

Species, Location, Years	Methods and Sample	Hypotheses Tested	Summary of Findings, Comments	Reference
Rhinolophus ferrumequinum, England 1948-1958	Bands, 1,808, primarily hibernacula . Number known alive each yr after banding.	Descriptive	Simple reporting of number banded and number known alive by yr.	Hooper (1983)
Rhinolophus ferrumequinum, England, ca. 1970- 1986	Bands, toe daw dipping J, hiber- nacula and nurseries, hand captures. IR/LT, UAC and KAC separately.	Descriptive: AM vs. AF, J vs. A survival, survival by season.	M, F SC similar. Survival to ages 1 (0.65) and 2 (0.62) lowest. Annual survival increases to 0.86 at age 9 . Survival lowest winter, % varied by yr from 0.55 to 0.85 .	Stebbins and Arnold (1987)
Tadanda <i>brasiliensis</i> , Texas, 1957-1958	Ad hoc extrapo- lation from relative areas of hypothetical SCs, and best fit by age ratios based on 3 classes of tooth wear in 22,498 Fs.	Descriptive	AF survival of 70- 80% "reasonable" (Davis et al. 1962: 337) based on age class ratios.	Davis et al. (1962)
<i>Taphozous georgianus</i> , Australia, 1965-1969	Bands, 229 J , mist nets at caves, sub- tropical. IR/LT.	Descriptive	Annual survival F 0.42-0.75 , M 0.24-0.66 .	Jolly (1990)

16

Evaluating Methods for Monitoring Populations of Mexican Spotted Owls: A Case Study

Joseph L. Ganey, Gary C. White,
David C. Bowden, and Alan B. Franklin

Monitoring **population** status of rare or elusive species presents special challenges. Understanding population trends requires separating signal (true and important changes in abundance) from noise (normal temporal and sampling variation; e.g., Block et al. 2001). This is **particularly** difficult when small numbers or elusive habits make it difficult to obtain precise estimates of population parameters (Thompson et al. 1998:68). We conducted a pilot study to evaluate a sampling design proposed for **monitoring populations** of the threatened Mexican spotted owl (*Strix occidentalis lucida*; USDI Fish and Wildlife Service 1995). Here, we discuss this effort as a case study illustrating some pitfalls and issues involved in sampling rare **and/or** elusive **populations**. We begin with a brief history of events leading up to the pilot study to provide a context for the study. We then describe study design and implementation and summarize results of the study and conclusions following from those results. Future monitoring efforts may benefit from our efforts and the lessons we learned.

Background and History

The Mexican spotted owl inhabits forested mountains and canyonland terrain throughout the southwestern United States and Mexico (Gutiérrez et al. 1995; Ward et al. 1995). This owl is associated with late-successional

forests throughout much of its range (Ganey and Dick 1995; **Gutiérrez et al.** 1995) and was listed as threatened in 1993 (USDI Fish and Wildlife Service 1993) because of concerns about the effects of timber harvest and wildfire on amount and distribution of late-successional forest.

A recovery plan produced for this owl contained five delisting **criteria** that must be met to remove the owl from the list of threatened species. One criterion called for monitoring populations of owls in three of the **six** "Recovery Units" identified in the United States (USDI Fish and Wildlife Service 1995:76-77; see also Figure 16.1). The monitoring criterion specified that delisting should occur only if the populations monitored were shown to be stable or increasing using a monitoring design capable of detecting a 20% decline over 10 **yrs** with a power of 90% and a Type I error rate of 5%. The specificity in this delisting criterion represented a deliberate attempt to provide a rigorous and unambiguous measure of population status and was a direct response to the history of litigation and administrative appeals surrounding the spotted owl issue (e.g., **Marcot** and Thomas 1997).

The recovery plan also outlined a general monitoring approach. Briefly, this approach involved (1) surveying for owls on randomly located sample "quadrats" approximately 40-75 **km²** in area (number of quadrats to be determined); (2) capturing and color-banding owls so that individuals could be uniquely identified; (3) estimating abundance of owls on the quadrats using capture-recapture models for closed populations; and (4) monitoring changes in abundance over time. **As** a first step in evaluating this approach, the USDA Forest Service, Southwestern Region (hereafter the **SW Region**), provided funding to evaluate the sampling methods on four quadrats in Arizona. Results of this test indicated that the field methodology was feasible at the limited scale tested (May et al. 1996).

The SW Region formally committed to "monitor changes in owl populations and habitat needed for delisting" in an amendment to Land Management Plans covering 11 **national** forests in the region (USDA Forest Service 1996:88). The SW Region also engaged in formal consultation with the U.S. Fish and Wildlife **Service** on the effects of this amendment on the owl, under Section 7 of the Endangered Species Act (Stanford Environmental Law Society 2001:Chapter 3). The resulting Biological Opinion stated "Population monitoring will follow the design in the proposed action (i.e., the amendment; USDA Forest **Service** 1996) and beginning on page 107 of the Recovery Plan" (USDI Fish and Wildlife Service 1996:34). It also called for a pilot study to evaluate the monitoring approach and

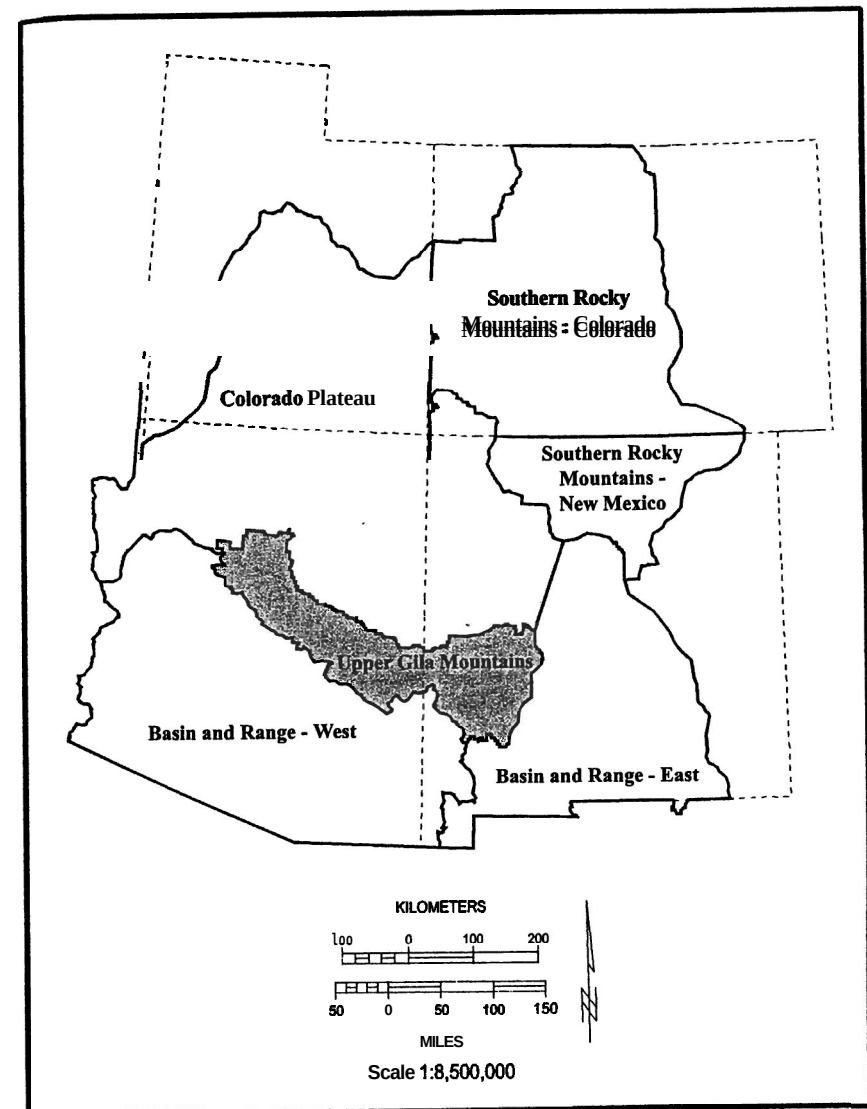


Figure 16.1. Recovery Units recognized for the Mexican spotted owl within the United States (from USDI Fish and Wildlife Service 1995:fig. ILB.1). The Upper Gila Mountains Recovery Unit is highlighted.

specified that the Forest Service should initiate the pilot study within 1 yr and "make timely progress thereafter towards full implementation" (USDI Fish and Wildlife Service 1996:34).

In late 1997, the SW Region requested that the Rocky Mountain Research Station (RMRS) assist in implementing a population monitoring program. RMRS appointed J. L. Ganey to head this effort in January 1998, and Ganey recruited the other authors of this paper to assist in planning, implementing, and evaluating the pilot study. The SW Region provided preliminary funding in 1998 to begin planning for the pilot study and funded implementation of the pilot study in 1999.

Based on the legal and administrative record discussed above, we concluded that our charter was to evaluate the specific monitoring approach described in the recovery plan. Consequently, rather than considering alternative approaches, we designed and conducted a pilot study to further evaluate the methods proposed in the recovery plan. Objectives of this pilot study were to (1) evaluate the feasibility of mark-recapture sampling at the spatial scale specified in the recovery plan; (2) collect preliminary data on owl density, capture probabilities, and spatial variation in those parameters; and (3) use these data to estimate sample-size requirements and costs for conducting a long-term population monitoring program for the Mexican spotted owl.

The Pilot Study

The target population identified in the recovery plan for the long-term monitoring program included the population of territorial Mexican spotted owls in three Recovery Units (Upper Gila Mountains, Basin and Range-West, and Basin and Range-East; Figure 16.1; see Rinkevich et al. 1995 for discussion of Recovery Units). These Recovery Units were chosen because they included what likely are the core populations within the range of the Mexican spotted owl in the United States (Ward et al. 1995). The design focused on territorial owls because no techniques were available to locate nonterritorial owls; hence, the number of nonterritorial owls could not be estimated reliably.

To simplify the pilot study, we restricted the scope of this study to the population of territorial owls in the Upper Gila Mountains Recovery Unit outside of the White Mountain and San Carlos Apache reservations. The Upper Gila Mountains Recovery Unit was chosen because it appeared to contain a large population of Mexican spotted owls (i.e., 424 occupied

"sites" [56% of known occupied sites] were documented in this Recovery Unit as of 1993 [Ward et al. 1995]). Tribal lands, which comprised about 18% of the Recovery Unit, were excluded from the pilot study because working on these lands would have required special permissions and access to these lands was not essential to meet the objectives of the pilot study.

Study Area

The Upper Gila Mountains Recovery Unit, approximately 54,860 km² in area, corresponds loosely to Bailey's (1980) Upper Gila Mountains Forest Province and William's (1986) Datil-Mogollon Section. This area is transitional between the canyonlands of the Colorado Plateau province to the north and the Basin and Range province to the south. It is characterized by steep mountains and entrenched river drainages dissecting high plateaus. For further information on vegetation patterns, land uses, and other features of this area, see Rinkevich et al. (1995).

Design

Sampling units for the pilot study consisted of randomly located quadrats approximately 40–76 km² in area. Quadrat size represented a compromise between the desire for spatial replication and unbiased, precise density estimates. Franklin et al. (1990) found that density estimates for northern spotted owls (*S. o. caurina*) in northwestern California stabilized at a study area size of 90–130 km². This was larger than our proposed quadrat size, but there were mitigating circumstances. First, Franklin et al. (1990) did not use ecological boundaries in subsampling their study area, and edge effects consequently may have been exaggerated in their analysis. Second, visual inspection of their figure 4 (a plot of the first derivative of change in density versus study-area size) indicates that the rate of change in density as study area size increased approached zero above 50 km². Therefore, we concluded that our quadrat size was both large enough to reduce edge effects and estimate density accurately and small enough to allow spatial replication.

The sampling frame for quadrat selection was developed using spatial modeling in a geographical information systems (GIS) environment. We first developed a GIS coverage that delineated the entire Recovery Unit into separate quadrats of 40–76 km² using size and shape constraints, topography (1:250,000 digital elevation models), and other spatial infor-

mation. To the extent possible, quadrat boundaries followed ecological features such as **ridgelines** and watersheds in an attempt to reduce **edge** effects and minimize the probability that a quadrat boundary ran **through** an owl's activity center. Further details on developing the quadrat coverage are contained in **Arundel (1999)**.

Once the quadrat sampling frame was developed, quadrats were **selected** using stratified random sampling. Random sampling was used to ensure an unbiased, representative sample so that inferences about owl **abundance** could be extended to the entire **Recovery Unit** (exclusive of tribal lands), rather than being **restricted** to the sample quadrats. Stratification was **used** to reduce the extent of among-quadrat variability in owl density.

We were unable to locate a useful vegetation-based **GIS** coverage to aid in **stratifying** quadrats, so instead stratified quadrats based on elevation. Quadrats with $\geq 33\%$ of their area occurring at elevations $\geq 1,982$ m and $< 2,745$ m were placed in a "high-density" stratum, and all other quadrats were placed in a "low-density" stratum. These represented strata with higher and lower expected owl density, respectively. Most of the quadrat

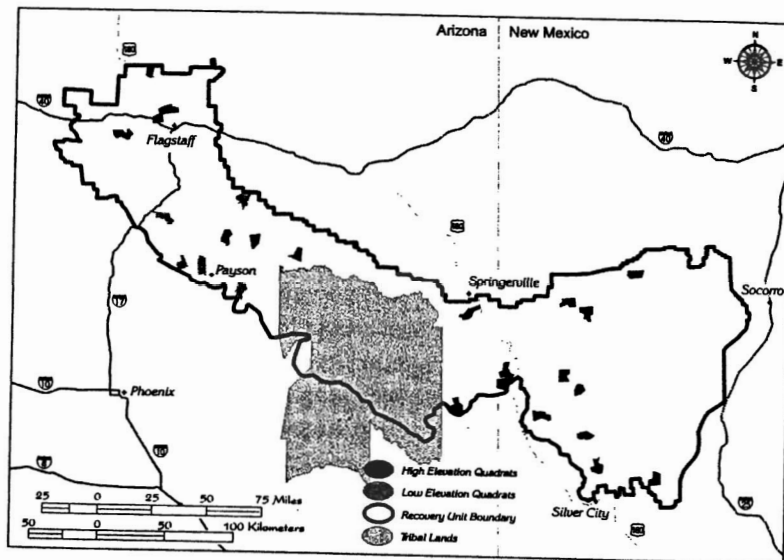


Figure 16.2. Sampling quadrats included in a study of abundance of Mexican spotted owls, Upper Gila Mountains Recovery Unit, Arizona and New Mexico, 1999. Also shown are tribal lands intersecting the Recovery Unit; these lands were not included in the sampling frame.

area within high-density quadrats fell within the elevational range where most Mexican spotted owls occur, whereas low-density quadrats were dominated by areas lower or higher than those where most spotted owls are found (Fletcher and Hollis 1994; Ganey and **Dick 1995**).

We selected 20 quadrats from the high-density and five from the low-density strata (Figure 16.2). The reduced emphasis on sampling quadrats from the low-density stratum was based on the expectation that few owls would be found in such **quadrats** and that spatial variation in owl density therefore would be low in that stratum. Conversely, greater expected **vari-**ation in the high-density stratum resulted in a need for greater sampling intensity. For descriptions of quadrats sampled, see Ganey et al. (1999).

Field Methods

All field sampling for this study was accomplished from April–September 1999. Sampling followed methods established for studies of spotted owl demography (Franklin et al. **1996**), with some differences. Fixed call points were established to ensure that the entire area within the quadrat was surveyed effectively. This generally meant that call points were established at intervals of ≤ 0.8 km along roads, trails, **ridge** tops, or drainage bottoms, depending on terrain. Crew leaders experienced in conducting spotted owl surveys guided establishment of call points.

Nocturnal calling surveys (Forsman 1983; Franklin et al. 1996) were **conducted** from call points to locate general areas occupied by owls. Surveyors spent 10 min at each call point, alternately calling and listening for a response from territorial owls.

We attempted to complete four survey passes through the **quadrats**, except for quadrats where no owls were located by the end of the third survey pass. We did not survey those quadrats a fourth time. A survey pass was considered completed when **all** call points were surveyed and **all** required daytime **follow-up** surveys were completed. Daytime follow-up surveys were conducted wherever an owl was detected during nocturnal surveys, to locate nest and/or roost areas, capture and mark owls, **resight** previously marked owls, and/or determine the reproductive status of resident owls. Two follow-up surveys were allowed per response per survey pass.

Crews attempted to capture and individually mark all territorial adult **and subadult** owls observed on the quadrat. Owls were captured using noose poles and board traps (Forsman 1983; Johnson and Reynolds 1998) and marked with a numbered **locking** aluminum band on one leg and a

unique color band on the other leg (Forsman et al. 1996). After an initial physical capture, owls were considered to be "recaptured" on subsequent passes if we were able to resight colored leg bands. Thus, each survey pass was treated as a potential capture occasion. Banding records were not reviewed before resighting attempts, to avoid potential bias in recognizing color combinations.

Survey Results

We established 2,345 call points across the 25 sample quadrats. The required number of survey passes was completed on 21 of the 25 quadrats (Table 16.1). Of the remaining quadrats, three survey passes were completed on one, a third pass was largely completed on a second, and two passes were completed on a third. On the fourth quadrat, four passes were completed on the southern half, whereas only two passes were completed on the northern half, where no owls were located during these passes. Failure to complete surveys in these areas was primarily due to limited numbers of surveyors working in roadless areas that featured difficult terrain.

Total survey effort involved calling 8,257 points (including repeat visits) over the course of all passes. This resulted in 434 nocturnal detections of owls, which triggered 400 daytime follow-up surveys. One or more owls were located on 202 of these follow-up surveys, and 57 territorial adult and subadult owls were captured and color-banded.

Spotted owls were heard or seen on 18 quadrats. 16 (80%) in the high-elevation stratum and two (40%) in the low elevation stratum. Of these, we estimated that 14 quadrats in the high-elevation stratum and one in the low-elevation stratum actually supported resident owls whose activity center was located within the quadrat boundary (70% and 20% of total quadrats within strata, respectively). Ganey et al. (1999) provided further information on numbers of territories resolved, reproductive histories, and numbers of owls banded by quadrat.

Initial Estimates of Population Size and Spatial Variation in Owl Density

We used the following steps, each of which is outlined in more detail below, to estimate the total number of Mexican spotted owls (N_{RU}) and its standard error ($SE[N_{RU}]$) for the Upper Gila Mountains Recovery Unit. First, we used the capture-recapture data to estimate capture probabilities

Table 16.1.

General location, area, number of survey passes completed, and number of call points for 25 quadrats surveyed for Mexican spotted owls, Upper Gila Mountains Recovery Unit, 1999. Quadrat numbers begin with H or L to indicate expected high- and low-density quadrats, respectively.

Quadrat				Survey	Call	
No.	Name	Area (km ²)	National forest	District	passes	points
H01	Red Mtn.	43.7	Coconino/Kaibab	Peaks/Chalender	3 ^a	60
H02	Peaks	61.2	Coconino	Peaks	4	89
H03	W i g Mtn.	46.5	Coconino	Peaks	3 ^a	67
H04	White Horse	76.4	Kaibab	Chalender	4	90
H07	Gen. Springs	59.6	Coconino	Blue Ridge	4	66
H08	Chevelon	55.7	Apache/Sitgreaves	Chevelon	4	86
H09	Heber	54.9	Apache/Sitgreaves	Heber	3 ^a	96
H11	Datil	57.9	Cibola	Magdalena	3 ^a	102
H12	Slaughter Mesa	63.2	Apache ^b	Quemado	4	77
H13	Springerville	66.8	Apache/Sitgreaves	Springerville	4	105
H14	Mangas Mtn.	68.1	Apache ^b	Quemado	4	134
H16	Brushy Mtn.	69.0	Apache ^b	Glenwood	3	153
H17	Telephone Canyon	62.3	Gila	Reserve	4	102
H18	Pueblo Creek	66.9	Apache ^b	Glenwood/Alpine	2	148
H19	Pitchfork Canyon	49.9	Gila	Reserve	4	37
H20	Rose Peak	71.0	Apache/Sitgreaves	Clifton	4	85
H21	Whitewater Creek	72.8	Gila	Glenwood	3 ^c	123
H22	Cliff Dwellings	52.5	Gila	Mimbres	4	123
H23	Tadpole Ridge	66.3	Gila	Silver City	4 ^d	149
H24	Hillsboro Peak	66.9	Gila	Silver City/Black Range	4	168
L01	Lake Montauma	40.9	Coconino	Beaver Creek	3 ^a	47
L02	jacks Canyon	66.1	Coconino	Blue Ridge	4	114
L03	Buckhead Mesa	68.5	Tonto	Payson	3 ^a	108
L05	The Gorge	45.0	Tonto	Payson	3 ^a	47
L06	Spring Creek	51.3	Tonto	Pleasant Valley	4	52

^a Fourth survey pass not required; no owls found through this survey passes.

^b Apache National Forest administered by the Gila National Forest.

^c A third survey pass was largely but not completely finished.

^d Four survey passes were completed on the southern half of the quadrat, which contained spotted owls. Due to time constraints, only two passes were completed on the northern half where no spotted owls were located during the first two passes.

(p) for owls on each quadrat. Second, we determined the numbers of banded and unbanded owls observed on each quadrat. Third, we used the estimates of p to correct the observed counts of banded and unbanded owls to estimate the total number of owls ($N_{quadrat}$) for each quadrat. The sampling variances and covariances associated with these estimates formed a variance-covariance (VC) matrix that represented the precision of the $N_{quadrat}$ estimates (sampling variances on the diagonal of the VC matrix) and the degree to which the estimates were spatially dependent (sampling

Table 16.2.

Distribution of quadrats among and characteristics of the two strata used to estimate abundance of Mexican spotted owls in the Upper Gila Mountains Recovery Unit, Arizona and New Mexico, 1999. Areas are in km².

Stratum	Stratum area	Area sampled	Total quadrats	Quadrats sampled
Low	10,635.20	271.81	186	5
High	34,795.66	1,231.4	559	20
Total	45,430.86	1,505.21	745	25

covariances in the off-diagonal elements of the VC matrix) because p 's were estimated with a capture-recapture model jointly across qua&.

Fourth, density (D_{quadrat}) was estimated for each quadrat by dividing each N_{quadrat} by quadrat area. Again, an associated VC matrix was estimated. Finally, we estimated the total number of owls (N_{RV}) and the standard error in the Recovery Unit by (a) multiplying the density for each stratum by the total area of that stratum within the sampling frame from which the sample quadrats were drawn (Table 16.2), and (b) summing across strata (e.g., Bowden et al. 2003).

We use the following notation (after Thompson et al. 1998) in the discussion that follows (see Table 16.2). We used U_h to denote the number of quadrats in the sampling frame for strata h , and u_h to define the number of quadrats sampled in strata h . The usual notation for sampling theory uses N and n , but we reserved N for the size of the biological population being estimated.

ESTIMATING CAPTURE PROBABILITY (p)

We used the capture histories of banded owls on quadrats where owls were banded and subsequently resighted (Table 16.3) to estimate p , the probability of capture on a given trapping occasion (Huggins 1989). We used a closed capture-recapture modeling procedure developed by Huggins (1989, 1991) and implemented in Program MARK (White and Burnham 1999). A dosed-capture model was appropriate because (1) the population estimate focused on territorial adults; and (2) the study was conducted over a short time period at a time of year when territorial adults are sedentary and little emigration or immigration occurs in this population (personal observation).

The goal at this stage was to estimate p s as precisely as possible because the sampling variances of the p 's contribute to the sampling variances of

Table 16.3.

Sample quadrats used to estimate capture probabilities of color-banded Mexican spotted owls in the Upper Gila Mountains Recovery Unit, Arizona and New Mexico, 1999. Quadrats were included if owls were color-banded and subsequently resighted on the quadrat.

Quadrat	Number of marked owls		Number of survey passes completed	Road access
	Male	Female		
H02	3	3	4	Roaded
H04	1	1	4	Roaded
H08	1	0	4	Roaded
H16	4	3	3	Roaded
H17	1	1	4	Roaded
H18	1	2	2	Unroaded
H20	1	0	4	Roaded
H21	4	4	3	Unroaded
H22	2	2	4	Unroaded
H23	3	2	4	Roaded
H24	5	5	4	Roaded

the estimated N s. In addition to p , the probability of recapture (c) also can be estimated, adding an additional parameter to be modeled. Both of these probabilities actually represent a combination of events, each with its own probability. For example, capture probability (p) is a function of (1) detecting an owl during a nocturnal survey; (2) locating the owl during a subsequent daytime follow-up survey; and (3) physically capturing the owl. Thus, capture probability is a combination of the probabilities of detecting the owl on both a nocturnal and diurnal survey and then physically capturing it. Recapture probability (c) requires largely the same steps, except that the owl does not need to be physically captured. Instead, it is necessary only to resight and correctly read the owl's color-band combination.

In standard dosed capture-recapture models, maximum-likelihood estimation is used to estimate both p and N simultaneously (Otis et al. 1978), so the resulting estimates represent the joint maximum-likelihood estimates. The Huggins models used here differ from the standard models in that only p and c are modeled, with N estimated as a derived parameter (N is computed algebraically from p and the number of individual owls

observed). Thus, our initial efforts centered on modeling the capture-recapture data to obtain parsimonious estimates of p .

To estimate p , we ran 26 closed-capture models in Program MARK (Table 16.4; notation follows Lebreton et al. 1992). In this set of models, we modeled the effects on p of sex, road access to the quadrat, occasion-specificity, and behavioral response to initial capture (i.e., inclusion of the recapture parameter c in the model). We used a bias-corrected version of Akaike's Information Criterion, AIC_c (Akaike 1973; Hurvich and Tsai 1995; Burnham and Anderson 1998), to rank models. The model best explaining the structure in p and c had the lowest AIC_c . This best model was $p = c_{T+roadless+sex}$ (Table 16.4), which constrained p 's equal to c 's (capture and recapture probabilities did not differ), changed linearly across occasions (T), had an additive effect of roadless versus roaded quadrats, and had an additive sex effect. The linear occasion, roadless, and sex effects were all negative and different from zero ($\beta_T = -0.350$, 95% CI = -0.637, -0.063; $\beta_{roadless} = -1.614$, 95% CI = -2.742, -0.486; $\beta_{sex} = -0.983$, 95% CI = -1.764, -0.203). This model indicated that capture probabilities declined over occasions in a linear fashion, were lower in roadless than in roaded quadrats, and were lower for females than for males.

We used model averaging to estimate the p 's rather than using the p 's from just the best model (Stanley and Burnham 1998a,b). This process, which incorporates model uncertainty into the estimates of p , involved estimating Akaike weights (the AIC_c weights in Table 16.4) for each model in Program MARK. These weights represented the likelihood that a given model was the best model to explain this particular data set, relative to the other models examined in our set of models (Buckland et al. 1997; Burnham and Anderson 1998). We then used these weights to derive a weighted mean estimate of capture probabilities (p_i) for each occasion for each sex and within roaded and unroaded quadrats across all models (see Stanley and Burnham 1998a,b). These weighted estimates of p_i had estimated standard errors that included a variance component due to model selection uncertainty that is, uncertainty about which model was best for providing an adequate structure on the p 's (Buckland et al. 1997; Burnham and Anderson 1998).

Thus, because the "best" model included occasion, road access, and sex effects, we ended up with 16 unique estimates of p (four occasions $\times$ two types of quadrats [roaded vs. unroaded] $\times$ two sexes; Table 16.5). These 16 unique values were expanded to 32 estimates of p assigned to the different sex, quadrat type, and pass number combinations. Associated with these 32

Table 16.4.

Models considered in Program MARK for estimating capture probabilities for Mexican spotted owls in quadrats listed in Table 16.3, and resulting summary statistics, including the AIC_c weights used for model averaging.

Model	AIC_c^a	ΔAIC_c^b	weight ^c	No. of parameters ^d	Deviance
$[p(T+Roadless+Sex) = c(T+Roadless+Sex), 0 \text{ passes}]$	221.62	0.00	0.41	4	231.41
$[p(T*Roadless+Sex) = c(T*Roadless+Sex), 0 \text{ passes}]$	222.99	1.37	0.21	5	212.68
$[p(T+Roadless+Sex) = c(T+Roadless+Sex)+\text{constant}, 0 \text{ passes}]$	223.62	2.00	0.15	5	213.31
$[p(T+Roadless*Sex) = c(T+Roadless*Sex), 0 \text{ passes}]$	223.68	2.06	0.14	5	213.37
$[p(T+Roadless) = c(T+Roadless)+\text{constant}, 0 \text{ passes}]$	227.75	6.13	0.02	4	219.55
$[p(Roadless) c(Roadless), 0 \text{ passes}]$	228.37	6.75	0.01	4	220.16
$[p(.) c(Roadless), 0 \text{ passes}]$	228.64	7.02	0.01	3	222.51
$[p(T+Roadless+Sex) c(T+Roadless+Sex), 0 \text{ passes}]$	229.49	7.87	0.01	8	212.73
$[p(Roadless) = c(Roadless), 0 \text{ passes}]$	229.74	8.12	0.01	2	225.68
$[p(T+Sex) = c(T+Sex), 0 \text{ passes}]$	229.75	8.13	0.01	3	223.62
$[p(Sex) c(Sex), 0 \text{ passes}]$	230.21	8.59	0.01	4	222.00
$[p(T*Sex) = c(T*Sex), 0 \text{ passes}]$	231.41	9.79	<0.01	4	223.20
$[p(T+Sex) = c(T+Sex)+\text{constant}, 0 \text{ passes}]$	231.62	10.00	<0.01	4	223.42
$[p(Roadless \text{ continuous}) = c(Roadless \text{ continuous}), 0 \text{ passes}]$	231.76	10.14	<0.01	2	227.70
$[p(Sex) = c(Sex), 0 \text{ passes}]$	232.23	10.61	<0.01	2	228.16
$[p(T*Sex) = c(T*Sex)+\text{constant}, 0 \text{ passes}]$	233.25	11.63	<0.01	5	222.94
$[p(t+Sex) = c(t+Sex), 0 \text{ passes}]$	233.50	11.88	<0.01	5	223.18
$[p(Roadless) c(.), 0 \text{ passes}]$	233.50	11.88	<0.01	3	227.37
$[p(.) c(.), 0 \text{ passes}]$	233.79	12.17	<0.01	2	229.73
$[p(T) = c(T)+\text{constant}, 0 \text{ passes}]$	235.70	14.08	<0.01	3	229.58
$[p(.) = c(.), 0 \text{ passes}]$	236.77	15.15	<0.01	1	234.75
$[p(t) = c(t), 0 \text{ passes}]$	238.12	16.50	<0.01	4	229.91
$[p(Quadrat) = c(Quadrat), 0 \text{ passes}]$	239.38	17.76	<0.01	11	215.98
$[p(t*Sex) = c(t*Sex), 0 \text{ passes}]$	239.41	17.79	<0.01	8	222.66
$[p(Quadrat) c(Quadrat), 0 \text{ passes}]$	247.59	25.97	<0.01	22	197.87
$[p(.) = c(.)]$	268.57	46.95	<0.01	1	266.55

AIC_c = A bias-corrected version of Akaike's Information Criterion for the model currently under consideration (Akaike 1973; Hurvich and Tsai 1989).

ΔAIC_c = The change in AIC_c between the model currently under consideration and the "best" model tested.

^c AIC_c weight = The weight given to the model currently under consideration in model averaging.

^d Number of parameters estimated in the current model.

Table 16.5.

Estimates of occasion-specific capture probabilities ($\hat{p}_i$) and indexing of overall capture probability ($\hat{p}^*$) among quadrats surveyed for Mexican spotted owls in the Upper Gila Mountains Recovery Unit, 1999. Estimates and indices were assigned based on combinations of sex, road access, and number of survey passes completed, based on modeling of capture probabilities (Table 16.4).

Gender	Access	Number of survey passes	Number of quadrats*	p_i	$\hat{p}^*$
Male	Roaded	3	1	p_1, p_2, p_3	1
	Roaded	4	20	p_1, p_2, p_3, p_4	2
	Unroaded	2	1	p_5, p_6	3
	Unroaded	3	1		
	Unroaded	4	2	p_5, p_6, p_7, p_8	4
Female	Roaded	3	1	p_9, p_{10}, p_{11}	5
	Roaded	4	20	$p_9, p_{10}, p_{11}, p_{12}$	6
	Unroaded	2	1	p_{13}, p_{14}	7
	Unroaded	3	1		8
	Unroaded	4	2	$p_{13}, p_{14}, p_{15}, p_{16}$	10

* Number of quadrats that were covered by a particular set of capture probabilities.

estimates of p was the estimated VC matrix $\mathbf{V}\hat{\mathbf{a}}\mathbf{r}(\hat{\mathbf{p}})$ (bold terms represent matrices). The VC matrix of the original 16 estimates from the model averaging procedure in MARK was used to build the 32×32 matrix $\mathbf{V}\hat{\mathbf{a}}\mathbf{r}(\hat{\mathbf{p}})$. The variances for each $\hat{p}$ were placed on the diagonal of this matrix, with the covariances between $\hat{p}$ in the appropriate off-diagonal elements and zeros elsewhere.

From the 32 estimates of p , we estimated an overall probability of seeing an owl (p^*) for each of the 10 sex, quadrat type, and pass-number combinations (rows in Table 16.5), as

$$p^* = 1 - (1 - \hat{p}_1)(1 - \hat{p}_2)(1 - \hat{p}_3)(1 - \hat{p}_4).$$

Subscripts 1 through 4 refer to survey pass, which was treated as a capture occasion. Thus, they correspond to subscripts in Table 16.5 only for the first two rows. For all other rows, sequential subscripts refer to passes 1 through the highest number pass completed. For quadrats with only three passes, $\hat{p}_4$ was set equal to zero, and for quadrats with only two

passes, $\hat{p}_3$ and $\hat{p}_4$ were set equal to zero ($\hat{p}_3 = \hat{p}_4 = 0$) when p 's were modeled. Ten values of p^* were required because there were 10 combinations of road access $\times$ number of passes $\times$ sex (Table 16.5).

Using $\mathbf{V}\hat{\mathbf{a}}\mathbf{r}(\hat{\mathbf{p}})$ (a 32×32 matrix) and a 10×32 matrix of partial derivatives of p^* with respect to p_i , we used the delta method (Seber 1982) to compute the VC matrix $[\mathbf{V}\hat{\mathbf{a}}\mathbf{r}(\hat{\mathbf{p}}^*)]$:

$$\mathbf{V}\hat{\mathbf{a}}\mathbf{r}(\hat{\mathbf{p}}^*) = \frac{\partial p^*}{\partial \mathbf{p}} \mathbf{V}\hat{\mathbf{a}}\mathbf{r}(\hat{\mathbf{p}}) \frac{\partial p^*}{\partial \mathbf{p}}^T,$$

where T indicates the transpose of the matrix of partial derivatives. This resulted in the 10×10 VC matrix $\mathbf{V}\hat{\mathbf{a}}\mathbf{r}(\hat{\mathbf{p}}^*)$.

ESTIMATING NUMBERS OF UNBANDIED OWLS PER QUADRAT

We estimated abundance of both banded and unbanded owls observed on quadrats. Numbers of banded owls were based on a direct count. To estimate numbers of unbanded owls observed we first identified unique owl "territories," then determined how many owls had been conclusively observed on those territories, based on daytime observations or other conservative criteria. We identified unique territories using a combination of nocturnal and/or diurnal observations clustered in a distinct geographic location. We assumed that a territory existed wherever (a) a nesting pair or juveniles were located; (b) ≥ 1 owl was located roosting in the same area (roost locations within 400 m of each other) on two or more passes, with all locations before 1 September; or (c) ≥ 1 owl was heard at night on two or more passes and one diurnal roost was located, with all locations before 1 September (again, locations within 400 m of each other).

Once unique territories were identified, we assessed their occupancy status to estimate numbers of unbanded birds. We counted unbanded birds where they were (a) unbanded mates of banded owls; or (b) unbanded members of nesting pairs (i.e., both pair members unbanded). We also classified an area as occupied by a pair if a male and female were observed within 400 m of each other on ≥ 1 daytime surveys, with all locations before 1 September. We counted only a single owl where we had daytime observations of only one owl in an area. Only daytime observations of known-sex owls were used in estimating numbers of unbanded owls, so that all observations could be adjusted by the correct sex-specific capture probability (see above).

Table 16.6.

Sex-specific estimates of Mexican spotted owl abundance in 25 quadrats surveyed within the Upper Gila Mountains Recovery Unit, Arizona and New Mexico, 1999.

sex-specific numbers of banded and unbanded owls observed, quadrat index (p^*) used in estimating capture probabilities, estimated capture probability ($\hat{p}^*$), corrected estimate of owl abundance ($\hat{N}$), and the estimated standard error of $\hat{N}$.

Quadrat	Gender	Number of owls		p^*	$\hat{p}^*$	$\hat{N}$	$SE(\hat{N})$
		Banded	Unbanded				
H01	Male	0	0	2	0.98	0	0
H02	Male	3	0	2	0.98	3.04	0.04
H03	Male	0	0	2	0.98	0	0
H04	Male	1	0	2	0.98	1.02	0.01
H07	Male	0	1	2	0.98	1.02	0.01
H08	Male	1	0	2	0.98	1.02	0.01
H09	Male	0	0	2	0.98	0	0
H11	Male	0	0	2	0.98	0	0
H12	Male	0	1	2	0.98	1.02	0.01
H13	Male	0	1	2	0.98	1.02	0.01
H14	Male	0	0	2	0.98	0	0
H16	Male	4	0	1	0.97	4.13	0.09
H17	Male	1	0	2	0.98	1.02	0.01
H18	Male	1	1	3	0.58	3.45	1.13
H19	Male	0	0	2	0.98	0	0
H20	Male	1	0	2	0.98	1.02	0.01
H21	Male	4	5	4	0.69	13.01	3.64
H22	Male	2	1	5	0.76	3.95	0.99
H23	Male	3	0	2	0.98	3.04	0.04
H24	Male	5	3	2	0.98	8.12	0.11
L01	Male	0	0	2	0.98	0	0
L02	Male	0	0	2	0.98	0	0
L03	Male	0	0	2	0.98	0	0
L05	Male	0	0	5	0.76	0	0
L06	Male	0	0	2	0.98	0	0
H01	Female	0	0	7	0.90	0	0
H02	Female	3	0	7	0.90	3.34	0.28
H03	Female	0	0	7	0.90	0	0
H04	Female	1	0	7	0.90	1.11	0.09
H07	Female	0	0	7	0.90	0	0
H08	Female	0	1	7	0.90	1.11	0.09
H09	Female	0	0	7	0.90	0	0
H11	Female	0	0	7	0.90	0	0
H12	Female	0	1	7	0.90	1.11	0.09
H13	Female	0	1	7	0.90	1.11	0.09
H14	Female	0	0	7	0.90	0	0
H16	Female	3	1	6	0.85	4.69	0.48

Quadrat	Gender	Number of owls		p^*	$\hat{p}^*$	$\hat{N}$	$SE(\hat{N})$
		Banded	Unbanded				
H17	Female	1	0	7	0.90	1.11	0.09
H18	Female	2	0	8	0.33	6.61	3.51
H19	Female	0	0	7	0.90	0	0
H20	Female	0	0	7	0.90	0	0
H21	Female	4	4	9	0.42	19.07	10.44
H22	Female	2	2	10	0.48	8.27	4.39
H23	Female	2	0	7	0.90	2.22	0.19
H24	Female	5	2	7	0.90	7.79	0.66
L01	Female	0	0	7	0.90	0	0
L02	Female	0	0	7	0.90	0	0
L03	Female	0	0	7	0.90	0	0
L05	Female	0	0	10	0.48	0	0
L06	Female	0	1	7	0.90	1.11	0.09

ESTIMATING THE NUMBER AND DENSITY OF OWLS PER QUADRAT

It is highly unlikely that all resident owls on the quadrats were observed during surveys. Consequently, we used the estimates of p^* derived earlier to correct the number of owls banded (plus the additional number of unbanded owls known to exist) on each of the 25 quadrats (Table 16.6).

Counts were corrected as:

$$\hat{N}_i = \frac{M_{i+1}}{\hat{p}_m},$$

where i indexes quadrat, m indexes the combination of sex, quadrat type, and number of passes, and M_{i+1} is the number of known owls on the quadrat (Table 16.7).

On each quadrat, we estimated N_i separately for males and females. Thus, we had 50 estimates (2 estimates $\times$ 25 quadrats) of N_i . To compute the VC matrix of the 50 estimates of N_i , that is, $\text{Var}(N)$, $\text{Var}(\hat{p}^*)$ was first expanded to be a 50×50 matrix, in which the variances for each estimate of p were placed on the diagonal corresponding to the appropriate N_i and the covariances between respective p 's were placed in the appropriate off-diagonal elements, with zeros elsewhere. This matrix then was used in the delta method (Seber 1982) to estimate $\text{Var}(\hat{N})$:

$$\text{Var}(\hat{N}) = \frac{\partial N}{\partial p} \text{Var}(\hat{p}^*) \frac{\partial N^T}{\partial p}.$$

Table 16.7.

Estimated abundance ($\hat{N}_{hq}$) and density ($\hat{D}_{hq}$) of Mexican spotted owls (males and females combined) in 25 surveyed quadrats. Observed counts (M_{i+1}) of banded and unbanded owls were corrected by capture probabilities to generate these estimates.

Quadrat	Area (km ²)	Owls observed	$\hat{N}_{hq}$	$\hat{SE}(\hat{N}_{hq})$	$\hat{D}_h$	$\hat{SE}(\hat{D}_h)$
H01	43.7	0	0	0	0	0
H02	61.2	6	6.38	0.29	0.10	0
H03	46.5	0	0	0	0	0
H04	76.4	2	2.13	0.10	0.03	0
H07	59.6	1	1.01	0.01	0.02	0
H08	55.7	2	2.13	0.10	0.04	0
H09	54.9	0	0	0	0	0
H11	57.9	0	0	0	0	0
H12	63.2	2	2.13	0.10	0.03	0
H13	66.8	2	2.13	0.10	0.03	0
H14	68.1	0	0	0	0	0
H16	69.0	8	8.82	0.52	0.13	0
H17	62.3	2	2.13	0.10	0.03	0
H18	66.9	4	9.52	4.35	0.14	0.07
H19	49.9	0	0	0	0	0
H20	71.0	1	1.01	0.01	0.01	0
H21	72.8	17	32.08	13.16	0.44	0.18
H22	52.5	7	12.21	5.10	0.23	0.10
H23	66.3	5	5.27	0.20	0.08	0
H24	66.9	15	15.9	0.69	0.24	0.01
L01	40.9	0	0	0	0	0
L02	66.1	0	0	0	0	0
L03	68.5	0	0	0	0	0
L05	45.0	0	0	0	0	0
L06	51.3	1	1.11	0.10	0.02	0

To compute the estimate of the total number of owls (males plus females) on each of the 25 quadrats, the matrix B was defined as consisting of two 25×25 identity matrices (one for each sex) set one on top of the other. Then $\hat{N}_{\text{quadrat}} = B^T \hat{N}$, where $\hat{N}$ is a 50×1 vector and $\hat{N}_{\text{quadrat}}$ is a 25×1 vector, with the estimated variance-covariance matrix $\text{Var}(\hat{N}_{\text{quadrat}}) = B^T \text{Var}(\hat{N}) B$.

We estimated density (owls/km²) for each of the 25 quadrats as $D = E \hat{N}_{\text{quadrat}}$, where the matrix E was a 25×25 diagonal matrix with diagonal elements consisting of the reciprocal of the area of each quadrat, with $\text{Var}(\hat{D}) = E \text{Var}(\hat{N}_{\text{quadrat}}) E^T$ (Table 16.7).

ESTIMATING TOTAL POPULATION SIZE ON THE RECOVERY UNIT

To compute the total population size for the recovery unit ($\hat{N}_{RU}$), we used a ratio estimator following Cochran (1977) and Bowden et al. (2003). We used the ratio of estimated population size ($\hat{N}_{hq}$, obtained from the $\hat{N}_{\text{quadrat}}$ vector, where h is the strata and q is the quadrat) to quadrat area (a_{hq} , with A_h the area of each strata h), such that:

$$\hat{N}_{RU} = \sum_{h=1}^2 \hat{N}_h = \sum_{h=1}^2 \hat{R}_h A_h,$$

where

$$\hat{R}_h = \frac{\sum_{q=1}^{u_h} \hat{N}_{hq}}{\sum_{q=1}^{u_h} a_{hq}}.$$

In our case, we had only two strata (low- or high-density). Because sampled quadrat population sizes were estimates instead of **exact** counts, and because of the covariances of the $\hat{N}_{hq}$ induced by estimating **common** resighting probabilities across quadrats and strata, the estimated variance of $\hat{N}_{RU}$, $\text{Var}(\hat{N}_{RU})$, was considerably more complicated than the usual case:

$$\begin{aligned} \text{Var}(\hat{N}_{RU}) = & \sum_{h=1}^2 \left(\frac{A_h}{\bar{a}_h} \right)^2 \left(\frac{1}{u_h} - \frac{1}{U_h} \right) \sum_{q=1}^{u_h} \frac{(\hat{N}_{hq} - \hat{R}_h a_{hq})^2}{u_h - 1} \\ & + \sum_{h=1}^2 \left(\frac{A_h}{\bar{a}_h} \right) \left[\sum_{q=1}^{u_h} \frac{\text{Var}(\hat{N}_{hq})}{u_h} + \sum_{q=1}^{u_h} \sum_{q' \neq q} \frac{\text{Cov}(\hat{N}_{hq}, \hat{N}_{hq'})}{u_h} \right] \\ & + \sum_{h=1}^2 \sum_{h' \neq h} \left(\frac{A_h}{\bar{a}_h} \right) \left(\frac{A_{h'}}{\bar{a}_{h'}} \right) \sum_{q=1}^{u_h} \sum_{q'=1}^{u_{h'}} \text{Cov}(\hat{N}_{hq}, \hat{N}_{h'q'}) \\ & - \sum_{h=1}^2 \left(\frac{A_h}{\bar{a}_h} \right)^2 \left(\frac{1}{u_h} - \frac{1}{U_h} \right) \left[\sum_{q=1}^{u_h} \frac{\text{Var}(\hat{N}_{hq})}{u_h} - \sum_{q=1}^{u_h} \sum_{q' \neq q} \frac{\text{Cov}(\hat{N}_{hq}, \hat{N}_{hq'})}{u_h(u_h - 1)} \right], \end{aligned}$$

where $\bar{a}_h$ is the average area of quadrats in the sample. The first term of this equation is the variation in the $\hat{N}_{hq}$ multiplied by a finite correction factor. The second term **incorporates** both sampling variation due to estimating the number of owls on the sampled **quadrats** and the covariances among quadrat estimates within the same stratum induced by model averaging. The third **term** incorporates the covariances between quadrats, and

the final term is a correction term that subtracts out mean **sampling variance** and covariances adjusted by a finite population correction **factor**. Finite population correction factors were incorporated into the **equation** because we sampled from a finite sampling frame. A reasonable **approximation** to this equation in which the finite population correction is **ignored** and $u_h^2 \approx u_h(u_h - 1)$ is:

$$\begin{aligned} \text{Var}(\hat{N}_{RU}) = & \sum_{h=1}^2 \frac{\left(\frac{A_h}{\bar{a}_h}\right)^2}{u_h} \left[\sum_{q=1}^{u_h} \frac{(\hat{N}_{hq} - \hat{R}_h \bar{a}_{hq})^2}{u_h - 1} \right] \\ & + \sum_{h=1}^2 \frac{\left(\frac{A_h}{\bar{a}_h}\right)^2}{u_h(u_h - 1)} \sum_{q=1}^{u_h} \sum_{q' \neq q}^{u_h} \text{Cov}(\hat{N}_{hq}, \hat{N}_{hq'}) \\ & + \sum_{h \neq h'}^2 \frac{\left(\frac{A_h}{\bar{a}_h}\right) \left(\frac{A_{h'}}{\bar{a}_{h'}}\right)}{u_h u_{h'}} \sum_{q=1}^{u_h} \sum_{q'=1}^{u_{h'}} \text{Cov}(\hat{N}_{hq}, \hat{N}_{hq'}). \end{aligned}$$

In this equation, the first **term** is the variation in the $\hat{N}_{hq}$, the second **term** incorporates the **covariances** induced within strata, and the third term incorporates the covariances induced among quadrats in different strata. These equations are extensions of the formulae given by **Skalski** (1994) because they incorporate the covariances of the $\hat{N}_{hq}$ **across** quadrats and strata.

Our estimate of total population for the Recovery Unit (exclusive of tribal lands) was imprecise (Table 16.8). For comparison with this estimate, we also computed a "naive" estimate of population size using raw counts of observed owls without adjusting these counts by p^* . These naive estimates thus represent counts of owls assuming complete detectability (i.e., $p^* = 1$). Resulting estimates for high and low strata were 2,091.0 ($\text{SE} = 574.0$) and 39.1 ($\text{SE} = 37.4$), **respectively, giving** a naive estimate of 2,130.1 ($\text{SE} = 575.3$) for the recovery unit (95% confidence interval = 930–3,330 owls). The difference in the standard **errors** for the naive estimate and $\hat{N}_{RU}$ was substantial, illustrating the impact of a few quadrats in greatly increasing the variance of the estimate when capture probability corrections are applied. For example, **quadrats H21, H22, and H18** had some of the lowest capture probabilities, and hence much larger variances for $\hat{N}_{hq}$. These three quadrats contributed 99.6% of the variance to the term:

$$\sum_{h=1}^2 \sum_{q=1}^{u_h} \text{Var}(\hat{N}_{hq}).$$

Table 16.8.

Estimates of population size ($\hat{N}$) of Mexican spotted owls for high- and low-density strata, and for the Upper Gila Mountains Recovery Unit (exclusive of tribal lands).

Stratum	$\hat{N}$	$\text{SE}(\hat{N})$	CV (%)
High density	2,896.6	1,073.6	37.1
Low density	44.0	44.2	100.5
Recovery Unit (without tribal lands)	2,940.6	1,075.4	36.6

Initial Power Analyses

Using the data from the **pilot study**, we evaluated statistical power using two approaches. In the first approach we regressed annual population estimates (calculated assuming a 20% decline over 10 yrs, see below) versus time and estimated the rate of change of the population (A) from the slope of the regression. In the second approach, we estimated A directly from the quadrat counts. If there is less among-quadrat variance in A than in population size, this approach should remove much of the among-quadrat variance.

REGRESSION APPROACH TO POWER ANALYSIS

A population declining by 20% over 10 yrs would decrease by $1 - 0.8^{1/9} = 0.02449$ per year. We assessed the power to detect this rate of decline using the methods of **Gerrodette** (1987) as described by Thompson et al. (1998). Here, we denote $N_{RU,t}$ as the population estimate of owls within the recovery unit in year t . We conducted a one-sided test with a sample of $n = 10$ yrs, $\alpha = 0.05$, and $\tau = -0.02449$ in the multiplicative model $N_{RU,t} = N_{RU,1}(1 + \tau)^{t-1}\epsilon_t$, using three assumed error **structures**. Error structures assessed included (1) CV, (the variation [CV] for the estimate of population size in year t) proportional to $1/\sqrt{\hat{N}_{RU,t}}$; (2) CV_t constant; and (3) CV_t proportional to $\sqrt{\hat{N}_{RU,t}}$. Statistical power, modeled as a function of the $\text{CV}(\hat{N}_{RU})$, was similar for each error structure (Figure 16.3).

This analysis clearly showed that the current level of effort was inadequate to **detect** a 20% decline with 10 yrs of surveys and would result in a power of approximately 18% when $\text{CV} = 36\%$ (Table 16.8). Even if the $\hat{N}_{hq}$ were estimated with no **error**, this level of effort with the current stratification would be inadequate to meet the power requirements in the Recovery Plan. This **can** be shown by examining the naive estimator based on

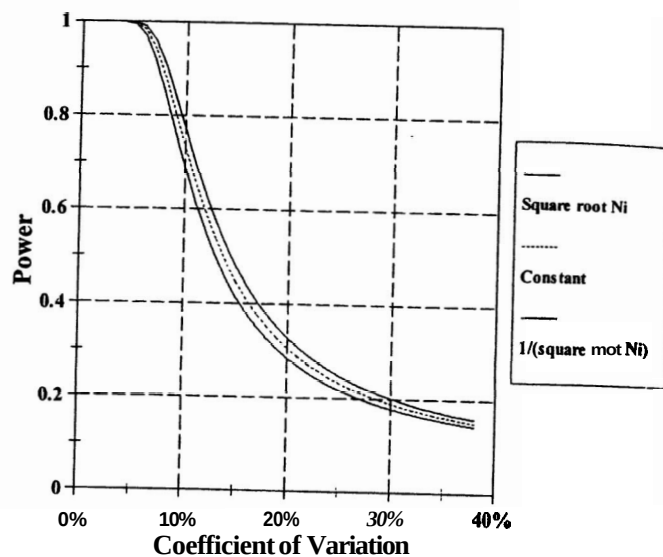


Figure 16.3. Estimated power to detect a 20% decline in Mexican spotted owl abundance over 10 yrs with a power of 90% for $\alpha = 0.05$, shown as a function of the coefficient of variation (CV) of the population estimate. Power was modeled assuming three separate error structures: CV proportional to $\sqrt{N_i}$, CV constant, and CV proportional to $1/\sqrt{N_i}$ (shown from top to bottom curves, respectively).

the minimum number of owls known to be on a quadrat (discussed above). The CV of this naive estimate was still 29%, resulting in power of approximately 20%, depending on the error structure assumed (Figure 16.3).

Meeting the power requirements in the Recovery Plan would necessitate that the CV for the annual estimates of $\hat{N}_{RU}$ be reduced to approximately 7% (Figure 16.3). To assess the feasibility of achieving such a reduction, we identified and evaluated several modifications to the existing sampling plan that could potentially reduce CV. These included (1) raising capture probabilities, especially on quadrats where capture probabilities were low; (2) better a priori stratification of quadrats to reduce among-quadrat variance within strata; and (3) increasing sample size.

As noted earlier, low capture probabilities in three high-density quadrats introduced considerable variance into the estimator of N_{RU} . We identified two changes in field techniques that should allow us to raise these capture probabilities. One would involve simply putting more surveyors in difficult roadless areas. A second would involve requiring sur-

veyors to carry and use the proper equipment. Surveyors working in these backcountry quadrats sometimes carried small binoculars rather than the heavier binoculars they were issued. These smaller binoculars proved inadequate for resighting color bands. These changes likely would result in greater capture probabilities but would be of limited help with respect to statistical power to detect trends. Comparisons with the naive estimator based on minimum number known alive suggest that consistently high capture probabilities would lower $CV(\hat{N}_{RU})$ from approximately 36% to approximately 29%. This reduction by itself is insufficient to meet the specified power requirements.

Better a priori stratification of quadrats could reduce among-quadrat variance in owl abundance within strata, especially in the high-density stratum. The estimate for the low-density stratum ranged from 0–1 owls per quadrat and contributed little variance to the total. However, naive estimates for the high-density stratum ranged from 0–17 owls per quadrat. The large variance in $\hat{N}_{RU}$ comes predominantly from this high variability across the high-density quadrats.

We were unable to determine the magnitude of potential improvements in a priori stratification of quadrats. We stratified by elevation in the pilot study because we were unable to locate a digital coverage of vegetation types that was mapped at a reasonable scale and covered the entire study area. This problem still exists and severely constrains our ability to stratify more precisely. Consequently, the problem here is similar to the problem with capture probabilities: improvements can be made, but those improvements by themselves are unlikely to be great enough to result in adequate statistical power.

The final alternative considered was to increase the sample size. Absent improvements in stratification, roughly a 10-fold increase in sampling effort would be required to obtain the necessary precision to detect a 20% decrease in 10 yrs (i.e., a $CV(\hat{N}_{RU}) = 7\%$) for the naive estimates based on the minimum number known alive. Approximately an 18-fold increase in sampling effort would be required to obtain the necessary precision for the exact estimator of the variance of $\hat{N}_{RU}$ when the current variability of capture probabilities is used. The effect of better stratification cannot be modeled here, as discussed above. Given the already large expense of this Sampling plan and the practical difficulties encountered in sampling even 25 quadrats, we concluded that such large increases in sampling effort were not feasible. This conclusion led us to consider a second approach to estimating λ .

APPROACH TO ESTIMATING λ DIRECTLY FROM QUADRAT DATA

Because the large among-quadrat variance in $\hat{N}_{RU}$ caused a large variance in estimates of λ obtained by taking ratios of consecutive $\hat{N}_{RU}$ values, we considered an alternative approach in which λ was estimated directly from the sample and then extrapolated to the population. To illustrate, consider the 20 values of $\hat{N}_{hq}$ for the high-density strata (i.e., the owls observed on each quadrat, given in Table 16.7). Assuming a second survey 1 yr later, an estimate of λ for the year from t to $t+1$ for strata h is:

$$\hat{\lambda}_t = \frac{\sum_{q=1}^{u_h} \hat{N}_{t+1,hq}}{\sum_{q=1}^{u_h} \hat{N}_{t,hq}}$$

If survey techniques were improved sufficiently to eliminate the few large standard errors for $\hat{N}_{hq}$, the standard errors of $\hat{N}_{hq}$ could be ignored. We simulated this by using the M_{t+1} values from Table 16.7 in place of $\hat{N}_{hq}$ in the following power calculation. The sampling variance of $\mathbf{I}$ can be estimated by recognizing that λ is a simple ratio estimator (e.g., Cochran 1977:150-188). For a given strata h , and finite population correction fpc :

$$\text{Var}(\hat{\lambda}_t) = \left[\frac{1 - fpc}{\frac{1}{u_h} \left(\sum_{q=1}^{u_h} \hat{N}_{t,hq} \right)^2} \right] \left[\frac{\sum_{q=1}^{u_h} (\hat{N}_{t+1,hq} - \hat{\lambda} \hat{N}_{t,hq})^2}{u_h - 1} \right]$$

The overall estimate of λ across a 10-yr period would consist of the product of the nine $\hat{\lambda}$ values as calculated by the above formula. The variance of the λ estimate for the 10-yr period can be obtained as the variance of the product of the nine estimates by repeatedly applying the formula (Goodman 1960) $\text{Var}(xy) = x^2 \text{Var}(y) + y^2 \text{Var}(x) - \text{Var}(x) \text{Var}(y)$. However, the product $\prod_{t=1}^9 \hat{\lambda}_t$ simplifies to the ratio estimator for the surveys at time $t = 1$ and $t = 10$ (the first year and the last year of the monitoring period), that is,

$$\hat{\lambda} = \prod_{t=1}^9 \hat{\lambda}_t = \frac{\sum_{q=1}^{u_h} \hat{N}_{t+9,hq}}{\sum_{q=1}^{u_h} \hat{N}_{t,hq}}$$

because the intermediate terms cancel out of the equation. Thus, the variance for the decline across 10 yrs can be estimated as:

$$\text{Var}(\hat{\lambda}_t) = \left[\frac{1 - fpc}{\frac{1}{u_h} \left(\sum_{q=1}^{u_h} \hat{N}_{t,hq} \right)^2} \right] \left[\frac{\sum_{q=1}^{u_h} (\hat{N}_{t+9,hq} - \hat{\lambda} \hat{N}_{t,hq})^2}{u_h - 1} \right]$$

The idea that **only** estimates of N from the first and last years are needed to estimate λ was not intuitive, but can be demonstrated mathematically with a simple example. Given a 5-yr monitoring period, we obtain

four estimates of λ via $\hat{\lambda}_1 = \frac{\hat{N}_2}{\hat{N}_1}$, $\hat{\lambda}_2 = \frac{\hat{N}_3}{\hat{N}_2}$, $\hat{\lambda}_3 = \frac{\hat{N}_4}{\hat{N}_3}$ and $\hat{\lambda}_4 = \frac{\hat{N}_5}{\hat{N}_4}$. A product of

λ over the 5-yr period can be estimated as $\hat{\lambda} = \hat{\lambda}_1 \cdot \hat{\lambda}_2 \cdot \hat{\lambda}_3 \cdot \hat{\lambda}_4$, which can be rewritten as:

$$\hat{\lambda} = \left(\frac{\hat{N}_2}{\hat{N}_1} \right) \cdot \left(\frac{\hat{N}_3}{\hat{N}_2} \right) \cdot \left(\frac{\hat{N}_4}{\hat{N}_3} \right) \cdot \left(\frac{\hat{N}_5}{\hat{N}_4} \right)$$

The numerator of the first term and the denominator of the second term ($\hat{N}_2$) cancel out, as do $\hat{N}_3$ and $\hat{N}_4$ in the second, third, and fourth terms. This leaves us with $\hat{\lambda} = \hat{N}_5 / \hat{N}_1$, which includes only the first and last years of the monitoring period.

For the following power analysis, we again simulated declines of 80% over a 10-yr period (i.e., annual $\lambda = 0.80^{(1/9)}$). We used two sets of population parameters to model annual rate of change of the population. Set 1 had survival - emigration (ϕ) equal to 0.865 and immigration + recruitment (f) equal to 0.110, giving $\lambda = \phi + f = 0.975$. Set 2 had $\phi = 0.845$ and $f = 0.130$, again giving $\lambda = 0.975$. The parameter ϕ is the probability that an owl on the quadrat at time t remains alive and on the quadrat at time $t+1$. The parameter f is the number of new recruits into the population at time t divided by the number of owls present at time $t - 1$. New recruits can be either offspring of individuals on the quadrat or new immigrants. These parameter sets were derived from demographic data from two long-term study areas in Arizona and New Mexico (Seamans et al. 1999) and were biologically reasonable. These study areas yielded mean estimates of 0.845 for ϕ and 0.110 for f . We adjusted these values slightly so that both parameter sets gave a rate of change of exactly 80% across 10 yrs.

For this **analysis**, the initial number of owls per quadrat was selected at random (with replacement) from the observed distribution of owls on the quadrats sampled. Demographic variation was modeled as a random binomial variable. Thus, the population size on a quadrat at time $t + 1$ was computed as the random binomial variable of the owls surviving from time t plus another random binomial variable of the number of new immigrants and recruits since time t . Once a quadrat reached a zero population level, the recolonization probability was zero, that is, quadrats never experienced immigration unless at least one animal was present. This assumption was biologically unrealistic but made little difference in terms of statistical power because it had little effect on the variance of the estimate. That is, colonization reduced effect size but not variance.

We conducted simulations using sample sizes of 25, 40, 50, 60, 75, 100, 125, 150, 175, and 200 quadrats. For each sample size, 100,000 simulations were conducted to estimate power. Estimates of β (where $\beta = [1 - \text{power}]$) were computed by determining the proportion of confidence intervals on the estimate of λ for the 9-yr interval that included 1. Results indicated that 90% power was achieved when between 100 and 150 quadrats were sampled

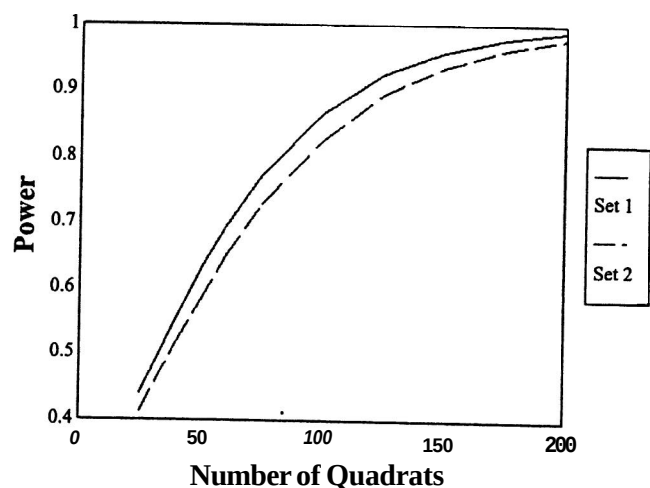


Figure 16.4. Power to detect a decline of 20% in Mexican spotted owl abundance over a 10-year period when randomly selected quadrats were sampled in years 1 and 10. Two sets of population parameters were used to model annual rate of change of the population. Set one (top curve) had survival-emigration (ϕ) = 0.865 and immigration + recruitment (f) = 0.110. Set two (bottom curve) had ϕ = 0.845 and f = 0.131. For both sets, annual λ = 0.975511 and 10-year λ = 0.8.

in year 1 and again in year 10 (Figure 16.4). Additional analyses demonstrated that sampling during the intervening years did not increase the power of this design. This was because temporal variation in the population growth process affected the probability that the population would decline by 20% but did not affect the power of the survey to detect that decline.

This method thus appears to offer powerful advantages over the regression approach. Using this method, the number of quadrats required to be sampled was considerably reduced, and sampling was required in only 2 yrs. The second advantage is largely illusory, however, because understanding the magnitude of temporal variation is important in an ecological and interpretive context. For example, we might find that the population regularly fluctuates by as much as 20%, suggesting that a 20% decline may not be cause for alarm and that the delisting criterion should be revised. Conversely, we might note a change of < 20% at the end of 10 yrs but observe large fluctuations in population size during the intervening years. In this case, delisting might not be indicated, as populations that undergo such large fluctuations may be especially vulnerable to extinction (Goodman 1987). Therefore, we would be reluctant to recommend a monitoring program that did not provide information on the magnitude of temporal variation in population size at intervals shorter than a decade.

Secondary Analyses Aimed at Increasing Precision of Estimates

Our overall conclusion from the previous section mirrored our earlier conclusion: the large increases necessary in sampling effort were not feasible. This led us to conduct a second set of analyses aimed at evaluating ways to improve the precision of estimates without large increases in sampling effort. We focused on two approaches: reducing quadrat size and using covariates to aid in estimating population size.

EFFECTS OF QUADRAT SIZE ON MEXICAN SPOTTED OWL DENSITY ESTIMATES

Smaller quadrats could be sampled for less money than large quadrats, allowing for greater spatial replication for a fixed level of funding. This greater spatial replication should in turn reduce the spatial variation component. Consequently, we explored the potential effects of reducing quadrat size to approximately 35–50 km². Parameters evaluated included (1) the magnitude and sampling variance of density estimates, (2) tempo-

ral process variation in density estimates, and (3) incidence of movement across quadrat boundaries by owls holding territories near quadrat boundaries (i.e., edge effects). Density was used as the basis for comparison to control for differences in quadrat area.

Briefly, comparisons were made between quadrats of the size used in the pilot study conducted in 1999 and quadrats approximately half the size of those sampled. Two relatively large study areas delineated to investigate the demography of Mexican spotted owls in Arizona and New Mexico (585 and 323 km², respectively; Seamans et al. 1999) were used to develop these comparisons. Spotted owls were color-banded and resighted annually on each study area from 1991 through 1999. Personnel conducting these studies provided data on spotted owl locations (roost and nest sites occupied by pairs, single males, or single females), with one location representing a unique spotted owl territory center for each year. Territory locations were delineated based on color-marked birds and geographic locations. These data provided the basis for estimating density within quadrats.

Using GIS, we subdivided the study areas into large quadrats (similar in size to those used in the pilot study) and small quadrats (approximately half the size of those sampled in 1999). This involved first delineating watersheds within the demography areas, then subdividing these into sub-watersheds in the appropriate size range, using topographic features. We then overlaid owl locations on the resulting quadrats and computed annual estimates of density (owls/km²) for both large and small quadrats where (1) the number of individuals was computed for each quadrat and year (including quadrats with no owls); (2) the density of each quadrat was computed based on number of individuals and quadrat area; and (3) mean density, with its standard error, was estimated for each year.

In this analysis, we assumed that the number of individuals within a quadrat was estimated without error, that is, with no sampling variance, and therefore assumed that the arithmetic standard deviation associated with mean annual densities estimated spatial process standard deviation (σ_{spatial}) among quadrats within each year. Annual estimates of $\sigma_{\text{spatial}}^2$

were expressed as coefficients of spatial process variation, $\hat{C}\hat{V}_{\text{spatial}} = \frac{\hat{\sigma}_{\text{spatial}}^2}{\hat{D}^2}$

We estimated temporal process variation only for small quadrats because our interest centered on whether or not small quadrats could be used. Because the mean annual estimates had sampling variance associated with them, $\text{Var}(\hat{D}) = [\hat{SE}(\hat{D})]^2$, we used a method-of-moments random-

effects model using shrinkage estimators to estimate $\sigma_{\text{temporal}}^2 \hat{D}$, and $\text{SE}(\hat{D})$, using an intercepts-only model, and β_1 (trend in estimates over time) and $\sigma_{\text{residual}}^2$ using a linear trend model. These models removed the sampling variation from the total variation to estimate temporal process variation. In the linear trend models, $\sigma_{\text{residual}}^2$ was the amount of temporal process variation remaining after accounting for a linear trend. We conducted separate analyses using estimates for (1) all 9 yrs and (2) for only the last 7 yrs. The latter analysis reflected the potential for a "learning" effect by which numbers of owls may have been underestimated in early years because the investigators were still becoming familiar with the study areas and the territorial owl populations.

Annual estimates of density were similar between large and small quadrats (Figure 16.5), indicating that reducing quadrat size did not increase

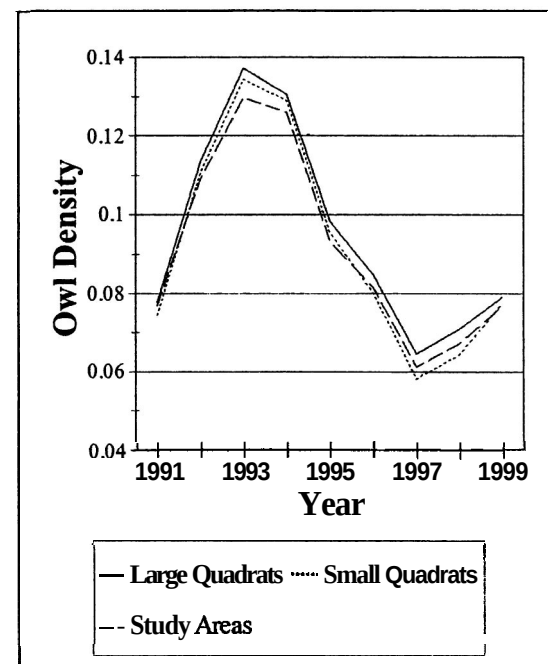


Figure 16.5. Trends in annual density (owls/km²) of Mexican spotted owls derived from large and small quadrats delineated in two demography study areas in Arizona and New Mexico. Annual density estimates averaged over the two study areas are shown for comparison.

bias in density estimates. In addition, density estimates from the large and small quadrats were similar to annual density estimates averaged across the two demography study areas (Figure 16.5). Mean standard errors of density estimates were 12.5% smaller for small quadrats than for large quadrats. In contrast, annual estimates of spatial process variation were approximately 24% higher for small quadrats than for large quadrats (Figure 16.6), likely due to the patchy distribution of owls across the landscape. We expect that the sample size could be approximately doubled with smaller quadrats, however. This increase in sample size should reduce the variance of the mean by $1/\sqrt{2} = 0.707$. Thus, use of small quadrats should result in a net decrease of approximately 12% in the CV of the density estimate (i.e., 0.707×1.239 [ratio of process variation on small quadrats relative to large quadrats] = 0.88).

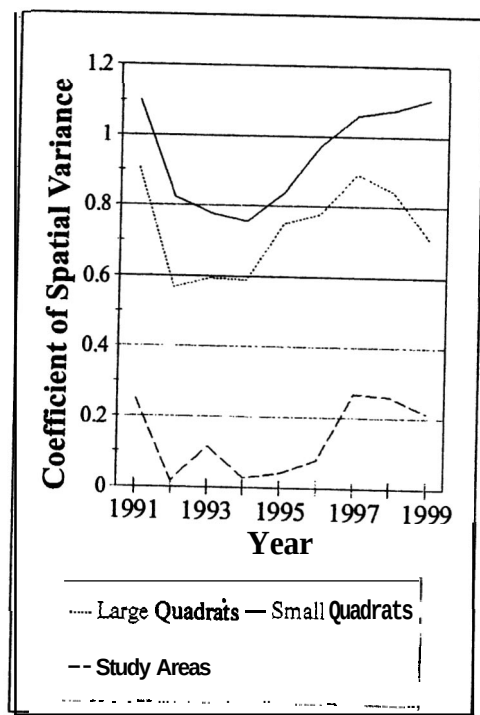


Figure 16.6. Trends in annual estimates of the coefficient of spatial process variation for estimates of density of Mexican spotted owls in large and small quadrats delineated in two demography study areas in Arizona and New Mexico. Annual estimates averaged over the two study areas are shown for comparison.

The estimates of temporal process standard variation (based on the random effects means models) were high for both the 9- and 7-yr periods (Table 16.9). Process CVs were 0.251 and 0.296 for the 9-yr and 7-yr periods, respectively. The linear model reduced temporal process variation substantially for the 7-yr period, but not for the 9-yr period (Table 16.9). This suggests that temporal process variation around the trend line was minimal for small quadrats where there was both a learning effect and a linear trend.

The degree to which territories crossed quadrat boundaries in different years was evaluated in two ways for large and small quadrats separately. First, we computed the total number of territories that crossed quadrat boundaries (e.g., a territory found in one quadrat in one year was found in another quadrat in a different year) across all years. Second, we estimated annual rates of territories crossing boundaries. This involved dividing the number of territories in year $t+1$ that were on quadrats different from those in year t by the total number of territories in year t that were available for reobservation in year $t+1$ (i.e., territories that were observed in one year but not the next were not included).

Annual rates of territories crossing boundaries were almost identical for small and large quadrats (Table 16.10). These rates varied in only 2 yrs (1997 and 1998), with this difference due to one territory crossing small quadrat boundaries in each of these years (Table 16.10). Rates of territories crossing quadrat boundaries appeared to increase over time, which may indicate a general pattern of shifts in territory locations over time.

Table 16.9.

Parameter estimates from means and linear trends models of Mexican spotted owl density estimated from small quadrats over 9- and 7-year periods. Estimates of σ^2 from the means model represent temporal process variation, whereas estimates from the linear trend model represent residual temporal variation remaining from that variation accounted for by the model.

Parameter	Estimates from means model		Estimates from trend model	
	9 yrs	7 yrs	9 yrs	7 yrs
β_0	0.0894	0.0893	0.1168	0.1369
$SE(\beta_0)$	0.0088	0.0113	0.0181	0.0159
β_1	—	—	-0.0054	-0.0120
$SE(\beta_1)$	—	—	0.0032	0.0034
σ^2	0.0005	0.0007	0.0004	0.0001
(95% CI)	(0.0002, 0.0034)	(0.0001, 0.0030)	(0.0001, 0.0023)	(0, 0.0006)

Table 16.10.

Annual rates at which Mexican spotted owl territories crossed boundaries of large and *small* quadrats delineated from demography study areas (*Seamans* et al. 1999) in the Upper Gila Mountains Recovery Unit, Arizona and New Mexico.

Year	Number of territories in year t	Number of territories found in different quadrat in year $t + 1$		Rate of territories crossing quadrat boundaries	
		Large quadrats	Small quadrats	Large quadrats	Small quadrats
1991	42	—	—	—	—
1992	57	1	1	0.024	0.024
1993	62	1	1	0.018	0.018
1994	51	2	2	0.032	0.032
1995	44	1	1	0.020	0.020
1996	32	7	7	0.159	0.159
1997	32	4	5	0.125	0.156
1998	29	2	3	0.063	0.094
1999	—	5	5	0.172	0.172

In summary, reducing quadrat size did not bias estimates of owl density and did not inflate "edge effects" in terms of owls moving among quadrats between years. Further, because more small quadrats could be sampled for a given funding level, use of smaller quadrats should improve the precision of estimates of owl abundance, as well as allow for greater spatial replication. It is impossible to realistically assess the cost per small quadrat, however, as this cost will depend largely on the actual sample of quadrats drawn. For example, this cost is a function of quadrat distribution (e.g., travel time to access quadrats) and logistics (e.g., road access or lack thereof, as well as **topography**).

EVALUATION OF TOPOGRAPHIC COVARIATES TO AID IN ESTIMATING POPULATION SIZE

We used a ratio estimator with covariates in our initial estimation of population size to reduce spatial variability relative to a ratio estimator that did not use covariates (**Bowden** et al. 2003). We used quadrat area as a covariate in this estimate for lack of alternatives. Quadrat area was not tightly linked to owl density, however, and use of covariates that are linked

to owl density should reduce spatial variation and improve the precision of the estimate. Consequently, we developed alternative terrain-based covariates and evaluated their use with this ratio estimator. We focused on terrain-based covariates because they could be computed from digital elevation models, which were readily available for the study area. A **combination** of terrain-based and habitat-based covariates (e.g., forest types) likely would work even better, but development of habitat-based covariates was beyond the scope of this study.

We developed and screened numerous terrain-based covariates but focus here on a covariate that provided an index of topographic roughness. This index (hereafter **TIN ratio - 1**) represented the ratio of true surface area to planar area for each quadrat, with true surface area derived from a triangulated irregular network (TIN). Because this ratio is always 21, we subtracted 1 from the ratio to set the minimum value to zero and force the relationship through the origin.

This covariate was highly correlated with owl abundance on sampled quadrats (Figure 16.7) and including it improved the precision of the estimate considerably. Using the CV as an index of variability, use of this covariate reduced CV from 37% (when quadrat area was used as the covariate; **Bowden** et al. 2003) to 24%. The relationship between abundance and **TIN ratio - 1** appeared to be nonlinear, **however**, suggesting that further increases in precision might be possible using nonlinear functions

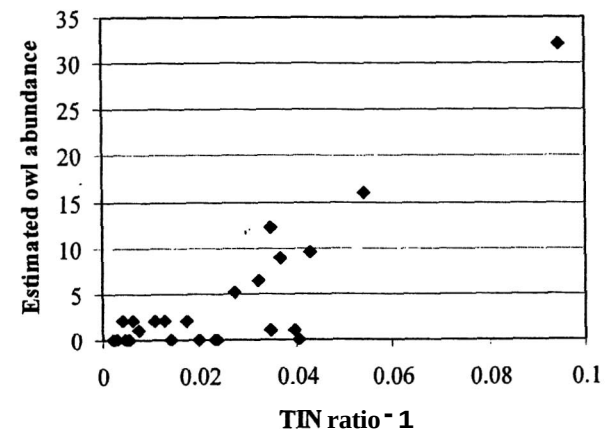


Figure 16.7. The relationship between estimated abundance of Mexican spotted owls and a topographic covariate (**TIN ratio - 1**) for 25 quadrats sampled in Arizona and New Mexico, 1999.

of TIN ratio - 1. Consequently, we explored several nonlinear functions of TIN ratio - 1 as covariates. The best fit (CV = 21%) was obtained using (TIN ratio - 1)^{1.52}. Thus, we reduced variability in the estimate of abundance by 43% through use of an appropriate topographic covariate. We suspect that further reductions would be possible using a multivariate ratio estimator with both habitat- and terrain-based covariates. This analysis thus suggests that considerable reductions in variability are possible, with concurrent increases in the precision of the estimate and in our ability to detect trends in owl abundance.

Evaluating the Effect of Temporal Variation in Abundance

As a final step in evaluating the proposed monitoring program, we conducted a set of analyses to evaluate the effect of temporal process variation on (1) the probability of observing a 20% decline over 10 yrs; and (2) the estimated power to detect population trend. These analyses used estimates of temporal variation derived from the two demography study areas (Seamans et al. 1999). No such estimates were available when the recovery plan was produced or when the pilot study was initiated.

ESTIMATION OF THE PROBABILITY OF A 20% DECLINE

Because of temporal process variation in owl abundance, the Mexican spotted owl population could decline by 20% over a 10-yr period even if the population was stable over longer time horizons. To determine the probability of such a scenario, we estimated the process variance of λ , σ_λ^2 , using the capture-recapture data from the demographic study areas in Arizona and New Mexico (Seamans et al. 1999). We used two approaches to estimate σ_λ^2 . The first compared consecutive annual counts of owls observed on the study areas (i.e., $\lambda = N_{t+1}/N_t$, where N was the combined number of owls observed on both study areas in year t). The first two estimates of A (for the intervals 1991-1992 and 1992-1993) were discarded because of the potential learning effect by observers during the first years of the study, leaving six estimates of A for the combined study areas. The standard deviation of these six estimates ($SD = \sigma_\lambda = \sqrt{\sigma_\lambda^2} = 0.175$) represents the process standard deviation of the population growth rate ($\bar{\lambda} = 0.925$) assuming that annual "censuses" were accomplished. This estimate should

be biased high because the counts used to estimate A likely contained some sampling variation.

The second approach used estimates of A obtained using capture-recapture data with the Pradel (1996) model in Program MARK (White and Burnham 1999). Five estimates of A from the model $\{\phi(t), p(\text{area} \cdot t), \lambda(t)\}$ for the two study areas were used to estimate σ_λ . The first two estimates again were discarded because of potential learning effects by observers, and A cannot be estimated for the first and last intervals with this model because it is confounded with estimates of p . The variance components estimator of Program MARK (White et al. 2002) estimated process standard deviation for the remaining five estimates as $\hat{\sigma}_\lambda = 0.114$ (95% confidence interval = 0.040-0.377; $\lambda = 0.905$; $\hat{SE} = 0.0557$). This estimate should be less biased than the value based on consecutive counts because it incorporated owl detection probabilities and, hence, sampling variances for the estimates.

Each of these estimates of temporal variability was used to generate 1,000,000 values of the product $\sum_{i=1}^n \lambda_i$, where λ_i was drawn from a normal distribution with a mean of 1 and a standard deviation equal to the appropriate estimate of σ_λ . The proportion of the simulations with the product less than 0.9, 0.8, and 0.5 then represent the probability of the owl population declining by 10, 20, and 50%, respectively, over a 10-yr period.

Results of these simulations indicated that the likelihood of observing a 20% decline in owl abundance over a 10-yr period was high given current estimates of temporal variation in abundance (Table 16.11). To assess the sensitivity of these results to the assumption of a normal distribution, two beta distributions also were examined. To set the bounds on the distribution of A , a projection matrix was developed:

$$L = \begin{bmatrix} 0 & s_{SA}fR & s_AfR \\ s_J & 0 & 0 \\ 0 & s_{SA} & s_A \end{bmatrix},$$

where s_A = adult survival, s_{SA} = subadult survival, s_J = juvenile survival, f = fecundity, and R = proportion of young that are female. To estimate an upper bound on A , we set $s_A = 0.95$, $s_{SA} = 0.95$, $s_J = 0.60$, $f = 2.8$, and $R = 0.50$. These values were very liberal compared to observed vital rates (Seamans et al. 1999). We obtained an asymptotic value of $A = 1.49$ based on the dominant eigenvalue of the matrix:

Table 16.11.

Probability of the Mexican spotted owl population declining by 10, 20, or 50%, assuming that the population rate of growth (λ) is distributed with process standard deviation $\sigma_\lambda = 0.175$ or **0.114**. We simulated both a normal and a beta *distribution*. Probabilities shown were based on **1,000,000** simulations, so standard errors of the estimates were $\sqrt{\hat{p}(1-\hat{p})/1,000,000}$.

Statistical distribution	Bounds	Decline (%)	Probability of decline	
			$\sigma_\lambda = 0.175$	$\sigma_\lambda = 0.114$
Normal	$-\infty, \infty$	10	0.515	0.439
		20	0.429	0.312
		50	0.156	0.037
Beta	0.60, 1.49	10	0.521	0.441
		20	0.434	0.312
		50	0.151	0.033
Beta	0.75, 1.49	10	0.527	0.446
		20	0.436	0.313
		50	0.138	0.027

$$\lambda = \frac{s_A + \sqrt{s_A^2 + 4Rs_s s_{SA} f}}{2}$$

To estimate a lower bound on λ , we set $s_A = 0.60$, $s_{SA} = 0.60$, $s_f = 0$, $f = 0$, and $R = 0.50$. These values, which were very conservative (Seamans et al. 1999), yielded an asymptotic value of $\lambda = 0.60$. As can be seen from the eigenvalue equation, iff $= 0$, $\lambda = s_A$. The value $s_{SA} = 0.60$ was taken from Franklin et al. (2000) for northern spotted owls. A lower bound on $\lambda = 0.75$ also was considered.

Values of λ were simulated from a beta distribution as

$$B(\alpha, \beta)(\lambda_{\text{upper}} - \lambda_{\text{lower}}) + \lambda_{\text{lower}}, \text{ where } B(\alpha, \beta) \text{ had a mean of } \mu = \frac{\bar{\lambda} - \lambda_{\text{lower}}}{\lambda_{\text{upper}} - \lambda_{\text{lower}}}$$

$$\text{and standard deviation of } \sigma = \frac{SD(\lambda)}{\lambda_{\text{upper}} - \lambda_{\text{lower}}}, \text{ yielding } \alpha = \frac{-\mu(\mu^2 - \mu + \sigma^2)}{\sigma^2}$$

$$\text{and } \beta = \frac{(\mu - 1)(\mu^2 - \mu + \sigma^2)}{\sigma^2}. \text{ Use of these alternate distributions did not}$$

greatly affect the results of the simulations (Table 16.11).

To verify that these simulations were approximately correct, we derived analytical results (as discussed earlier) to provide approximate estimates.

This analysis documented that the expected value of the product $\prod_{i=1}^9 \lambda_i$ was 1, as we found in the simulations. Further, the approximate variance of this product based on a Taylor series expansion (delta method) was $\text{Var}(\prod_{i=1}^9 \lambda_i) = \prod_{i=1}^9 \lambda_i \sum_{i=1}^9 \text{CV}(\lambda_i)^2 = 9\sigma_\lambda^2$, although we know that this estimate is biased low. Again, this analytical result was consistent with simulation results.

The delisting criterion in the Mexican spotted owl Recovery Plan (USDI Fish and Wildlife Service 1995) specified monitoring for a 20% decline in owl abundance over a 10-yr period. Our results demonstrated that the likelihood of observing such a decline was high (e.g., Tables 16.11, 16.12) even when the overall population trend was stable (i.e., $\bar{\lambda} = 1$), given the level of process variation observed in the demography studies (Seamans et al. 1999). This suggests that observing a 20% decline in owl abundance over a 10-yr period does not provide unambiguous evidence that the owl population is in trouble. In other words, such a decline could occur with relatively high probability even though the owl population was stable over longer time horizons. Consequently, we considered alternative approaches to deriving a less ambiguous delisting criterion.

One such approach would involve basing the criterion on the probability of observing a decline of specified magnitude. To illustrate this approach, we modeled the percent decline in abundance expected as a func-

Table 16.12.

The percent decline expected in the Mexican spotted owl population over 10 yrs, given the specified probability levels and levels of temporal process variation (σ_λ).

Statistical distribution	Bounds	Probability	Expected percent decline	
			$\sigma_\lambda = 0.175$	$\sigma_\lambda = 0.114$
Normal	$-\infty, \infty$	0.05	65.7	47.3
		0.10	57.4	39.8
		0.25	39.4	25.1
Beta	0.60, 1.49	0.05	64.3	46.7
		0.10	56.4	39.4
		0.25	39.3	25.1
Beta	0.75, 1.49	0.05	61.8	45.5
		0.10	54.5	38.7
		0.25	38.5	25.0

tion of various probability levels, using the three distributions and two estimates of process standard deviation discussed above. Results suggested that neither the particular distribution used nor the lower bound on the beta distribution had much effect on the predictions (Table 16.12). In contrast, the predictions were extremely sensitive to the process standard deviation. Thus, one of the biggest uncertainties in devising an appropriate delisting criterion for the Mexican spotted owl population is the true magnitude of the process standard deviation. The available estimates may overestimate overall temporal variation because localized temporal variation may influence the populations on the demography areas. However, no other estimates of σ_λ were available at this time.

ESTIMATION OF POWER TO DETECT A DECLINE

We also evaluated how process variation affected the power to detect trends in the population, because (1) the process variance of λ (i.e., temporal variability in owl abundance) strongly influences predicted probabilities of decline, and (2) considerable uncertainty exists concerning the true magnitude of this process variance (see above). Most research evaluating the power of monitoring programs to detect a trend has not considered process variance of λ directly. For example, Gerrodette (1987) developed analytical formulae for determining power but assumed that process variance was zero. Hatfield et al. (1996) considered serial correlation of population estimates but did not consider process variance explicitly. Gibbs (1999, 2000) provided a program (MONITOR) to simulate power of a monitoring program that "can accommodate random trend variation among plots or sites if estimates of its magnitude are available" (Gibbs 2000:228), but he assumed "deterministic linear trends are projected from the initial abundance index on each plot over the series of survey years" (Gibbs 2000:225) for analyses presented. Gibbs also presented estimated CVs to aid in designing population monitoring programs but did not separate sampling variance from temporal process variance in these estimates. Thompson et al. (1998) recognized that temporal process variation influences the appropriate level of decline for which to monitor but did not directly incorporate process variation into monitoring programs. Rather, Thompson et al. (1998) suggested that the analytical results presented by Gerrodette (1987) could be used with nonzero process variance by adding the process variance to the sampling variance when estimating power.

We evaluated the usefulness of Gerrodette's (1987) formulae when process variance was added to the sampling variance (Thompson et al.

1998) by comparing power estimates obtained from those formulae with power estimates from Monte Carlo simulations. Ten years of population estimates were considered, with a process standard deviation for λ of $\hat{\sigma}_\lambda = 0.114$, obtained from the Pradel (1996) model λ estimates from the two demographic study areas. We considered seven values of the sampling CV, ranging from 0 to 30% in increments of 5%. Sampling CV was assumed constant for population size, and the exponential model of decline, $N_i = N_1 \lambda^{i-1}$, $i = 1, \dots, 10$, was used to detect trend. Taking the natural logarithm of both sides of this equation recast it in the form of a linear regression ($y = a + bx$), such that $\ln(\hat{N}_i) = \ln(\hat{N}_1) + \ln(\lambda)(i - 1)$ and $\hat{N}_1 = \exp(\hat{a})$, $\hat{\lambda} = \exp(\hat{b})$, $SE(\hat{N}_1) \equiv \exp(\hat{a})SE(\hat{a})$, and $SE(\hat{\lambda}) \equiv \exp(\hat{b})SE(\hat{b})$.

We conducted Monte Carlo simulations with 10,000 replications, where λ_{i-1} was generated as a random normal deviate with mean = 1 and standard deviation = 0.114. Then, $\hat{N}_i = N + \sigma_i$, where σ_i was generated as a random normal deviate with mean zero and standard deviation $CV_1 N_i$. Resulting power estimates differed considerably between the analytical approach and Monte Carlo simulations, where power estimates determined via simulation were considerably lower than estimates from the analytical procedure (Figures 16.8, 16.9). Thus, we concluded that simulation procedures were required to determine power for monitoring populations with nonzero temporal process variation, rather than using the approach in Thompson et al. (1998).

We also evaluated the percent relative bias (PRB) of estimates of N_1 and λ , $\hat{PRB}(\hat{\theta}) = (\hat{E}(\hat{\theta}) - \theta)/\theta$. Response surface models were fit for both $\hat{\lambda}$ and $\hat{N}_1$ with independent variables of process standard deviation (σ_λ), decline, decline squared, sampling CV, and sampling CV squared. The squared terms for decline and sampling CV were included to examine potential nonlinear, quadratic relationships. Based on AIC model selection, the best models were $\hat{PRB}(\hat{\lambda}) = 0.0528 - 10.404 \sigma_\lambda + 0.00008182 CV^2 - 0.00003257 \text{ decline}^2$ and $\hat{PRB}(\hat{N}_1) = -0.47877 + 9.97573 \sigma_\lambda + 0.00796 CV - 0.00380 CV^2 - 0.00002171 \text{ decline}^2$. Relative bias was $< 4\%$ and $< 1.5\%$ for $\hat{N}_1$ and λ , respectively, suggesting that the regression estimators used in simulations were useful for evaluating trends over the range of process standard deviations, sampling CVs, and declines considered.

To illustrate how temporal variation simultaneously influenced the power to detect a trend in abundance and the probability of occurrence of declines of specific magnitude, we again modeled power to detect a linear trend versus specified probabilities of decline. Unlike our earlier analysis, here we explicitly included temporal process variation. We

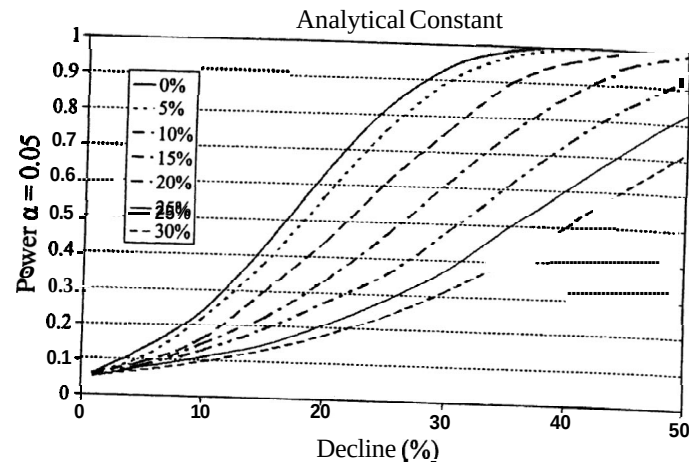


Figure 16.8. Power to detect a decline in Mexican spotted owl abundance modeled for declines of varying magnitude. Power curves were generated with the analytical formulae of Gerrodette (1987) for seven values of the coefficient of sampling variation assuming process standard deviation was 0.114. The coefficient of sampling variation was assumed to be constant and the exponential trend model was used with 10 yrs of population estimates. Curves shown represent CVs of 0–30% (from top to bottom, respectively).

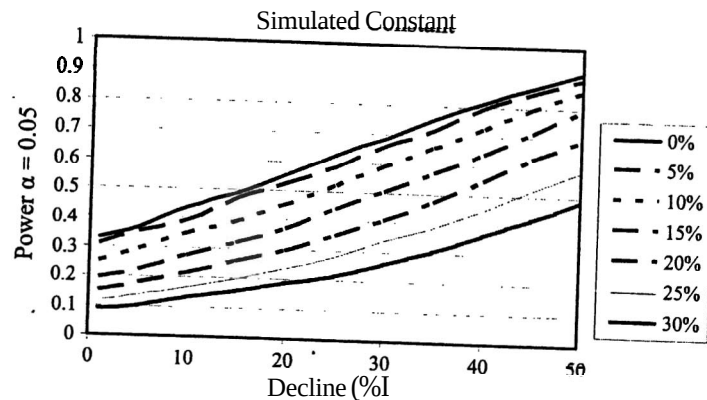


Figure 16.9. Simulation results for models relating power to percent decline in abundance of Mexican spotted owls, using seven values of the sampling coefficient of variation assuming process standard deviation was 0.114. An exponential model (Gerrodette 1987) was used to detect a trend over 10 yrs of population estimates. Curves represent CVs of 0–30% (from top to bottom, respectively).

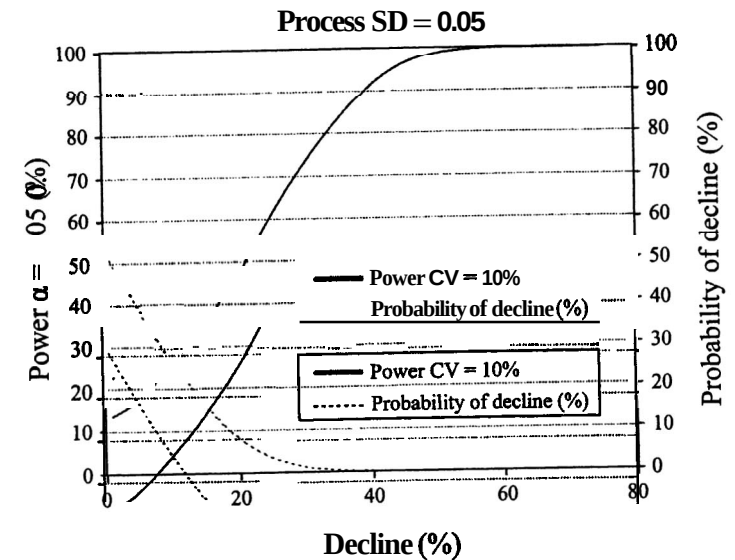


Figure 16.10. Probability of observing a decline in abundance of Mexican spotted owls of specific magnitude (descending curve) when mean $\lambda = 1$ and process standard deviation = 0.05. This probability is plotted at the same scale as the power to detect a decline (ascending curve) with a coefficient of sampling variation = 10%. Power was estimated from 10,000 simulations using 10 yrs of population estimates and the exponential model (Gerrodette 1987).

assumed CV = 10% for sampling variation and considered three levels of process variation: 0.05, 0.10, and 0.15 (Figures 16.10–16.12). We discuss these results relative to a decline in abundance of 20% (the magnitude specified in the current delisting criterion for the Mexican spotted owl). The expected probability of observing a 20% decline was approximately 10% for $\sigma_\lambda = 0.05$, 28% for $\sigma_\lambda = 0.10$, and 35% for $\sigma_\lambda = 0.15$. Although power curves varied among the three levels of process variance simulated, power to detect a 20% decline was approximately 40% in all cases (Figures 16.10–16.12). Thus, our results suggest that reasonable levels of temporal variation compound problems with both power to detect a trend and the probability of occurrence of declines of specified magnitude. Both factors

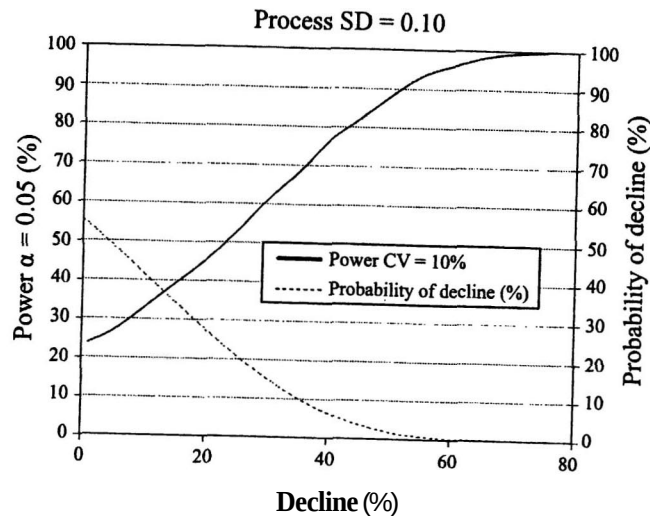


Figure 16.11. Probability of observing a decline in abundance of Mexican spotted owls of specific magnitude (descending curve) when mean $A = 1$ and process standard deviation = 0.10. This probability is plotted at the same scale as the power to detect a decline (ascending curve) with a coefficient of Sampling variation = 10%. Power was estimated from 10,000 simulations using 10 yrs of population estimates and the exponential model (Gerrodette 1987).

thus complicate devising a reasonable and unambiguous delisting criterion for the Mexican spotted owl.

Conclusion

Our experience in this pilot study suggests that mark-recapture sampling of Mexican spotted owls can be conducted and coordinated at large spatial scales, but that such sampling is relatively impractical. It requires large numbers of well-qualified and highly motivated field assistants, and finding and training these numbers of such individuals consistently on a seasonal basis will be difficult. The approach evaluated also is highly labor-intensive and therefore requires high funding levels. Both of these factors present serious practical hurdles to implementing such a program.

We also found that sample quadrats were too large to survey effectively in roadless areas containing large numbers of owls given limited person-

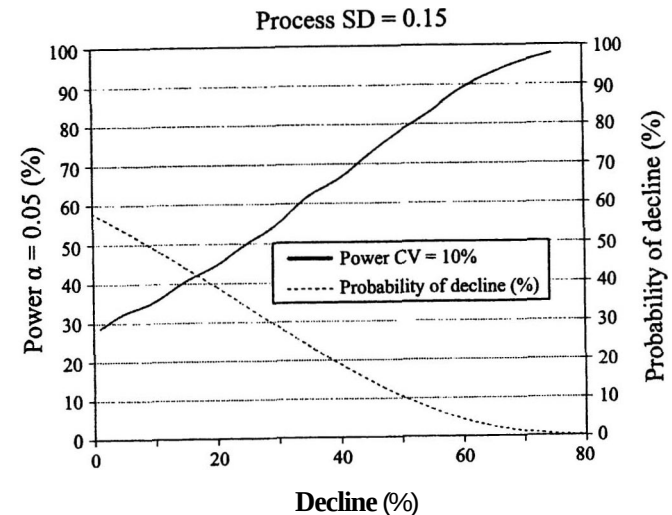


Figure 16.12. Probability of observing a decline in abundance of Mexican spotted owls of specific magnitude (descending curve) when mean $A = 1$ and process standard deviation = 0.15. This probability is plotted at the same scale as the power to detect a decline (ascending curve) with a coefficient of Sampling variation = 10%. Power was estimated from 10,000 simulations using 10 yrs of population estimates and the exponential model (Gerrodette 1987).

nel. Survey passes in such areas typically were not completed in a short time period, which is undesirable given the sampling design, and the required number of passes was never completed on some of these areas. Reducing quadrat size could alleviate both of these problems. Our analysis suggested that sampling smaller quadrats would not result in biased estimates of owl density or exaggerated edge effects. Thus, reducing quadrat size appears to be a feasible option. This should allow for an increase in spatial replication of quadrats, a decrease in overall variance, and an increase in the number of quadrats sampled for a given funding level.

We identified several practical ways to improve sampling efficiency, including placing more surveyors in roadless areas and ensuring that surveyors carry proper equipment. Despite such improvements, however, the mark-recapture sampling called for remains impractical at the required scale.

The use of a ratio estimator with quadrat area as a covariate increased precision in estimates of abundance over a simple estimator without covariates (Bowden et al. 2003), and use of appropriate topographical

covariates resulted in further improvements in precision. It should be possible to increase precision further by using a combination of habitat-based and topographic covariates. Appropriate habitat-based covariates were not available to us but could be developed in future efforts.

Our analyses suggest that the approach of estimating a population trend directly from quadrat data holds more promise than the more typical regression approach. Despite proposed and actual improvements in efficiency of field sampling and estimation procedures, however, power to detect a 20% decline over a 10-yr period (as required by the delisting criterion in USDI Fish and Wildlife Service [1995]) remained low given current estimates of process variation. Further, there was a high probability of observing a 20% decline by chance alone, given current estimates of temporal process variation. This suggests that the delisting criterion does not **provide** an unambiguous monitoring target. We present results that may aid in devising a more appropriate delisting criterion, but recommending a specific **criterion** represents a decision-theory problem beyond the scope of this study.

Given the high economic costs involved in large-scale mark-recapture sampling, the serious logistical hurdles involved in such sampling, and uncertainty about an appropriate delisting criterion, we cannot recommend full-scale implementation of the monitoring design proposed in USDI Fish and Wildlife Service (1995). Instead, we recommend revising the delisting criterion to incorporate current data on temporal variation. This may require monitoring for a larger decline, an idea likely to prove unpopular with segments of the American public. Given the difficulty inherent in implementing the approach evaluated here, we also recommend considering practical aspects of implementing a monitoring program. This likely will require evaluating alternative approaches to monitoring that require less labor-intensive sampling. For example, we are currently working on a design based on simple presence-absence monitoring of a large number of small (1 km²) quadrats.

General Lessons

This effort provides insight into several potential problems that may be encountered when sampling rare and elusive populations. The first is the potential magnitude of spatial variation. In this case study, spatial variation in **abundance** was the most significant source of variation encountered. This may not be a significant problem in all populations, but it will

undoubtedly prove **problematic** in some, particularly populations that are **widely** but patchily distributed.

A second **significant** problem encountered in this study was temporal variation. Again, the magnitude of this problem likely will vary among populations, but our results suggest that it should not be ignored. In particular, choosing an appropriate monitoring target becomes difficult in the face of **significant** temporal variation. In our case, monitoring for a decline that would occur with low probability (e.g., 5–10% of the time) would have required us to monitor for a very large **decline** (roughly 30–60%, depending on the extent of temporal variation; Figure 16.12) within the 10-yr period. Monitoring for a decline of such magnitude is likely to prove **socially** or politically unacceptable when dealing with a threatened species. **Monitoring** for longer time periods may alleviate this problem somewhat, a possibility that we have not yet explored. The obvious drawbacks to that approach are delayed decisions on listing status and greater funding requirements.

A related problem concerns the power to detect a trend. In this case study, power was low due to spatial variation when temporal variation was ignored, and lower still when both sources of variation were considered explicitly. Our results also suggested that traditional analytical analyses of power to detect trends did not **provide** valid results when temporal variation was significant and that simulations were required to accurately estimate power in such situations.

It is unclear at this time whether the Mexican spotted owl presents a **best-** or worst-case scenario relative to these points. This owl likely is both more abundant and more easily detected than many rare and elusive species. **All** else being equal, both factors should aid in generating precise estimates and adequate power to detect trends. **However**, both spatial and temporal variation may be higher for the Mexican spotted owl than for some **rare** and elusive species. Both sources of variation strongly affect **precision** of estimates and power to detect trends. Thus, although we can note general problems likely to be encountered **by** similar efforts, we cannot at this time estimate the **magnitude** of problems likely to be encountered by such efforts.

Our results clearly demonstrate that monitoring population trends in a variable world is a difficult and expensive task. Many federal agencies operate under mandates to monitor multiple species of **plants** and animals, however. Our experience suggests that **fulfilling** this mandate will present great practical difficulties. Recent advances in analysis of presence-absence data (e.g., MacKenzie et al. 2003; Royle and Nichols 2003) may help alleviate

this problem. Nevertheless, we recommend that agenaes proceed extremely carefully when identifying particular species to monitor and when designing monitoring criteria and protocols. Particular attention should be paid to the appropriate level of decline for which to monitor, power to detect a decline of that magnitude, sample sizes required to achieve that power, and associated costs and feasibility issues. Failure to consider these aspects could result in poorly designed monitoring schemes and unattainable goals, which in turn could place agenaes in legal jeopardy.

ACKNOWLEDGMENTS

This study was made possible by the efforts of many dedicated individuals. Special thanks to field crew leaders S. Ackers, P. Fonken, J. Jenness, C. Kessler, P. Shaklee, and E. Swarthout and crew members D. April, J. Bennett, S. Bird, B. Coyle, J. Cummings, K. Damm, R. Davis, C. Dodge, G. Dunn, B. Gill, K. Gilligan, J. Gulbransen, J. Hagerty, M. Holley, T. Holt, R. Hunt, J. Justus, K. Krause, A. Lavoie, M. Layes, M. Luad, D. McCallum, M. McCarty, H. McClure, S. Meares, B. Millay, J. Moser, M. Moyer, J. Palmer, A. Ringia, M. Schenk, S. Schmitz, T. Shewan, A. Shovlain, A. Stein, J. Trent, A. Trombley, E. Vincent, S. Vuturo, R. Wagner, P. Wenninger, T. Williams, A. Winters, and J. York. Special thanks also to K. Nodal, administrative assistant extraordinaire, and to T. Garito for data entry. Funding was provided by the Southwestern Region, U.S. Forest Service, and numerous Forest Service district personnel helped in innumerable ways. S. Arundel created the quadrat sampling frame, and J. S. Jenness computed the topographic covariates. J. P. Ward, Jr., helped considerably during the initial design phase. Numerous individuals from the Rocky Mountain Research Station also assisted in numerous ways, including B. Block, J. Dwyer, S. Elefant, K. Gurley-Davis, S. Kyle, D. Parker, D. Prince, B. Strohmeyer, and B. Whiteman, Flagstaff; and L. Bemis, R. King, and T. Pues, Fort Collins. C. May M. Petersburg, M. Seamans, and R. J. Gutiérrez kindly allowed us to use unpublished data from their demography studies to evaluate the effects of quadrat size and temporal variability. W. L. Thompson and an anonymous reviewer reviewed earlier drafts of this chapter.

REFERENCES

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. pp. 267–281 in B. N. Petran and F. Csaki, eds., Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.
- Arundel, S. 1999. Developing a Sampling Frame to Guide Quadrat Selection for a

- Program to Monitor Population Trend of the Mexican Spotted Owl: Methodology. Unpublished report. USDA Forest Service, Rocky Mountain Research Station, Flagstaff, Arizona.
- Bailey, R. G. 1980. Descriptions of the Ecoregions of the United States. USDA Forest Service Miscellaneous Publication 1391, Intermountain Region, Ogden, Utah.
- Block, W. M., A. B. Franklin, J. P. Ward Jr., J. L. Ganey, and G. C. White. 2001. Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. *Restoration Ecology* 9:293–303.
- Bowden, D. C., G. C. White, A. B. Franklin, and J. L. Ganey. 2003. Estimating population size with correlated sampling unit estimates. *Journal of Wildlife Management* 67:1–10.
- 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. 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.
- Cochran, W. G. 1977. Sampling Techniques, 3rd ed. Wiley, New York.
- Fletcher, K. W., and H. E. Hollis. 1994. Habitats Used, Abundance, and Distribution of the Mexican Spotted Owl (*Strix occidentalis* luada) on National Forest System Lands in the Southwestern Region. Unpublished report. USDA Forest Service, Southwestern Region, Albuquerque, New Mexico.
- Forsman, E. D. 1983. Methods and Materials for Locating and Studying Spotted Owls. USDA Forest Service General Technical Report PNW-162, Pacific Northwest Research Station, Portland, Oregon.
- Forsman, E. D., A. B. Franklin, F. M. Oliver, and J. P. Ward Jr. 1996. A color band for spotted owls. *Journal of Field Ornithology* 67:507–510.
- Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. W. Wagner. 1996. Methods for collecting and analyzing demographic data on the Northern spotted owl. *Studies in Avian Biology* 17:12–20.
- Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in Northern spotted owl populations in northwestern California. *Ecological Monographs* 70:69–120.
- 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.
- Ganey, J. L., S. Ackers, P. Fonken, J. S. Jenness, C. Kessler, K. Nodal, P. Shaklee, and E. Swarthout. 1999. Monitoring Populations of Mexican Spotted Owls in Arizona and New Mexico: 1999 Progress Report, USDA Forest Service Rocky Mountain Research Station, Flagstaff, Arizona. Available from <http://www.nns.nau.edu/lab/4251/spowmonitoring.hd>.
- Ganey, J. L., and J. A. Dick. 1995. Habitat relationships of Mexican spotted owls: Current knowledge. Chapter 4:1–42 in Recovery Plan for the Mexican Spotted Owl. Vol. II • Technical Supporting Information. USDI Fish and Wildlife Service, Albuquerque, New Mexico.
- Gerrodette, T. 1987. A power analysis for detecting trends. *Ecology* 68:1364–1372.
- Gibbs, J. P. 1999. Effective monitoring for adaptive wildlife management: Lessons from the Galapagos Islands. *Journal of Wildlife Management* 63:1055–1065.
- _____. 2000. Monitoring populations. pp. 213–252 in L. Boitani and T. K. Fuller, eds., Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York.

- Goodman, D. 1987. The demography of chance extinction. pp. 11–34 in M. E. Soulé, ed., *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
- Goodman, L. 1960. On the exact variance of products. *Journal of the American Statistical Association* 55:708–713.
- Gutiérrez, R. J., A. B. Franklin, and W. S. LaHaye. 1995. Spotted owl (*Strix occidentalis*). No. 179 in A. Poole and F. Gill, eds., *The Birds of North America*. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists Union, Washington, D.C.
- Hatfield, J. S., W. R. Gould IV, B. A. Hoover, M. R. Fuller, and E. L. Lindquist. 1996. Detecting trends in raptor counts: Power and Type I error rates of various statistical tests. *Wildlife Society Bulletin* 24:505–515.
- Huggins, R. M. 1989. On the statistical analysis of capture-recapture experiments. *Biometrika* 76:133–140.
- _____. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725–732.
- Hurvich, C. M., and C.-L. Tsai. 1995. Model selection for extended quasi-likelihood models in small samples. *Biometrics* 51:1077–1084.
- Johnson, C. L., and R. T. Reynolds. 1998. A new trap design for capturing spotted owls. *Journal of Raptor Research* 32:181–182.
- 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.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.
- Marcot, B. G., and J. W. Thomas. 1997. Of *Spotted Owls, Old Growth, and New Policies: A History Since the Interagency Scientific Committee Report*. USDA Forest Service General Technical Report PNW-GTR-408, Pacific Northwest Research Station, Portland, Oregon.
- May, C. A., M. Z. Peery, R. J. Gutiérrez, M. E. Seamans, and D. R. Olson. 1996. *Feasibility of a Random Quadrat Study Design to Estimate Changes in Density of Mexican Spotted Owls*. USDA Forest Service Research Paper RM-RP-322, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on dosed animal populations. *Wildlife Monographs* 62:1–135.
- Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709.
- Rinkevich, S. E., J. L. Ganey, W. H. Moir, F. P. Howe, F. Clemente, and J. F. Martinez-Montoya. 1995. Recovery Units. pp. 36–51 in *Recovery Plan for the Mexican Spotted Owl*. USDI Fish and Wildlife Service, Albuquerque, New Mexico.
- Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84:777–790.
- Seamans, M. E., R. J. Gutiérrez, C. A. May, and M. Z. Peery. 1999. Demography of two Mexican spotted owl populations. *Conservation Biology* 13:744–754.
- Seber, G. A. F. 1982. *The Estimation of Animal Abundance and Related Parameters*, 2nd ed. Griffin, London.
- Skalski, J. R. 1994. Estimating wildlife populations based on incomplete area surveys. *Wildlife Society Bulletin* 22:192–203.

- Stanford Environmental Law Society. 2001. *The Endangered Species Act*. Stanford University Press, Stanford California.
- Stanley, T. R., and K. P. Burnham. 1998a. Estimator selection for closed-population capture-recapture. *Journal of Agricultural, Biological, and Environmental Statistics* 3:131–150.
- _____. 1998b. Information-theoretic model selection and model averaging for dosed-population capture-recapture studies. *Biometrical Journal* 40:475–494.
- Thompson, W. L., G. C. White, and C. Gowan. 1998. *Monitoring Vertebrate Populations*. Academic Press, San Diego.
- USDA Forest Service. 1996. *Record of Decision for Amendment of Forest Plans. Arizona and New Mexico*. USDA Forest Service, Southwestern Region, Albuquerque, New Mexico.
- USDI Fish and Wildlife Service. 1993. Endangered and threatened wildlife and plants: Final rule to list the Mexican spotted owl as a threatened species. *Federal Register* 58:14248–14271.
- _____. 1995. *Recovery Plan for the Mexican Spotted Owl (Strix occidentalis lucida), Vol. I*. USDI Fish and Wildlife Service, Albuquerque. Available from http://mso.fws.gov/recovery_plan.htm.
- _____. 1996. *Final Biological Opinion. Mexican Spotted Owl and Critical Habitat and Forest Plan Amendments: U. S. Forest Service, Southwestern Region*. USDI Fish and Wildlife Service, Albuquerque.
- Ward, J. P., Jr., A. B. Franklin, S. E. Rinkevich, and F. Clemente. 1995. Distribution and abundance of Mexican spotted owls. Chap. 11–14 in *Recovery Plan for the Mexican Spotted Owl. Vol. II - Technical Supporting Information*. USDI Fish and Wildlife Service, Albuquerque, New Mexico.
- White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 Supplement:S120–S138.
- White, G. C., A. B. Franklin, and T. M. Shenk. 2002. Estimating parameters of PVA models from data on marked animals. pp. 169–190 in S. R. Beissinger and D. R. McCullough, eds., *Population Viability Analysis*. University of Chicago Press, Chicago.
- Williams, J. L. 1986. *New Mexico in Maps*. University of New Mexico Press, Albuquerque, New Mexico.