Spatial Models and Spotted Owls: Exploring Some Biological Issues Behind Recent Events

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Few species will ever challenge conservation biology as much as the Northern Spotted Owl, *Strix occidentalis caurina*, has done (Simberloff 1987; Murphy & Noon 1992). The Forest Service and other U.S. agencies, mandated to protect the owl, face formidable pressures to neither under- nor overestimate its needs. Biologists were asked to produce the bottom line: what minimal amount of old-growth forest, in what spatial configuration, would give the owl a high likelihood of survival? This is a very difficult question in strictly biological terms. The owl's extreme sparsity—its distribution of about 3000 pairs over millions of acres in three states—means that existing formulas for "minimum viable population size" are clearly inapplicable. Spatial dynamics—the theoretically challenging issue of how populations are affected by their distribution across an irregular habitat—had to be central to any defensible analysis.

Recently, conservation biologists faced each other in the legal arena, some supporting a proposed plan for the owl and others backing lawsuits to block it. Metapopulation theory and the validity of mathematical modeling became the subjects of court testimony and rulings. Here we describe the biological issues in this unusually science-rich legal debate. We do so from a partisan perspective, as expert witnesses for the litigants, and we invite responses from other viewpoints.

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The Thomas Strategy

In 1989, the U.S. government created a commission of experts from the Forest Service, the Bureau of Land Management, the Fish and Wildlife Service, and the Park Service to coordinate these agencies' plans for managing the owl. The report of this commission (Thomas et al. 1990) marked a milestone in population viability analysis because of its explicit, quantitative treatment of spatial population dynamics (see below). Development of the commission's report, henceforth referred to as the "Thomas Strategy" after the commission's chairman Jack Ward Thomas, is described in detail by Murphy and Noon (1992).

The Thomas Strategy calls for the preservation of 7.7 million acres of old-growth forest in a system of large and evenly spaced blocks, called "habitat conservation areas," throughout the range of the owl. In Oregon and Washington, each block is to be large enough for at least 20 pair territories and no more than 12 miles from another block. In northern California, where forest fragments are smaller, the standards are at least 10 territories and no more than 7 miles. To permit dispersal between habitat conservation areas, forest between them is to be managed under the "50–11–40 rule," in which each quarter-township (9 miles^2) contains at least 50% forest with trees at least 11 inches in diameter at breast height and with at least 40% canopy closure.

At present, the habitat conservation areas designated by the Thomas Strategy consist of only 30% old-growth forest. The rest is secondary forest that will be allowed to regrow, requiring an estimated 50–100 years. The strategy meanwhile allows about 500,000 acres of old-growth forest outside of the habitat conservation areas to be cut. The strategy thus converts the present landscape of many small, partly connected fragments of old-growth forest into one of fewer, larger blocks in the course of one-half to one century.

Spatial Models and Threshold Effects

Why this particular plan, and how likely is it to succeed? The complexity and long timescale involved in this question make computer simulation modeling an indispensable tool. The Thomas Strategy utilizes two models, the "individual-territory model" and the "territory-cluster model," to address the interaction between the owl's demography and forest fragmentation (see McKelvey et al. 1992; Lamberson et al. 1992 for details of the models). These models use a basic approach developed by Lande (1988) and Doak (1989) and add greater complexity and realism.

Owl demography is linked to fragmentation by making juvenile dispersal success a function of the proportion of the landscape that is forested. A newly fledged juvenile in search of a territory is assumed to visit a limited number of sites, which are either suitable (forested) or unsuitable, and either occupied or vacant. A juvenile goes on to breed only if it finds a suitable vacant territory.

Thresholds for extinction are a key behavior of such models. When the percentage of landscape that is forested reaches a critical lower limit, the owl population collapses, because too few juveniles find territories to balance the mortality of existing territory holders. Extinction thus occurs well before the last old-growth disappears. Lande (1988), Doak (1989), and the Thomas Strategy all suggest that the threshold may lie near 20%, the current percentage of the landscape that is old-growth forest in the Northwest.

The individual-territory models adds further realism by requiring juveniles to encounter mates in order to breed. The result is a second extinction threshold (otherwise known as the Allee effect), a population density below which the owl population collapses because of mate-finding failure.

The individual-territory model is nonspatial; forest exists as a uniform percentage of the landscape, all of which is accessible to every owl. To examine the effects of patch size and spacing, the territory-cluster model of Doak (1989) and the Thomas Strategy portrays the landscape more realistically: forest exists in clusters of territories, corresponding to habitat-conservation areas. Owls disperse more readily within than between clusters. In Doak's model, all clusters are equally distant from one another, but the Thomas Strategy model has an explicit spatial structure: clusters are arranged in a regular fashion across an edgeless plane (a torus).

The territory-cluster model showed that owls would often become extinct in a universe of five territory-clusters, but would persist far better with a cluster size of 10. Gains in persistence are smaller as cluster size increases from 10 to 20. The Thomas Strategy concludes that a minimum of 20 territories per habitat-conservation area offers reasonable security. The Thomas Strategy stresses the consistency of these results with empirical studies of local population extinction.

Models Go to Court

Soon after its release, the Thomas Strategy was adopted by the U.S. Forest Service, manager of 74% of existing spotted owl habitat and 68% of known owl pairs. The Bureau of Land Management, with 22% of known owl pairs, opted instead for its own less restrictive strategy, and also asked the so-called "God Squad" (the Endangered Species Committee) to exempt 44 planned timber sales from the Endangered Species Act. (In early 1992, the God Squad granted 13 exemptions, but these were later declined by the Clinton Administration.)

But when the seemingly more cooperative Forest Service attempted to use the Thomas Strategy, it was promptly thwarted by environmentalist lawsuits. Ruling in *Seattle Audubon Society (SAS) et al. vs. Evans* in March 1991, and again in *SAS et al. vs. Moseley* in May 1992, U.S. District Judge William Dwyer blocked the Forest Service from selling timber under its new "Thomas-based" management plan. Dwyer ruled that this plan carried significant and unacknowledged risks to the owl, and also (in the 1992 ruling) that the Forest Service had neglected to consider the other species inhabiting old-growth forests.

Timber interests, already hostile to the Thomas Strategy, were outraged by Dwyer's rulings. Their calls for congressional intervention and modification of the Endangered Species Act intensified. Conservation biologists who participated in or supported the Thomas Strategy also questioned the "extremism" of the environmentalist litigants.

Weaknesses of the Thomas Strategy

The critics of the Thomas Strategy did not take issue with its general approach, including its use of models. But all models include some tenuous assumptions, and in the intense scrutiny generated by the legal process, some key weaknesses in the Thomas Strategy's analyses were identified.

One concerned the search behavior of juvenile owls. The cluster model portrays juveniles as searching their natal cluster thoroughly; then, if unsuccessful in finding a territory, they move away in linear paths until striking another cluster, which they again search thoroughly, and so on. This is a highly efficient search pattern, and the Thomas Strategy notes that the results depend fairly strongly on it. Unfortunately, details of how juvenile movements really respond to variable landscapes remain unknown.

Another issue was habitat geometry. The cluster model depicts round patches and an edgeless universe. Preliminary work on a model using maps of the actual landscape (Lamberson et al. 1992; McKelvey et al. 1992) shows, not surprisingly, that ragged patches and edge effects greatly reduce the viability of the owl population.

The Thomas Strategy scrupulously points out these and other limitations, but it nonetheless projects a high degree of confidence. Consideration of the above issues alone suggests that some optimism is required. But the litigants also raised an even more basic question: will the owl even survive until the day, 50 to 100 years from now, when its habitat consists of the prescribed array of patches?

The Transition Question

The Thomas Strategy calls for the near-term loss of 500,000 acres of old-growth forest, which will give way to net habitat gain after 50–100 years. In the "worst-case scenario," the report states, the owl population may decline by 50–60% during this time. Implicitly assumed is that the owl population will survive the transition and stabilize once loss of habitat ceases. But it could reach the threshold of either too little habitat or too low density and become extinct before the Thomas Strategy comes into full effect.

This issue could be assessed directly using models in which the landscape is dynamic; some work of this kind has already been performed (Lamberson et al. 1992). But the Forest Service argued that the models were "not yet sufficiently validated" to incorporate the issue into its risk analyses. In fact, the Forest Service did not even acknowledge the transition issue in its 1992 environmental impact statement, which was supposed to disclose all major risks of the proposed plan. Meanwhile, new demographic evidence suggests that the near-term extinction of the owl is a serious possibility.

Dire Demography?

Trends in the owl population are not estimated simply by counting owls, partly because the existence of "floater" owls lacking territories may conceal trends in the territorial breeding population (Thomas et al. 1990). Instead, estimates of survival and fecundity from studies of marked territorial owls are assembled into stage-projection matrices, from which lambda, the yearly rate of population increase, is calculated. Lande (1988), the first to apply these techniques, detected no trends: lambda = 0.96, not significantly different from 1.0. In sensitivity analyses, Lande found that adult survival is the most critical parameter influencing lambda for this long-lived iteroparous species. In the 1990 Thomas Strategy, this analysis is repeated using 3–6 years of data from three populations. One of these, in the Oregon Coast Range, was in sharp decline (lambda = 0.85). The other two, in the Olympic Peninsula and northern California, were in possible decline (lambda = 0.98 and 0.95; not statistically different from 1.0).

In 1991, U.S. Fish and Wildlife Service biostatisticians analyzed 4–7 years of data from over 2000 marked owls in five populations (Anderson & Burnham 1992). They found all populations to be declining at 7.5% to 10% per year, a rate at which about 15 pairs of owls would remain in 50 years. They also found the rate of decline to be accelerating, evidently due to an unsuspected and still unexplained decrease in the survival of adult territorial owls. (Increasing competition with the Barred Owl, an aggressive and more edge-tolerant congener of the Spotted Owl, is one possibility proposed by owl biologists.) These findings were a major basis for Judge Dwyer's 1992 ruling.

The Problem with Monitoring

The Thomas Strategy includes provisions for monitoring and modification (adaptive management). But the litigants argued that, according to the Thomas Strategy's own models, these safeguards won't work. Because of the owl's sparsity, its longevity, and the existence of the pool of "floaters," there will be a long lag between the time when the critical habitat threshold is reached and the time when the resulting population crash becomes detectable. Thus, by the time any trends can be proven, the fate of the population may already be sealed.

The Forest Service's Responses

In the 1992 ruling, Judge Dwyer focused on three sets of issues: (1) risks associated with new information about the owl; (2) risks to species besides the owl; (3) risks causing the refusal of the Bureau of Land Management to participate in the strategy. In March 1993, the Forest Service released a new report (the "Scientific Assessment Team Report") addressing these risks. Most pertinent here is the first set of issues, risks to the owl. The Scientific Assessment Team focuses on the validity of the new evidence for sharp demographic decline. Backed by some owl biologists, the team argues that (1) lambda may have been underestimated because of emigration from the study areas, and (2) some data on absolute *densities* of owls indicate only a moderate decline, roughly equal to the rate of habitat loss (1–3% per year). Thus the team argues that there is no evidence for a precipitous ("threshold effect") collapse of the owl population.

Counter-arguments exist to each of these claims. First, Lande, the Thomas Strategy authors, and Anderson and Burnham all showed that substantial *juvenile* emigration (which does occur), has little influence on estimates of lambda; conversely, substantial *adult* emigration, which would affect lambda, is not evident from any existing data. Second, the use of density data to estimate owl population trends was earlier disavowed by the Thomas Strategy itself for the reasons explained earlier. It can thus be argued that Anderson and Burnham used the best-accepted techniques on the most complete data set available, so that until disproven, their findings stand as strong grounds for doubting the owl's present security.

Summary

As litigants in the recent lawsuits against the Forest Service, we attempted to show that the Northern Spotted Owl may be in rapid decline, that the reason is loss and fragmentation of its habitat, and that the decline may become irreversible once a certain threshold of habitat loss is reached. Thus, on present evidence, any plan entailing further loss of old-growth forest is incompatible with the legal mandate to insure the owl's survival. In response, the Forest Service and its scientific supporters argue that the imminent collapse is not yet proven, and that the Thomas Strategy is a reasonable compromise between opposing interests.

Two fundamental issues emerge from this debate. One is the burden of proof question: if the consequences of the plan are uncertain, should it be allowed or not? (We would argue that the degree of risk is sufficiently high that the law says "not.") The other concerns the role of science in the process. We acknowledge the sincerity of the Thomas Strategy's creators and backers. But we also believe this case has highlighted a dangerous tendency among some conservation biologists to see political "realities" and compromise solutions as a paramount goal. Even if science is never value-free in practice, our aim in cases such as this should be to provide an accurate assessment of biological risks. Weighing these against other concerns and reaching compromises is the job of decision makers. In this case, we feel it would be more honest for the Forest Service to say "the Thomas Strategy is very risky for the owl, but we're going to do it anyway," than to claim that it is a safe strategy.

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