estimating temporal process variation ($\sigma_{\text{temporal}}^2$) in reproductive output. The capture–recapture data were initially modeled with time effects to determine whether temporal process variation existed. If a time-dependent model (ϕ_t or b_t) explained the data better than did a model with time-invariant parameters (ϕ or b), the annual estimates from that model were used to estimate $\sigma_{\text{temporal}}^2$. Temporal process variation in each of the life history parameters and rates of population change was estimated as the numerical solution of the following equation for $\sigma_{\text{temporal}}^2$ (after Burnham et al. 1987:263):

$$\left[\frac{1}{n-1} \right] [(\mathbf{P} - \hat{\theta}\mathbf{1})' \mathbf{D}(\mathbf{P} - \hat{\theta}\mathbf{1})]' = 1 \quad (23)$$

where

$$\hat{\theta} = [(\mathbf{DP})' \mathbf{1}][(\mathbf{D1})' \mathbf{1}]^{-1} \quad (24)$$

and $\mathbf{D} = (\sigma_{\text{temporal}}^2 \mathbf{I} + \mathbf{V})^{-1}$; \mathbf{P} is a vector containing the annual estimates of either ϕ , R , b , or λ ; n is the number of annual estimates; $\mathbf{1}$ is a vector of 1's; \mathbf{I} is an identity matrix; \mathbf{V} is the conditional (sampling) variance-covariance matrix for the estimates; and $\hat{\theta}$ is the weighted mean of the parameter of interest. We used the relationship for temporal variation where $\hat{\sigma}_{\text{temporal}}^2 = \hat{\sigma}_{\text{climate}}^2 + \hat{\sigma}_{\text{residual}}^2$ to estimate the amount of variation due to climate ($\sigma_{\text{climate}}^2$). Because $\sigma_{\text{residual}}^2$ was estimated when modeling reproductive output, $\sigma_{\text{climate}}^2$ was estimated as $\hat{\sigma}_{\text{temporal}}^2 - \hat{\sigma}_{\text{residual}}^2$ where $\sigma_{\text{temporal}}^2$ was estimated using Eq. 23. For survival and recruitment, the contribution of $\hat{\sigma}_{\text{climate}}^2$ in explaining $\hat{\sigma}_{\text{temporal}}^2$ was estimated by regressing annual estimates of logit(ϕ) or b , including their sampling variances and covariances, obtained from the time-dependent models (ϕ_i or b_i) against the climatic covariates included in the "best" climatic model selected for each life history trait. The form of the regression followed Eq. 14 to estimate $\sigma_{\text{residual}}^2$. The estimated amount of variation explained by the best climate model ($\sigma_{\text{climate}}^2$) could be assessed as $\hat{\sigma}_{\text{temporal}}^2 - \hat{\sigma}_{\text{residual}}^2$. Weighted means of parameters were estimated using Eq. 24.

To estimate the amount of spatial process variation ($\sigma_{\text{spatial}}^2$) in survival, we first estimated survival probabilities for each territory, using the same structure on the capture probabilities as the best approximating model. We estimated $\sigma_{\text{spatial}}^2$ using Eqs. 23 and 24. The amount of this variation explained by the best approximating model ($\hat{\sigma}_{\text{model}}^2$) was estimated as the empirical variance of the predicted estimates of $\phi(\hat{\phi}_i)$ from the following model:

$$\hat{\sigma}_{\text{model}}^2 = \frac{\sum_{i=1}^{95} (\hat{\phi}_i - \bar{\phi})^2}{n - 1} \quad (25)$$

where $n = 95$ territories. We estimated 95% confidence intervals as:

$$\frac{\sum_{i=1}^{95} (\hat{\phi}_i - \bar{\phi})^2}{\chi_{94, 0.975}^2} \leq \sigma_{\text{model}}^2 \leq \frac{\sum_{i=1}^{95} (\hat{\phi}_i - \bar{\phi})^2}{\chi_{94, 0.025}^2} \quad (26)$$

following Burnham et al. (1987:265).

In the general linear mixed model approach for estimating reproductive output, we estimated $\sigma_{\text{spatial}}^2$ using an intercepts-only ("means") model in PROC MIXED in SAS (SAS Institute 1997). This model retained the best covariance structure for \mathbf{E} (Eq. 15) used in the hypothesized model, included territories as a random effect, and used restricted maximum likelihood procedures (Wolfinger 1993). We also ran the best approximating model again, using restricted maximum likelihood procedures to obtain an estimate of the spatial process variation not accounted for by the fixed effects ($\hat{\sigma}_{\text{residual}}^2$). At this point, restricted maximum like-

hood procedures estimated variance components based on the residuals after the fixed effects had been fit to the model (Searle et al. 1992:250). Thus, the use of these two models allowed decomposition of $\hat{\sigma}_{\text{spatial}}^2$ into the component explained by the fixed-effects model ($\hat{\sigma}_{\text{model}}^2$) and the component not explained by the fixed-effects model ($\hat{\sigma}_{\text{residual}}^2$). If the best approximating model included only habitat covariates, then the amount of $\hat{\sigma}_{\text{spatial}}^2$ explained by habitat variation ($\hat{\sigma}_{\text{habitat}}^2$) equaled ($\hat{\sigma}_{\text{model}}^2$). However, if age effects were included in the best approximating model, then the amount of spatial process variation due to the age of individuals ($\hat{\sigma}_{\text{age}}^2$) was partitioned by estimating $\hat{\sigma}_{\text{residual}}^2$, using the design matrix for an age effects model and estimating $\hat{\sigma}_{\text{age}}^2$ as $\hat{\sigma}_{\text{spatial}}^2 - \hat{\sigma}_{\text{residual}}^2$. An estimate of $\hat{\sigma}_{\text{habitat}}^2$ was then found similarly, using the design matrix containing habitat covariates only from the best approximating model. Log-based 95% confidence intervals for $\hat{\sigma}_{\text{spatial}}^2$ were estimated using $\widehat{\text{SE}}(\hat{\sigma}_{\text{spatial}}^2)$ from PROC MIXED and formulas in Burnham et al. (1987:212). We directly estimated $\sigma_{\text{spatial}}^2$ for habitat fitness potential using Eqs. 22 and 23. Log-based 95% confidence intervals were also estimated for $\hat{\sigma}_{\text{spatial}}^2$ of habitat fitness potential.

Coefficients of process variation were estimated as

$$\frac{\sqrt{\hat{\sigma}_{\text{process}}^2}}{\hat{\theta}} \quad (27)$$

where $\hat{\theta}$ was the weighted mean (based on Eq. 24) of parameters of interest. Coefficients of process variation were used to estimate the degree to which parameters varied over time or space.

Relative contributions of climatic and habitat variation

We examined the importance of climatic and habitat variation by comparing models explaining variation due to climate and habitat, and by comparing components of process variation. In a model selection approach, we combined the effects in the best approximating model used to describe the effects of climate and habitat, respectively, on apparent survival and reproductive output. We used the model selection approach in the following manner to address the question of whether habitat quality buffered individuals from the extremes of climate. For each life history parameter, we analyzed models that combined the climate and habitat covariates from the best approximating models in additive models. We compared these models to ones that included all possible combinations of interactions between climate and habitat covariates. Only the full interactions between climate and habitat covariates were included. We used the notation of (climate covariates)*(habitat covariates) to indicate both main effects and their interactions.

Models with interactions between climate and habitat

suggest that habitat might buffer or intensify the effects of climate on individuals, depending on the sign of the slope parameter for the interaction. AICc and Akaike weights were used to determine whether an additive model (one indicating that habitat quality did not buffer climate effects) or a model with interactions (one indicating that habitat quality buffered climate effects) was the best approximating model for the data. In models examining effects on reproductive output, year was considered a fixed effect. Model selection was based on comparisons of AICc and Akaike weights computed for each model. If either of the models containing the climate or habitat covariates alone was strongly selected as the best approximating model, then this suggested that either climatic variation or habitat variation alone was responsible for variation in the life history trait being examined. However, if the model containing both sets of covariates was selected as the best approximating model, this suggested that both climate and habitat were important in influencing process variation of life history traits. This approach examined the relative importance of climate and habitat effects on survival and reproductive output.

In order to estimate the magnitude of the effects of climate and habitat on variation of survival and reproductive output, we used a components of process variation approach. We compared the estimates of the components of process variation separately for survival and reproductive output. The total process variation examined in this study for each life history trait (σ_{total}^2) can be expressed as

$$\sigma_{\text{total}}^2 = \sigma_{\text{temporal}}^2 + \sigma_{\text{spatial}}^2 = \sigma_{\text{model}}^2 + \sigma_{\text{residual}}^2 \quad (28)$$

where $\sigma_{\text{temporal}}^2$ and $\sigma_{\text{spatial}}^2$ are the estimates of total temporal and spatial process variation, respectively; σ_{model}^2 is the amount of process variation explained by both the models relating the life history trait to climate, habitat, and other effects; and $\sigma_{\text{residual}}^2$ is the amount of process variation unexplained by any of the modeled effects. The estimate of σ_{model}^2 can be further partitioned into

$$\sigma_{\text{model}}^2 = \sigma_{\text{climate}}^2 + \sigma_{\text{habitat}}^2 + \sigma_{\text{other}}^2 \quad (29)$$

where $\sigma_{\text{climate}}^2$ was estimated based on the best approximating model containing climate covariates; $\sigma_{\text{habitat}}^2$ was estimated from the best approximating model containing landscape habitat covariates; and σ_{other}^2 was any other effects, such as age or sex, that were included in the final models. The proportion of σ_{model}^2 accounted for by climate, habitat, or other effects can then be expressed as

$$\frac{\sigma_x^2}{\sigma_{\text{model}}^2} \quad (30)$$

where x is climate, habitat, or other. In this way, we estimated the relative contributions of climate, habitat, and other effects to total process variation.

RESULTS

Effects of climate on temporal variation in population processes

Survival probabilities.—From 1985 through 1994, we marked 57 1-yr-old, 45 2-yr-old, and 206 ≥ 3 -yr-old Northern Spotted Owls; these were roughly equal by sex (150 females and 158 males ≥ 1 yr old). A global model $\{\phi_{s \times a \times t}, p_{s \times a \times t}\}$ allowing survival and recapture probabilities to vary over time by sex (s) and age classes (a) with all interactions was found to adequately fit the data ($\chi^2 = 50.02$, $df = 79$, $P = 0.99$). No overdispersion was evident in the data ($\chi_{\text{good}}^2/df = 0.633$).

Before modeling with the climatic covariates, we first examined the capture–recapture data for significant time variation, in addition to sex and age class effects, and the interactions between those effects on ϕ and p . These models ranged from the global model with 84 parameters to the simplest model $\{\phi, p\}$ with only two parameters. Intermediate models included various combinations of pooled age classes with and without sex and time effects. Based on minimum AICc, model $\{\phi, p_{s+c}\}$ was selected as the best approximating model ($K = 12$ parameters), given only the sex, age, and time effects examined. This model indicated that survival probabilities varied over time, with no sex or age effects, and that recapture probabilities were best structured based on differences in recapture methods during the study that varied by sex. The next four time-only models ranked by AICc ($\Delta\text{AICc} = 0.461$ – 1.667) also included a year-dependent (t) structure in ϕ and included p_c .

We then examined the eight hypothesized climatic models (Table 2) in addition to 79 climatic models representing variations on the hypothesized models (e.g., quadratic structure on ϕ , different structures on p). Of these models, $\{\phi_{P_E+T_E}, p_{s+c}\}$ was selected as the best approximating model based on AICc (Table 4), where the annual estimates of P_E and T_E explained time variation better than just the time model $\{\phi_t, p_{s+c}\}$. The data did not support inclusion of sex effects or a quadratic term in the selected model to simulate the negative effects of drought (Table 5). Model $\{\phi_{P_E+T_E}, p_{s+c}\}$ still exhibited adequate goodness-of-fit to the capture–recapture data ($\chi^2 = 125.63$, $df = 157$, $P = 0.97$). Therefore, we retained $\{\phi_{P_E+T_E}, p_{s+c}\}$ as the most parsimonious explanation of survival in spotted owls ≥ 1 yr old. This model was a better explanation of the data than those based on variable or linear time models (Table 4). Model $\{\phi_{P_E+T_E}, p_{s+c}\}$ explained variation in survival as

$$\hat{\phi} = \frac{1}{1 + \exp[-(0.11164 - 0.06753P_E + 0.01035T_E)]} \quad (31)$$

where $\widehat{\text{SE}}(\hat{\beta}_0) = 1.0844$; $\widehat{\text{SE}}(\hat{\beta}_1) = 0.0346$ (95% CI = $-0.1353, 0.0003$); and $\widehat{\text{SE}}(\hat{\beta}_2) = 0.0038$ (95% CI = $0.0029, 0.0178$). Confidence intervals for both slope pa-

TABLE 4. Ranking of a priori hypothesized models relating climate covariates to apparent survival probabilities (owls ≥ 1 yr old), reproductive output, and recruitment for Northern Spotted Owls in northwestern California.

Model	Hypothesis [†]	K_{\ddagger}^{\dagger}	AICc	ΔAICc_i	w_i
Apparent survival models (all models with p_{s+c})					
$\phi_{P_E+T_E}$	3	6	1293.93	0.00	0.426
$\phi_{P_W+P_E}$	4	6	1294.19	0.27	0.373
$\phi_{P_W+T_W+P_E+T_E}$	6	8	1296.73	2.81	0.105
$\phi_{P_W+T_E}$	5	6	1298.15	4.22	0.052
$\phi_{P'_W+T'_E}$	8	6	1299.33	5.40	0.029
$\phi_{P_W+P'_W+T_W+P_E+P'_E+T_E}$	7	10	1300.80	6.88	0.014
ϕ_H	1	5	1303.72	9.80	0.003
$\phi_{P_W+T_W}$	2	6	1303.99	10.07	0.003
Reproductive output models					
$R_{P_L^2}$	2	3	-28.62	0.00	0.971
$R_{P_L+T_L}$	6	4	-21.19	7.42	0.024
$R_{P_E+P_L}$	3	4	-17.59	11.02	0.004
R_{P_E}	1	3	-14.99	13.63	0.001
$R_{P_W+T_W}$	4	4	-12.04	16.58	0.000
$R_{P_E+T_E}$	5	4	-9.16	19.46	0.000
$R_{P_W+T_L}$	10	4	-8.74	19.88	0.000
$R_{P_W+T_E}$	9	4	-8.01	20.61	0.000
$R_{P_W+T_E+T_L}$	11	5	0.26	28.88	0.000
$R_{P_E+T_E+P_L+T_L}$	7	6	2.04	30.65	0.000
$R_{P_W+T_W+P_E+T_E}$	8	6	11.69	40.31	0.000
Recruitment models (all models include $\phi_{P_E+T_E}, p_c$)					
$\psi_{P'_W+P'_E}$	ϕ_4	9	965.99	0.00	0.498
$\psi_{P_W+T_W+P_E+T_E}$	ϕ_6	11	967.11	1.11	0.286
$\psi_{P_D+P_W+P_E}$	4	10	968.51	2.51	0.142
$\psi_{P_D+T_D+P_W}$	5	10	972.18	6.18	0.023
$\psi_{P_D+P_W}$	2	9	972.64	6.65	0.018
$\psi_{P_W+T_W}$	ϕ_2	9	972.84	6.84	0.016
$\psi_{P_D+T_D+P_W+T_W}$	6	11	974.11	8.11	0.009
$\psi_{P_D+T_D}$	3	9	976.48	10.48	0.003
ψ_{P_E}	R1	8	976.90	10.90	0.002
$\psi_{P'_L}$	R2	8	977.68	11.68	0.001
ψ_{P_D}	1	8	977.80	11.80	0.001

Note: Ranking is based on AICc values; W_i values are Akaike weights.

[†] Numbers correspond to those in Table 2; ϕ indicates an a priori climate model proposed for survival probabilities; R indicates a model proposed for reproductive output (see Table 2).

[‡] Number of estimable parameters.

rameters suggested that the effects were real. Recapture probabilities were high, with $\hat{p} = 0.723$ ($\widehat{SE}(\hat{p}) = 0.050$) and 0.797 ($\widehat{SE}(\hat{p}) = 0.058$) for females and males in 1986–1987, respectively, and $\hat{p} = 0.912$ ($\widehat{SE}(\hat{p}) = 0.018$) and 0.940 ($\widehat{SE}(\hat{p}) = 0.022$) for females and males in 1988–1994, respectively. Under $\{\phi_{P_E+T_E}, p_{s+c}\}$, annual survival was negatively affected by increased precipitation (P) and positively affected by increased temperature (T) during the early nesting period (E). Thus, cold, wet springs had a negative effect on survival, whereas warm, dry springs had a positive effect (Fig. 4a). Changes in apparent survival predicted from Eq. 31 were most sensitive to changes in T_E (17.8% change in $\hat{\phi}$) followed by changes in P_E (4.5% change in $\hat{\phi}$). The model selected accounted for a substantial amount of the temporal process variation in survival probabilities (Table 6). However, the coefficient of temporal variation based on $\hat{\sigma}_{\text{temporal}}^2$ was relatively small, suggesting that temporal process variation in annual survival probabilities was low (Table 6).

One model, $\{\phi_{P_W+P_E}, p_{s+c}\}$, was weighed almost equally with $\{\phi_{P_E+T_E}, p_{s+c}\}$ and was considered a potential competitor to this model (Table 4), representing another possible explanation for survival that was still negatively affected by increased precipitation in the early nesting period, but positively affected by increased precipitation during the winter. The covariates P_E and P_W were not highly correlated ($r = 0.29$), which suggested that model $\{\phi_{P_W+P_E}, p_{s+c}\}$ was not competitive because of colinearity between P_E and P_W . However, inclusion of the covariate P_W in model $\{\phi_{P_E+T_E}, p_{s+c}\}$ (e.g., as $\{\phi_{P_W+P_E+T_E}, p_{s+c}\}$) was not well supported (Table 5). Therefore, we retained the selected model $\{\phi_{P_E+T_E}, p_{s+c}\}$ in analyses of population rates of change, but suspected that model $\{\phi_{P_W+P_E}, p_{s+c}\}$ may be important in future analyses when more data have been collected, or in other data sets.

Reproductive output.—Annual estimates of R varied from 0.150 to 0.810 (Fig. 4b). Estimation of R did not require the intermediate modeling process used with

TABLE 5. Ranking of the best approximating models for apparent survival, reproductive output, and recruitment for Northern Spotted Owls in northwestern California, relative to models in which specific effects were included, excluded, or changed.

Model	Change in best approximating model	AICc	ΔAICc_i	w_i
Apparent survival (ϕ)				
$\phi_{P_E+T_E, P_{S+c}}$	Best model (no change)	1293.93	0.00	0.291
$\phi_{P_E+T_E, P_c}$	Exclusion of sex in p	1294.60	0.68	0.207
$\phi_{P_W+P_E+T_E, P_{S+c}}$	Inclusion of p_W in ϕ	1294.89	0.96	0.180
$\phi_{P_E+P_E^2+T_E, P_{S+c}}$	Additional quadratic term for P_E in ϕ	1295.93	2.00	0.107
$\phi_{S+P_E+T_E, P_{S+c}}$	Inclusion of sex on ϕ	1295.94	2.01	0.106
$\phi_{T_E, P_{S+c}}$	Exclusion of P_E in ϕ	1296.14	2.21	0.096
$\phi_{P_E, P_{S+c}}$	Exclusion of T_E in ϕ	1300.38	6.45	0.012
$\phi_{t, P_{S+c}}$	Random time	1304.66	10.74	0.001
$\phi_{\cdot, P_{S+c}}$	No effects (means model)	1306.89	12.97	0.000
$\phi_{lt, P_{S+c}}$	Linear effect on time	1308.68	14.76	0.000
$\phi_{a2+t, P_{S+c}}$	Inclusion of age (1–2 vs. \geq 3-yr-old)	1310.55	16.62	0.000
$\phi_{a2'+t, P_{S+c}}$	Inclusion of age (1- vs. $>$ 2-yr-old)	1313.37	19.45	0.000
Reproductive output (R)				
$R_{P_L^2}$	Best model (no change)	-28.62	0.00	0.638
$R_{P_L^2+m}$	Inclusion of male age	-26.05	2.57	0.177
$R_{P_L^2+f}$	Additional quadratic term for P_L	-25.31	3.31	0.122
$R_{P_L^2}$	Inclusion of female age	-22.68	5.94	0.033
R_{P_L}	Exclusion of quadratic effect	-22.35	6.27	0.028
R_{\cdot}	No effects (means model)	-17.14	11.48	0.002
R_{lt}	Linear effect on time	-14.18	14.44	0.000
Recruitment models (ψ)				
All models include $\phi_{P_E+T_E, P_c}$				
$\psi_{P_W+P_E^2}$	Best model (no change)	965.99	0.00	0.355
$\psi_{P_W+P_E}$	No quadratic effect	966.42	0.42	0.288
$\psi_{P_W+P_W^2+P_E+P_E^2}$	Additional quadratic terms for P_W and P_E	967.11	1.11	0.204
ψ_{t, P_E}	Random time	968.51	2.51	0.101
ψ_{\cdot, P_E}	No effects (means model)	972.18	6.18	0.016
ψ_{lt, P_E}	Linear effect on time	972.64	6.65	0.013

Note: Ranking is based on AICc values; w_i values are Akaike weights.

the capture–recapture data. Therefore, resulting estimates were used directly in the components of variance analysis. We examined the 11 hypothesized climate models (Table 2) in addition to 56 intermediate models that included the age and sex covariate (m and f) and different nonlinear structures of the climatic covariates. Of the models examined, model $\{R_{P_L^2}\}$ had the lowest AICc (Table 4) and was selected as the best approximating model given the data. We were unable to compare other models with model $\{R_t\}$ using AICc because model $\{R_t\}$ was saturated (i.e., $K = n$). The form of model $\{R_{P_L^2}\}$ was

$$\hat{R} = 0.8394 - 0.0030 (P_L)^2 \quad (32)$$

where R was mean annual reproductive output and P_L was the number of days of measurable precipitation during the late nesting period. The goodness-of-fit test based on deviance indicated no evidence for lack of fit of the data to the model selected ($\chi^2 = 6.051$, $df = 7$, $P = 0.534$). Examination of residual plots did not suggest any violation of the key assumptions in linear regression. Therefore, model $\{R_{P_L^2}\}$ was considered an appropriate model for relating mean annual reproductive output with climatic variation in the linear modeling framework. Parameter estimates were precise for

this model, with $\widehat{SE}(\hat{\beta}_0) = 0.0538$ and $\widehat{SE}(\hat{\beta}_1) = 0.0004$ (95% CI = $-0.0040, -0.0021$). Confidence intervals for $\hat{\beta}_1$ did not overlap zero, supporting a negative trend in reproductive output with respect to precipitation during the late nesting period.

Model $\{R_{P_L^2}\}$ represented hypothesized model 2 (Table 2), which predicted a negative relationship between reproductive output and precipitation during the late nesting period. The quadratic effect in this, and in model $\{R_{P_L+P_L^2}\}$, was not indicative of a drought effect, as proposed in some of the models. Rather, it appeared to describe more of a plateau effect in reproductive output at lower levels of precipitation (Fig. 4b). The one extreme point in Fig. 4b was not considered an outlier, but a real event that represented a region-wide reduction in reproductive output throughout the range of the Northern Spotted Owl (see Burnham et al. 1996). In not including the P_L term in the quadratic, model $\{R_{P_L^2}\}$ restricts maximum reproductive output at zero number of days of precipitation. However, lack of this term in the selected model suggests that this was an appropriate restriction (Table 5). Based on Akaike weights, the selected model was heavily weighted (Table 4), suggesting that the other hypothesized models were not competitive with the selected model. Inter-

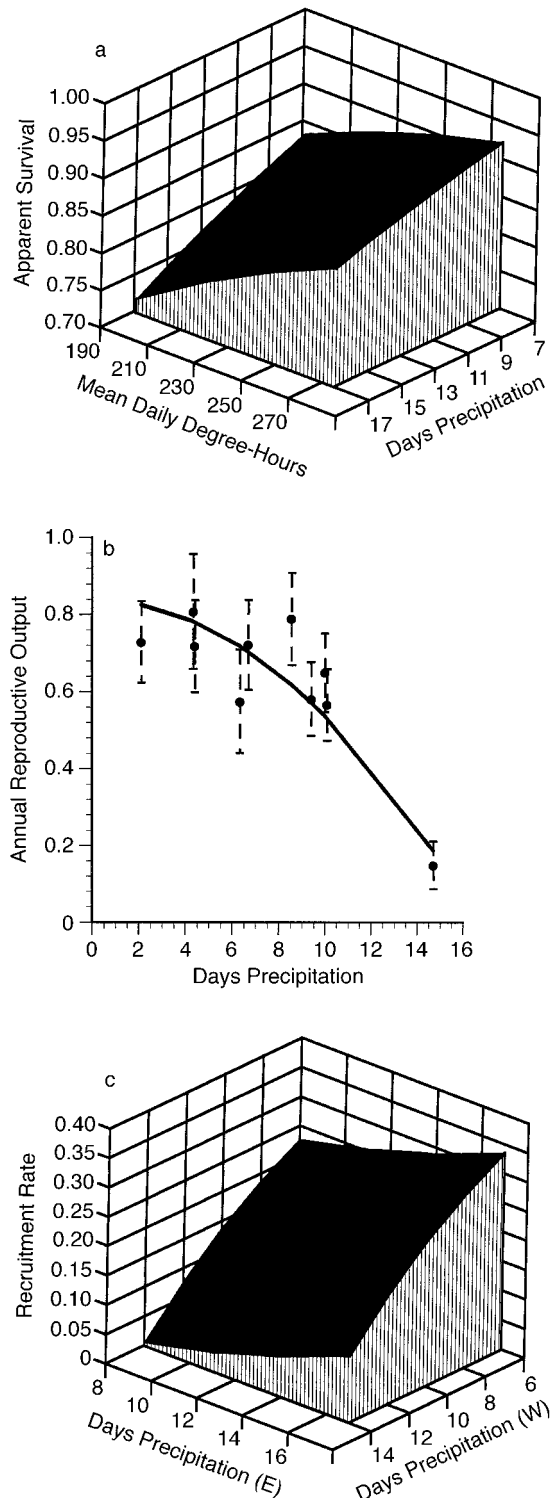


FIG. 4. Predicted values of (a) apparent survival of Northern Spotted Owls ≥ 1 yr old in relation to precipitation and temperature in the early nesting period; (b) annual reproductive output (mean ± 1 SE) of Northern Spotted Owls relative to number of days of precipitation in the late nesting period; and (c) recruitment rate of Northern Spotted Owls relative to number of days of precipitation in the winter stress period (W) and early nesting period (E) in northwestern California.

estingly, the covariate P_L was present in the first three models ranked by AICc (Table 4), suggesting that it was an important covariate for explaining reproductive output.

Model $\{R_{P_L}\}$ estimated no significant residual variation (Table 6), indicating that this model explained all of the estimable temporal process variation. The 95% confidence intervals for $\sigma_{\text{temporal}}^2$ for reproductive output did not overlap zero, and the coefficient of temporal process variation was much greater relative to survival probabilities (Table 6). All of these suggested that $\sigma_{\text{temporal}}^2$ in reproductive output was large and was mostly explained by climatic variation, primarily precipitation during the late nesting period.

Recruitment rate.—We relied on the results of the goodness-of-fit procedures used for the survival analysis as the basis for assessing goodness-of-fit in the recruitment models. Survival and recapture probabilities were modeled as $\{\phi_{P_E+T_E}, p_c\}$, the best climate model describing survival, in all models used to estimate recruitment. Recapture probabilities were structured as p_c rather than p_{s+c} (as in the best climate model for ϕ) for recruitment models because POPAN-4 did not allow for group (i.e., sex) effects in estimation procedures. When we examined time effects only, model $\{\psi_t, \phi_{P_E+T_E}, p_c\}$ had the lowest AICc among models with linear time $\{\psi_{lt}, \phi_{P_E+T_E}, p_c\}$ and no time $\{\psi., \phi_{P_E+T_E}, p_c\}$ (Table 5). Estimates of ψ from the time-dependent model were then transformed into recruitment rates (b), which were used to estimate components of temporal process variation in recruitment rates.

We examined 33 additional recruitment models that included the hypothesized models describing climatic effects on survival, reproductive output, and recruitment (see Table 2). Model $\{\psi_{P_W^2+P_E^2}, \phi_{P_E+T_E}, p_c\}$ was selected as the most parsimonious model based on minimum AICc (Table 4). Model $\{\psi_{P_W+T_W+P_E+T_E}, \phi_{P_E+T_E}, p_c\}$ was a potential competitor based on Akaike weights (Table 4). This model differed from the selected model by including temperature covariates, T_W and T_E . Otherwise, it included the same precipitation covariates as the selected model. We concluded that model $\{\psi_{P_W^2+P_E^2}, \phi_{P_E+T_E}, p_c\}$ was best supported by the data based on minimum AICc, but that inclusion of covariates T_W or T_E might be supported in models based on additional data. Estimates of ψ from the selected model were transformed into recruitment rates (b), which were regressed against the same climate covariates to yield (using random-effects models)

$$\hat{b} = 0.24732 - 0.00139(P_W)^2 + 0.00048(P_E)^2 \quad (33)$$

as the model explaining variation in recruitment rates, with $\widehat{\text{SE}}(\hat{\beta}_0) = 0.04121$, $\widehat{\text{SE}}(\hat{\beta}_1) = 0.00037$ (95% CI = $-0.00212, -0.00067$), and $\widehat{\text{SE}}(\hat{\beta}_2) = 0.00021$ (95% CI = $0.00007, 0.00089$). Confidence intervals for the slope parameters did not overlap zero, suggesting that the trends were meaningful. In this model, recruitment rates were negatively affected by increased winter precipitation and positively affected by increased precipitation during the

TABLE 6. Components of temporal variation for apparent survival, mean reproductive output, recruitment rate, and rate of population change for Northern Spotted Owls in northwestern California, with 95% confidence limits in parentheses.

Parameter	Apparent survival ($\hat{\phi}$)	Reproductive output (\hat{R})	Recruitment rate (\hat{b})	Rate of population change ($\hat{\lambda}$)
$\hat{\theta}^\dagger$	0.8755	0.6129	0.1379	1.0086
$\widehat{SE}(\hat{\theta})$	0.0173	0.0640	0.0300	0.0224
$\hat{\sigma}_{\text{temporal}}^2$	0.0013	0.0291	0.0063	0.0031
$CV(\hat{\theta})^\ddagger$	(0, 0.0087)	(0.0105, 0.1128)	(0.0015, 0.0309)	(0.0008, 0.011)
$\hat{\sigma}_{\text{climate}}^2$	0.0410	0.2784	0.5755	0.0552
$\hat{\sigma}_{\text{residual}}^2$	0.0013	0.0291	0.0063	0
	(0, 0.0008)	(0, 0.0103)	(0, 0.0036)	

Note: Survival probabilities are for owls ≥ 1 yr old.

† Weighted mean (see text for details).

‡ Coefficient of temporal process variation estimated as $\hat{\sigma}_{\text{temporal}}/\hat{\theta}$ and represented as proportions.

§ Estimated as $\hat{\sigma}_{\text{climate}}^2 = \hat{\sigma}_{\text{temporal}}^2 - \hat{\sigma}_{\text{residual}}^2$.

early spring (Fig. 4c). Changes in recruitment predicted from Eq. 33 were most sensitive to changes in P_w (516.1% change in \hat{b}) followed by changes in P_E (51.8% change in \hat{b}).

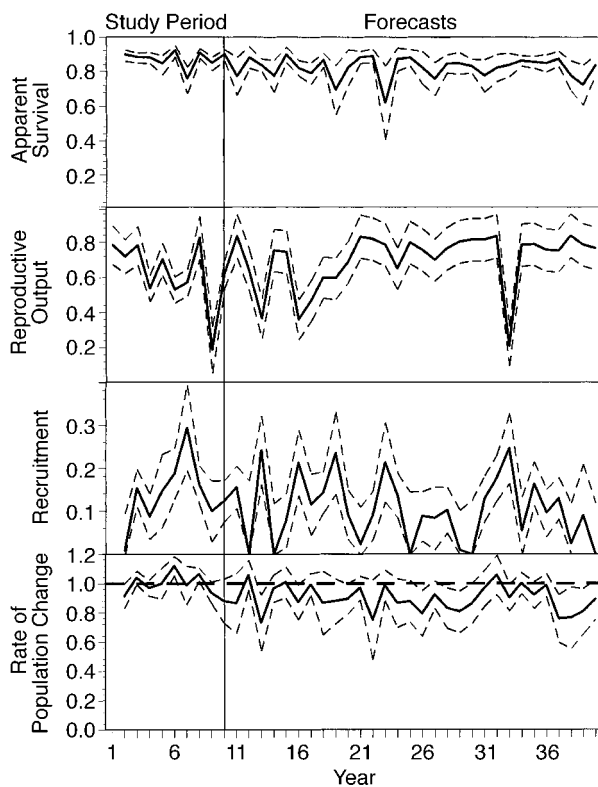


FIG. 5. Annual estimates (solid line) and 95% confidence intervals (dashed lines) for apparent survival, reproductive output, recruitment rate, and rates of population change, based on selected climate models for Northern Spotted Owls in northwestern California. The solid vertical line separates estimates for the study period and forecasts from a 30-yr climate trace recorded from 1955 to 1984, which does not represent future predictions beyond the study period. The horizontal dashed line represents $\lambda = 1$.

The climate model selected explained variation in ψ significantly better than did the random or linear time models (Table 5), with little residual variation estimated (Table 6). The coefficient of temporal process variation for b was substantially higher than those for the other life history parameters (Table 6), suggesting that it exhibited the greatest year-to-year variation relative to survival and reproductive output. Model $\{\psi_{P_w^2+P_E^2}, \phi_{P_E+T_E}, P_c\}$ explained all of the estimable temporal process variation, suggesting that the climatic covariates were primarily responsible for temporal process variation.

Population rates of change.—We used parameter estimates from the models selected to explain survival probabilities and recruitment rates to estimate annual rates of population change λ from Eq. 21 and their standard errors. Based on $\hat{\lambda}$ and $\widehat{SE}(\hat{\lambda})$, $\lambda = 1$ was contained within the 95% confidence intervals for $\hat{\lambda}$ (0.9594, 1.0578), suggesting that the population could be stationary during the study period. The level of temporal process variation in λ was low based on its coefficient of temporal process variation (Table 6).

Forecasts with climate models.—Fig. 5 shows the forecasts of point estimates, and their 95% confidence intervals, from the models selected to represent climatic variation in the demographic parameters and rate of population change, based on the 30-yr period from 1955 through 1984. These forecasts are properly interpreted as what might occur if a similar trend in climate were observed in the future, given that the models used are reasonably correct and other conditions affecting the estimates remain the same. Thus, the traces in Fig. 5 represent what could happen, given the conditions stated previously, rather than what will happen in future years. Therefore, inferences about small-scale variation in the long-term trends are limited. However, large-scale trends can provide some insights into how climate may affect these life history traits over time.

Three important results are evident in examining trends forecasted over 30 yr. First, point estimates of

survival and recruitment, the parameters used to estimate λ , were negatively correlated (Pearson's $r = -0.340$, $P = 0.07$), but not strongly so. This may reflect the influence of precipitation during the early nesting period, which negatively affected survival but positively affected recruitment. However, there is also inherent sampling covariance between survival and recruitment because these two parameters were estimated from the same data. As expected, both survival and recruitment were positively correlated with λ . However, recruitment had a stronger correlation ($r = 0.705$, $P < 0.001$) than survival ($r = 0.412$, $P = 0.024$). Second, long-term variation in life history traits differed among the three traits examined. Both survival and reproductive output appear to have longer periods of relative stability punctuated by shorter periods exhibiting severe declines in both survival and reproduction, which represent catastrophic events for each of these parameters. Forecasts of survival estimates revealed two years in which survival estimates dropped below 0.70, with survival in one year as low as 0.62. Reproductive output reached extremely low levels (<0.4) in at least three years. Thus, the probability of catastrophic events (C) can be crudely estimated as $\hat{C} = 2/30 = 0.067$ for survival probabilities and $\hat{C} = 3/30 = 0.10$ for reproductive output. Catastrophic periods did not occur simultaneously for both survival and reproduction, suggesting that events causing variation in these parameters may not be linked. In contrast, recruitment rate was highly and consistently variable, reaching extremely low levels (<0.01) in six of the 30 yr ($\hat{C} = 0.20$). Finally, an average $\hat{\lambda}$ of 0.9118 (based on Eq. 24 from the annual estimates from Eq. 21) for the 30-yr climate trace was less than that estimated during the study period. Annual estimates of λ were significantly lower than a stationary population in 11 of those years, based on 95% confidence intervals (Fig. 5).

Effects of landscape habitat configuration on spatial variation in population processes

Survival probabilities.—We analyzed 280 models to evaluate the effects of habitat, age, and elevation covariates and their interactions on apparent survival. The best approximating a priori hypothesized model for survival was $\{\phi_{a2+LSOCOR+LSOMP+LSOEDG}, p_{c^*ELEV}\}$ (model 13 in Table 7), which was twice as likely, based on Akaike weights, as the next ranked model, $\{\phi_{a2'+SOCOR+(SOCOR)^2+SODIS+(SODIS)^2}, p_{c^*ELEV}\}$ (model 9 in Table 7). The c^*ELEV structure on the recapture probabilities (p) was arrived at early in the modeling process where annual differences in capture technique interacted with mean elevation of territories. This structure on the p 's was checked again at the later stages of the modeling process, and remained the best structure for all models.

The effects of SOCOR and SOEDG on ϕ appeared to be most important in the pseudothreshold form (i.e.,

LSOCOR) because (1) they were more precise (coefficients of variation = 0.37–0.50); (2) 95% confidence intervals of their slope parameters never overlapped zero in the other hypothesized models; and (3) one or both of these covariates appeared in the top three ranked hypothesized models (Table 7). However, slope parameters for the two covariates overlapped zero to a greater degree when they appeared in the squared difference form (i.e., DSOCOR), although the slope parameters for SOCOR as a quadratic (SOCOR + SOCOR²) did not overlap zero (Table 7). The quadratic form of SOCOR had a shape similar to a pseudothreshold model, suggesting that SOCOR + SOCOR² was explaining the data as a pseudothreshold model similarly to LSOCOR.

The covariates SOMP, SOCOR, and SOHAB were all highly correlated ($r = 0.82$ – 0.96). The covariates LSOCOR and LSOMP in the best a priori hypothesized model also were highly correlated ($r = 0.88$). Therefore, we examined another model that incorporated all of the effects included in the top two a priori hypothesized models, $\{\phi_{a2+LSOCOR+LSOMP+LSOEDG}, p_{c^*ELEV}\}$ and $\{\phi_{a2'+SOCOR+(SOCOR)^2+SODIS+(SODIS)^2}, p_{c^*ELEV}\}$. This model $\{\phi_{a2'+LSOCOR+LSOEDG+SODIS+(SODIS)^2}, p_{c^*ELEV}\}$ (starred model in Table 7) was 2.4 times as likely, based on Akaike weights, as the best a priori hypothesized model. All of the covariates were more precise (coefficients of variation = 0.30–0.56) in this combined model, and none of the 95% confidence intervals of the slope parameters overlapped zero except for LSOEDG, which overlapped only slightly (Table 7). In addition, none of the covariates included in the combined model was highly correlated pairwise ($r = -0.22$ to -0.48). Models including sex-, and age-covariate, and between-covariate interactions were not supported by the data as well as was model $\{\phi_{a2'+LSOCOR+LSOEDG+SODIS+(SODIS)^2}, p_{c^*ELEV}\}$ (Table 8). However, the $\Delta AICc$ value between the model with an $a2$ vs. an $a2'$ age effect was very small, suggesting that either structure may be appropriate. This was also the case with the a priori hypothesized models in which the $\Delta AICc_i$ values between the same models, with one including an $a2$ and the other an $a2'$ structure, ranged from 0.01 to 5.61 with the $a2'$ structured model having a lower AICc value in 17 of 19 models. For this reason, we chose to retain the $a2'$ structure in model $\{\phi_{a2'+LSOCOR+LSOEDG+SODIS+(SODIS)^2}, p_{c^*ELEV}\}$. Further exploration of this model with additional covariates did not yield a better model. Although it resulted from some data exploration, model $\{\phi_{a2'+LSOCOR+LSOEDG+SODIS+(SODIS)^2}, p_{c^*ELEV}\}$ represented a minor alteration from two of the hypothesized models and, thus, retained much of the a priori thinking used to develop the models. Therefore, this model was retained for making inferences concerning the effects of landscape habitat features on survival. The form of the model was as follows:

TABLE 7. Rankings, based on AICc, and estimated slope parameters for the a priori hypothesized models used to relate landscape habitat features with apparent survival (ϕ) for Northern Spotted Owls in northwestern California.

Hypothesized model†	AICc	K_{\ddagger}	$\delta AICc_i$	w_i	Estimated slope parameters (95% CI)§
* $\phi_{a2'+LSOCOR+LSOEDG+SODIS+(SODIS)^2}$	1132.45	10	0.00	0.427	$\beta_1 = -0.503 (-0.986, -0.019)$ $\beta_2 = 0.213 (0.038, 0.388)$ $\beta_3 = 0.547 (-0.051, 1.144)$ $\beta_4 = 0.085 (0.030, 0.141)$ $\beta_5 = -0.001 (-0.002, -0.0004)$
13) $\phi_{a2'+LSOCOR+LSOMP+LSOEDG}$	1134.19	9	1.74	0.179	$\beta_1 = -0.811 (-1.500, -0.122)$ $\beta_2 = 0.493 (0.153, 0.833)$ $\beta_3 = -0.779 (-1.520, -0.039)$ $\beta_4 = 0.790 (0.221, 1.359)$
9) $\phi_{a2'+SOCOR+(SOCOR)^2+SODIS+(SODIS)^2}$	1135.44	10	2.99	0.096	$\beta_1 = -0.480 (-0.963, 0.003)$ $\beta_2 = 0.022 (0.003, 0.041)$ $\beta_3 = -0.002 (-0.0004, -0.00002)$ $\beta_4 = 0.067 (0.013, 0.121)$ $\beta_5 = -0.001 (-0.002, -0.0004)$
12) $\phi_{a2'+LSOCOR+LSOEDG}$	1136.20	8	3.75	0.065	$\beta_1 = -0.527 (-1.005, -0.049)$ $\beta_2 = 0.163 (0.016, 0.310)$ $\beta_3 = 0.652 (0.095, 1.209)$
4) $\phi_{a2'+DSOMP+DSODIS}$	1136.63	8	4.18	0.053	$\beta_1 = -0.500 (-0.981, -0.019)$ $\beta_2 = -0.010 (-0.024, 0.005)$ $\beta_3 = -0.305 (-0.596, -0.139)$
1) $\phi_{a2'+DSOHAB}$	1137.74	7	5.29	0.030	$\beta_1 = -0.526 (-1.002, -0.049)$ $\beta_2 = -0.019 (-0.034, -0.003)$
6) $\phi_{a2'+DSOMP+DSOEDG}$	1137.86	8	5.41	0.029	$\beta_1 = -0.506 (-0.985, -0.027)$ $\beta_2 = -0.006 (-0.023, 0.011)$ $\beta_3 = -0.015 (-0.031, 0.001)$
8) $\phi_{a2'+DSOCOR+DSONCA}$	1137.89	8	5.44	0.028	$\beta_1 = -0.535 (-1.013, -0.058)$ $\beta_2 = -0.0001 (-0.0003, 0.0001)$ $\beta_3 = -0.048 (-0.089, -0.006)$
5) $\phi_{a2'+SOMP+(SOMP)^2+SONP+(SONP)^2+SODIS+(SODIS)^2}$	1137.94	12	5.49	0.027	$\beta_1 = -0.454 (-0.939, 0.030)$ $\beta_2 = 0.208 (-0.028, 0.445)$ $\beta_3 = -0.013 (-0.029, 0.002)$ $\beta_4 = -0.224 (-0.587, 0.139)$ $\beta_5 = 0.016 (-0.020, 0.052)$ $\beta_6 = 0.099 (0.037, 0.161)$ $\beta_7 = -0.001 (-0.002, -0.0007)$
2) $\phi_{a2'+DSOMP}$	1139.02	7	6.57	0.016	$\beta_1 = -0.523 (-0.999, -0.047)$ $\beta_2 = -0.014 (-0.028, -0.0005)$
11) $\phi_{a2'+LSOCOR+LSOMP}$	1139.16	8	6.71	0.015	$\beta_1 = -0.538 (-1.016, -0.061)$ $\beta_2 = 0.367 (0.043, 0.692)$ $\beta_3 = -0.517 (-1.223, 0.190)$
7) $\phi_{a2'+LSOCOR}$	1139.91	7	6.74	0.015	$\beta_1 = -0.525 (-1.001, -0.049)$ $\beta_2 = 0.155 (0.002, 0.308)$
3) $\phi_{a2'+DSOMP+DSONP}$	1140.79	8	8.34	0.007	$\beta_1 = -0.521 (-0.997, -0.045)$ $\beta_2 = -0.014 (-0.028, -0.0004)$ $\beta_3 = -0.008 (-0.036, 0.021)$
$\phi_{a2'}$	1140.94	6	8.49	0.006	$\beta_1 = -0.534 (-1.008, -0.059)$
10) $\phi_{a2'+LSOCOR+LSONCA+LSODIS}$	1140.98	9	8.53	0.006	$\beta_1 = -0.535 (-1.011, -0.058)$ $\beta_2 = 0.193 (0.025, 0.361)$ $\beta_3 = 0.147 (-0.156, 0.450)$ $\beta_4 = 0.139 (-0.073, 0.350)$
ϕ .	1143.41	5	10.96	0.002	

Notes: Models $\{\phi_{a2'}\}$ and $\{\phi\}$ are included for comparison. All models have capture probabilities structured as $\{p_{c \geq \text{ELEV}}\}$. The starred model represents a combination of a priori hypothesized models 13 and 9. Covariates are described in Table 1.
 † Numbers correspond to hypothesized models in Table 3.
 ‡ Number of estimated parameters.
 § Slope parameters based on rescaled covariates (see Table 1).

$$\hat{\phi} = 1/\{1 + \exp[-(0.5489 - 0.5025(\text{AGE}) + 0.2129(\text{LSOCOR}) + 0.5465(\text{LSOEDG}) + 0.0853(\text{SODIS}) - 0.0011(\text{SODIS})^2]\} \quad (34)$$

where AGE (the a2' structure) is a dummy variable (1 is 1–2-yr-olds, 0 is ≥ 3 -yr-olds), LSOCOR is $\log_e(\text{SOCOR} + 0.5)$, and LSOEDG is $\log_e(\text{SOEDG} + 0.5)$. Standard errors for the parameter estimates were $\widehat{SE}(\hat{\beta}_0) = 0.8676$, $\widehat{SE}(\hat{\beta}_1) = 0.2465$, $\widehat{SE}(\hat{\beta}_2) = 0.0895$, $\widehat{SE}(\hat{\beta}_3) = 0.3050$, $\widehat{SE}(\hat{\beta}_4) = 0.0283$, and $\widehat{SE}(\hat{\beta}_5) = 0.0003$. This model suggested that apparent survival

TABLE 8. Ranking of best approximating model of apparent survival (ϕ) or reproductive output (R) for Northern Spotted Owls in northwestern California relative to models where specific effects in the best approximating model were included, excluded, or changed.

Change in effect	Model	$\Delta AICc_i$	w_i
Apparent survival (ϕ)			
None (best approximating model)	$\phi_{a2'}+LSOCOR+LSOEDG+SODIS+(SODIS)^2, P_{c*ELEV}$	0.00	0.19
Change of age effect to a2 on ϕ	$\phi_{a2}+LSOCOR+LSOEDG+SODIS+(SODIS)^2, P_{c*ELEV}$	0.07	0.19
Addition of LSOMP effect on ϕ	$\phi_{a2'}+LSOCOR+LSOMP+LSOEDG+SODIS+(SODIS)^2, P_{c*ELEV}$	0.51	0.15
Exclusion of LSOEDG effect on ϕ	$\phi_{a2'}+LSOCOR+SODIS+(SODIS)^2, P_{c*ELEV}$	1.02	0.12
Exclusion of age effect	$\phi_{LSOCOR+LSOEDG+SODIS+(SODIS)^2, P_{c*ELEV}}$	1.83	0.08
Exclusion of c*ELEV interaction in p	$\phi_{a2'}+LSOCOR+LSOEDG+SODIS+(SODIS)^2, P_{c+ELEV}$	1.96	0.07
Addition of sex effect	$\phi_{s+a2'}+LSOCOR+LSOEDG+SODIS+(SODIS)^2, P_{c*ELEV}$	2.03	0.07
Change of SODIS+SODIS ² to DSODIS on ϕ	$\phi_{a2'}+LSOCOR+LSOEDG+DSODIS, P_{c*ELEV}$	4.06	0.03
Change of SODIS+SODIS ² to LSODIS on ϕ	$\phi_{a2'}+LSOCOR+LSOEDG+LSODIS, P_{c*ELEV}$	4.46	0.02
Change of SODIS+SODIS ² to DIS on ϕ	$\phi_{a2'}+LSOCOR+LSOEDG+SODIS, P_{c*ELEV}$	5.74	0.01
Exclusion of c effect on p	$\phi_{a2'}+LSOCOR+LSOEDG+SODIS+(SODIS)^2, P_{ELEV}$	11.59	0.00
Exclusion of ELEV effect on p	$\phi_{a2'}+LSOCOR+LSOEDG+SODIS+(SODIS)^2, P_c$	106.3	0.00
Reproductive output (R)			
None (best approximating model)	$R_{a2'}+LSOCOR+LSOEDG+SONP+(SONP)^2$	0.00	0.34
Exclusion of quadratic form in SONP	$R_{a2'}+LSOCOR+LSOEDG+SONP$	1.25	0.18
Inclusion of ELEV effect	$R_{a2'}+LSOCOR+LSOEDG+SONP+(SONP)^2+ELEV$	1.81	0.14
Exclusion of LSOCOR	$R_{a2'}+LSOEDG+SONP+(SONP)^2$	2.02	0.12
Exclusion of SONP	$R_{a2'}+LSOCOR+LSOEDG$	2.39	0.10
Inclusion of 3 age-class effect	$R_{a3}+LSOCOR+LSOEDG+SONP+(SONP)^2$	3.36	0.06
Change of age effect to a2	$R_{a2}+LSOCOR+LSOEDG+SONP+(SONP)^2$	3.68	0.05
Exclusion of age effect (a2')	$R_{LSOCOR+LSOEDG+SONP+(SONP)^2}$	9.18	0.00
Exclusion of SOEDG effect	$R_{a2'}+LSOCOR+SONP+(SONP)^2$	9.85	0.0
Exclusion of SOCOR and SOEDG effect	$R_{a2'}+SONP+(SONP)^2$	12.12	0.0

Note: Covariates are described in Table 1.

increased in parallel for both age classes with increasing amounts of spotted owl habitat, increasing edge between spotted owl and other habitats, and increasing mean nearest neighbor distance between patches of spotted owl habitat at ~400 m, after which apparent survival declined with increasing distance (Fig. 6). Owls 1–2 yr old had lower survival than owls ≥3 yr old, and this difference was constant across changes in the habitat covariates (i.e., there was no interaction between age class and habitat covariates). Changes in apparent survival predicted from the model in Eq. 34 were most sensitive to changes in edge between spotted owl habitat and other habitats (11.1% change in $\hat{\phi}$), followed by changes in spotted owl core habitat (5.4% change in $\hat{\phi}$), mean nearest neighbor distance between spotted owl habitat patches (3.8% change in $\hat{\phi}$) and age class of the territorial occupants (2.0% change in $\hat{\phi}$).

In estimating $\sigma^2_{spatial}$ for apparent survival, we encountered problems with some of the estimates of sampling variances for ϕ (see Appendix B). Based on the estimates of $\sigma^2_{spatial}$ and the weighted mean survival probability across territories (Table 9), the coefficient of spatial process variation was 0.085, suggesting that spatial process variation in ϕ was relatively low. The habitat covariates in model $\{\phi_{a2'}+LSOCOR+LSOEDG+SODIS+(SODIS)^2, P_{c*ELEV}\}$ accounted for 66.7% of $\hat{\sigma}^2_{spatial}$, whereas age accounted for 8.8% of $\hat{\sigma}^2_{spatial}$. There was considerable uncertainty in the estimates of spatial process variation in survival based on the 95% confidence intervals, all of which included

zero for each of the variance components (Table 9). This uncertainty was probably due to large sampling variation in the territory-specific estimates of ϕ relative to $\hat{\sigma}^2_{spatial}$ (Table 9). The cause of this large sampling variation was probably due to some territory-specific estimates based on only one or two individuals.

Reproductive output.—In running the general linear mixed models for reproductive output, we found a covariance structure that used low, medium, and high variance years to have the best approximating structure, based on minimum AICc computed from the restricted maximum log likelihood. This structure was used on all subsequent models examining the fixed effects in the hypothesized models and their variations.

We examined 122 models that included the 13 a priori hypothesized models in addition to variations on those models, which included effects due to age, elevation, and interactions. From this suite of models, the best approximating a priori model was $\{R_{a2'}+SOCOR+SOEDG\}$, based on minimum AICc (model 12 in Table 10). However, model $\{R_{a2'}+SOMP+SOEDG\}$ was a close competitor based on approximately equal Akaike weights. In these two models, the estimated slope parameter for SOEDG had greater precision (CV = 0.298–0.383), and was different from zero, based on confidence intervals, than slope parameter estimates for the habitat amount covariates, SOMP and SOCOR, which were much less precise (CV = 1.231–6.402), with confidence intervals that overlapped zero considerably (Table 10). The poor es-

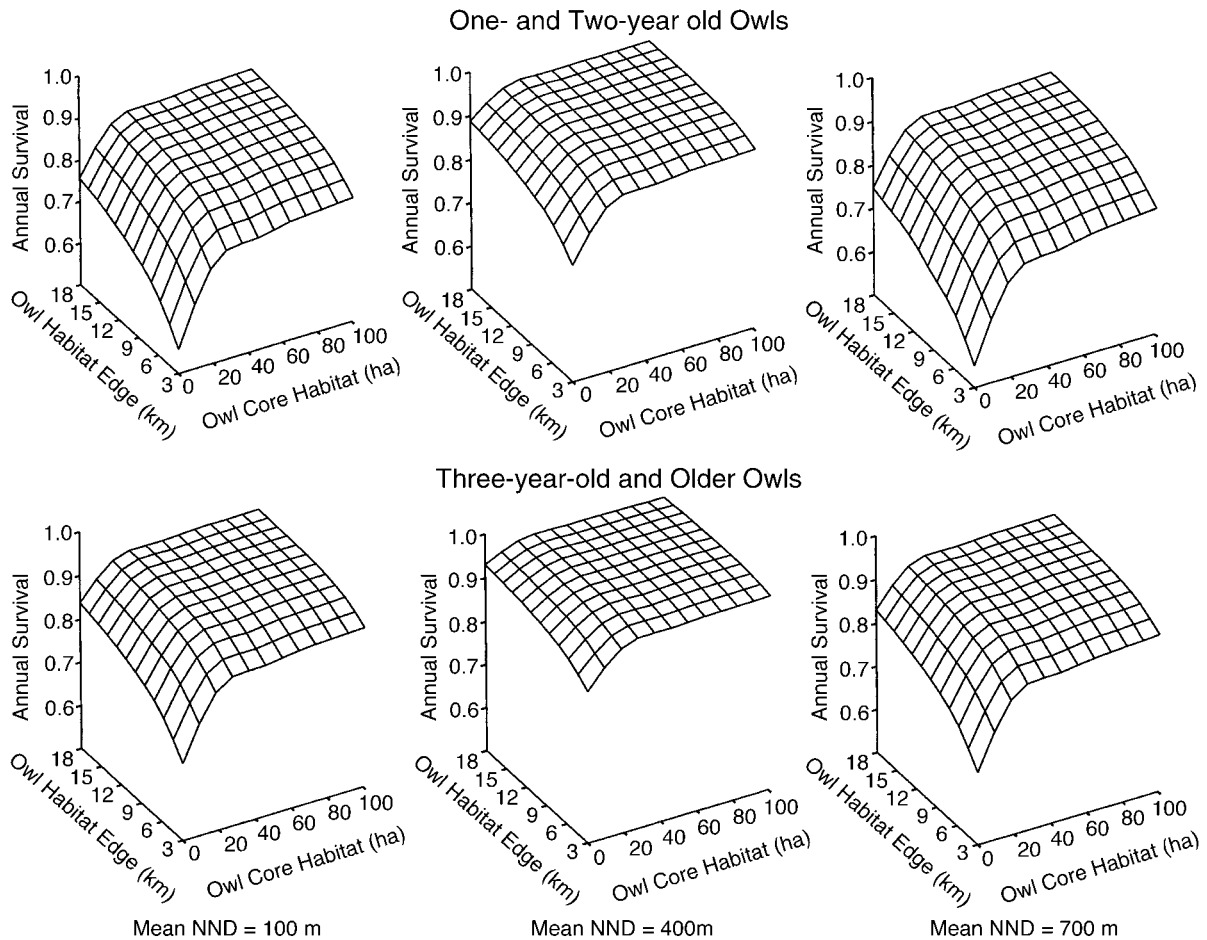


FIG. 6. Annual apparent survival (ϕ) of 1- and 2-yr-old and ≥ 3 -yr-old Northern Spotted Owls in relation to the amount of core habitat, edge between spotted owl and other habitats, and nearest neighbor distance (NND) between patches of spotted owl habitat on territories in northwestern California. Estimates of apparent survival are based on model $\{\phi_{a2} + LSOCOR + LSOEDG + SODIS + (SODIS)^2, P_c \cdot ELEV\}$.

TABLE 9. Components of spatial variation for apparent survival (ϕ), reproductive output (R), and habitat fitness potential (λ_H) in Northern Spotted Owls in northwestern California.

Parameter†	Apparent survival ($\hat{\phi}$)	Reproductive output (\hat{R})	Habitat fitness potential ($\hat{\lambda}_H$)
$\hat{\theta}$	0.8822	0.6006	1.0750
SE($\hat{\theta}$)	0.0141	0.0412	0.0100
$\hat{\sigma}_{spatial}^2$	0.0057	0.0302	0.0031
	(0.0003, 0.0165)	(0.0090, 0.1017)	(0.0019, 0.0051)
$\hat{\sigma}_{habitat}^2$	0.0038	0.0226	‡
	(0.0029, 0.0052)	(0.0058, 0.0882)	
$\hat{\sigma}_{age}^2$	0.0005	0.0008	
	(0.0004, 0.0007)	(0.0002, 0.0040)	
$\hat{\sigma}_{residual}^2$	0.0013	0.0068	
	(0.0001, 0.0269)	(0, 0.0408)	

Note: Ninety-five percent confidence intervals are in parentheses.

† The parameter $\hat{\sigma}_{spatial}^2$ is an estimate of spatial process variation, $\hat{\sigma}_{habitat}^2$ is the amount of $\hat{\sigma}_{spatial}^2$ explained by variation in selected habitat covariates, $\hat{\sigma}_{age}^2$ is the amount of $\hat{\sigma}_{spatial}^2$ explained by age of territory occupants, and $\hat{\sigma}_{residual}^2$ is the unexplained amount of $\hat{\sigma}_{spatial}^2$.

‡ Not estimated.

TABLE 10. Rankings, based on AICc, and estimated slope parameters for the a priori hypothesized models used to relate landscape habitat features to reproductive output (R) in Northern Spotted Owls in northwestern California.

Hypothesized model†	AICc	$K‡$	$\Delta AICc_i$	w_i	Estimated slope parameters (95% CI)§
* $R_{a2'+LSOCOR+LSOEDG+SONP+(SONP)^2}$	1317.31	9	0.00	0.532	$\beta_1 = 0.344 (0.145, 0.544)$ $\beta_2 = -0.074 (-0.145, -0.003)$ $\beta_3 = 0.473 (0.220, 0.727)$ $\beta_4 = -0.151 (-0.280, -0.022)$ $\beta_5 = 0.013 (-0.001, 0.026)$
12) $R_{a2'+SOCOR+SOEDG}$	1319.88	8	2.58	0.147	$\beta_1 = 0.349 (0.147, 0.550)$ $\beta_2 = -0.002 (-0.005, 0.002)$ $\beta_3 = 0.042 (0.011, 0.074)$
6) $R_{a2'+SOMP+SOEDG}$	1320.28	8	2.97	0.121	$\beta_1 = 0.354 (0.153, 0.556)$ $\beta_2 = -0.006 (-0.029, 0.017)$ $\beta_3 = 0.047 (0.019, 0.075)$
13) $R_{a2'+SOCOR+SOMP+SOEDG}$	1321.83	9	4.52	0.056	$\beta_1 = 0.345 (0.142, 0.547)$ $\beta_2 = -0.003 (-0.010, 0.005)$ $\beta_3 = 0.023 (-0.037, 0.054)$ $\beta_4 = 0.040 (0.006, 0.074)$
1) $R_{a2'+SOHAB+(SOHAB)^2+ELEV+ELEV*SOHAB+ELEV*(SOHAB)^2}$	1322.98	11	5.67	0.031	$\beta_1 = 0.333 (0.131, 0.532)$ $\beta_2 = -0.544 (-1.179, 0.091)$ $\beta_3 = 0.028 (-0.010, 0.065)$ $\beta_4 = -0.347 (-0.645, -0.049)$ $\beta_5 = 0.082 (0.009, 0.155)$
9) $R_{a2'+SOCOR+SODIS}$	1323.54	8	6.23	0.024	$\beta_1 = 0.341 (0.139, 0.544)$ $\beta_2 = -0.005 (-0.008, -0.001)$ $\beta_3 = -0.010 (-0.022, 0.002)$
3) $R_{a2'+SOMP+(SOMP)^2+SONP+(SONP)^2}$	1323.60	10	6.28	0.023	$\beta_1 = 0.345 (0.144, 0.546)$ $\beta_2 = 0.083 (-0.013, 0.179)$ $\beta_3 = -0.008 (-0.014, -0.002)$ $\beta_4 = -0.188 (-0.330, -0.046)$ $\beta_5 = 0.017 (0.002, 0.031)$
7) $R_{a2'+SOCOR}$	1324.14	7	6.83	0.017	$\beta_1 = 0.335 (0.132, 0.538)$ $\beta_2 = -0.427 (-0.007, -0.001)$
11) $R_{a2'+SOCOR+SOMP}$	1324.73	8	7.41	0.013	$\beta_1 = 0.325 (0.122, 0.528)$ $\beta_2 = -0.007 (-0.014, -0.001)$ $\beta_3 = 0.028 (-0.016, 0.071)$
8) $R_{a2'+SOCOR+SONCA}$	1324.93	8	7.62	0.012	$\beta_1 = 0.337 (0.134, 0.539)$ $\beta_2 = -0.002 (-0.007, 0.0001)$ $\beta_3 = 0.026 (-0.019, 0.070)$
10) $R_{a2'+SOCOR+SONCA+SODIS}$	1325.04	9	7.72	0.011	$\beta_1 = 0.342 (0.140, 0.544)$ $\beta_2 = -0.004 (-0.008, -0.001)$ $\beta_3 = 0.018 (-0.028, 0.063)$ $\beta_4 = -0.009 (-0.021, 0.003)$
2) $R_{a2'+SOMP+(SOMP)^2}$	1326.29	8	8.98	0.006	$\beta_1 = 0.343 (0.140, 0.546)$ $\beta_2 = 0.0781 (-0.022, 0.179)$ $\beta_3 = -0.006 (-0.013, 0.0002)$
4) $R_{a2'+SOMP+SODIS}$	1327.43	8	10.11	0.003	$\beta_1 = 0.355 (0.151, 0.558)$ $\beta_2 = -0.022 (-0.047, 0.003)$ $\beta_3 = -0.010 (-0.022, 0.003)$
5) $R_{a2'+SOMP+SONP+SODIS+SONP*SODIS}$	1328.65	11	11.34	0.002	$\beta_1 = 0.356 (0.154, 0.559)$ $\beta_2 = 0.008 (-0.059, 0.076)$ $\beta_3 = -0.037 (-0.067, -0.007)$ $\beta_4 = 0.004 (-0.022, 0.031)$ $\beta_5 = -0.007 (-0.018, 0.004)$
$R_{a2'+DELEV}$	1328.97	7	11.66	0.002	$\beta_1 = 0.350 (0.146, 0.555)$ $\beta_2 = -0.004 (-0.014, 0.007)$
$R.$	1336.18	5	18.87	0.000	

Notes: Models $\{R_{a2'+DELEV}\}$, and $\{R.\}$ are included for comparison. The starred model was achieved after further exploration. Covariates are described in Table 1.

† Numbers correspond to hypothesized models in Table 2.

‡ Number of estimated parameters.

§ Slope parameters based on re-scaled covariates (see Table 1).

timation of SOMP and SOCOR effects suggested that the top three a priori models may have been the best from the suite of models examined, but did not model the data very well. Therefore, we explored additional models that included other combinations of the covariates, with the best approximating a priori model as

a starting point. We did not explore any additional models that included the covariates SOCOR, SOMP, and SOHAB together, because of the high correlations among these covariates.

We examined 55 additional models outside of the hypothesized models. From this suite of models, the best

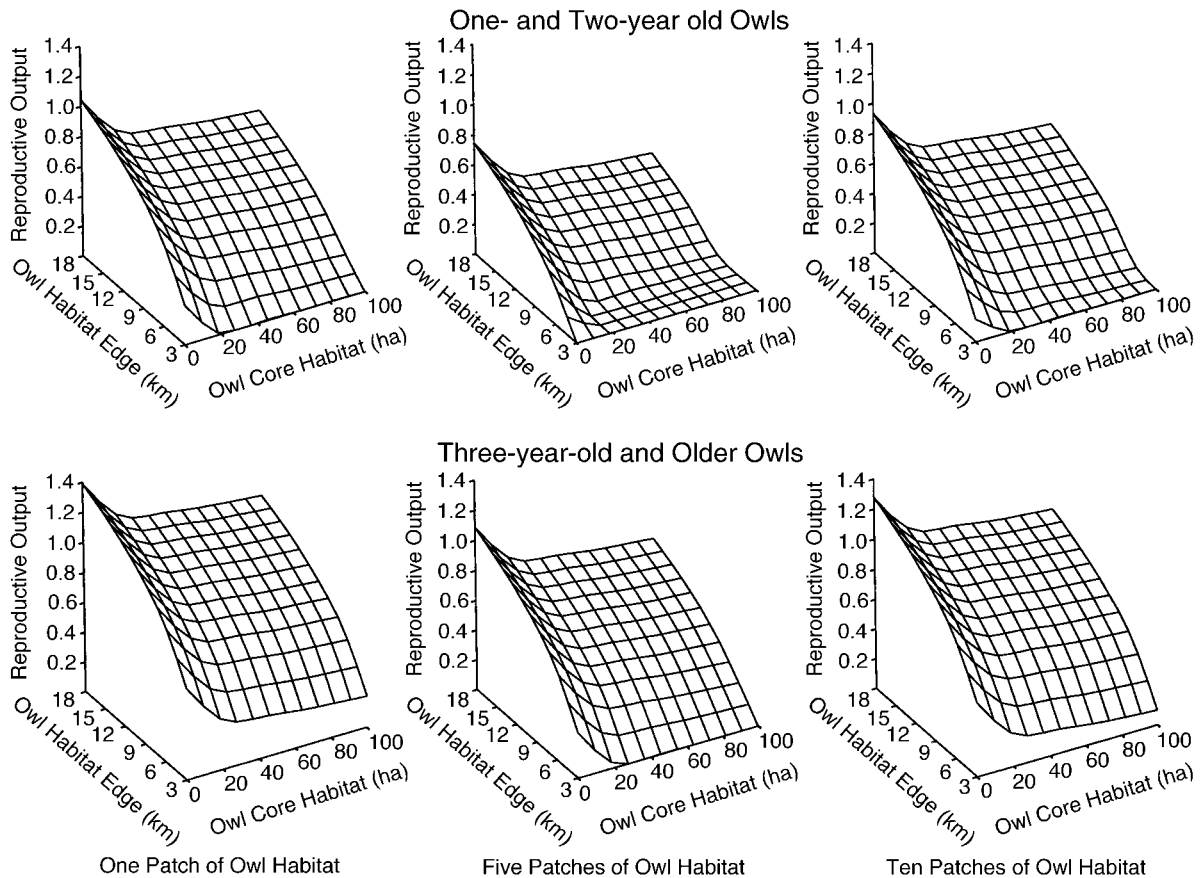


FIG. 7. Reproductive output (R) of 1- and 2-yr-old and ≥ 3 -yr-old Northern Spotted Owls in relation to amount of core spotted owl habitat, edge between spotted owl and other habitats, and number of patches of spotted owl habitat on territories in northwestern California. Estimates of reproductive output are from model $\{R_{a2'+LSOCOR+LSOEDG+SONP+(SONP)^2}\}$.

approximating model based on minimum AICc was $\{R_{a2'+LSOCOR+LSOEDG+SONP+(SONP)^2}\}$, which was also a much better approximating model than any of the a priori hypothesized models (starred model in Table 10). The Akaike weight for model $\{R_{a2'+LSOCOR+LSOEDG+SONP+(SONP)^2}\}$ indicated that it was 3.6 times more likely than the nearest a priori hypothesized model. Close competitors within one AICc unit of this model, within the suite of models involved in data exploration, retained a similar structure but without the log effects and with some age interactions (Table 8). The form of model $\{R_{a2'+LSOCOR+LSOEDG+SONP+(SONP)^2}\}$ was

$$\begin{aligned} \hat{R} = & -0.245 + 0.344(\text{AGE}) - 0.074(\text{LSOCOR}) \\ & + 0.473(\text{LSOEDG}) - 0.151(\text{SONP}) \\ & + 0.013(\text{SONP})^2 \end{aligned} \quad (35)$$

where AGE was a dummy variable (0, either 1 or 2 yr old; 1, ≥ 3 yr old). The standard errors for the parameter estimates were $\widehat{SE}(\hat{\beta}_0) = 0.377$, $\widehat{SE}(\hat{\beta}_1) = 0.102$, $\widehat{SE}(\hat{\beta}_2) = 0.036$, $\widehat{SE}(\hat{\beta}_3) = 0.129$, $\widehat{SE}(\hat{\beta}_4) = 0.066$, and $\widehat{SE}(\hat{\beta}_5) = 0.0068$. All of the slope parameters were relatively precise (CV = 0.27–0.54).

This model was similar to the best hypothesized

model $\{R_{a2'+SOCOR+SOEDG}\}$, except that there was a pseudothreshold effect on SOCOR and SOEDG, and the model included SONP. We used model $\{R_{a2'+LSOCOR+LSOEDG+SONP+(SONP)^2}\}$ with the understanding that inferences were somewhat limited because this model was developed by further exploration beyond the a priori hypothesized models. However, this model was based mostly on one of the a priori hypotheses (model 12 in Table 3). This model indicated that reproductive output was (1) negatively associated with female age class, with 1- and 2-yr-old owls fledging fewer young than owls ≥ 3 yr old (the dummy variable was scored 1 for owls ≥ 3 yr old); (2) negatively associated with the amount of core spotted owl habitat in a nonlinear fashion; (3) positively associated with the amount of edge between spotted owl habitat and other habitats in a nonlinear fashion; and (4) associated with the number of patches of spotted owl habitat by an inverse quadratic relationship in which reproductive output was highest when the number of patches was either few or many, and lowest when the number of patches was intermediate (Fig. 7). Changes in reproductive output predicted from Eq. 35 were most sensitive to changes in edge between spotted owl habitat

and other habitats (382.0% change in \hat{R}), followed by changes in spotted owl core habitat (30.4% change in \hat{R}), number of spotted owl habitat patches (23.9% change in \hat{R}), and age class of the territorial occupants (22.4% change in \hat{R}).

Using the weighted mean for reproductive output (Table 9), the coefficient of spatial variation was 0.289, suggesting that reproductive output was relatively variable among territories, much more so than survival. The habitat covariates in model $\{R_{a2} + \text{LSOCOR} + \text{LSOEDG} + \text{SONP} + (\text{SONP})^2\}$ explained 74.8% of this spatial process variation, whereas the age effect explained 2.7% (see Table 9).

Habitat fitness potential.—We estimated the habitat fitness potential of each spotted owl territory using the Leslie stage projection matrix in (22). As inputs to (22) for each territory, we estimated apparent survival ($\hat{\phi}$) using Eq. 34, and we estimated fecundity (\hat{m}) from Eq. 35 using the relevant landscape covariates from each of the territories. For example, we used the measures of LSCOR, LSOEDG, and SODIS from territory A to estimate age-specific ϕ for that territory using Eq. 34, and we used the measures of LSCOR, LSOEDG, and SONP from territory A to estimate age-specific R for that territory using Eq. 35. Estimates of m were derived by dividing \hat{R} by 2. An estimate of λ_H was then obtained for territory A using the age-specific estimates of ϕ and m as inputs to matrix 22.

Estimated values of territory-specific habitat fitness potential ($\hat{\lambda}_H$) varied from 0.438 to 1.178 (Fig. 8a), with a weighted mean (using Eq. 24 with territory-specific estimates from matrix 22) of 1.075 (95% CI = 1.061, 1.089). The median coefficient of sampling variation among territories was 0.028, indicating that estimates of λ_H were quite precise. Based on estimates in Table 9, the coefficient of spatial process variation for $\hat{\lambda}_H$ was 0.052, suggesting that spatial process variation in the predicted habitat fitness potential among territories was relatively low. However, territory-specific estimates of λ_H followed a smooth progression from territories with relatively high fitness (with point estimates substantially greater than one), to territories that had low fitness (with values less than one; Fig. 9a). Based on the 95% confidence intervals of $\hat{\lambda}_H$ for each territory, three territories (3.2%) had point estimates less than one, with confidence intervals that did not overlap one; 26 territories (27.4%) had estimates either less than or greater than one, with confidence intervals that overlapped one; and 66 territories (69.4%) had estimates that were greater than one and confidence intervals that did not overlap one. This indicated that females on at least two-thirds of the territories more than replaced themselves and were potentially contributing a surplus to the population.

The components used to estimate λ_H , age-specific apparent survival and age-specific fecundity, appeared to contribute differently to the spatial process variation among territory-specific λ_H . First, $\hat{\lambda}_H$ was highly cor-

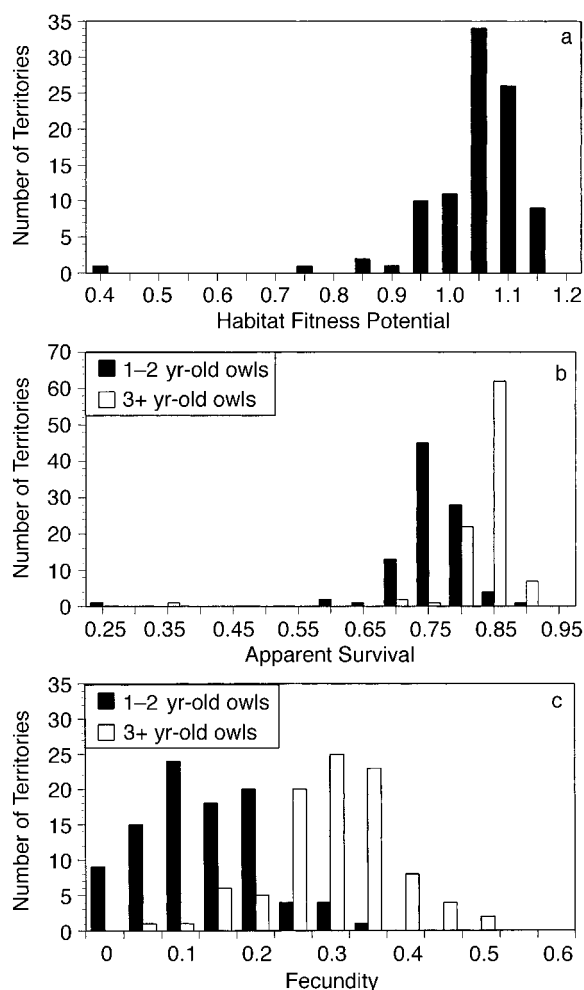


FIG. 8. Distributions of (a) estimated habitat fitness potential ($\hat{\lambda}_H$), (b) predicted estimates of apparent survival used to estimate λ_H , and (c) predicted estimates of fecundity used to estimate λ_H for 95 Northern Spotted Owl territories in northwestern California.

related with apparent survival ($r = 0.83$), but less so with fecundity ($r = 0.57$). Estimates of apparent survival used in estimating λ_H varied little when compared with fecundity estimates (Table 9, Fig. 8b, c). This was also apparent when estimates of apparent survival and fecundity for owls ≥ 3 yr old were compared along the gradient of territories ranked by $\hat{\lambda}_H$; apparent survival appeared to be relatively constant except for owls in territories that had very low fitness (Fig. 9b), whereas fecundity declined (Fig. 9c). This suggested that small changes in apparent survival were responsible for relatively large changes in $\hat{\lambda}_H$.

The combination of effects of landscape habitat characteristics on apparent survival and fecundity (and, hence, habitat fitness potential) can be illustrated by examining territories with relatively high, medium, and low habitat fitness potentials (Fig. 10). There are evident trade-offs in landscape habitat configurations

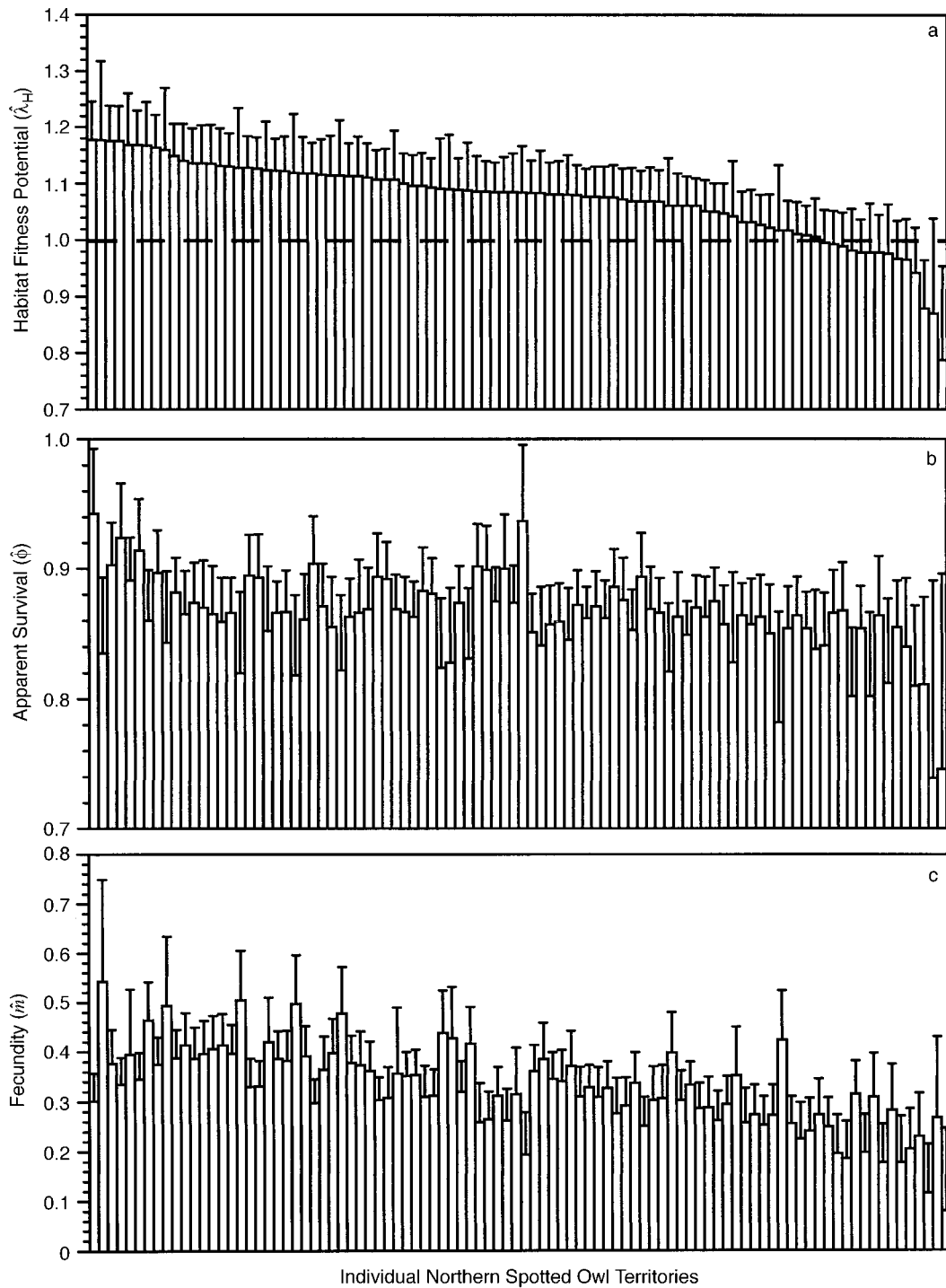


FIG. 9. Northern Spotted Owl territories in northwestern California (a) sorted by descending habitat fitness potential values with (b) corresponding estimates of apparent survival for owls ≥ 3 yr old, and (c) estimates of fecundity for owls ≥ 3 yr old. Each histogram bar is an individual territory. Error bars represent $+2$ SE of the mean. One territory with $\hat{\lambda}_H = 0.44$ was not included, for ease in comparisons.

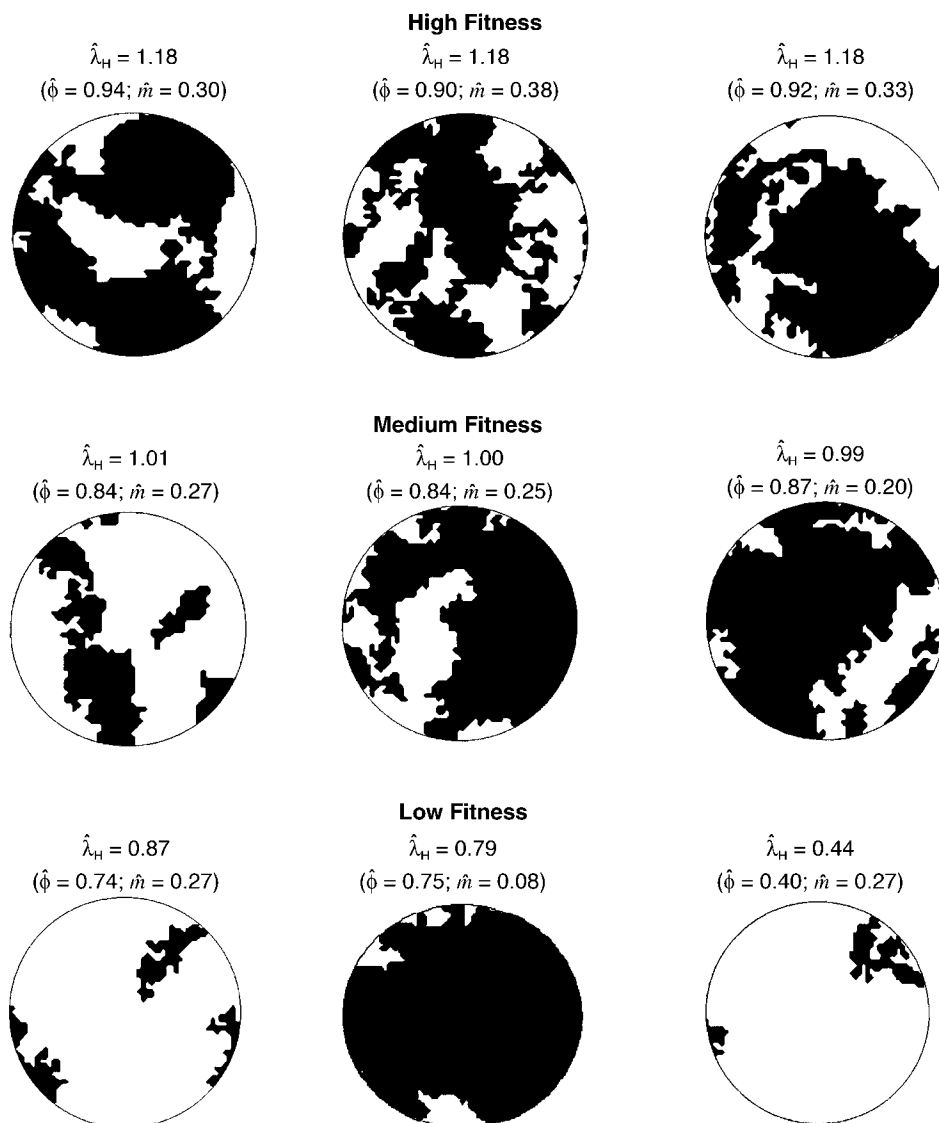


FIG. 10. Landscape habitat characteristics (within 0.71 km radius circles used to define Northern Spotted Owl territories) at three levels of habitat fitness potential in northwestern California. Dark areas are Northern Spotted Owl habitat; white areas are other vegetation types. Estimates of ϕ (apparent survival) and m (fecundity) are for owls ≥ 3 yr old.

within spotted owl territories where survival is maximized by maintaining relatively large core areas of habitat with some edge (see Eq. 34). In contrast, fecundity was maximized by minimizing the core area of spotted owl habitat, maximizing the amount of edge between spotted owl and other habitats, and either minimizing or maximizing the number of discrete patches of spotted owl habitat (see Eq. 35). In territories with high $\hat{\lambda}_H$, it appears that both adult survival and fecundity were high (Fig. 10). In territories with medium and low $\hat{\lambda}_H$, $\hat{\lambda}_H$ was a function of low survival and high fecundity, high survival and low fecundity, or low survival and low fecundity. Thus, the landscape configurations in territories with medium and low values of $\hat{\lambda}$ could maximize either one or the other of the components

used to estimate $\hat{\lambda}_H$, but not necessarily both. In addition, high $\hat{\lambda}_H$ in territories appears to be associated with a mixture of spotted owl habitat vs. other vegetation types (e.g., some degree of heterogeneity). On the other hand, too much homogeneity in either spotted owl habitat or other vegetation types appears to result in low $\hat{\lambda}_H$.

Relative contributions of climatic and habitat variation to population processes

The coefficient of total process variation for apparent survival was 9.5%, based on the weighted mean for either temporal (Table 6) or spatial (Table 9) variation. Spatial process variation accounted for most of the total process variation in apparent survival (Table 11). The

TABLE 11. Sources of process variation in apparent survival and reproductive output in Northern Spotted Owls in northwestern California, with 95% confidence intervals in parentheses.

Type of variation	Survival probability		Reproductive output	
	Estimate	Percentage	Estimate	Percentage
Total process				
$\hat{\sigma}_{\text{total}}^2$ †	0.0070 (0.0021, 0.0227)	100.0	0.0593 (0.0215, 0.1635)	100.0
$\hat{\sigma}_{\text{temporal}}^2$	0.0013 (0, 0.0087)	18.6	0.0291 (0.0105, 0.1128)	49.1
$\hat{\sigma}_{\text{spatial}}^2$	0.0057 (0.0003, 0.0165)	81.4	0.0302 (0.0090, 0.1017)	50.9
Modeled process				
$\hat{\sigma}_{\text{model}}^2$	0.0056 (0.0041, 0.0077)	100.0	0.0525 (0.0141, 0.1959)	100.0
$\hat{\sigma}_{\text{climate}}^2$	0.0013 (0, 0.009)	23.2	0.0291 (0.0105, 0.1128)	55.4
$\hat{\sigma}_{\text{habitat}}^2$	0.0038 (0.0029, 0.0052)	67.9	0.0226 (0.0058, 0.0882)	43.1
$\hat{\sigma}_{\text{age}}^2$	0.0005 (0.0001, 0.0269)	8.9	0.0008 (0.0002, 0.0040)	1.5

† Total variation accounted for by temporal and spatial process variation only (residual variation not included).

variation in apparent survival that was accounted for by the climate and habitat models ($\hat{\sigma}_{\text{model}}^2$) explained 80.0% of the total process variation ($\hat{\sigma}_{\text{model}}^2/\hat{\sigma}_{\text{total}}^2$ in Table 11), suggesting that these influences were primarily responsible for the observed process variation in this study. This left little residual variation (20.0%) to be explained by other factors not modeled here. Based on model selection, both climate and habitat influences appeared to be important in explaining variation in apparent survival; the additive model $\{\phi_{a2'+P_E+T_E+LSOCOR+LSOEDG+SODIS+(SODIS)^2}\}$ containing both climate and habitat effects was ≥ 52 times as likely (based on Akaike weights) as either the habitat-only

model $\{\phi_{a2'+LSOCOR+LSOEDG+SODIS+(SODIS)^2}\}$ or the climate-only model $\{\phi_{P_E+T_E}\}$ (Table 12).

Spatial and temporal process variation accounted for roughly equal amounts of the total process variation in reproductive output (Table 11). The coefficient of total process variation was 39.7–40.5%, depending on whether we used the weighted mean for temporal (Table 6) or spatial (Table 9) variation. The variation in reproductive output that was explained by the climate and habitat models ($\hat{\sigma}_{\text{model}}^2$) accounted for 88.5% of the total observed process variation ($\hat{\sigma}_{\text{model}}^2/\hat{\sigma}_{\text{total}}^2$ in Table 11). Again, little residual variation (11.5%) was left to be explained by factors other than

TABLE 12. Comparison of climate, habitat, and combined climate and habitat models for apparent survival and reproductive output in Northern Spotted Owls in northwestern California. Models with problems in identifiability of parameters are not included (see Appendix B).

Model	AICc	K	ΔAICc_i	w_i
Apparent survival (ϕ)				
$\phi_{a2'+(P_E+T_E)+(LSOEDG+SODIS)+LSOCOR+(SODIS)^2}$	1121.46	16	0.00	0.627
$\phi_{a2'+P_E+T_E+LSOCOR+LSOEDG+SODIS+(SODIS)^2}$	1124.23	12	2.77	0.157
$\phi_{a2'+(P_E+T_E)+(LSOEDG)+LSOCOR+SODIS+(SODIS)^2}$	1125.42	14	3.96	0.087
$\phi_{a2'+(P_E+T_E)+(LSOCOR)+LSOEDG+SODIS+(SODIS)^2}$	1125.48	14	4.02	0.084
$\phi_{a2'+(P_E+T_E)+(LSOCOR+LSOEDG)+SODIS+(SODIS)^2}$	1126.87	16	5.41	0.042
$\phi_{a2'+LSOCOR+LSOEDG+SODIS+(SODIS)^2}$	1132.45	10	10.99	0.003
$\phi_{P_E+T_E}$	1136.01	7	14.55	0.000
Reproductive output (R)				
$R_{a2'+P_L^2+LSOCOR+LSOEDG+SONP+(SONP)^2}$	1291.73	11	0.00	0.438
$R_{a2'+P_L^2+LSOCOR+LSOEDG+SONP+(SONP)^2}$	1293.65	12	1.92	0.168
$R_{a2'+P_L^2+LSOEDG+LSOCOR+SONP+(SONP)^2}$	1293.82	12	2.09	0.154
$R_{a2'+P_L^2+LSOEDG+LSOCOR+SONP+(SONP)^2}$	1294.88	13	3.15	0.090
$R_{a2'+P_L^2+[SONP+(SONP)^2]+LSOCOR+LSOEDG}$	1295.75	13	4.02	0.059
$R_{a2'+P_L^2+[LSOCOR+SONP+(SONP)^2]+LSOEDG}$	1296.31	14	4.58	0.044
$R_{a2'+P_L^2+[LSOEDG+SONP+(SONP)^2]+LSOCOR}$	1296.96	14	5.23	0.032
$R_{a2'+P_L^2+[LSOCOR+LSOEDG+SONP+(SONP)^2]}$	1298.42	15	6.69	0.015
$R_{P_L^2}$	1314.72	10	22.99	0.000
$R_{a2'+LSOCOR+LSOEDG+SONP+(SONP)^2}$	1317.31	6	25.58	0.000

TABLE 13. Estimates of slope parameters ($\hat{\beta}$) for habitat and climate covariates, with their coefficients of variation (CV) and 95% confidence intervals, in the best approximating models (including both climate and habitat covariates) of apparent survival ($\hat{\phi}$) and reproductive output (R) for Northern Spotted Owls in northwestern California.

Effect	$\hat{\beta}^\dagger$	CV	95% CI
Model $\{\phi_{a2'+(P_E+T_E)*(LSOEDG+SODIS)+LSOCOR+(SODIS)^2}\}$			
P_E	5.799	0.50	0.093, 911.151
T_E	7.186	0.44	1.005, 13.367
LSOCOR	0.214	0.44	0.031, 0.397
LSOEDG	8.765	0.44	1.212, 16.317
$P_E \times$ LSOEDG	-2.452	0.48	-4.736, -0.168
$T_E \times$ LSOEDG	-2.250	0.57	-4.748, 0.247
SODIS	0.053	0.35	0.017, 0.091
$P_E \times$ SODIS	-0.060	0.69	-0.142, 0.021
$T_E \times$ SODIS	-0.158	0.45	-0.298, -0.018
SODIS ²	-0.091	0.49	-0.178, -0.003
Model $\{R_{a2'+P_L^2+LSOCOR+LSOEDG+SONP+(SONP)^2}\}$			
P_L^2	-0.003	0.19	-0.004, -0.002
LSOCOR	-0.075	0.48	-0.144, -0.005
LSOEDG	0.495	0.26	0.245, 0.744
LSONP	-0.146	0.44	-0.273, -0.019
LSONP ²	0.012	0.56	-0.001, 0.025

† Based on rescaled climate covariates: $P_E/10$ and $T_E/100$. Habitat covariates are re-scaled as in Table 1.

climate or habitat. The importance of both temporal and spatial process variation in explaining total process variation was supported by model selection. Model $\{R_{a2'+P_L^2+LSOCOR+LSOEDG+SONP+(SONP)^2}\}$, which contained the additive effects of the best climate and habitat models, was >400 times as likely as either model $\{R_{P_L^2}\}$, with climate effects only, or model $\{R_{a2'+LSOCOR+LSOEDG+SONP+(SONP)^2}\}$, with habitat effects only (Table 12).

Effects of variation in climate on habitat quality.—

In survival estimation, we used a structure on recapture probabilities (p) of p_{c*ELEV} for all models that differed from the structure of p_{s+c} used in models relating survival to climatic covariates. We used the p_{c*ELEV} structure in this analysis because it was used in models relating survival to habitat covariates, and it still incorporated some of the structure of p 's used in the climate models.

Four models supported interactions between climate and habitat in apparent survival better than did model $\{\phi_{a2'+P_E+T_E+LSOCOR+LSOEDG+SODIS+(SODIS)^2}\}$, which included only additive effects between climate and habitat (Table 12). However, there were a number of problems encountered in modeling interactions with these data, because the form of the sample data did not allow for unique identifiability of parameters in models that contained certain interactions (see Appendix B). Thus, the best approximating model for apparent survival was $\{\phi_{a2'+(P_E+T_E)*(LSOEDG+SODIS)+LSOCOR+(SODIS)^2}\}$ (Table 12), which contained interactions between both climate covariates and habitat covariates LSOEDG and SODIS (Table 13). Based on Akaike weights, this model was four times as likely as the additive model containing both

climate and habitat covariates but no interactions between the two sets of covariates (Table 12). Inferences from model $\{\phi_{a2'+(P_E+T_E)*(LSOEDG+SODIS)+LSOCOR+(SODIS)^2}\}$ were very limited because of the problems encountered in modeling interactions and the removal of the quadratic effect from any interactions with climate covariates (see Appendix B). The precision of slope parameters in model $\{\phi_{a2'+(P_E+T_E)*(LSOEDG+SODIS)+LSOCOR+(SODIS)^2}\}$ (Table 13) was similar to the best approximating models that included only climate effects or only habitat effects.

Model $\{\phi_{a2'+(P_E+T_E)*(LSOEDG+SODIS)+LSOCOR+(SODIS)^2}\}$ indicated that higher quality Northern Spotted Owl habitat, as described by the habitat covariates, buffered the adverse effects of climate (Fig. 11). In Fig. 11, we arbitrarily defined “good” habitat as habitat covariates (SOCOR = 65 ha of interior forest, SOEDG = 9 km, SODIS = 100 m) yielding $\hat{\phi} = 0.91$; “medium” habitat as habitat covariates (SOCOR = 25 ha, SOEDG = 9 km, and SODIS = 50 m) yielding $\hat{\phi} = 0.86$; and “poor” habitat as habitat covariates (SOCOR = 5 ha, SOEDG = 6 km, and SODIS = 50 m) yielding $\hat{\phi} = 0.78$ when climate effects are ignored. The effects of interactions between climate and habitat covariates were examined in this more qualitative manner along a hypothetical climate gradient, because of the poor support for the best approximating model, $\{\phi_{a2'+(P_E+T_E)*(LSOEDG+SODIS)+LSOCOR+(SODIS)^2}\}$. The climate gradient used in Fig. 11 was based on data within the range of conditions observed during the study.

Of the three different habitat qualities, apparent survival declined 7.1% in good habitat as the climate gradient progressed from an optimal warm, dry spring to a cold, wet spring. Along the same climate gradient,

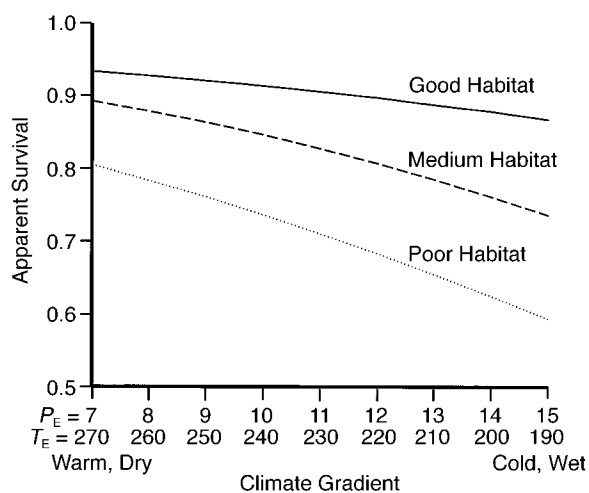


FIG. 11. Effects of climate on apparent survival of Northern Spotted Owls in three qualities of habitat in northwestern California. Predicted effects on apparent survival are based on model $\phi_{a2'+(P_E+T_E)*(LSOEDG+SODIS)+LSOCOR+(SODIS)^2}$. The climate gradient is a function of both P_E and T_E . Habitat quality is defined in Results: Effects of variation in climate on habitat quality.

apparent survival decreased 17.5% and 26.3% in medium and poor habitats, respectively (Fig. 11). These results indicate that individuals in good habitat had a much slower decline in survival as climatic conditions deteriorated than did individuals in poorer habitats. Thus, high habitat quality, as defined in this study, buffered the survival of territory occupants from the negative effects of climate. Aspects of habitat quality that buffered apparent survival were the habitat covariates LSOEDG (\log_e transform of SOEDG) and SO-DIS, both of which describe patch configurations of mature and old-growth forest. In addition, predicted estimates of survival had $\hat{\sigma}_{\text{temporal}}^2 = 0.0005$ for "good" habitat, $\hat{\sigma}_{\text{temporal}}^2 = 0.0029$ for "medium" habitat, and $\hat{\sigma}_{\text{temporal}}^2 = 0.0053$ for "poor" habitat. Thus, survival in "poor" habitat varied more than 10 times as much as survival in "good" habitat under the same conditions.

The best approximating model for reproductive output, $\{R_{a2'+P_L^2+LSOCOR+LSOEDG+SONP+(SONP)^2}\}$, was an additive model that included both climate and habitat covariates (Table 12). Based on the best approximating model, interactions between the climate and habitat covariates were not supported by the data. Based on Akaike weights, model $\{R_{a2'+P_L^2+LSOCOR+LSOEDG+SONP+(SONP)^2}\}$ was more than twice as likely as the next ranked model, which included interactions between the climate covariates and the habitat covariate LSOCOR (the \log_e transform of SOCOR) (Table 12). The selection of model $\{R_{a2'+P_L^2+LSOCOR+LSOEDG+SONP+(SONP)^2}\}$ suggested that reproductive output of individuals was similarly affected by climate changes, regardless of the quality of the habitats they occupied. In other words, if habitat were classified similar to Fig. 11, then slopes of the three lines would be parallel for reproductive output and would differ by the slope parameter for P_L^2 (Table 13).

DISCUSSION

Magnitude of temporal process variation in life history traits

Based on coefficients of temporal process variation, survival of adult Northern Spotted Owls varied the least, whereas recruitment varied the most, >15 times more than adult survival. In a variable environment, Northern Spotted Owls appear to follow a pattern in life history traits in which (1) adult survival is high with low temporal variation, (2) recruitment is low with high temporal variation, and (3) survival of territory holders and recruitment into the territorial population appear to be negatively correlated. Variation in reproductive output was intermediate between survival and recruitment, and was characterized more by infrequent catastrophes than by regular rises and falls in rates, such as in recruitment. Such a pattern suggested that spotted owls may employ a life history strategy similar to "bet hedging," by which selection favors adult survival at the expense of present fecundity when the re-

cruitment of offspring is unpredictable from year to year (Stearns 1976). This strategy does not necessarily impose a cost of reproduction when negative correlations exist between survival and recruitment, based on simulations by Benton and Grant (1996). However, the negative correlation in our study includes both process and sampling variation because of the sampling covariances between survival and recruitment estimates.

At least six scenarios underlie the bet-hedging tactic (Boyce 1988), and application of the observed pattern in Northern Spotted Owls to any one of these scenarios (or other patterns in life history traits) is premature without additional work. In a broad sense, the life history pattern exhibited by this owl does follow the trend of increased iteroparity in response to environmental stochasticity (Orzack and Tuljapurkar 1989), in which a long reproductive life-span allows for some eventual recruitment of offspring even if that recruitment does not occur each year.

Role of climatic variation in temporal process variation of life history traits

After accounting for sampling and demographic variation, climate explained almost all of the temporal process variation observed in the life history traits estimated for Northern Spotted Owls. This suggested that temporal variation in these populations may be driven primarily by annual variation in climate. The lack of sex and age effects within years was consistent with previous analyses of these data (Franklin et al. 1996b). The climate models developed here have the advantage of being empirically based, with good statistical rigor. However, the complexity of these models depended on the amount of available data and the observed climatic variation during the study. We expect that future parsimonious models will support additional climatic covariates with additional years of study. Therefore, the climate models that we developed to describe environmental variation here should be considered first approximations.

The climate models that we described do not demonstrate cause and effect. Unfortunately, neither the climate models nor the effects that they describe can be adequately tested with experiments because of the uncontrollable nature of climatic variation. Model validation is possible only through additional observations within the Klamath province of the Pacific Northwest, or by using a similar approach in other study areas. This also makes it difficult to test forecasts of the model back in time; no adequate estimates of reproductive output exist for northern California prior to 1983, and survival probabilities and recruitment rates were not estimated prior to this study. With additional years of data, we predict that the form of the climate models may change, as well as the importance of some of the covariates.

Based on the climate models selected, the period when life history traits for Northern Spotted Owls are

generally affected by climate is during the spring rather than the winter. In terms of energetic costs, owls have their highest daily energy expenditures during the breeding season rather than the winter (Wijnandts 1984, Meczewa 1986). A plausible mechanism during this energetically stressful period is that precipitation may decrease hunting efficiency, prey activity, and prey populations, as we proposed during the formulation of the models that were ultimately selected as explanations of climatic variation. Extreme climate conditions during the early nesting period may exacerbate an energetic stress on an individual by decreasing its time to starvation. At a body mass of 550–650 g (Blakesley et al. 1990), Northern Spotted Owls would reach starvation levels, about 25% of their body mass (Handrich et al. 1993), within about 8 d at maintenance metabolic rates (based on an allometric equation in Kirkwood 1981). This rate is similar to those observed for captive Barn Owls, *Tyto alba* (Handrich et al. 1993). As energetic stress due to reproductive effort is added to maintenance metabolic rates, time to starvation will decrease and, hence, will increase the potential for lowered survival probabilities. In several other species of raptors, extremes in precipitation affect reproductive output, after young have hatched, by preventing efficient foraging by adults, reducing prey supplies, and causing direct mortality of young through chilling (Schipper 1979, Davis and Newton 1981, Village 1986, Mearns and Newton 1988, Kostrzewa and Kostrzewa 1990). These are the same mechanisms that were proposed for our hypothesized climate model, which was selected as the most appropriate model. However, we have the least confidence in the ability of the selected climate model to explain variation in reproductive output, because of the lack of additional extreme values and the absence of positive extreme values (e.g., very high reproductive output). Although the selected model may adequately explain negative effects of climate, this model does not encompass unknown climate effects that positively affect reproductive output.

The winter period was only important for explaining variation in recruitment. The negative effects of winter precipitation may have resulted through impacts on survival of young experiencing their first year of independence. The positive relationship of recruitment with spring precipitation supported the prediction that factors negatively affecting survival of territory holders would positively affect recruitment if floaters were present in sufficient numbers in the population; floaters would fill immediate vacancies resulting from the deaths of territory holders.

Long-term consequences of climatic variation on population growth and stability

The pattern of variation in rates of population change under the 30-yr climate trace suggested that Northern Spotted Owl populations may experience periods of decline caused solely by climatic variation. However,

the inferences that we made here are relevant only if conditions other than climate remain the same as when the models were developed. Inferences here do not include what will occur, regardless of changes in other conditions that may affect Northern Spotted Owl populations. Thus, even if habitat conditions remain unchanged, Northern Spotted Owl populations may experience declines. Whether or not these long periods of decline would lead to extinction is unknown.

Despite the highly variable nature of recruitment, estimates of rates of population change have very low coefficients of temporal process variation. Recruitment may be the dynamic that controls Northern Spotted Owl populations, because of its highly variable nature. Noon and Biles (1990) and Lande (1991) found λ estimated for Northern Spotted Owls with deterministic, empirically based matrix models to be highly sensitive to small changes in adult survival. However, this type of model sensitivity does not necessarily imply that survival contributes much to variation in rates of population change (Boyce 1994) and, hence, to population dynamics. We argue that rates of population change in Northern Spotted Owls are at least as sensitive to recruitment as to survival, in the presence of temporal variation. Survival of ≥ 1 -yr-olds exhibits little temporal process variation and, thus, sets the relative magnitude for rates of population change (e.g., λ can never be less than the ≥ 1 -yr-old survival rate in Eq. 21). In this study, variation at or above the baseline value of λ set by ≥ 1 -yr-old survival is determined by recruitment rates. Therefore, variation in recruitment determines the variation in λ above its relative magnitude set by ≥ 1 -yr-old survival. For this reason, rates of population change were more correlated with recruitment in forecasts with the 30-yr climate trace than with ≥ 1 -yr-old survival. If certain long-term climate trends can cause negative rates of population change, as suggested in this study, then climatic variation has the potential to negatively affect Northern Spotted Owl populations, even if no further habitat loss occurs. Thus, we conclude that temporal variation, as influenced by climate, is an additional factor to strongly consider in developing conservation strategies.

Most conservation plans for the Northern Spotted Owl assume that their overall population will decline from habitat loss and then stabilize as habitat amount eventually stabilizes (Gutiérrez et al. 1996). However, as populations decrease in size, the effects of catastrophes on life history traits will gain increasing importance in determining rates of population change. Catastrophic events can be characterized as density-independent, physical catastrophes (Boyce 1984) that may reduce the number of territorial holders in an unpredictable manner. The extent to which these catastrophic events in parameters affect the population as a whole is dependent on population size, spatial distribution, and regulatory mechanisms (Mangel and Tier 1993). In addition, climatic conditions that will cata-

strophically affect all parameters simultaneously over several years will occur with some unknown probability at some unpredictable time. Such a "megacatastrophe" will have a much stronger impact on a reduced population (Lande 1993).

Effects of landscape habitat characteristics on life history traits

There are many levels of uncertainty in the estimates of survival, reproductive output, and, hence, habitat fitness potential. First, there is model uncertainty, which was expressed in terms of the Akaike weights. Whenever a model is developed from empirical data, there is uncertainty as to whether the model selected is indeed the best model. Second, there was some data dredging used to select a best approximating model for both survival and reproductive output. However, data dredging here was limited, and was closer to the a priori approach rather than an approach based on unlimited data exploration. Third, there is the issue of scale. These results are scale dependent in both habitat and landscape extent. In terms of habitat within a territory scale, scale is relevant only to discrete habitat patches and not to within-patch variation. In addition, landscape extent in this study is limited to the territory scale and not to larger or smaller scales. Therefore, differences (or lack thereof) can only be attributed to the territory scale. Other scales such as a home range scale or cluster of territories may produce different results and should be appropriately analyzed. Fourth, there is uncertainty in the classifications of habitats and their distribution (see also Mowrer et al. 1996). Although we were able to classify Northern Spotted Owl habitat with a high level of certainty, we were unable to classify other habitats well. In addition, we were unable to determine whether estimated habitat patch configurations accurately matched those existing on the ground.

Although these levels of uncertainty do not negate the results of this study, our results should be considered more as working hypotheses from an observational study that require further experimental verification. Clearly, part of the value of this work is in reducing the number of potential landscape configurations that might affect Northern Spotted Owls in this area to a small subset, which then can form the basis of field experiments.

The habitat covariates in the best approximating models for apparent survival and reproductive output explained a large proportion of spatial process variation in these two life history traits. The best approximating models explaining variation in both apparent survival and reproductive output contained two covariates in common: the amount of core spotted owl habitat and the amount of edge between spotted owl and other habitats. However, the relationship between these two life history traits was reversed with respect to the amount of core spotted owl habitat; apparent survival was pos-

itively associated with the amount of core habitat, whereas reproductive output was negatively associated with core habitat. However, both life history traits were positively associated with the amount of edge between spotted owl and other habitats. In addition, the models relating habitat to both survival and reproductive output were strongly sensitive to the amount of edge.

Apparent survival among territories appeared to vary little in terms of spatial process variation. There may be several reasons for this low variation in survival among territories. First, high sampling variation of among-territory estimates increased the uncertainty in estimating process variation, even though some extremes (survival below 0.80) were noted on certain territories. Second, Northern Spotted Owls may only select a territory to defend that will promote high survival (T. Shenk, *personal communication*). Hunter et al. (1995) found that, at the territory scale of this study, areas used for nesting and roosting by Northern Spotted Owls in our study area contained larger amounts of mature and old-growth forests than did random areas. Thus, an owl has the following options: it defends an area that contains sufficient mature and old-growth forest to maintain high survival, it does not bother defending a territory, it disperses, or it dies. Once the owl selects a territory to defend, variation in its expected survival rate should be low if the habitat is of sufficient quality. We call this the "all-or-nothing defense" hypothesis. Our surveys included only owls exhibiting territorial behavior; hence, we estimated survival only for territorial individuals. Owls that did not acquire territories were not included in the sample because they were rarely found.

The spatial process variation in reproductive output among spotted owl territories was large compared with variation in survival. Reproductive output was dependent on a high degree of spotted owl habitat edge, a low amount of core area, and either few or many patches of spotted owl habitat. Although a high degree of spotted owl habitat edge implies large amounts of spotted owl habitat within a finite territory size, the requisite amount of edge can be also be achieved with minimal amounts of interior spotted owl habitat and numerous small patches or a highly convoluted single patch that minimizes the amount of interior habitat. However, low amounts of spotted owl habitat within a territory will not supply the high degree of edge predicted to support high reproductive output.

Gutiérrez (1985) outlined four hypotheses as alternative explanations for why Northern Spotted Owls require mature and old-growth forests, three of which are relevant to the "all-or-nothing" defense hypothesis: predation, thermoregulation, and sufficiency of prey. The predation hypothesis suggests that mature and old-growth forests provide sufficient cover for spotted owls to avoid predation from other avian predators such as Great Horned Owls, which are a primary predator of Northern Spotted Owls (Johnson 1992). Carey et al.

(1992) found densities of Great Horned Owls encountered near Northern Spotted Owls to be highest in the mixed-conifer forests of the Klamath Mountains province in southern Oregon. Great Horned Owls hunt primarily using vision (Johnsgard 1988) and probably lack the auditory morphology used by spotted owls to hunt effectively by sound alone in a vertically structured habitat such as mature and old-growth forests (see Volman and Konishi 1990). Therefore, Northern Spotted Owls may use areas of mature and old-growth forests that are not useable by Great Horned Owls, thus minimizing their risk of predation.

Under the thermoregulation hypothesis, mature and old-growth forests provide a more stable microclimate, and the complex vertical structure of these forests provides protection from inclement weather (Forsman et al. 1984, Ting 1998).

Under the prey hypothesis, mature and old-growth forests provide an abundant and accessible source of prey not available in other habitats. However, the primary prey species of Northern Spotted Owls in this study area is the dusky-footed woodrat (*Neotoma fuscipes*), which is most abundant in brush areas that are inaccessible to the owl, and has low abundance in mature and old-growth forests (Sakai and Noon 1993). Another important prey item, the northern flying squirrel (*Glaucomys sabrinus*), achieves high densities in both mid- and late-seral stage forests in northeastern California (Waters and Zabel 1995) and southern Oregon (Carey et al. 1992, Rosenberg and Anthony 1992). Northern flying squirrels have about one-half of the biomass of woodrats (Ward et al. 1998), and owls eating a high proportion of woodrats have smaller home ranges than those eating flying squirrels (Zabel et al. 1995). In addition, spotted owls in the Klamath Mountains province hunt along edges of mature and old-growth forests (Zabel et al. 1995). Ward et al. (1998) suggested that some degree of fragmentation within their territories may provide an energetic benefit to the owls; Northern Spotted Owls in California first selected dusky-footed woodrats over other species, and then selected foraging areas near ecotones between late- and early-seral forests where woodrats were both abundant and accessible. Our results corroborate this. Woodrats are probably more accessible at ecotones because of their lateral nocturnal movements from early-seral stages and other vegetation types with dense understories to late-seral stages with more open understories (Sakai and Noon 1997). By remaining within late-seral stage forests at these ecotones, spotted owls may avoid predation by Great Horned Owls while gaining access to prey in the ecotones (Zabel et al. 1995). Thus, sufficient core area interspersed with other vegetation types may provide protection from predators while offering a source of large, accessible prey. In addition, White (1996) found that owls on our study area that successfully fledged young ate significantly more large prey (mostly woodrats) than did unsuccessful

owls. Thus, there appears to be a direct link from landscape habitat configuration, to the ability of owls to successfully capture large prey, to reproductive output. Here, we were able to establish a link between landscape habitat configuration on individual territories and survival and reproductive output of owls. This link seems plausible, based on interactions among owls, woodrats, and the juxtaposition of habitats supporting both.

At some level, all three of the hypotheses outlined by Gutiérrez (1985) probably account for the use of mature and old-growth forests by spotted owls, and also support the "all-or-nothing defense" hypothesis. For example, the presence of sufficient core habitat may allow Northern Spotted Owls to actively defend an area while avoiding predation, whereas sufficient edge may provide foraging opportunities where prey are both abundant and accessible. The age effect seen in both survival and reproductive output may be due to differences in the ability of the two age classes to survive (such as experience or hunting ability), and physiological differences in terms of reproduction, rather than differences in habitat. Interactions between age of the owls and habitat were not supported by the best approximating model; apparently, younger birds were not necessarily relegated to poorer habitat that lowered their potential for survival.

Effects of landscape habitat on fitness

Estimates of habitat fitness potential are female-based and a territory must necessarily be occupied by a pair in order for habitat fitness potential to be realized. Territory occupancy is best estimated where detectability of birds can be modeled, such as in a capture-recapture framework. We were unable to estimate occupancy because detectability, territory abandonment, and territory reoccupation were all confounded. Although ad hoc estimators could be used, we chose not to do this because such estimators ignore detectability.

There appears to be a dichotomy between the effects of landscape habitat characteristics on survival and on reproductive output. Survival seems positively associated with some level of interior mature and old-growth coniferous forest and the edge between those forests and other vegetation types, whereas reproductive output is enhanced by convoluted edge with little interior habitat. Thus, there is evidently a trade-off in potential need for interior habitat and potential need for ecotones within a territory. This trade-off was expressed in estimates of habitat fitness potential in Northern Spotted Owls, where high fitness balanced having both core owl habitat for maintaining high survival and having some mosaic of older forest and other vegetation types for maximizing reproduction and maintaining high survival. This mosaic was expressed as small patches of other vegetation types with convoluted edges, dispersed within and around a main patch of mature and old-growth forest (Fig. 10). Ex-

amining the effects of just one of the components of habitat fitness potential as a surrogate for fitness would be misleading. A landscape pattern within a territory that promotes either high survival or high fecundity alone does not necessarily promote high fitness (Fig. 10). McGraw and Caswell (1996) found a similar problem in relating lifetime reproductive output with individual fitness of the European Sparrowhawk (*Accipiter nisus*); lifetime reproductive output was a poor surrogate for fitness.

Based on differences in estimates of spatial process variation, habitat-related variation in fecundity is probably most responsible for variation in fitness. Reproductive output had much higher spatial variation than did survival. However, this qualitative assessment is tempered by the fact that Leslie matrix models, such as those used here to estimate fitness, tend to be most sensitive to changes in adult survival (Noon and Biles 1990). Low spatial variation in survival can still have large effects on estimates of fitness because the matrix model used to estimate habitat fitness potential tends to be sensitive to small changes in adult survival (Noon and Biles 1990). The high positive correlation between point estimates of survival and habitat fitness potential suggests that changes in habitat fitness potential were tracking smaller changes in survival.

Thus, we propose that, once a territory with suitable habitat characteristics is selected for defense, individuals enjoy high survival. The quality of that territory then determines the reproductive output of individuals. Habitat fitness potential is then determined more by within-territory landscape configurations that control reproductive output than by survival rates, as long as the landscape configuration controlling survival remains intact.

Forest fragmentation and fitness

In conservation biology, forest fragmentation generally has a negative connotation, especially with respect to potentially interior forest species such as the Northern Spotted Owl (Wiens 1994). In the early years of wildlife management, edge (and hence fragmentation) was often promoted as generally beneficial for wildlife (Yoakum and Dasmann 1971). Fragmentation can be beneficial for populations of some species and deleterious for others. Andr en (1992) found that densities of five sympatric species of corvids differed along a gradient of landscape fragmentation; differing degrees of fragmentation were beneficial to some species but not to others. Other organisms appear to react little to fragmentation at different scales (Beyer et al. 1996, Johannesen and Ims 1996).

The mosaics of older forest and other vegetation types that we observed on spotted owl territories resulted from human-caused (e.g., logging) and natural disturbances (e.g., fire), as well as edaphic and topographic factors. Heterogeneity of vegetation types within spotted owl territories in the Klamath Mountains

province has been determined by both past and present landscape disturbances. Past disturbances were governed primarily by wildfires, and present disturbances by logging. Thus, our measures of fragmentation do not strictly conform to the definition of Wiens (1989b) for habitat fragmentation, because the mosaics that we observed were not entirely due to conversion of continuous habitat into smaller patches through some disturbance process. Although edge between mature and old-growth forest and other vegetation types appeared to be a key habitat component, we emphasize that this component is still poorly understood because of our inability to discriminate among other vegetation types. For example, edge, as we measured it, could represent ecotones with a clearcut from logging, or an oak forest resulting from edaphic conditions.

Two key questions are (1) to what degree are the mosaics observed in Northern Spotted Owl territories having a high habitat fitness potential due to fine-scale fragmentation of mature and old-growth forest from disturbance; and (2) can logging practices mimic this fine-scale fragmentation? Current logging practices probably do not generate the type of mosaic that we observed in high-fitness territories; clear-cut logging leaves large, regularly shaped patches with clean edges. Fire disturbance, on the other hand, tends to leave smaller, irregularly shaped patches having convoluted edges (see Agee 1991). In addition, fire disturbance leaves a variety of seral stages based on the frequency of low, moderate, and severe burns over time. However, it is poorly understood how fire shaped past landscape mosaics. The appearance of landscape mosaics prior to fire suppression and logging would greatly increase our ability to develop silvicultural practices that might be neutral or possibly beneficial to Northern Spotted Owls in the Klamath Mountains province. In addition, our definition of edge needs to be further examined in terms of which seral stages adjacent to mature and old-growth forest most strongly affect spotted owl reproduction.

Are Northern Spotted Owls ideal-free or ideal-despotic?

The presence of spatial process variation among habitat fitness potentials estimated for individual territories suggested that Northern Spotted Owls follow an ideal-despotic distribution. Although the coefficient of spatial process variation for habitat fitness potential was small (5%), spatial process variation in habitat fitness potential differed from zero and there was a clear gradient in habitat fitness potential. However, extremes were not great in terms of relative magnitude. Unfortunately, no other studies have directly estimated habitat fitness potential for a species with a life history similar to that of the Northern Spotted Owl. The closest was McGraw and Caswell (1996), who estimated individual fitness for European Sparrowhawks, which ranged from 0.75 to 3.00. However, these estimates of fitness were on an individual basis rather than a habitat

basis, and comparisons with our estimates are difficult. If reproductive output is considered the primary driving force in defining habitat fitness potential, then the larger spatial process variation in reproductive output could be considered sufficient evidence that Northern Spotted Owls follow an ideal-despotic distribution. The possibility also exists that habitat fitness potential has been reduced on spotted owl territories because of past changes in the landscape caused by logging. To assess this possibility requires examination of the patch characteristics on territories with different estimated habitat fitness potentials, e.g., assessing the source and timing of disturbance that created other habitats within the mature and old-growth forest matrix.

An ideal-despotic distribution suggests that there is a source-sink relationship among Northern Spotted Owl territories. Territories with habitat fitness potentials >1 act as sources of recruits, whereas territories with habitat fitness potentials <1 act as sinks, in that birth rates by individuals in those territories do not compensate for mortality (Pulliam 1988). However, source-sink models are usually based on discrete habitats. Northern Spotted Owls, and probably a number of other species as well, seem to follow a continuous gradient of habitat quality in which territories may be considered sources at one end of the gradient and sinks at the other end with a number of territories in between that can be relative sources or sinks, or simply balance birth and death rates with $\lambda_H \approx 1$. Regardless, territories at one end of the spectrum are those that contribute surplus recruits to the population, whereas those at the other end may act as sinks if occupied on a regular basis.

An important but unresolved question is: how does habitat fitness potential, λ_H , relate to the overall population rate of change (λ)? If a 1:1 correspondence is assumed, the weighted average of habitat fitness potential that we estimated would be a measure of the overall population rate of change in the absence of temporal variation. In this study, the estimate of λ would be 1.075, the weighted mean of λ_H , which indicates a growing population. On the other hand, the rate of population change estimated using more conventional means was $\hat{\lambda} = 1.009$, which indicates that this same population was stationary over the same time period. The reason for the discrepancy between the two estimates is due to occupancy. For λ_H and λ to be roughly equivalent, all territories need to be occupied. Therefore, to understand the relationship between λ_H and λ , some measure of occupancy on territories needs to be included in some function that also includes λ_H . Such a function might be simply $\lambda = (\lambda_H)(p_o)$, where p_o is some measure of occupancy. However, as discussed previously, we were unable to estimate occupancy appropriately.

Although theoretical models have been developed integrating ideal-free and ideal-despotic distributions with source-sink dynamics (Pulliam and Danielson

1991), they include only discrete habitats and use only reproductive success as a measure of habitat quality. Thus, these models need to be extended to include continuous gradients of habitat quality and estimates of survival.

Sources of variation in Northern Spotted Owl populations

Based on estimated total process variation, apparent survival varied the least, whereas reproductive output varied the most during this study. Two factors, climate and habitat, appeared to have the greatest effect on these two life history traits. However, the effects of these two factors were not similar on apparent survival and reproductive output. Apparent survival exhibited more spatial variation than temporal variation, whereas temporal and spatial variation contributed about equally to total observed variation in reproductive output. Based on our results, spatial and temporal variation appeared to operate independently on reproductive output because of the lack of interaction between climate and habitat covariates. Habitat quality did not appear to buffer the effects of climatic variation on reproductive output of individuals. In other words, temporal variation in reproductive output would be similar if habitat quality were uniformly "good" or uniformly "bad" among territories. However, temporal and spatial variation did not appear to be independent in their effects on survival, based on the interactions between the climate covariates and the habitat covariates, edge between mature and old-growth forest, and distance between patches of these forests. As habitat quality decreased, the effects of climatic variation on survival increased.

One source of variation that we did not consider was individual variation, which is a function of phenotypic or genotypic differences among individuals (White 2000). Although age effects were accounted for in the models, they contributed little in explaining total process variation. In reality, age effects probably account for little in terms of individual variation, which is more related to individual fitness. A better expression of individual variation would be variation in true individual fitness, those individuals genetically predisposed to surviving better and producing more offspring and, hence, contributing more to future generations. If an ideal-despotic distribution were operating in spotted owls, then habitat quality, as defined by habitat fitness potential, was probably confounded with individual fitness. Individuals with higher intrinsic fitness would be more competitive (despotic) and able to garner the best resources to ensure that their fitness was realized. Partitioning individual fitness from habitat fitness potential requires identification of genetic or phenotypic traits to allow for separation of individual fitness from fitness bestowed on individuals by habitat quality.

Climatic variation and habitat quality

For apparent survival, the best approximating model included interactions between climate and habitat covariates (SOEDG and SODIS) that described the mosaic of mature and old-growth forests and other vegetation types. There appears to be an optimal type of mosaic that defines high-quality spotted owl habitat. In the face of climatic variation, these areas may also provide a more stable prey base by providing more distinct patches of prey populations and, possibly, greater prey diversity if other habitats are a mosaic of different seral stages. Radio-marked Northern Spotted Owls traverse their home ranges less, and hence expend less energy, in areas of older forest mixed with different seral stages than do owls in areas with similar amounts of older forest mixed with clearcuts (Carey and Peeler 1995). The period when climatic variation affects spotted owls is during the early breeding season, when energetic stress is high. Increased movements would only add to an already stressed energetic burden. In addition, spotted owls may exhaust patches of prey through repeated visits (Carey et al. 1992). Thus, dispersed patches of different vegetation types and seral stages within a matrix of mature and old-growth forest may provide a stable prey resource that buffers against the effects of climate on prey populations and, hence, spotted owls. Although speculative, this argument suggests a link in the interaction of climate and habitat quality, with prey abundance and availability as a potential mechanism behind that interaction. This also suggests that habitat maintenance is essential at landscape scales because excessive loss of key landscape habitat components, such as mature and old-growth forest, can exacerbate the effects of unfavorable climatic conditions on survival.

The best approximating model for reproductive output does not support any interactions between climate and habitat covariates. Climate affects reproductive output during the late breeding season. We surmise that climatic effects during this period could inhibit prey populations or the ability of parents to capture prey for their offspring, or could cause direct mortality of young owls. The lack of interaction between climate and habitat supports the idea that increased precipitation during the late breeding season may directly affect survival of young outs before they fledge and are counted during surveys. However, we cannot discount the possibility that, although these particular data during this time period did not support climate-habitat interactions, they might have been present given a longer time period.

Implications for Northern Spotted Owl population dynamics

Dennis and Taper (1994) and Turchin (1995) define a regulated population as one with a long-term stationary probability distribution of population densities.

This definition implies some mean level of density around which a regulated population fluctuates with some bounded variance (Turchin 1995). Thus, this definition of a regulated population can be rephrased in terms of rates of population change (λ) as *a population with a long-term mean λ of one ($\bar{\lambda} = 1$) that follows some probability distribution with variance σ_{λ}^2* . From this, limitation can be defined as the process that sets long-term $\bar{\lambda} = 1$, and regulation as the process that maintains the population at $\bar{\lambda} = 1$ within σ_{λ}^2 . Density dependence can then be viewed as the dependence of population rates of change on past and/or present population densities (Murdoch and Walde 1989). We were only able to speculate about the role of density-dependent factors with respect to Northern Spotted Owl populations. We did not incorporate density into our analyses, largely because of the problems in detecting density dependence from only 10 yr of field data (see Shenk 1997). The following discussion attempts to integrate simple population dynamics with our empirical evidence on life history traits, their process variation influenced by climate and habitat variation, and their relationship to population rates of change.

Based on estimates of apparent survival and recruitment, the spotted owl population in this study appeared to be stationary ($\bar{\lambda} \approx 1$) during the 10-yr study period. This population was stationary under fluctuating climate conditions and habitat quality that varied spatially, but varied little over time. The stationary nature of the study population suggested that this population was regulated. In addition, temporal process variation in λ for this population was low, suggesting little variation around $\bar{\lambda}$. This evidence suggested a well-regulated population, which may be typical of bird populations (Murdoch 1994), especially raptor populations (Newton 1989c).

Habitat may proximally limit spotted owl populations in northwestern California. Here, we use the term *habitat* in reference to the landscape configurations of mature and old-growth forests at the territory scale, which collectively defined the life history traits and habitat fitness potential. Ultimately, the abundance and availability of prey within spotted owl habitat may limit populations, because the habitat covariates most closely associated with survival and reproduction are best explained in terms of prey abundance and availability. Lack (1954, 1966) argues that food supply ultimately limits avian populations. Newton (1980) extends this argument to limitation in raptor populations. Field experiments using food supplementation of raptors support this argument in terms of reproductive output, which increases with increasing available food (Ward and Kennedy 1996, Wiehn and Korpimäki 1997). Unfortunately, empirical evidence is scant concerning the effects of food supply on survival of territory holders. If habitat configurations within Northern Spotted Owl territories are limiting, then both survival and fecundity may be density dependent *if* habitat selection is density

dependent, as suggested by an ideal-despotic distribution in spotted owls (Morris 1989). However, this idea needs further empirical examination.

Previously, we argued that survival of territorial individuals determines the magnitude of λ in Northern Spotted Owls, whereas recruitment determines temporal variation in λ above the relative magnitude set by survival. In terms of total process variation, survival varied little, relative to reproductive output, over the course of this study. However, most of the variation in survival was based on habitat variation, whereas variation in reproductive output was based equally on climatic and habitat variation. By affecting apparent survival, habitat quality may determine the magnitude of λ , whereas reproductive output and recruitment may determine variation around λ . If habitat conditions remain unchanged, then density-dependent factors (habitat) control the magnitude of λ , and combined density-independent (climate) and density-dependent factors (habitat) control the variation around λ . However, if habitat conditions change, e.g., from less "good" habitat to more "poor" habitat, then density-independent factors influence the variation in survival and, hence, variation around λ . In other words, as habitat quality decreases, density-independent factors become more important in determining variation around λ . Thus, there is probably some range of habitat quality where $\bar{\lambda}$ will remain at 1 but variation around $\bar{\lambda}$ will increase. Theoretically, an increase in variation around $\bar{\lambda}$, with a greater proportion of this variation caused by climate, will increase the probability of extinction (Lande 1993). At some point, lower habitat quality will cause the population to be unregulated (i.e., $\bar{\lambda} < 1$), and it will decline, eventually to extinction.

The argument as to whether a single general factor, such as habitat quality or climate, regulates or limits populations becomes moot when interactions are considered (Holmes 1995). These two factors can increase or decrease in importance, depending on changes in the other factor. We believe that understanding the magnitude, strength, and relative importance of different factors under varying conditions provides a deeper understanding of population dynamics.

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LITERATURE CITED

- Agee, J. K. 1991. Fire history of Douglas-fir forests in the Pacific Northwest. Pages 25–33 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical coordinators. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. Forest Service General Technical Report **PNW-GTR-285**.
- Agee, J. K. 1993. Fire ecology of the Pacific Northwest forests. Island Press, Washington, D.C., USA.
- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petran and F. Csaki, editors. International symposium on information theory. Second edition. Akademiai Kiado, Budapest, Hungary.
- Akaike, H. 1974. A new look at the statistical model identification. IEEE (Institute for Electrical and Electronics Engineers). Transactions on Automatic Control **AC-19**:716–723.
- Allen, J. C. 1976. A modified sine wave method for calculating degree days. Environmental Entomology **5**:388–396.
- Andr n, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology **73**:794–804.
- Arnason, A. N., C. J. Schwarz, and G. Boyer. 1995. POPAN-4: a data maintenance and analysis system for mark-recapture data. University of Manitoba, Winnipeg, Canada.
- Atsatt, P. R., and T. Ingram. 1983. Adaptation to oak and other fibrous, phenolic-rich foliage by a small mammal, *Neotoma fuscipes*. Oecologia (Berlin) **60**:135–142.
- Bajpai, A. C., I. M. Calus, and J. A. Fairley. 1978. Statistical methods for engineers and scientists. John Wiley, New York, New York, USA.
- Barrows, C. W. 1981. Roost selection by spotted owls: an adaptation to heat stress. Condor **83**:302–309.
- Bart, J., and S. Earnst. 1992. Suitable habitat for Northern Spotted Owls: an update. Pages 281–317 in J. Bart, R. G. Anthony, M. Berg, J. H. Beuter, W. Elmore, J. Fay, R. J. Guti rrez, H. T. Heintz, Jr., R. S. Holthausen, K. Starkey,

- and J. C. Tappeiner. Recovery plan for the Northern Spotted Owl: final draft. U.S. Department of the Interior, Washington, D.C., USA.
- Bart, J., and E. D. Forsman. 1992. Dependence of Northern Spotted Owls *Strix occidentalis caurina* on old-growth forests in the western USA. *Biological Conservation* **62**:95–100.
- Beardeley, D., and R. Warbington. 1996. Old growth in north-western California National Forests. U.S. Forest Service Research Paper **PNW-RP-491**.
- Benton, T. G., and A. Grant. 1996. How to keep fit in the world: elasticity analyses and selection pressures on life histories in a variable environment. *American Naturalist* **147**:115–139.
- Berryman, A. A., A. P. Gutierrez, and R. Arditi. 1995. Credible, parsimonious and useful predator–prey models—a reply to Abrams, Gleeson, and Sarvelle. *Ecology* **76**:1980–1985.
- Beyer, D. E., Jr., R. Costa, R. G. Hooper, and C. A. Hess. 1996. Habitat quality and reproduction of Red-cockaded Woodpecker groups in Florida. *Journal of Wildlife Management* **60**:826–835.
- Blakesley, J. A., A. B. Franklin, and R. J. Gutiérrez. 1990. Sexual dimorphism in Northern Spotted Owls from north-western California. *Journal of Field Ornithology* **61**:320–327.
- Blakesley, J. A., A. B. Franklin, and R. J. Gutiérrez. 1992. Spotted owl roost and nest site selection in northwestern California. *Journal of Wildlife Management* **56**:388–392.
- Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology: theory and applications. Pages 35–91 in D. M. Powers, editor. *Current Ornithology*. Volume 11. Plenum Press, New York, New York, USA.
- Blondel, J. 1991. Birds in biological isolates. Pages 45–72 in C. M. Perrins, J.-D. Lebreton, and G. J. M. Hiron, editors. *Bird population studies: relevance to conservation*. Oxford University Press, Oxford, UK.
- Bolsinger, C. L., and K. L. Waddell. 1993. Area of old-growth forests in California, Oregon and Washington. U.S. Forest Service Resource Bulletin **PNW-RB-197**.
- Box, G. E. P., W. G. Hunter, and J. S. Hunter. 1978. *Statistics for experimenters*. John Wiley, New York, New York, USA.
- Boyce, M. S. 1984. Restitution of *r*- and *K*-selection as a model of density-dependent natural selection. *Annual Review of Ecology and Systematics* **15**:427–447.
- Boyce, M. S. 1988. Bet hedging in avian life histories. Pages 2131–2139 in H. Ouellet, editor. *Acta International Ornithological Congress XIX*. Volume 2. University of Ottawa Press, Ottawa, Canada.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* **23**:481–506.
- Boyce, M. S. 1994. Population viability analysis exemplified by models for the Northern Spotted Owl. Pages 3–18 in D. J. Fletcher and B. F. J. Manly, editors. *Statistics in ecology and environmental monitoring*. University of Otago Press, Dunedin, New Zealand.
- Bronson, F. H. 1989. *Mammalian reproductive biology*. University of Chicago Press, Chicago, Illinois, USA.
- Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. *Biometrics* **53**:603–618.
- Burnham, K. P., and D. R. Anderson. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. Pages 16–30 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001: populations*. Elsevier Applied Science, London, UK.
- Burnham, K. P., and D. R. Anderson. 1998. *Model selection and inference: a practical information theoretic approach*. Springer-Verlag, New York, New York, USA.
- Burnham, K. P., D. R. Anderson, and G. C. White. 1995. Model selection strategy in the analysis of capture–recapture data. *Biometrics* **51**:888–898.
- Burnham, K. P., D. R. Anderson, and G. C. White. 1996. Meta-analysis of vital rates of the Northern Spotted Owl. *Studies in Avian Biology* **17**:92–101.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release–recapture. *American Fisheries Society Monograph* **5**:1–437.
- Burns, R. M., and B. H. Honkala. 1990. *Silvics of North America*. Two volumes. Agricultural Handbook 654, U.S. Department of Agriculture, Washington, D.C., USA.
- Carey, A. B. 1991. The biology of arboreal rodents in Douglas-fir forests. U.S. Forest Service General Technical Report **PNW-GTR-276**.
- Carey, A. B., S. P. Horton, and B. L. Bisell. 1992. Northern Spotted Owls: influence of prey base and landscape character. *Ecological Monographs* **62**:223–250.
- Carey, A. B., and K. C. Peeler. 1995. Spotted owls: resources and space use in mosaic landscapes. *Journal of Raptor Research* **29**:223–239.
- 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**:1–17.
- Caswell, H. 1989a. *Matrix population models*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Caswell, H. 1989b. Life-history strategies. Pages 285–307 in J. M. Cherrett, editor. *Ecological concepts*. Blackwell Scientific, Oxford, UK.
- Cézilly, F., A. Viallefont, V. Boy, and A. R. Johnson. 1996. Annual variation in survival and breeding probability in Greater Flamingos. *Ecology* **77**:1143–1150.
- Charlesworth, B. 1970. Selection in populations with overlapping generations. I. The use of Malthusian parameters. *Theoretical Population Biology* **1**:352–370.
- Chatfield, C. 1995. Model uncertainty, data mining and statistical inference. *Journal of the Royal Statistical Society, Series A* **158**:419–466.
- Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* **5**:74–86.
- Cooper, J., and J. R. E. Lutjeharms. 1992. Correlations between seabird breeding success and meteorological conditions on Marion and Gough Islands. *Suid-Afrikaanse Tydskrifvir Wetenskap* **88**:173–175.
- Danchin, E., G. González-Dávila, and J.-D. Lebreton. 1995. Estimating bird fitness correctly by using demographic models. *Journal of Avian Biology* **26**:67–75.
- Davis, P. E., and I. Newton. 1981. Population and breeding of Red Kites in Wales over a 30-yr period. *Journal of Animal Ecology* **50**:759–772.
- Dennis, B., and M. L. Taper. 1994. Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs* **64**:205–224.
- Diggle, P. J. 1988. An approach to the analysis of repeated measurements. *Biometrics* **44**:959–971.
- Dixon, K. R., and T. C. Juelson. 1987. The political economy of the spotted owl. *Ecology* **68**:772–776.
- Draper, N., and H. Smith. 1981. *Applied regression analysis*. Second edition. John Wiley, New York, New York, USA.
- Dykstra, C. R., and W. H. Karasov. 1993. Nesting energetics of House Wrens (*Troglodytes aedon*) in relation to maximal rates of energy flow. *Auk* **110**:481–491.
- ESRI. 1987. *ARC/INFO users manual*. Environmental Systems Research Institute, Redlands, California, USA.
- Fitter, A. H., R. S. R. Fitter, I. T. B. Harris, and M. H. Williamson. 1995. Relationships between first flowering date and temperature in the flora of a locality in central England. *Functional Ecology* **9**:55–60.

- Forsman, E. D. 1980. Habitat utilization by spotted owls in the west-central Cascades of Oregon. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Forsman, E. D. 1983. Methods and materials for locating and studying spotted owls. U.S. Forest Service General Technical Report **PNW-GTR-12**.
- Forsman, E. D., A. B. Franklin, F. B. Oliver, and J. P. Ward. 1996. A color band for spotted owls. *Journal of Field Ornithology* **67**:507–520.
- Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984. Distribution and biology of the spotted owl in Oregon. *Wildlife Monographs* **87**:1–64.
- Franklin, A. B. 1992. Population regulation in Northern Spotted Owls: theoretical implications for management. Pages 815–827 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001: populations*. Elsevier Applied Science, London, UK.
- Franklin, A. B. 1997. Factors affecting temporal and spatial variation in Northern Spotted Owl populations in northwest California. Dissertation. Colorado State University, Fort Collins, Colorado, USA.
- Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. F. Wagner. 1996a. Methods for collecting and analyzing demographic data on the Northern Spotted Owl. *Studies in Avian Biology* **17**:12–20.
- Franklin, A. B., R. J. Gutiérrez, B. R. Noon, and J. P. Ward. 1996b. Demographic characteristics and trends of Northern Spotted Owl populations in northwestern California. *Studies in Avian Biology* **17**:83–91.
- Franklin, A. B., J. P. Ward, R. J. Gutiérrez, and G. I. Gould, Jr. 1990. Density of Northern Spotted Owls in northwest California. *Journal of Wildlife Management* **54**:1–10.
- Freedman, D. A. 1983. A note on screening regression equations. *American Statistician* **37**:152–155.
- Fretwell, S. D., and H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* **19**:16–36.
- Ganey, J. L., R. P. Balda, and R. M. King. 1993. Metabolic rate and evaporative water loss of Mexican Spotted and Great Horned Owls. *Wilson Bulletin* **105**:645–656.
- Gentry, J. B., F. B. Golley, and J. T. McGinnis. 1966. Effect of weather on captures of small mammals. *American Midland Naturalist* **75**:526–530.
- Geographic Resource Solutions. 1996. The California Timberland Task Force: Klamath province mapping pilot study report. California Department of Forestry and Fire Protection, Sacramento, California, USA.
- Goodman, D. 1987. The demography of chance extinction. Pages 11–34 in M. E. Soulé, editor. *Viable populations for conservation*. Cambridge University Press, Cambridge, UK.
- Grant, B. R., and P. R. Grant. 1989. *Evolutionary dynamics of a natural population*. University of Chicago Press, Chicago, Illinois, USA.
- Graybill, F. A., and H. K. Iyer. 1994. *Regression analysis: concepts and applications*. Duxbury Press, Belmont, California, USA.
- Groom, M. J., and N. Schumaker. 1993. Evaluating landscape change: patterns of worldwide deforestation and local fragmentation. Pages 24–44 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Gutiérrez, R. J. 1985. An overview of recent research on the spotted owl. Pages 39–49 in R. J. Gutiérrez and A. B. Carey, technical coordinators. *Ecology and management of the spotted owl in the Pacific Northwest*. U.S. Forest Service General Technical Report **PNW-GTR-185**.
- Gutiérrez, R. J., E. D. Forsman, A. B. Franklin, and E. C. Meslow. 1996. History of demographic studies in the management of the Northern Spotted Owl. *Studies in Avian Biology* **17**:6–11.
- Gutiérrez, R. J., A. B. Franklin, and W. S. LaHaye. 1995. Spotted owl (*Strix occidentalis*). In A. Poole and F. Gill, editors. *The Birds of North America* 179. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, D.C., USA.
- Handrich, Y., L. Nicolas, and Y. L. Maho. 1993. Winter starvation in captive common Barn Owls: physiological states and reversible limits. *Auk* **110**:458–469.
- Hirons, G. J. M. 1982. The effects of fluctuations in rodent numbers on breeding success in the Tawny Owl *Strix aluco*. *Mammal Review* **12**:155–157.
- Hofacker, C. F. 1983. Abuse of statistical packages: the case of the general linear model. *American Journal of Physiology* **245**:R299–R302.
- Holmes, J. C. 1995. Population regulation: a dynamic complex of interactions. *Wildlife Research* **22**:11–19.
- Howell, A. B. 1926. Voles of the genus *Phenacomys*. II. Life history of the red tree mouse *Phenacomys longicaudus truei*. *North American Fauna* **48**:39–64.
- Howell, T. R. 1964. Notes on incubation and nestling temperatures and behavior of captive owls. *Wilson Bulletin* **76**:28–36.
- Hunter, J. E., R. J. Gutiérrez, and A. B. Franklin. 1995. Habitat configuration around spotted owl sites in northwestern California. *Condor* **97**:684–693.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* **76**:297–307.
- Husch, B., C. I. Miller, and T. W. Beers. 1982. *Forest mensuration*. Third edition. John Wiley, New York, New York, USA.
- Jameson, E. W. 1952. Food of deer mice, *Peromyscus maniculatus*, and *P. boylei*, in the northern Sierra Nevada, California. *Journal of Mammalogy* **33**:50–60.
- Jennrich, R. I., and M. D. Schluchter. 1986. Unbalanced repeated-measures models with structured covariance matrices. *Biometrics* **42**:805–820.
- Jensen, T. S. 1982. Seed production and outbreaks of non-cyclic rodent populations in deciduous forests. *Oecologia* **54**:184–192.
- Johannesen, E., and R. A. Ims. 1996. Modeling survival rates: habitat fragmentation and destruction in root vole experimental populations. *Ecology* **77**:1196–1209.
- Johnsgard, P. A. 1988. *North American owls: biology and natural history*. Smithsonian Institution Press, Washington, D.C., USA.
- Johnson, A. R., R. E. Green, and G. J. M. Hirons. 1991. Survival rates of Greater Flamingos in the west Mediterranean region. Pages 249–271 in C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, editors. *Bird population studies: relevance to conservation and management*. Oxford University Press, Oxford, UK.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**:65–71.
- Johnson, D. H. 1992. Spotted owls, Great Horned Owls, and forest fragmentation in the central Oregon Cascades. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Johnson, D. H. 1995. Statistical sirens: the allure of non-parametrics. *Ecology* **76**:1998–2000.
- Jolly, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration–stochastic model. *Biometrika* **52**:225–247.
- Jouventin, P., and H. Weimerskirch. 1991. Changes in the population size and demography of southern seabirds: management implications. Pages 297–314 in C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, editors. *Bird population*

- studies: relevance to conservation and management. Oxford University Press, Oxford, UK.
- Karr, J. R., and K. E. Freemark. 1983. Habitat selection and environmental gradients: dynamics in the "stable" tropics. *Ecology* **64**:1481–1494.
- Kindvall, O. 1995. The impact of extreme weather on habitat preference and survival in a metapopulation of the bush cricket *Metrioptera bicolor* in Sweden. *Biological Conservation* **73**:51–58.
- Kirkwood, J. K. 1981. Maintenance energy requirements and rate of weight loss during starvation in birds of prey. Pages 153–157 in J. E. Cooper and A. G. Greenwood, editors. *Proceedings of a Symposium on Diseases of Birds of Prey*. Chiron Publishing, London, UK.
- Kostrzewa, A., and R. Kostrzewa. 1990. The relationship of spring and summer weather with density and breeding performance of the Buzzard *Buteo buteo*, Goshawk *Accipiter gentilis* and Kestrel *Falco tinnunculus*. *Ibis* **132**:550–559.
- Kostrzewa, R., and A. Kostrzewa. 1991. Winter weather, spring and summer density, and subsequent breeding success of Eurasian Kestrels, Common Buzzards and Northern Goshawks. *Auk* **108**:342–347.
- Küchler, A. W. 1977. The map of the natural vegetation of California. Pages 909–938 in M. Barbor and J. Majors, editors. *Terrestrial vegetation of California*. John Wiley, New York, New York, USA.
- Kundel, W. 1980. Adaptations of mediterranean-climate oaks to environmental stress. Pages 43–54 in T. R. Plumb, technical editor. *Proceedings of a Symposium on the Ecology, Management and Utilization of California Oaks*. U.S. Forest Service General Technical Report **PSW-GTR-44**.
- Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, London, UK.
- Lack, D. 1966. *Population studies of birds*. Clarendon Press, Oxford, UK.
- Lahaye, W. S. 1988. Nest site selection and nesting habitat of the Northern Spotted Owl (*Strix occidentalis caurina*) in northwest California. Thesis. Humboldt State University, Arcata, California, USA.
- Lande, R. 1988. Demographic models of the Northern Spotted Owl (*Strix occidentalis caurina*). *Oecologia* **75**:601–607.
- Lande, R. 1991. Population dynamics and extinction in heterogeneous environments: the Northern Spotted Owl. Pages 566–580 in C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, editors. *Bird population studies: relevance to conservation and management*. Oxford University Press, Oxford, UK.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**:911–927.
- Larcher, W. 1980. *Physiological plant ecology*. Second edition. Springer-Verlag, Berlin, Germany.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**:67–118.
- Li, H., and J. F. Reynolds. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology* **75**:2446–2455.
- Lindsey, A. A., and J. E. Newman. 1956. Use of official weather data in spring time—temperature analysis of an Indiana phenological record. *Ecology* **37**:812–823.
- Linsdale, J. M., and L. P. Tevis, Jr. 1951. *The dusky-footed wood rat*. University of California Press, Berkeley, California, USA.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. *SAS system for mixed models*. SAS Institute, Cary, North Carolina, USA.
- Lomnicki, A. 1988. *Population ecology of individuals*. Princeton University Press, Princeton, New Jersey, USA.
- Luoma, D. L., R. E. Frenkel, and J. M. Trappe. 1991. Fruiting of hypogeous fungi in Oregon Douglas-fir forests: seasonal and habitat variation. *Mycologia* **83**:335–353.
- Major, J. 1977. California climate in relation to vegetation. Pages 11–74 in M. Barbor and J. Majors, editors. *Terrestrial vegetation of California*. John Wiley, New York, New York, USA.
- Mangel, M., and C. Tier. 1993. Dynamics of metapopulations with demographic stochasticity and environmental catastrophes. *Theoretical Population Biology* **44**:1–31.
- Marcot, B. G., and R. Holthausen. 1987. Analyzing population viability of the spotted owl in the Pacific Northwest. *Transactions of the North American Wildlife and Natural Resource Conference* **52**:333–347.
- Marten, G. G. 1973. Time patterns of *Peromyscus* activity and their correlation with weather. *Journal of Mammalogy* **54**:169–188.
- Martinson, R. K., and C. R. Grondahl. 1966. Weather and pheasant populations in southwestern North Dakota. *Journal of Wildlife Management* **30**:74–81.
- Maser, C., Z. Maser, J. W. Witt, and G. Hunt. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. *Canadian Journal of Zoology* **64**:2086–2089.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models*. Second edition. Chapman and Hall, New York, New York, USA.
- McDonald, P. M., and J. C. Tappeiner II. 1987. Silviculture, ecology and management of tanoak in northern California. Pages 64–70 in T. R. Plumb and N. H. Pillsbury, technical editors. *Proceedings of the Symposium on Multiple-use Management of California Hardwood Resources*. U.S. Forest Service General Technical Report **PSW-GTR-100**.
- McGarigal, K., and B. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. U.S. Forest Service General Technical Report **PNW-GTR-351**.
- McGraw, J. B., and H. Caswell. 1996. Estimation of individual fitness from life-history data. *American Naturalist* **147**:47–64.
- Mearns, R., and I. Newton. 1988. Factors affecting breeding success of peregrines in south Scotland. *Journal of Animal Ecology* **57**:903–916.
- Meczewa, R. 1986. Bioenergetic parameters and energy flow through the population of the Tawny Owl *Strix aluco* L. *Zeszyty Naukowe Uniwersytetu Jagiellońskiego* **32**:29–58.
- Meyer, J. S., L. L. Irwin, and M. S. Boyce. 1998. Influence of habitat abundance and fragmentation on Northern Spotted Owls in western Oregon. *Wildlife Monographs* **139**:1–51.
- Meyers, P., L. L. Master, and R. A. Garrett. 1985. Ambient temperature and rainfall: an effect on sex ratio and litter size in deer mice. *Journal of Mammalogy* **66**:289–298.
- Mitchell, J. H. 1977. *A robustness study of the analysis of variance on negative binomial data*. Thesis. University of Washington, Seattle, Washington, USA.
- Moen, C. A., A. B. Franklin, and R. J. Gutiérrez. 1991. Age determination of subadult Northern Spotted Owls in northwest California. *Wildlife Society Bulletin* **19**:489–493.
- Morris, D. W. 1989. Density-dependent habitat selection: testing the theory with fitness data. *Evolutionary Ecology* **3**:80–94.
- Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. *Wildlife-habitat relationships: concepts and applications*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Mowrer, H. T., R. L. Czaplewski, and R. H. Hamre. 1996. Spatial accuracy assessment in natural resources and environmental sciences: second international symposium.

- U.S. Forest Service General Technical Report **RM-GTR-277**.
- Murdoch, W. W. 1994. Population regulation in theory and practice. *Ecology* **75**:271–287.
- Murdoch, W. W., and S. J. Walde. 1989. Analysis of insect population dynamics. Pages 113–140 in P. J. Grubb and J. B. Whittaker, editors. *Towards a more exact ecology*. Blackwell Scientific, Oxford, UK.
- Neal, J. C., D. A. James, W. G. Montague, and J. E. Johnson. 1993. Effects of weather and helpers on survival of nestling Red-cockaded Woodpeckers. *Wilson Bulletin* **105**:666–673.
- Nelson, R. J. 1993. Simulated drought affects male reproductive function in deer mice (*Peromyscus maniculatus bairdii*). *Physiological Zoology* **66**:99–114.
- Newton, I. 1980. The role of food in limiting bird numbers. *Ardea* **68**:11–30.
- Newton, I. 1989a. Habitat variation and population regulation in sparrowhawks. *Ibis* **133**:76–88.
- Newton, I. 1989b. Synthesis. Pages 441–469 in I. Newton, editor. *Lifetime reproduction in birds*. Academic Press, New York, New York, USA.
- Newton, I. 1989c. Population limitation in raptors. Pages 3–12 in B. G. Pendleton, M. N. LeFranc, Jr., C. E. Ruibal, M. A. Knighton, and D. L. Krahe, editors. *Proceedings of the Northeast Raptor Management Symposium and Workshop*. National Wildlife Federation Scientific Technical Series **13**.
- Noon, B. R., and C. M. Biles. 1990. Mathematical demography of spotted owls in the Pacific Northwest. *Journal of Wildlife Management* **54**:18–27.
- Noon, B. R., and K. S. McKelvey. 1996. Management of the spotted owl: a case history in conservation biology. *Annual Review of Ecology and Systematics* **27**:135–162.
- Nur, N. 1987. Population growth rate and the measurement of fitness: a critical reflection. *Oikos* **48**:338–341.
- Nur, N., and J. Clobert. 1988. Measuring Darwinian fitness in birds: a field guide. Pages 2122–2130 in H. Ouellet, editor. *Acta International Ornithological Congress XIX*. Volume 2. University of Ottawa Press, Ottawa, Canada.
- Orzack, S. H., and S. Tuljapurkar. 1989. Population dynamics in variable environments. VII. The demography and evolution of iteroparity. *American Naturalist* **133**:903–923.
- Peach, W. J., P. S. Thompson, and J. C. Coulson. 1994. Annual and long-term variation in the survival rates of British Lapwings *Vanellus vanellus*. *Journal of Animal Ecology* **63**:60–70.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**:652–661.
- Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* **137**:S50–S66.
- Raphael, M. G. 1988. Long-term trends in abundance of amphibians, reptiles and mammals in Douglas-fir forests of northwestern California. Pages 23–31 in R. C. Szaro, K. E. Severson, and D. R. Patton, technical coordinators. *Management of amphibians, reptiles, and small mammals in North America*. U.S. Forest Service General Technical Report **RM-GTR-166**.
- Rhodes, O. E., Jr., and E. P. Odum. 1996. Spatiotemporal approaches in ecology and genetics: the road less traveled. Pages 1–7 in O. E. Rhodes, Jr., R. K. Chesser, and M. H. Smith, editors. *Population dynamics in ecological space and time*. University of Chicago Press, Chicago, Illinois, USA.
- Ricklefs, R. E. 1983. Comparative avian demography. Pages 1–32 in R. F. Johnston, editor. *Current Ornithology*. Volume 1. Plenum Press, New York, New York, USA.
- Ripple, W. J., G. A. Bradshaw, and T. A. Spies. 1991. Measuring forest landscape patterns in the Cascade range of Oregon, USA. *Biological Conservation* **57**:73–88.
- Ripple, W. J., P. D. Latin, K. T. Hershey, F. F. Wagner, and E. C. Meslow. 1997. Landscape composition and pattern around Northern Spotted Owl nest sites in southwest Oregon. *Journal of Wildlife Management* **61**:151–158.
- Rogers, C. M., J. N. M. Smith, W. M. Hochachka, A. L. E. V. Cassidy, M. J. Taitt, P. Arcese, and D. Schluter. 1991. Spatial variation in winter survival of Song Sparrows *Melospiza melodia*. *Ornis Scandinavica* **22**:387–395.
- Rosenberg, D. K., and R. G. Anthony. 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. *Canadian Journal of Zoology* **70**:161–166.
- Rotenberry, J. T., and J. A. Wiens. 1991. Weather and reproductive variation in shrubsteppe sparrows: a hierarchical analysis. *Ecology* **72**:1325–1335.
- Sadleir, R. M. F. S. 1974. The ecology of the deer mouse, *Peromyscus maniculatus* in a coastal coniferous forest. II. Reproduction. *Canadian Journal of Zoology* **52**:119–131.
- 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.
- Sakai, H. F., and B. R. Noon. 1997. Between-habitat movement of dusky-footed woodrats and vulnerability to predation. *Journal of Wildlife Management* **61**:343–350.
- Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. Akaike information criterion statistics. KTK Scientific Publishing, Tokyo, Japan.
- SAS Institute. 1990. SAS/STAT user's guide, Version 6. Fourth edition. Volume 2. SAS Institute, Cary, North Carolina, USA.
- SAS Institute. 1997. SAS/STAT Software: changes and enhancements through release 6.12. SAS Institute, Cary, North Carolina, USA.
- Scheibe, J. S. 1984. The effects of weather, sex and season on the nocturnal activity of *Peromyscus truei* (Rodentia). *Southwestern Naturalist* **29**:1–5.
- Schipper, W. J. A. 1979. A comparison of breeding ecology in European Harriers (*Circus*). *Ardea* **66**:77–102.
- Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of capture–recapture experiments in open populations. *Biometrics* **52**:860–873.
- Searle, S. R., G. Casella, and C. E. McCulloch. 1992. Variance components. John Wiley, New York, New York, USA.
- Shaffer, M. L. 1987. Minimum viable populations: coping with uncertainty. Pages 69–86 in M. E. Soulé, editor. *Viable populations for conservation*. Cambridge University Press, Cambridge, UK.
- Shenk, T. M. 1997. Detecting density dependence in natural populations. Dissertation. Colorado State University, Fort Collins, Colorado, USA.
- Skalski, J. R., and D. S. Robson. 1992. Techniques for wildlife investigations: design and analysis of capture data. Academic Press, San Diego, California, USA.
- Smith, J. N., P. Arcese, and W. M. Hochachka. 1991. Social behavior and population regulation in insular bird populations: implications for conservation. Pages 148–167 in C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, editors. *Bird population studies: relevance to conservation and management*. Oxford University Press, Oxford, UK.
- Solis, D. M., Jr., and R. J. Gutiérrez. 1990. Summer habitat ecology of Northern Spotted Owls in northwestern California. *Condor* **92**:739–748.
- Southern, H. N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). *Journal of Zoology, London* **162**: 197–285.
- Spies, T. A., W. J. Ripple, and G. A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. *Ecological Applications* **4**:555–568.

- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* **51**:3–47.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.
- Swenson, J. E., L. Saari, and Z. Bonczar. 1994. Effects of weather on Hazel Grouse reproduction: an allometric perspective. *Journal of Avian Biology* **25**:8–14.
- Temple, S. A. 1986. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. Pages 301–304 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Tevis, L., Jr. 1956. Responses of small mammal populations to logging of Douglas-fir. *Journal of Mammalogy* **37**:189–196.
- Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the Northern Spotted Owl. Interagency Committee to Address the Conservation of the Northern Spotted Owl. U.S. Department of Interior, Portland, Oregon, USA.
- Thornburgh, D. A. 1982. Succession in the mixed evergreen forests of northwestern California. Pages 87–91 in J. E. Means, editor. *Forest succession and stand development research in the Northwest*. Oregon State University Forestry Research Laboratory, Corvallis, Oregon, USA.
- Ting, T.-F. 1998. The thermal environment of Northern Spotted Owls in northwestern California: possible explanations for use of interior old growth and coastal early successional stage forest. Thesis. Humboldt State University, Arcata, California, USA.
- Tompa, F. S. 1971. Catastrophic mortality and its population consequences. *Auk* **88**:753–759.
- Tuhkanen, S. 1980. Climatic parameters and indices in plant geography. *Acta Phytogeographica Suecica* Number 67. Almqvist and Wiksell International, Stockholm, Sweden.
- Tuljapurkar, S. 1989. An uncertain life—demography in random environments. *Theoretical Population Biology* **35**:227–294.
- Turchin, P. 1995. Population regulation: old arguments and a new synthesis. Pages 19–40 in N. Cappuccino and P. W. Price, editors. *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, California, USA.
- U.S. Fish and Wildlife Service. 1990. Endangered and threatened wildlife and plants: determination of threatened status for the Northern Spotted Owl. *Federal Register* **55**:26114–26194.
- U.S. Forest Service. 1992. Final environmental impact statement on management for the Northern Spotted Owl in the national forests. Two volumes. U.S. Forest Service, National Forest System, Portland, Oregon, USA.
- Van Horne, B. 1981. Demography of *Peromyscus maniculatus* populations in seral stages of coastal coniferous forest in southeast Alaska. *Canadian Journal of Zoology* **59**:1045–1061.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* **47**:893–901.
- Van Horne, B., G. Olson, R. L. Schooley, J. G. Corn, and K. P. Burnham. 1997. Effects of drought and prolonged winter on Townsend's ground squirrel demography in shrubsteppe habitats. *Ecological Monographs* **67**:295–315.
- Vickery, W. L., and J. R. Bider. 1981. The influence of weather on rodent activity. *Journal of Mammalogy* **62**:140–145.
- Village, A. 1986. Breeding performance of Kestrels at Eskdalemuir, south Scotland. *Journal of Zoology, London* **208**:367–378.
- Volman, S. F., and M. Konishi. 1990. Comparative physiology of sound localization in four species of owls. *Brain, Behavior, and Evolution* **36**:196–215.
- Ward, J. M., and P. L. Kennedy. 1994. Approaches to investigating food limitation hypotheses in raptor populations: an example using the Northern Goshawk. *Studies in Avian Biology* **16**:114–118.
- Ward, J. M., and P. L. Kennedy. 1996. Effects of supplemental food on size and survival of juvenile Northern Goshawks. *Auk* **113**:200–208.
- Ward, J. P., Jr., R. J. Gutiérrez, and B. R. Noon. 1998. Habitat selection by Northern Spotted Owls: the consequences of prey selection and distribution. *Condor* **100**:79–92.
- Waters, J. R., and C. J. Zabel. 1995. Northern flying squirrel densities in fir forests of northeastern California. *Journal of Wildlife Management* **59**:858–866.
- Watts, C. H. S. 1969. The regulation of wood mice (*Apodemus sylvaticus*) numbers in Wytham woods, Berkshire. *Journal of Animal Ecology* **38**:285–304.
- Wells-Gosling, N., and L. R. Heaney. 1984. *Glaucomys sabrinus*. *Mammalian Species* **229**:1–8.
- White, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pages 288–331 in L. Boitani and T. K. Fuller, editors. *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York, New York, USA.
- White, G. C., and R. E. Bennetts. 1996. Analysis of frequency count data using the negative binomial distribution. *Ecology* **77**:2549–2557.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**: Supplement:120–139.
- White, K. 1996. Comparison of fledging success and sizes of prey consumed by spotted owls in northwestern California. *Journal of Raptor Research* **30**:234–236.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**:279–338.
- Wiehn, J., and E. Korpimäki. 1997. Food limitation on brood size: experimental evidence in the Eurasian Kestrel. *Ecology* **78**:2043–2050.
- Wiens, J. A. 1989a. The ecology of bird communities. Volume 1. Foundations and patterns. Cambridge University Press, Cambridge, UK.
- Wiens, J. A. 1989b. The ecology of bird communities. Volume 2. Processes and variation. Cambridge University Press, Cambridge, UK.
- Wiens, J. A. 1994. Habitat fragmentation: island vs. landscape perspectives on bird conservation. *Ibis* **137**:s97–s104.
- Wijnandts, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). *Ardea* **72**:1–92.
- Witt, J. W. 1991. Fluctuations in the weight and trap response for *Glaucomys sabrinus* in western Oregon. *Journal of Mammalogy* **72**:612–615.
- Wolfinger, R. 1993. Covariance structure selection in general mixed models. *Communications in Statistics-Simulation and Computation* **22**:1079–1106.
- Yoakum, J., and W. P. Dasmann. 1971. Habitat manipulation practices. Pages 173–231 in R. H. Giles, editor. *Wildlife management techniques*. Wildlife Society, Washington, D.C., USA.
- Zabel, C. J., K. McKelvey, and J. P. Ward, Jr. 1995. Influence of primary prey on home-range size and habitat-use patterns of Northern Spotted Owls (*Strix occidentalis caurina*). *Canadian Journal of Zoology* **73**:433–439.

APPENDIX A

BIOLOGICAL BACKGROUND

Biological basis for delineation of life history periods

The *winter stress period* (November–February) and the *heat stress period* (July and August) were defined based on when maximum climatic stresses occurred. The winter stress period averaged the highest precipitation and coldest temperatures during the year, whereas the heat stress period averaged the highest maximum temperatures $\geq 32^{\circ}\text{C}$ (Fig. 2). The winter stress period is when female owls may develop fat reserves prior to laying eggs in the spring. Hirons (1982) observed that ovarian follicles failed to develop in Tawny Owl (*Strix aluco*) females that had insufficient fat reserves from the winter. Although individuals do not undergo stresses from rearing young and molting during this period, they may encounter stress from poor hunting conditions during extended periods of rain. Thus, climatic conditions during the winter stress period can affect reproductive output in the following spring, as well as over-winter survival. Extremely hot conditions during the heat stress period, regardless of precipitation, could negatively affect survival in fledged young and ≥ 1 -yr-olds. Although counting of most fledged young occurs before this period, survival of fledged young during this period might affect estimates of recruitment of young birds into the territorial population the following year.

Two periods were defined in which reproduction may require additional energetic demands on individuals. The *early nesting period* (March and April) occurs when owls initiate nesting and incubate eggs, and the *late nesting period* (May) occurs when young are brooded with decreasing frequency until they fledge in late May and early June (Forsman et al. 1984). These two periods can be optimal, given appropriate conditions, for plant growth that optimizes maintenance and production of prey populations. However, severe inclement weather may affect reproductive output during these two periods. In addition, conditions during the early nesting period may affect survival of owls ≥ 1 yr old, because winter-like conditions can still occur. The last period we considered was the *dispersal period* in September and October, when juveniles disperse from their natal territories and first begin fending for themselves (Gutiérrez et al. 1995). This period is relevant only to recruitment, because juvenile survival affects potential recruitment of these individuals into the territorial population.

Biological basis for development of hypothesized climate models

In terms of direct effects, it is unlikely that cold temperatures alone affect survival of Northern Spotted Owls ≥ 1 yr old because they have plumage characteristics similar to those of boreal owl species (Barrows 1981). However, young owls have poor thermoregulatory ability while still in the nest (Howell 1964, Wijnandts 1984) and may be negatively affected by cold temperatures, especially in combination with precipitation. Conversely, Northern Spotted Owls may be prone to heat stress. They appear to have a lower upper critical

temperature (25.2°C) than do Great Horned Owls, exhibiting heat stress at $\sim 32^{\circ}\text{C}$ under laboratory conditions and in the wild (Barrows 1981, Ganey et al. 1993).

In terms of indirect effects, precipitation combined with cold temperatures may inhibit the owls' ability to forage successfully at night when they rely primarily on hearing to locate and capture prey (Forsman et al. 1984). Although precipitation does not inhibit nocturnal movements of radio-tagged Northern Spotted Owls (Forsman 1980), it reduces the hunting success of Tawny Owls (*Strix aluco*), presumably by limiting the owls' ability to hear prey movement at night (Hirons 1982). Therefore, precipitation may not inhibit movements of owls, but may inhibit their success in capturing prey. Large prey may also limit their movements during rainy weather (Linsdale and Tevis 1951, Wells-Gosling and Heaney 1984, Gentry et al. 1966), whereas small prey may increase their activity (Gentry et al. 1966, Marten 1973, Vickery and Bider 1981, Scheibe 1984). However, small prey may decrease their activity during low ambient temperatures (Marten 1973, Vickery and Bider 1981, Scheibe 1984). We postulate that hunting success for Northern Spotted Owls is lowest during cold, rainy periods when prey activity and the hearing ability of owls are both suppressed. Hunting success determines both individual survival and reproductive success. Female owls do all of the incubation and early brooding of young, with the male providing food (Forsman et al. 1984). Nest desertion in Tawny Owls is influenced by the inability of the male to provide sufficient food for the female during bad weather (Southern 1970). Conversely, hunting success should be highest during dry, warm conditions and neutral during wet, warm or dry, cold conditions that represent trade-offs between detection ability of owls and activity of prey (Table A1).

We also postulate that (1) wet, cold conditions and severe drought conditions, in general, would negatively affect prey survival; (2) drought conditions, regardless of temperature, would negatively affect prey reproduction and plant production; and (3) only warm, wet conditions would have a positive effect on both (Table A1). Extended rainy periods increase parasitism and disease in *Neotoma* (Linsdale and Tevis 1951), whereas *Peromyscus* has reduced body mass under drought conditions (Nelson 1993). Prey reproduction can be inhibited by both drought conditions and reduced ambient temperatures, which reduce sperm production and litter size (Meyers et al. 1985, Nelson 1993) and delay breeding seasons (Sadleir 1974). Production of forage also affects successful reproduction in prey species because of increased energetic demands during breeding (Bronson 1989). In northern California, the vegetative growing season is restricted to the spring when higher temperatures coincide with adequate water supplies, which are lacking in the summer (Major 1977). Fitter et al. (1995) suggest that ambient temperature may be the most important determinant of flowering in the spring.

TABLE A1. Potential indirect effects of climate conditions on Northern Spotted Owls and their prey that were used to develop statistical models of the effects of climate on life-history traits: 0 indicates a neutral effect, – a negative effect, and + a positive effect.

Climate condition	Hunting success	Prey survival	Prey reproduction	Prey forage production	Net effect
Warm wet	0	0	+	+	+
Cold wet	–	–	–	–	–
Warm drought	+	–	–	–	–
Cold drought	0	–	–	–	–

However, lack of available water also has a direct inhibitory effect on photosynthesis (Larcher 1980). Hypogeous fungi reach higher biomass in mesic conditions (Luoma et al. 1991), whereas tanoak requires relatively high levels of moisture and mild temperatures for production, even though it is adapted to withstand drought conditions (McDonald and Tappeiner 1987). There could also be lag effects of climate on plant production, which in turn could affect spotted owl prey. Over-

winter survival and density of small mammals have been positively correlated with forage production in the previous year (Watts 1969, Jensen 1982). For example, acorn production of *Quercus* oaks in California is positively associated with total precipitation during the previous growing season (Kundel 1980). Therefore, life history parameters of Northern Spotted Owls in time $t + 1$ may be indirectly affected by the growing season in time t .

APPENDIX B

A further consideration of survival models, including models with problems in identifiability of parameters, is available electronically in ESA's Electronic Data Archive: *Ecological Archives* M070-003.