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META-ANALYSIS OF VITAL RATES OF THE NORTHERN SPOTTED OWL

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INTRODUCTION

Beginning in the mid-1980s a number of large "demographic" study areas were established within the range of the Northern Spotted Owl (*Strix occidentalis caurina*). Anderson and Burnham (1992) presented an analysis of data from five of these study areas. By the fall of 1993, 14 such demographic study areas had at least four years of capture-recapture and fecundity data. We provide results here for 11 of the 14 demographic data sets available; data from two studies areas in northern California conducted by the timber industry were not made available at the workshop, and the industry-sponsored study on the Wenatchee National Forest was withdrawn on the final day of the 12-day workshop. Thus, none of the three study areas sponsored by the timber industry was available for use in this paper. The 11 study areas where data were available are shown in Fig. 1 of Franklin et al. (*this volume*). These are large study areas, several are contiguous with others, and have as few as four years to as many as nine years of banding (Table 1) and fecundity data. The sample size for individual owls first banded as territorial "adults" (i.e., non-juvenile birds) was over 6,500 capture-and-releases events (Table 1).

Our main objective was to conduct a rigorous and objective analysis of the empirical population data available on the Northern Spotted Owl and provide the statistical inferences that were justified about the owl's vital rates. We emphasized a science-based, data analysis agenda during the 12-day workshop. Many quality controls were established, data were formally certified prior to analysis, analysis protocols were determined *a priori,* and these were followed. Several people with special expertise in capture-recapture and population dynamics theory were invited to supervise the analyses, and every effort was made to assure the integrity of the data analyses and inferences. Considerable published formal theory and computer software existed to guide the sophisticated analysis of these data. Direct inferences were limited to the years where data were available. Because of the number, large size, and wide distribution of the study areas, we assume the statistical inferences extend beyond these specific study areas to the range of this subspecies.

At and after the workshop we were asked repeatedly to provide insights to managers and policy people such as *"What do these results and inferences mean to managers?"* or *"Is Option 9 of the President's forest plan viable, given the results from these 11 studies?"* Those subjects lie beyond our expertise, and hence this chapter is a "science only" document with but few of our interpretations expressed. Other papers in this volume delve into these management issues (e.g., Gutiérrez *this volume,* Raphael et al. *this volume*).

METHODS

Most of the presentation of methods is in Franklin et al. (*this volume*). However, there are a few aspects of analyses herein that are not covered in Franklin et al. (*this volume*); it is these matters we cover below, in particular the estimation (and use of) emigration rate, *E,* from radio-tracking data.

CAPTURE-RECAPTURE DATA

Most of the data analysis effort focused on the Northern Spotted Owl capture-recapture (CR) data sets from 11 studies (see Table 1). The CR data from each individual study were thoroughly analyzed as described in the previous chapters. Also several "meta-analyses" were done, because the data sets were partitioned into short- and long-term studies. The global model for a meta-analysis here is $\{\phi_{a*s*g*t}, p_{a*s*g*t}\}$. This model can have hundreds of parameters. No new ideas are introduced in doing a meta-analysis, but meta-analysis models are much more difficult because so many data are being dealt with. The advantage of such overall analyses is that we learn of effects and trends common in all the data sets. A meta-analysis is more powerful than the set of separate analyses.

The meta-analysis on the short term studies included the Wenatchee Demographic Study (N.E. Washington) data because those analyses were done, and could not be re-done, when the investigators withdrew their WDS data. They did, however, agree that the WDS data could remain in the meta-analysis.

The data used in the meta-analyses were the capture histories of just those birds initially caught as territory-holders; for simplicity we refer to

TABLE 1. Summary Information on Sampling Effort for 11 Northern Spotted Owl Demographic Studies. Number Banded Is the Number of Distinct Birds Caught and Banded, Whereas Sample Size $N = R_1 + R_2 + \ldots + R_{K-1}$ in the Capture-recapture *M*-array (Lebreton et al. 1992). Study Area Acronyms Are Defined in Franklin et al. (*This Volume*)

Study area	First year	Number of years	Adults banded		Juveniles banded	Subadults banded	Adult sample size	
			Male	Female			Male	Female
CAL	1985	9	99	91	274	84	369	257
RSB	1985	9	262	214	429	117	692	520
SCS	1985	9	560	491	680	189	1032	823
SAL	1986	8	74	68	101	17	151	129
HJA	1987	7	123	109	226	57	294	286
OLY	1987	7	127	129	249	43	295	278
CLE	1989	5	60	56	186	30	131	96
EUG	1989	5	49	52	59	16	117	98
COO	1990	4	99	93	136	49	178	157
SIU	1990	4	82	72	72	25	135	112
SIS	1990	4	38	31	31	10	75	55
		Totals	1573	1406	2443	637	3469	2811

these birds here as adults although they can be <3 years old. Birds banded as juveniles that survived to be adults and were then re-encountered were not part of the data set used in the meta-analysis. These additional data were a minor part of all the possible data on territorial owls. In principle, program SURGE can use all the data in a meta-analyses; in fact, limitations of computer capability and the workshop time frame prevented us from using this additional information (known adults first banded as juveniles).

Fecundity Data

The field studies involved finding and monitoring territorial females to determine their breeding success. The basic data are, for each territorial female (hence for potential breeders), the number of offspring that were fledged, which ranged from 0 to 3. A 50:50 sex ratio is assumed at fledging and is supported by genetic sex markers (see Franklin et al. *this volume,* Reid et al. *this volume*). The parameter of interest, fecundity rate b, is the average number of young fledged per territorial female, hence statistical analysis is straightforward. Despite the integer nature of the data, sample sizes are sufficient to justify ANOVA inference methods. Hence, data analysis was done using SAS PROCs MEANS, GLM, and VARCOMP (SAS Institute 1985). PROC MEANS was used to produce means and standard errors by various categories (e.g., female age, year, study area, age and study, etc.). PROC GLM, with area and time effects random (age is a fixed effect), was used to test for significance of effects and interactions. PROC VARCOMP, using option MIVQUE, was used to estimate variance components from the fecundity rates, $\hat{b}$, over years, areas, and for interactions.

Population Rate of Change

For one study area, we can test $H_o : \lambda \geq 1$ vs. $H_a : \lambda < 1$ with a one-sided z-test (Franklin et al. *this volume*). With multiple studies a broader scope of inference is possible with an empirical t-test based on independent estimates of λ for each site. A less robust test is a z-test based on the estimated average $\hat{\bar{\lambda}}$ and its estimated theoretical standard error where

$$\hat{\bar{\lambda}} = \frac{1}{k}\sum_{i=1}^{k}\hat{\lambda}_i,$$

$$\widehat{\text{SE}}(\hat{\bar{\lambda}}) = \frac{1}{k}\sqrt{\sum_{i=1}^{k}\widehat{\text{var}}(\hat{\lambda}_i)}.$$

Hence, as an inference over all study areas, we can test H_0: $\bar{\lambda} \geq 1$ vs. H_a: $\bar{\lambda} < 1$ with the one-sided z-test

$$z = \frac{1 - \hat{\bar{\lambda}}}{\widehat{\text{SE}}(\hat{\bar{\lambda}})}.$$

The corresponding t-test is more robust because it uses an empirical estimate of $\text{SE}(\hat{\bar{\lambda}})$, but it can have less power for this same reason.

Emigration Estimation and a Common λ

In recent years some juveniles have had radios attached so that their movements and fate could be determined. These radio-tracking data can be used to directly estimate juvenile emigration, based on counts of surviving juveniles in the next spring. Emigration is defined here as: the juvenile moves out of its original study area, where it would be at risk of capture, is not captured by any other researchers, and survives its first year. The radio-tracking data include counts of survivors in and out of the specific study areas, and include information on whether the emigrated birds were captured in other areas.

Let n be the total number of survivors in spring, year $t + 1$, of birds radioed in summer, year t. Then $n = n_s + n_{ed} + n_{en}$, where n_s = number that stayed in their natal study area and survived the year, n_{ed} = number that emigrated off the natal area, survived the year, and were detected by the routine CR study methods (with no aid from telemetry), and n_{en} = number that emigrated off the natal area, survived the year, and were not detected by the routine CR study methods. Then the emigration estimate is

$$\hat{E} = \frac{n_{en}}{n}, \text{ with } \widehat{\text{SE}}(\hat{E}) = \sqrt{\frac{\hat{E}(1 - \hat{E})}{n}}.$$

This estimator is robust to some problems that would bias an estimator of annual juvenile survival probability based on the radio-tracking data. Birds are radioed (on average) about a month after fledging and their survival is not always monitored until mid-June. Thus, a survival estimate covers a shorter time period than the requisite one year needed to match with adult survival probability in population dynamics evaluation. This emigration estimate is based only on birds surviving to spring. Assuming all emigration has occurred by then, and that by that spring, subsequent mortality of birds is the same for emigrants and non-emigrants, then it is not required that the survivors be monitored until mid-June to get a reliable emigration estimator.

Let S_s and S_e represent the annual survival probability of juveniles that stay and those that emigrate, respectively. Then true juvenile survival probability is

$$S_J = S_s(1 - E) + S_eE = \phi_J + S_eE.$$

Without reliable, large samples of radio-tracking data on annual survival probability of juveniles (residents vs. emigrants), to estimate E from these data it is necessary to assume $S_s = S_e \equiv S_J$. Then $S_J = \phi_J + S_e E$, and therefore

$$\hat{S}_J = \frac{\hat{\phi}_J}{1 - \hat{E}}.$$

To estimate SE($\hat{\lambda}$) we need the variances and covariance below (derived by the delta-method):

$$[\text{var}(\hat{S}_J)]^2 = (S_J)^2[[\text{cv}(\hat{\phi}_J)]^2 + [\text{cv}(1 - \hat{E})]^2],$$

$$\text{cov}(\hat{S}_J, \hat{\phi}_A) = \frac{\text{cov}(\hat{\phi}_J, \hat{\phi}_A)}{1 - \hat{E}}.$$

We note that while SE($\hat{E}$) $\equiv$ SE($1 - \hat{E}$),

$$\text{cv}(1 - \hat{E}) = \frac{\hat{E}}{1 - \hat{E}}\,\text{cv}(\hat{E}).$$

RESULTS

GOODNESS-OF-FIT TESTS FOR CAPTURE-RECAPTURE DATA

Table 2 gives the summarized results of the goodness-of-fit (GOF) tests to the global model $\{\phi_{a*t}, p_{a*t}\}$, separately for males and females and each study area, for the adult data. The CR data on releases of juveniles and subadults were also tested for goodness-of-fit; those tests are additive to the tests for the adult data. However, these latter data were so sparse in terms of captures that they contributed relatively little to the overall GOF test (a total of $\chi^2_{(36)} = 28.49$, P = 0.8095 for those test components with enough data to be reliable), and we therefore give the detailed results here only for the adults.

From Table 2, the overall GOF test result was $\chi^2_{(225)} = 292.47$, P = 0.0016. Given the sample size (about 3,000 individuals banded as adults) this is a decent fit for data of this magnitude and complexity. This judgment of a "decent fit" is based on the ratio 292.47/225 = 1.3 (and 220.47/193 = 1.14) being "near" 1 despite the huge sample size here (given sufficiently large sample size, one can get an extremely small P-value even for a trivial effect size). Lack of fit here comes from mostly the SCS and OLY areas. The GOF test components for these areas, and HJA and RSB, were carefully scrutinized. It was found that the significant test components were associated with only a few birds and failure to fit was not because of any systematic patterns that could be modeled with CR models more general than CJS. Much of the lack of fit for area SCS is attributed to about five birds that showed temporary emigration (one adult female was not seen for six years after initial banding, and this alone caused much of the GOF failure of the female data for SCS). In the case of OLY, there was one released cohort of 18 newly banded birds in 1992 that was captured in 1993 at a very different rate from previously banded birds. Basically, most of the lack of fit indicated in Table 2 can be related to about 30 to 40 birds out of 3,000. Without those few birds, the chi-squared to df ratio (i.e., a variance inflation factor) was 1.14. Therefore, we maintained that the global model was satisfactory and analysis could proceed without any compelling need for quasi-likelihood variance inflation.

MODELS OF THE CAPTURE-RECAPTURE DATA

The models with the minimum AIC value for each study area are summarized in Table 3 for data from owl adults and for all age-classes. Five of the 11 minimum AIC models contain a negative time trend in survival (i.e., ϕ_T) for the adult data, while three of the 11 show this negative trend for the data including all age-classes. Other

TABLE 2. GOODNESS-OF-FIT (GOF) TESTS FOR NORTHERN SPOTTED OWL ADULT CAPTURE-RECAPTURE DATA SETS. SEE FRANKLIN ET AL. (*THIS VOLUME*) FOR INFORMATION ABOUT THE TESTS USED

Study area	Sex	TEST 2 + 3 χ^2	df	P	TEST 2 P	TEST 3 P
CAL	Males	11.22	14	0.6688	0.2399	0.8382
	Females	4.75	14	0.9890	1.0000	0.9428
RSB[a]	Males	29.02	19	0.0656	0.0087	0.5393
	Females	26.93	20	0.1374	0.0831	0.3288
SCS[a]	Males	31.69	15	0.0071	0.0001	0.5714
	Females	40.54	17	0.0011	0.0000	0.5300
SAL	Males	12.89	14	0.5354	0.1420	0.8152
	Females	14.86	16	0.5350	0.9040	0.2753
HJA[a]	Males	16.23	12	0.1810	0.1239	0.3138
	Females	19.87	13	0.0984	0.5854	0.0482
OLY[a]	Males	19.89	12	0.0691	0.3937	0.0499
	Females	34.36	13	0.0011	0.2021	0.0008
CLE	Males	5.11	7	0.6466	0.3280	0.7185
	Females	6.03	7	0.5368	0.0612	0.9942
EUG	Males	0.85	4	0.9323	1.0000	0.9323
	Females	3.30	7	0.8559	1.0000	0.6539
COO	Males	2.98	4	0.5605	1.0000	0.3941
	Females	6.47	3	0.0910	0.0128	0.8787
SIU	Males	3.83	4	0.4295	1.0000	0.2804
	Females	1.15	4	0.8858	1.0000	0.7644
SIS	Males	0.50	3	0.9199	1.0000	0.9199
	Females	0.23	3	0.9734	1.0000	0.9734
Total χ^2 GOF		292.70	225	0.0016		
χ^2 GOF w/o SCS		220.47	193	0.0853		

[a] Examined in detail for lack of fit in the component tests (as per Burnham et al. 1987, Lebreton et al. 1992).

study areas had negative time trends in survival for models within 1 or 2 AIC units of the low-AIC model. Thus, even for individual data sets, where sample size is small and statistical power is expected to be low, there are indications of negative time trends in survival probabilities.

There is also evidence in these and other analyses of time trends in the capture probabilities, although this has no relevance to owl population dynamics. In general, within a study capture probabilities tended to increase over time because funding and field experience tended to increase.

ESTIMATES OF AGE-SPECIFIC SURVIVAL UNDER THE MINIMUM AIC MODELS

Estimated apparent juvenile survival ($\hat{\phi}_J$) varied from 0.140 (CLE) to 0.418 (RSB), excluding SIS, which had little data for the estimation of this parameter (Table 4). An unweighted average across study areas yielded an estimate of apparent juvenile survival of 0.258 (empirical SE = 0.036). These estimates include the rate at which juvenile birds left the area and survived a year (i.e., $\phi_J = S_J\ (1 - E\ )$). Adults had estimated survival probabilities varying over a small range from 0.821 (HJA) to 0.868 (CAL). The unweighted average survival of adults was 0.844 (empirical SE = 0.0052) (Table 4). Emigration is a minor issue in territorial birds (see chapters on individual studies). The effect of emigration and senescence produce negative and positive bias,

TABLE 3. SUMMARY OF THE MODEL WITH THE MINIMUM AIC VALUE BY STUDY AREA, FOR THE NORTHERN SPOTTED OWL. "ADULTS ONLY" USE ONLY CR DATA ON BIRDS INITIALLY BANDED AS AN ADULT; "AGE MODELS" USE ALL THE DATA. NOTATION IS EXPLAINED IN THE APPENDIX

Study area	Best model, adults only	Best model, age models
CAL[a]	$\{\phi_{s*T},\ p_c\}$	$\{\phi_{\mathrm{J,A1}},\ p_{a4',\mathrm{Ac}}\}$
RSB	$\{\phi_T,\ p_{s+T}\}$	$\{\phi_{a2},\ p_{a4'+s}\}$
SCS	$\{\phi_T,\ p_s\}$	$\{\phi_{a2},\ p_{a4'+s}\}$
SAL	$\{\phi_T,\ p\}$	$\{\phi_{a2+T},\ p_{a4'+s}\}$
HJA	$\{\phi,\ p_{s+T}\}$	$\{\phi_{a2+t},\ p_{a3'+s}\}$
OLY	$\{\phi_s,\ p_T\}$	$\{\phi_{a2},\ p_{a5'+T}\}$
CLE	$\{\phi_T,\ p_s\}$	$\{\phi_{a2+T},\ p_{s+T}\}$
EUG[b]	$\{\phi_{t_1=t_2,t_3,t_4},\ p_{t+s}\}$	$\{\phi_{a2+T},\ p_{a2+s*T}\}$
COO	$\{\phi_t,\ p_s\}$	$\{\phi_{a2+t},\ p_{a2+s}\}$
SIU	$\{\phi,\ p_{s+t}\}$	$\{\phi_{a2},\ p_{a2}\}$
SIS	$\{\phi,\ p_T\}$	$\{\phi,\ p_T\}$

[a] Capture technique (c): a binary variable to index physical recapture vs. resighting.

[b] Here $\phi_{t_1-t_2,t_3,t_4}$ denotes model $\{\phi_t\}$ with the constraint that survival probabilities are same over time periods 1 to 2 and 2 to 3 (i.e., $\phi_1 = \phi_2$).

TABLE 4. ESTIMATES OF JUVENILE AND ADULT SURVIVAL PROBABILITIES, FROM THE BEST MODEL, FOR THE NORTHERN SPOTTED OWL DATA. NOTATION IS EXPLAINED IN THE APPENDIX

Study area	Best model, age models	Juvenile survival		Adult survival	
		ϕ_J	SE(ϕ_J)	ϕ_A	SE(ϕ_A)
CAL	$\{\phi_{J,A1}, p_{a4',Ac}\}$	0.330	0.043	0.868	0.012[a]
RSB	$\{\phi_{a2}, p_{a4'+s}\}$	0.418	0.042	0.843	0.010
SCS	$\{\phi_{a2}, p_{a4'+s}\}$	0.320	0.038	0.824	0.009
SAL	$\{\phi_{a2+T}, p_{a4'+s}\}$	0.402	0.105[a]	0.851	0.022[a]
HJA	$\{\phi_{a2+t}, p_{a3'+s}\}$	0.288	0.052[a]	0.821	0.016[a]
OLY	$\{\phi_{a2}, p_{a5'+T}\}$	0.245	0.064[a]	0.862	0.017[a]
CLE	$\{\phi_{a2+T}, p_{s+T}\}$	0.140	0.026[a]	0.850	0.031[a]
EUG	$\{\phi_{a2+T}, p_{a2+s*T}\}$	0.232	0.078[a]	0.853	0.026[a]
COO	$\{\phi_{a2+t}, p_{a2+s}\}$	0.218	0.045[a]	0.862	0.019[a]
SIU	$\{\phi_{a2}, p_{a2}\}$	0.243	0.092	0.822	0.027
SIS	$\{\phi, p_T\}$	0.000	—	0.830	0.045
Mean, and empirical SE on 10 *df*		0.258	0.036	0.844	0.005

[a] Standard error is an approximation based on the nearest (in AIC) model with no time effects on survival probability; we did not have general enough software to get exact standard errors in these cases.

respectively; thus, for adults (these were all territory holders, due to the sampling methods) we assumed $\phi_A = S_A$. The average survival of adults is very precisely estimated, cv = 0.6%.

META-ANALYSIS OF SURVIVAL

Anderson and Burnham (1992) conducted a comprehensive "meta-analysis" of the data from adult females on the five study areas available at that time. Because more data are used in the estimation of parameters, there is greater power to detect various "effects" and reveal more structure in the data. Here, we partitioned the study areas into six short-term data sets (<6 years; the WDS data were included in this analysis, with the investigators consent) and six long-term data sets (>6 years) to test the null hypothesis that there were no decreasing time trends in survival against the one-sided alternative that survival was decreasing. Thus, interest was focused on three models for survival $\{\phi, \phi_T, \text{ and } \phi_t\}$, while allowing the minimum AIC parameterization of the capture probabilities (e.g., p_{g*T}). The data were in no way "pooled" during this analysis; rather, the data from several study areas were jointly used to estimate the same parameter set.

Long-term study areas

We tested for a time trend in survival of females captured as adults using a likelihood ratio test of model $\{\phi, p_{g*T}\}$ vs. model $\{\phi_T, p_{g*T}\}$ and found evidence of a time trend ($\chi^2_{(1)} = 4.889$, P = 0.0270). A further test of model $\{\phi_T, p_{g*T}\}$ vs. model $\{\phi_t, p_{g*T}\}$ was also significant ($\chi^2_{(6)} = 15.015$, P = 0.0201). Some of this additional time variation in ϕ_t (beyond just a linear time effect) is related to study area effects. This general finding is shown in Fig. 1 where a nearly linear negative trend in adult female survival is seen (it is linear on logit(ϕ)) corresponding to model $\{\phi_T, p_{g*T}\}$ and the year-specific estimates are also plotted, corresponding to model $\{\phi_t, p_T\}$. The average standard error for points along the line was 0.014, cv $\doteq$ 1.7%.

A similar finding was made for a joint analysis of males and females captured as adults. That is,

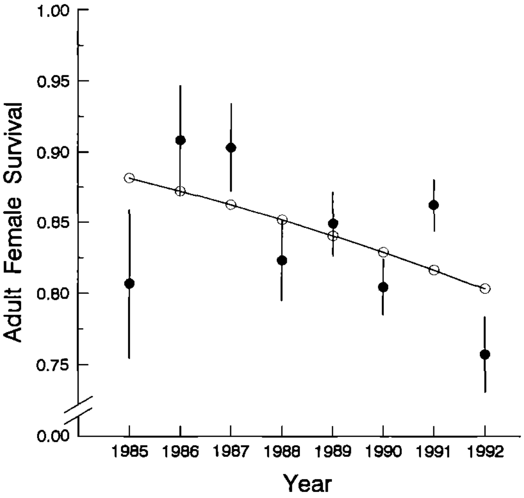

FIGURE 1. Estimated survival probability of adult female Northern Spotted Owls as a function of years, 1985–1992. A significant negative time trend (open circles) is indicated by the nearly linear line (estimated under model $\{\phi_T, p_{g*T}\}$). The solid circles are estimates under model $\{\phi_t, p_{g*T}\}$ with one standard error plotted. The standard error for points along the line averaged 0.014.

TABLE 5. NUMBER OF RECORDS OF NORTHERN SPOTTED OWL FEMALES THAT PRODUCED 0, 1, 2, OR 3 YOUNG, BASED ON DATA COMBINED OVER 11 STUDY AREAS, BY YEAR.

Year	Number of young produced 0	1	2	3	Totals
1985	79	14	22	1	116
1986	60	26	39	0	125
1987	154	19	44	0	217
1988	153	63	68	1	285
1989	264	66	89	2	421
1990	431	216	192	0	839
1991	660	146	194	3	1003
1992	469	280	466	31	1246
1993	1013	61	51	0	1125
Totals	3283	891	1165	38	5377

a significant negative time trend in survival was shown ($\chi^2_{(1)} = 15.307$, $P = 0.0001$), testing model $\{\phi, p_{g \cdot T+s}\}$ vs. $\{\phi_T, p_{g \cdot T+s}\}$. Less evidence was found for a similar negative time trend in the survival of adult males ($\chi^2_{(1)} = 2.053$, $P = 0.1519$), testing model $\{\phi, p_{g \cdot t}\}$ vs. model $\{\phi_T, p_{g \cdot t}\}$.

Short-term study areas

Power to detect time trends from the short-term study areas is surely low, because so few years were available and sample sizes tended to be low (Table 2.). A negative time trend in survival was detected only for females ($\chi^2_{(1)} = 3.476$, $P = 0.0623$), testing model $\{\phi, p_{g+t}\}$ vs. model $\{\phi_T, p_{g+t}\}$. The result for the joint analysis of males and females was inconclusive ($\chi^2_{(1)} = 1.707$, $P = 0.1914$), as was that for the males alone ($\chi^2_{(1)} = 0.754$, $P = 0.3852$). Two points are of interest here, first a significant negative trend was shown for females and second, the sign of the non-significant relationships for males and females and males alone was negative in both cases.

FECUNDITY DATA

Across all 11 studies and years, there were 5,377 females checked for reproduction. Of these, 3,283

TABLE 6. ANALYSIS OF VARIANCE RESULTS, AND YEARLY MEANS, FOR NUMBER OF FEMALE YOUNG FLEDGED PER TERRITORIAL FEMALE. THE EXACT F-TESTS USE EXPECTED MEAN SQUARES TO CONSTRUCT A DENOMINATOR MEAN SQUARE; VARIANCE COMPONENTS ESTIMATED BY THE MIVQUE METHOD IN SAS PROC VARCOMP (AGE IS A FIXED-EFFECT, HENCE FOR IT THERE IS NO VARIANCE COMPONENT)

Source	df	SS	Mean square	F-value	P
AGE	2	9.4096	4.7048	8.18	0.0003
		(exact F-test based on expected mean squares		8.14	0.0004)
YEAR	8	39.5056	4.9382	8.58	0.0001
		(exact F-test based on expected mean squares		5.07	0.0001)
AGE*YEAR	16	14.5058	0.9068	1.58	0.0665
STUDY	11	12.4231	1.1294	1.96	0.0280
		(exact F-test based on expected mean squares		1.84	0.0534)
AGE*STUDY	21	5.7360	0.2731	0.47	0.9791
YEAR*STUDY	57	129.9290	2.2795	3.96	0.0001
ERROR	4406	2534.4290	0.5752		

Variance components estimates

Var(YEAR)	0.02087
Var(STUDY)	0.00256
Var(YEAR*STUDY)	0.00000
Var(YEAR*AGE)	0.02682
Var(STUDY*AGE)	0.00000
Var(ERROR)	0.13932

Average yearly fecundity

Year	Mean	N
1985	0.2630	116
1986	0.4160	125
1987	0.2466	217
1988	0.3544	285
1989	0.2969	421
1990	0.3576	839
1991	0.2707	1003
1992	0.5237	1246
1993	0.0725	1125

TABLE 7. ESTIMATES OF AGE-SPECIFIC FECUNDITY (B_X) FOR FEMALE NORTHERN SPOTTED OWLS (B_X = THE NUMBER OF JUVENILE FEMALES FLEDGED/FEMALE OF AGE X)

Study area	Subadult 1 (12 mos.)		Subadult 2 (24 mos.)		Adult (≥36 mos.)	
	$\hat{b}_1$	SE($\hat{b}_1$)	$\hat{b}_2$	SE($\hat{b}_2$)	$\hat{b}_A$	SE($\hat{b}_A$)
CAL	0.094	0.067	0.205	0.077	0.333	0.029
RSB	0.080	0.056	0.144	0.062	0.321	0.022
SCS	0.013	0.019	0.145	0.056	0.313	0.016
SAL[a]	0.500	0.408	0.500	0.408	0.381	0.051
HJA[a]	0.154	0.102	0.154	0.102	0.348	0.034
OLY[a]	0.206	0.106	0.206	0.106	0.380	0.036
CLE[a]	0.360	0.126	0.360	0.126	0.565	0.061
EUG[a]	0.167	0.236	0.167	0.236	0.272	0.049
COO	0.156	0.124	0.167	0.113	0.323	0.044
SIU[a]	0.071	0.101	0.071	0.101	0.231	0.043
SIS[a]	0.000	0.000	0.000	0.000	0.282	0.072
Average[b]	0.068	0.027	0.205	0.034	0.339	0.010

[a] Data for subadults 1 and 2 were pooled, to estimate a common fecundity, because of small sample size ($n_1 + n_2 < 30$ for total sample size of subadults).

[b] These averages are based directly on all the data pooled over ages, not on averaging the column means.

(61.1%), 891 (16.6%), 1,165 (21.7%), and 38 (0.7%) had fledged 0, 1, 2 and 3 young, respectively (Table 5). These data were converted into fecundity values (see Franklin et al. *this volume*) for subsequent analyses.

Key results for the fecundity data are given in Table 6, along with the overall means for each year. These means are numbers of female young fledged per territorial (hence potentially breeding) female; these yearly means use all data (known and unknown aged females). Table 7 gives estimates of fecundity (b) by study area and age of parent female; these means use only data from known-aged female parents. The variance components in Table 6 are for females fledged per territorial female.

From the ANOVA results in Table 6, age of the female parent and year are significant factors in variation among true fecundities. There may be small, but real, differences in fecundity by study area ($P = 0.0534$). With year and study area effects and interactions of these effects treated as random, the estimated variance components are given in Table 6. Because of the large year effects, Table 6 also gives the mean fecundity by year. The most striking features of these means are the high fecundity in 1992 and low fecundity in 1993. We believe no meaningful linear trend in fecundity is observed over these 9 years; formal regression-based statistical tests for a linear trend are strongly influenced by the results in 1993 (these data points have very high leverage) and therefore tend to have a negative trend.

As Table 7 shows, fecundity of 1–2 year old birds is much less than for birds 3+ years old ($P = 0.0004$). Within the subadult age class, 2-year old females are more productive than 1-year old birds ($P = 0.0045$).

JUVENILE EMIGRATION (RADIO-TRACKING DATA)

The only radio-tracking data available for these analyses relative to emigration were from post-fledging juveniles in the OLY and RSB areas in 1991 and 1992 (Forsman, unpublished data; Reid, unpublished data). These data were analyzed to see if estimates of juvenile survival could be obtained that would validly apply to the same annual time period as the CR data. Because the radios were put on 3–6 weeks after fledging and there was a lot of censoring (radio failure and birds that were lost), we did not obtain an estimate of S_J from the radio-tracking data. However, it became apparent during the workshop that these data did allow estimation of the parameter E needed to adjust the CR estimator, $\hat{\phi}_J$, for permanent emigration.

To estimate E we need only counts of juveniles surviving until after emigration occurs (plus the unavoidable assumption that the annual survival probability is the same for emigrating and not emigrating juveniles). The relevant data are given below:

Area	Year	n_{en}	n
OLY	1991	8	11
OLY	1992	3	8
RSB	1991	2	26
RSB	1992	11	31
Totals:		24	76

Based on these data, $\hat{E} = 24/76 = 0.3158$, with SE($\hat{E}$) = 0.05332 and a 95% confidence interval of 0.2113 to 0.4203.

POPULATION RATE OF CHANGE, λ

Our estimates of λ based on $\hat{\phi}_J$ (Table 8) are biased low because of the confounding effect of

TABLE 8. ESTIMATES OF THE RATE OF ANNUAL POPULATION CHANGE, λ, FOR FEMALE NORTHERN SPOTTED OWLS IN 11 INDEPENDENT STUDY AREAS THROUGHOUT THEIR RANGE. ALSO SHOWN ARE TEST STATISTICS AND P-VALUES FOR THE TEST OF THE NULL HYPOTHESIS THAT $\lambda \geq 1$ VS. THE ALTERNATIVE THAT $\lambda < 1$

Study area	$\hat{\lambda}$	SE($\hat{\lambda}$)	*t* or z	P
CAL	0.9656	0.0165	2.08	0.0188
RSB	0.9570	0.0146	2.94	0.0016
SCS	0.9105	0.0121	7.39	0.0000
SAL	1.0191	0.0729	−0.26	0.6064
HJA	0.9106	0.0212	4.22	0.0000
OLY	0.9472	0.0255	2.07	0.0192
CLE	0.9240	0.0323	2.35	0.0094
EUG	0.9134	0.0314	2.76	0.0029
COO	0.9274	0.0223	3.25	0.0006
SIU	0.8738	0.0312	4.04	0.0000
SIS	0.8302	—	—	—
Simple average and t-test, 10 df	0.9253	0.0148	5.04	0.0003
Simple average and z-test	0.9349[a]	0.0103	6.32	0.0000

[a] Excludes SIS area because no theoretical SE($\hat{\lambda}$) could be obtained for that area.

emigration. Still, it is worth testing these $\hat{\lambda}$ against 1 because if, with such a test, they are not significantly less than 1 we may conclude we do not have statistical evidence that λ is less than 1. Given that the results in Table 8 suggest true λ might be less than 1, we computed Table 9 results. Table 9 allows a subjective assessment of whether it is reasonable or not to believe $\lambda < 1$. Overall, to believe $\lambda \geq 1$, one must believe average juvenile survival probability (S_J) is ≥ 0.565, or (equivalently) that emigration probability is ≥ 0.51. In the previous section we derived $\hat{E}$ = 0.3158 with a 95% confidence interval of 0.2113 to 0.4203. This is indirect, but strong, evidence that, on average, $\lambda < 1$ during the years of these studies.

Given this data-based estimate of E, we can adjust $\hat{\phi}_J$ for emigration to obtain $\hat{S}_J$ and compute a less biased $\hat{\lambda}$. We did not do this for each area because we do not have area-specific $\hat{E}$. Instead, we obtained averages of the vital rates over time and study areas to use with the single estimate $\hat{E}$ to get one bias-adjusted $\hat{\lambda}$. This $\hat{\lambda}$ applies in general, as an average over the years 1985 to 1993, to Northern Spotted Owls. From Table 7 the fecundities are (standard errors in parentheses), $\hat{b}_1 = 0.068$ (0.027), $\hat{b}_2 = 0.205$ (0.034), $\hat{b}_A$ = 0.339 (0.010). Sampling correlations among these estimates are 0. From Table 4, $\hat{\phi}_J = 0.2579$ (0.03563), $\hat{S}_A = \hat{\phi}_A = 0.8441$ (0.00519), with empirical correlation between these estimates of 0.130 (note, we are using empirical not theoretical variances for the above point estimates). From above, we get $\hat{E} = 0.3158$ (0.05332), hence $\hat{S}_J = 0.3769$ (0.05979), and the estimated correlation between adult and juvenile survival estimates ($\hat{S}_A$, $\hat{S}_J$) is 0.13. Using these parameter estimates (and associated variances and covariances) we find $\hat{\lambda} = 0.9548$, SE($\hat{\lambda}$) = 0.01731. Because we used empirical variances we will consider that the standard error of $\hat{\lambda}$ is based on 10 df and do a one sided t-test, as well as construct a 95% confidence interval. This is conservative in the sense of producing a less powerful test and a wider interval than might be justified by a more exact evaluation of degrees of freedom to associate with the standard error of $\hat{\lambda}$. The t-test (H_o:

TABLE 9. THE VALUE OF JUVENILE SURVIVAL PROBABILITY NEEDED TO PRODUCE $\lambda = 1$, DENOTED AS $S_{J|\lambda=1}$ IS PRESENTED. THE CALCULATION OF $S_{J|\lambda=1}$ IS BASED ON THE ESTIMATES OF ADULT SURVIVAL (TABLE 4) AND FECUNDITY (TABLE 7) USED TO COMPUTE $\hat{\lambda}$ IN TABLE 7 (AND REPEATED BELOW). SIMILARLY, WE PRESENT THE JUVENILE EMIGRATION PROBABILITY ($E_{|\lambda=1}$) THAT WOULD RESULT IN THE OBSERVED $\hat{\phi}_J$ ESTIMATES GIVEN IN TABLE 5 UNDER THE ASSUMPTION THAT $\lambda = 1$. THIS INFORMATION IS USEFUL IN ASSESSING THE PLAUSIBLE DEGREE OF BIAS IN THE $\hat{\lambda}$ VALUES DUE TO EMIGRATION OF JUVENILE BIRDS

Study area	$\hat{\lambda}$	$S_{J\|\lambda=1}$	$E_{\|\lambda=1}$
CAL	0.9656	0.461	0.29
RSB	0.9570	0.607	0.31
SCS	0.9105	0.746	0.75
SAL	1.0191	0.360	−0.12
HJA	0.9106	0.630	0.54
OLY	0.9472	0.413	0.41
CLE	0.9240	0.297	0.53
EUG	0.9134	0.603	0.61
COO	0.9274	0.492	0.56
SIU	0.8738	0.995	0.77
SIS	0.8302	0.607	1.00
Means	0.9253	0.565	0.51

: $\bar{\lambda} \geq 1$ vs. $H_a : \bar{\lambda} < 1$) is $t_{10} = 2.61$, $P = 0.0130$. The 95% confidence interval on $\bar{\lambda}$ (uses 97.5 percentile $t_{10} = 2.228$) is 0.9162 to 0.9934.

DISCUSSION

The first important result was that annual survival probabilities of females capture as adults have declined at a significant, negative rate. Several individual data sets revealed this negative time trend, as did the meta-analyses for both the short-term and long-term data sets. This is an important finding and must be weighed heavily in decisions concerning land management policy in the future and in view of the fact that this is a Threatened subspecies under the Endangered Species Act. The survival results for adult males were less convincing, but the pattern of declining survival was still there. The meta-analysis of males and females also showed a highly significant negative time trend. The adult female population component is the most important, and it is this component where the evidence is strongest for a negative time trend (Fig. 1) (we again note that λ applies only to the female owls).

We did not detect any trend in juvenile survival probabilities; these data are somewhat sparse and the power to detect a trend was low. Several areas did seem to show a negative time trend in ϕ_J (Table 3), but we will not pursue this further here. We found no time trends that we felt were biologically significant in fecundity, but note that 1993 was a year of very poor production.

We make here two comments on methodology. Firstly, the tests for time trend in survival are based on a ideas of fixed time effects, because we are not making any inference to other time periods. To be consistent with this philosophy, the ANOVAs on the fecundity data could have treated time main-effects as fixed (Table 6). Inferences about fecundity would not have changed under a fixed time-effects model.

Secondly, the issue was raised about whether tag loss or senescence could be factors confounded with time, hence mislead us about a true time decline in adult survival rates. We have considered these issues. There was no loss of leg bands. The design of the studies, especially in regards to the sample sizes, over time, of numbers of newly banded adults precludes senescence as a confounding factor with time-effects.

The second important result is that average λ, corrected for juvenile emigration, is significantly <1. We will restrict our inference to the specific years of study; we do not intend that this $\hat{\lambda}$ be used to project the size or rate of change of the population into the distant future (≥ 10 years). We use λ to answer the following question, *"given a population with estimated average vital rates for females (i.e., the $\hat{\hat{S}}_x$ and $\hat{\hat{b}}_x$, where x = age), what is the rate of population change if these rates remained constant over an appropriately long time period?"* Thus, these estimates of λ answer a hypothetical question that remains of prime interest. No assumptions concerning a stationary age distribution are required under this interpretation. Finally, $\hat{\lambda}$ relates to the population of resident, territorial female birds. In this sense, λ answers the question, *"Have the resident, territorial female birds replaced themselves?"* This is an inference to the entire population of owls, not just the banded birds.

The ability to make definitive statements concerning λ is hampered by undetected emigration of some juvenile birds to places outside the study areas. To the degree that juvenile owls emigrate from the study area, survive the year, and are not captured, a negative bias exists if one takes $\hat{\phi}_J$ as an estimator of the parameter S_J, because of the relationship $\phi_J = S_J(1 - E)$. To evaluate the bias in $\hat{\phi}_J$, we have given the value of S_J required for $\lambda = 1$ (see Table 9). In addition, during 1991 and 1992 there were birds fitted with radio transmitters, which allowed an estimate of emigration probability (E). This also leads to insights concerning the degree to which $\lambda < 1$ may be true. Generally, we conclude from Table 8 that the population of resident females is declining on most of the 11 areas (perhaps SAL is an exception; but note the large estimated standard error for SAL).

Past studies (e.g., Anderson and Burnham 1992) have shown significant rates of immigration (much of this may be recruitment from a floater component of the owl population) and this seems likely to be the case here. Time constraints did not permit the estimation of these rates during the December, 1993, workshop. Thus, if a census could be done over several years to completely enumerate all the birds within some study area boundary, it is likely that these numbers might be fairly stationary (i.e., $N_1 \doteq N_2 \doteq N_3 \doteq \ldots \doteq N_k$). This hypothetical result is not inconsistent with our findings that $\lambda < 1$ and that populations of resident territorial birds are declining. In this latter case, the population within a particular bounded study area is being temporarily augmented by recruitment into the territorial population.

The third important result is that the rate of population decline is accelerating. This result stems from the fact that λ is estimated using time-averages of the vital rates (the $\bar{\phi}_x$ and $\bar{b}_x$, where x = age); however, it is clear that the survival probability of territorial females has a significant, negative time trend (Fig. 1). Thus, we conclude that the rate of population decline is accelerating. This acceleration was not expected by, for example, the Interagency Scientific Committee (Thomas et al. 1990) or other groups who have examined these general issues. If the next 100 years are thought to be "highly risky" for the owl, then the findings concerning accelerating declines offer no comfort for the long-term viability for this subspecies.

SUMMARY

We used all available demographic data on the northern spotted owl to estimate vital rates of this population to assess the current status of the subspecies. We used capture-recapture analysis and information-theoretic methods to analyze survival data from 1985–1993 on the Northern Spotted Owl from 11 large study areas. That analysis of all the capture-recapture data showed a declining annual survival rate for adult Northern Spotted Owls on the study areas during 1985–1993. We used general linear models to analyze recruitment data; no time trend was found. Survival and recruitment rates were combined in a Leslie matrix demography analysis. Using data from the 11 study areas we estimated $\hat{\lambda} = 0.9548$ (SE = 0.017). This is the average annual rate of population change under the estimated vital rates. We rejected the null hypothesis that $\lambda \geq 1$ vs. the one-sided alternative hypothesis that $\lambda < 1$ ($t = 2.61$, $P = 0.0130$). We restrict our interpretation of $\hat{\lambda}$ to the specific years of the studies; $\hat{\lambda}$ should not be used to project the size, or rate of change, of the population into the distant future (10+ years). From either the trend in adult survival rate, or $\hat{\lambda}$, there is a plausible inference of a declining population during the study period. This inference concerning declining populations of resident, territorial female owls applies to the entire population, not just the banded birds on the 11 study areas. Based on the capture-recapture analyses alone, the annual survival probability of adult female owls declined during the study years. Therefore, we conclude that the rate of population decline is accelerating.

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