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SURVIVAL AND HOME-RANGE SIZE OF NORTHERN SPOTTED OWLS IN SOUTHWESTERN OREGON

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ABSTRACT.—In the Klamath province of southwestern Oregon, Northern Spotted Owls (*Strix occidentalis caurina*) occur in complex, productive forests that historically supported frequent fires of variable severity. However, little is known about the relationships between Spotted Owl survival and home-range size and the characteristics of fire-prone, mixed-conifer forests of the Klamath province. Thus, the objectives of this study were to estimate monthly survival rates and home-range size in relation to habitat characteristics for Northern Spotted Owls in southwestern Oregon. Home-range size and survival of 15 Northern Spotted Owls was monitored using radiotelemetry in the Ashland Ranger District of the Rogue River–Siskiyou National Forest from September 2006 to October 2008. Habitat classes within Spotted Owl home ranges were characterized using a remote-sensed vegetation map of the study area. Estimates of monthly survival ranged from 0.89 to 1.0 and were positively correlated with the number of late-seral habitat patches and the amount of edge, and negatively correlated with the mean nearest neighbor distance between late-seral habitats. Annual home-range size varied from to 189 to 894 ha ($\bar{x}$ = 576; SE = 75), with little difference between breeding and nonbreeding home ranges. Breeding-season home-range size increased with the amount of hard edge, and the amount of old and mature forest combined. Core area, annual and nonbreeding season home-range sizes all increased with increased amounts of hard edge, suggesting that increased fragmentation is associated with larger core and home-range sizes. Although no effect of the amount of late-seral stage forest on either survival or home-range size was detected, these results are the first to concurrently demonstrate increased forest fragmentation with decreased survival and increased home-range size of Northern Spotted Owls.

KEY WORDS: *Northern Spotted Owl; Strix occidentalis caurina; habitat characteristics; home-range size; Klamath Province; Oregon; survival.*

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SUPERVIVENCIA Y TAMAÑO DEL ÁREA DE ACCIÓN DE *STRIX OCCIDENTALIS CAURINA* EN EL SUROESTE DE OREGÓN

RESUMEN.—En la provincia de Klamath, al suroeste de Oregón, *Strix occidentalis caurina* habita bosques complejos y productivos que históricamente han soportado incendios frecuentes de intensidad variable. Sin embargo, se sabe poco acerca de las relaciones entre la supervivencia de *S. o. caurina* y el tamaño del área de acción y las características de los bosques mixtos de coníferas propensos a incendios de la provincia de Klamath. Por ello, los objetivos de este estudio fueron estimar las tasas de supervivencia mensuales y el tamaño del área de acción en relación con las características del hábitat de *S. o. caurina* en el suroeste de Oregón. Se monitorearon el área de acción y la supervivencia de 15 individuos de *S. o. caurina* usando radiotelemetría en el Distrito de Guardabosque Ashland del Bosque Nacional Rogue River–Siskiyou desde septiembre del 2006 a octubre del 2008. Las clases de hábitat dentro de las áreas de acción de *S. o. caurina* fueron caracterizadas usando un mapa de vegetación del área de estudio elaborado con sensores remotos. Las estimaciones de supervivencia mensual oscilaron entre 0.89 y 1.0 y estuvieron positivamente correlacionadas con el número de parches de hábitat de la etapa sucesional tardía y la cantidad de hábitat de borde, y negativamente correlacionados con la distancia media al vecino más cercano entre hábitats sucesionales tardíos. El área de acción anual varió de 189 a 894 ha ($\bar{x}$ = 576; EE = 75), con una pequeña diferencia entre las áreas de acción reproductivas y no reproductivas. El área de acción de la época reproductiva se incrementó con la cantidad de borde tajante y con la cantidad de bosques viejos y maduros combinados. El área núcleo y las áreas de acción de la época reproductiva y no reproductiva se incrementaron con el aumento de hábitats de borde tajante, lo que sugiere que el incremento de la fragmentación se asocia con áreas núcleo y áreas de acción de mayor tamaño. Aunque no se detectó el efecto de la cantidad de bosque de la etapa sucesional tardía en la supervivencia o el tamaño del área de acción, estos resultados son los primeros en demostrar simultáneamente el incremento de la fragmentación del bosque con la disminución de la supervivencia y el aumento del tamaño del área de acción en *S. o. caurina.*

[Traducción del equipo editorial]

Habitat requirements for Northern Spotted Owl (*Strix occidentalis caurina*) include structurally complex forests characterized by a multispecies and multistoried canopy as well as large standing snags and downed wood (Forsman et al. 1984, Gutiérrez et al. 1995). The vertical complexity of these forests provides the components utilized by Spotted Owls for nesting, roosting, and foraging, and forest structure and configuration has been linked to overall fitness of the species (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). For example, annual survival has been positively correlated with the amount of late-seral forest and amount of edge between old forests and other vegetation types within the territory (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). In addition, reproductive success (Dugger et al. 2005) and colonization rates of territories (Dugger et al. 2011) are both positively affected by increased amounts of old forest habitat near the core of the home range. However, most of the relationships observed between habitat characteristics and Northern Spotted Owl occupancy, survival, and reproduction are associated with the predominantly Douglas-fir forests of the western Cascade Mountains in southern Oregon (Olson et al. 2004, Dugger et al. 2005, Dugger et al. 2011),

and the mixed-conifer, mixed-evergreen forests of northern California (Franklin et al. 2000).

In the Klamath province, Northern Spotted Owls are associated with structurally diverse stands that are currently susceptible to high-severity wildfire because of the increased fuel loads and ladder fuels associated with these forest types (Agee and Edmonds 1992, Sensenig 2002). This region has a unique fire-regime history that differs from that of Northern Spotted Owl habitat found within the dry ecosystems of the eastern Cascades and mesic forests of the western Cascades and coastal mountains (Agee 1993, Sensenig 2002, Skinner et al. 2006). The eastern Cascades are more at risk to high-severity wildfires due to the effects of fire suppression, while the western Cascades experience less frequent high-severity fires (Agee and Edmonds 1992, Agee 1993). Recent wildfires in the Klamath provinces, such as the 2002 Biscuit fire, have burned hundreds of thousands of acres of Northern Spotted Owl habitat. For this reason, the Klamath region has become the focus of fuels-reduction projects that simplify stands (e.g., thinning and prescribed burning; U.S. Fish and Wildlife Service 2008), but may also lower habitat quality for Spotted Owls.

Spotted Owls have large home ranges compared to other owls (Forsman et al. 2005, Clark 2007, Hamer et al. 2007), but home ranges in southwestern Oregon (Clark 2007) and northern California (Zabel et al. 1995) tend to be smaller than those in other parts of the subspecies' range (Carey et al. 1990, Glenn et al. 2004, Forsman et al. 2005, Hamer et al. 2007). These differences have been attributed to factors such as the proportion of old forest within home ranges (Carey et al. 1990, Forsman et al. 2005), amount of hard edge (Clark 2007), and prey abundance (Carey et al. 1992, Zabel et al. 1995). However, only Clark (2007) has linked habitat characteristics to home-range size and survival in mixed-conifer forests in southwestern Oregon. Thus, information is limited on the relationships between survival and home-range size and the characteristics of mixed-conifer forests of the Klamath province in southwestern Oregon (Wagner and Anthony 1999, Clark 2007). To inform and advise the proposed management actions to reduce fuel loads in these forests, we need to understand the relationship between current habitat characteristics and owl demographics and home-range size. Thus, the objectives of this study were to estimate monthly survival rates and home-range size in relation to habitat characteristics for Northern Spotted Owls in southwestern Oregon.

METHODS

Study Area. Our study area was within the Mt. Ashland Late Successional Reserve (LSR) on the Ashland Ranger District of the Rogue River–Siskiyou National Forest with small blocks of private and City of Ashland ownership interspersed (U.S. Forest Service 2005). The general study area lies within the Siskiyou Range of the Klamath Mountains and the mixed-conifer and Shasta Red Fir (*Abies magnifica* var *shastensis*) vegetation zones (Franklin and Dyrness 1973). A pronounced rain shadow from the Oregon coast to the Ashland watershed resulted in precipitation ranging from 25–89 cm annually, increasing with elevation (U.S. Forest Service 2005). Elevations within the study area ranged from 760–1830 m with moderate to steep (20–70%) slopes that were highly dissected and characterized by high rates of erosion (U.S. Forest Service 2005).

Radiotelemetry. Between September 2006 and June 2007, we captured Spotted Owls with a noose pole, foot snare, or by hand and fitted them with 5 g backpack-mounted radio transmitters which included mortality sensors and an expected life span of 12 mo (Holohil Systems Ltd. Model RI-2C, Ontario, Canada). We attached radios to all owls that occupied territories within the Ashland, Neil Creek, and Upper Little Applegate watersheds. We relocated these owls using a directional yagi antennae and a Telonics model TR-2 receiver (Telonics, Inc., Mesa, Arizona, U.S.A.) or a Communication Specialists model R-1000 receiver (Communication Specialists, Inc., Orange, California, U.S.A.). We monitored each owl for approximately 12 mo from the time it was initially captured, unless the bird died or left the study area. Five individuals were recaptured at the end of their radio's life span, radios were replaced, and they were then monitored for an additional year (25 mo total). We determined the location and fate of each owl approximately every other night for nocturnal locations and once per week for diurnal roost locations. An owl must have been verified alive and present on the study area at the beginning or end of a month; otherwise it was censored for that interval. If an owl's transmitter failed, it was located again and fitted with a new transmitter and censored for that month.

Habitat Classification. Factors affecting habitat selection of owls, such as understory structural quality associated with late-seral forest (Solis and Gutiérrez 1990, North et al. 1999, Irwin et al. 2000), occur at the microhabitat level and are unreliably measured with remotely sensed data. In contrast, landscape-scale factors affecting home-range sizes, such as the aggregation of late-seral habitats, occur at the macrohabitat level (Carey et al. 1990, Forsman et al. 2005, Hamer et al. 2007) and can be characterized across large geographic scales with reasonable accuracy using remotely sensed map layers (Glenn and Ripple 2004, Dugger et al. 2005).

For our analysis of survival rates and home-range size, we used an ArcGIS (Global Information Systems; ESRI, Redlands, California, U.S.A.) map layer created by Geographic Resource Solutions (GRS; Hill 1996), which used Landsat Thematic Mapper (TM) data acquired August 1993, and described canopy closure (%), average tree diameter at breast height (DBH), and dominant vegetation of all forest types for each 25-m^2 pixel. There were no major disturbance events (e.g., fire) or logging activities within the study area since the map layer was collected (D. Clayton, USDA Forest Service, pers. comm.). In addition, the accuracy of this satellite-based map was 86, 92, and 88% respectively, for canopy closure, average DBH, and the three cover types (late-seral forest, intermediate-aged forest, and non-habitat) we

Table 1. Definitions and acronyms of habitat covariates used to model monthly survival and home-range size for Northern Spotted Owls in southern Oregon from October 2006–October 2008. All covariates represent values found within 95% fixed kernel home ranges.

ACRONYM	DEFINITION
LATE	The percentage of late-seral forest for all forest types characterized by canopy closure $\geq$40% and DBH >50.8 cm.
INTER	The percentage of intermediate-aged forest characterized by canopy closure $\geq$40% and DBH 12.7–50.7 cm.
NON	The percentage of non-habitat (DBH $\leq$12.6 cm).
SUIT	Suitable habitat is the combined percentage of LATE and INTER habitat classes.
NUMP	The number of patches of late-seral forest.
MPS	The mean patch size of late-seral forest (ha).
EDGE	The amount of edge (km) between suitable and non-habitat.
MNN	The mean nearest neighbor distance, which is the average of the shortest distances (edge to edge in m) between patches of late-seral forest.
PERIM	Perimeter density, which is the length (m) of the perimeter of late-seral conifer forest patches divided by the amount (ha) of late conifer forest.
TCA	Total core area is the total amount (ha) of late-seral forest with a 100-m buffer to edge.

used to classify the vegetation layer (Table 1; Hill 1996). Young and pole cover types were combined because the young forest category made up a very small percentage of available habitats within the study area. For the same reason we combined sapling, early seral, and non-forest categories into a non-habitat cover type. These habitat classes were based on the system developed by Wagner and Anthony (1999) for habitat selection by Spotted Owls in southwestern Oregon.

We derived metrics of forest fragmentation within owl home ranges identified as important to Spotted Owls (Franklin and Gutiérrez 2002) from the map layers using the software program FRAGSTATS (McGarigal and Marks 1995) and included total core area of late-seral forest (TCA), mean patch size of old forest (MPS), number of late-seral patches (NUMP), mean nearest neighbor distance of old forest (MNN), and amount of edge in m (EDGE; Table 1). We defined edge as the interface between intermediate and late-successional forest habitat and non-habitat. We classified intermediate-aged forest types as "suitable" habitat because previous research in southwestern Oregon indicated that owls used these forest types in proportion to availability (Wagner and Anthony 1999).

Home-range Analysis. We used the program KERNELHR (Seaman et al. 1998) to estimate 95% fixed kernel home ranges for the breeding season (1 March–31 August), nonbreeding season (1 September–28 February), and annual periods (1 September–31 August). KERNELHR estimates densities using nonparametric kernel smoothing methods, which have less sample-size bias than harmonic

mean or minimum convex polygon methods (Worton 1989). Within each owl's home range, we estimated core use areas by using the greater than average observation density contour generated by KERNELHR.

All habitat covariates were generated from the individual 95% contour of the fixed kernel home range estimated by KERNELHR (Seaman et al. 1998) using ArcGIS 9.2. Fixed kernel estimates are less biased than adaptive kernel estimates when least squares cross-validation is used to select the smoothing parameter (Seaman and Powell 1996). We hypothesized nonlinear relationships between habitat characteristics and home-range size, so in addition to linear habitat variables, pseudo-threshold (log 10; lg), and mean-centered quadratic (q) structures of each habitat covariate were also included in our models. Mixed model multiple regression analysis in SAS (PROC MIXED; SAS 2009) was used to evaluate factors that may influence home-range and core use area size of individual owls based on a set of a priori models that included sex (male vs. female), season (defined above), and habitat covariates (Table 2). Initially only models with single habitat covariates were investigated, but if any of those single-factor models were competitive (<2 AIC$_c$), and the beta's on the covariates had 95% confidence limits that did not include zero, then exploratory, multifactor models were run a posteriori. We included a site identifier as a random effect because in some cases data were collected on both members of a pair.

Survival Analysis. We used radiotelemetry and known fate models in program MARK (White and Burnham 1999) to estimate monthly survival rates

Table 2. Model structure and predictions for habitat characteristics in relation to survival (S) and home-range size (HR) of Northern Spotted Owls in southern Oregon from September 2006 through October 2008.

MODEL	LINEAR	PSEUDO-THRESHOLD	QUADRATIC
S_{LATE}	$\beta_{(LATE)} > 0$	$\beta_{(lg\_LATE)} > 0$	$\beta_{(LATE)} > 0, \beta_{(LATE)}^2 < 0$
S_{INTER}	$\beta_{(INTER)} > 0$	$\beta_{(lg\_INTER)} > 0$	$\beta_{(INTER)} > 0, \beta_{(INTER)}^2 < 0$
S_{NON}	$\beta_{(NON)} < 0$	$\beta_{(lg\_NON)} < 0$	$\beta_{(NON)} > 0, \beta_{(NON)}^2 < 0$
S_{NUMP}	$\beta_{(NUMP)} > 0$	$\beta_{lg\_NUMP)} > 0$	$\beta_{(NUMP)} > 0, \beta_{(NUMP)}^2 < 0$
S_{MPS}	$\beta_{(MPS)} > 0$	$\beta_{lg\_MPS)} > 0$	$\beta_{(MPS)} > 0, \beta_{(MPS)}^2 < 0$
S_{EDGE}	$\beta_{(EDGE)} > 0$	$\beta_{lg\_EDGE)} > 0$	$\beta_{(EDGE)} > 0, \beta_{(EDGE)}^2 < 0$
S_{MNN}	$\beta_{(MNN)} < 0$	$\beta_{lg\_MNN\_)} < 0$	
S_{PERIM}	$\beta_{(PERIM)} < 0$	$\beta_{lg\_PERIM)} < 0$	
S_{TCA}	$\beta_{(TCA)} > 0$	$\beta_{lg\_TCA)} > 0$	$\beta_{(TCA)} > 0, \beta_{(TCA)}^2 < 0$
HR_{LATE}	$\beta_{(LATE)} < 0$	$\beta_{(lg\_LATE)} < 0$	$\beta_{(LATE)} < 0, \beta_{(LATE)}^2 > 0$
HR_{INTER}	$\beta_{(INTER)} < 0$	$\beta_{(lg\_INTER)} < 0$	$\beta_{(INTER)} < 0, \beta_{(INTER)}^2 > 0$
HR_{NON}	$\beta_{(NON)} > 0$	$\beta_{(lg\_NON)} > 0$	
HR_{NUMP}	$\beta_{(NUMP)} < 0$	$\beta_{(lg\_NUMP)} < 0$	$\beta_{(NUMP)} < 0, \beta_{(NUMP)}^2 > 0$
HR_{MPS}	$\beta_{(MPS)} < 0$	$\beta_{(lg\_MPS)} < 0$	$\beta_{(MPS)} < 0, \beta_{(MPS)}^2 > 0$
HR_{EDGE}	$\beta_{(EDGE)} > 0$	$\beta_{(lg\_EDGE)} > 0$	$\beta_{(EDGE)} > 0, \beta_{(EDGE)}^2 < 0$
HR_{MNN}	$\beta_{(MNN)} > 0$	$\beta_{(lg\_MNN)} > 0$	
HR_{PERIM}	$\beta_{(PERIM)} > 0$	$\beta_{(lg\_PERIM)} < 0$	
[1]HR_{TCA}	$\beta_{(TCA)} < 0$	$\beta_{(lg\_TCA)} < 0$	

[1] TCA was not included in the *a priori* model set for the core home-range size because we didn't believe it was a viable covariate at the core scale.

(S) and model the effects of covariates on survival (Kaplan and Meier 1958, Pollock et al. 1989). This method allows for censoring of owls that die or emigrate from the study area and also allows for the staggered entry of individuals into the analysis. We entered owls into the data set the first month their fate was known for the entire monthly interval. We recorded owls as being either alive, dead, or censored for each monthly interval.

We generated a list of *a priori* models based on hypotheses regarding the effects of sex, time, study area (i.e., Ashland watershed vs. outside Ashland watershed, the detection of Barred Owls, and habitat covariates (Table 2) and modeled these effects directly using Program MARK. We predicted that monthly survival rates of owls might be lower in winter compared to non-winter periods, so we included a model that tested for seasonal differences (winter: November–April; non-winter: May–October) in monthly survival rates. In addition, several recent studies of Northern Spotted Owls (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005) reported relationships between survival and habitat variables that were not linear in nature. We, therefore, modeled survival using three functional relationships for each variable including linear, pseudo-threshold (lg), and mean-centered quadratic (q). Fuels thinning treatments were planned for the Ashland watershed

shortly after we concluded our study. Thus, as a form of baseline monitoring (i.e., prior to the thinning activities) for future comparison with post-thinning parameters, we tested the hypothesis that survival was similar for birds in the Ashland watershed, vs. those outside the management activity zone. The Barred Owl variable for a particular month represented detections of single or paired Barred Owls, which were detected while surveying for Spotted Owls within the study area during the previous breeding season (Schilling 2009). Although our surveys each year were conducted specifically for Spotted Owls rather than Barred Owls, the cumulative probability of incidentally detecting Barred Owls on a territory each year in western Oregon is high (0.86) given the traditional three-visit Spotted Owl survey protocol used during our study (Wiens et al. 2011).

Model Selection. We used an information theoretic approach to select the best models and most important effects on survival and home-range size (Burnham and Anderson 2002). We ranked models according to AIC_c adjusted for small sample size. We considered the model with the lowest AIC_c and highest model weight as the "best" model (Burnham and Anderson 2002). We considered all models having an AIC_c value within two units of the best model as "competitive" and 95% confidence intervals on regression coefficients were used to determine the

Table 3. Model selection results for all competitive models (<2 AICc) in our *a priori* model set, estimating monthly survival rates for Northern Spotted Owls (*n* = 15) in southern Oregon from October 2006–October 2008. Models were ranked according to Akaike's Information Criterion adjusted for small sample size (AIC_c). The model deviance, number of parameters (*k*), ΔAIC_c, and AIC_c weights are given for all models. Models including the pseudo-threshold structure of covariates are designated as "lg" and the intercept-only model is included for comparison [S(.)]. Sign refers to the regression coefficient corresponding to the landscape variable, given as positive (+) or negative (−) if 95% confidence intervals for the coefficient do not overlap zero, and zero otherwise. See Table 1 for habitat covariate acronym definitions.

MODEL[A]	AICc	ΔAIC_c	AIC_c WTS	K	DEVIANCE	SIGN
S(lg_NUMP)	47.39	0.00	0.12	2	43.33	+
S(lg_LATE)	47.40	0.01	0.11	2	43.34	0
S(MNN)	47.69	0.31	0.10	2	43.64	−
S(lg_EDGE)	47.86	0.48	0.09	2	43.81	0
S(NON)	48.26	0.87	0.07	2	44.20	0
S(INTER)	48.41	1.03	0.07	2	44.35	0
S(lg_MPS)	48.68	1.30	0.06	2	44.63	0
S(PERIM)	49.34	1.95	0.05	2	45.28	0
S(.)	49.56	2.31	0.04	1	47.54	

strength of specific effects. After ranking all the habitat models by AIC_c, we reduced the total model list by retaining the best functional form (linear, pseudo-threshold, or quadratic) for each variable in the final model list. It is not possible or appropriate to test for goodness of fit for known-fate models (Cooch and White 1999), so we assumed minimal over-dispersion in the survival dataset ($\hat{c} = 1$). However, given most of our radio-marked owls were members of pairs (who were also marked), it is possible that the sample units in our survival data set (i.e., individual radio-marked owls) were not independent. We evaluated the potential over-dispersion in our survival data using the bootstrapping approach described in Bishop et al. (2008) to estimate $\hat{c}$ for our best models with individual covariates.

RESULTS

Owl Mortalities. We monitored a total of 15 individual radio-marked owls from seven different pairs, for varying lengths of time between September 2006 and October 2008. One owl disappeared from the study area in May 2007 and was never seen again despite multiple surveys and aerial telemetry searches. We censored this owl from the data set in addition to two other owls that briefly left the study area but later returned. Five of the 15 radio-marked owls (33%) died between October 2006 and September 2008, and the fate of one owl was never determined. Two females died early in the winter of 2007–08, just a few days before heavy snow fell on the study area. Although the mortality sensors

provided us with time and location of death of these birds, these owls were buried under snow and by the time the snow had melted in the spring their transmitters had failed.

Monthly Survival. The best *a priori* model for monthly survival for 25 mo of the study included the log of the number of late-seral forest patches (lg_NUMP) within the 95% fixed kernel home range (Table 3). Although this model accounted for only 11.5% of the model weight of all models, the direction of the effect of the number of late-seral forest patches on survival was positive as predicted (Fig. 1a), and the 95% CI on the β did not overlap zero (β = 2.51, SE = 1.22, 95% CI = 0.13–4.90). There were a number of other highly competitive survival models (<2 ΔAIC_c) including habitat covariates (Table 3). However, only the estimate of the slope coefficient for the mean nearest neighbor distance between late-seral forest patches (MNN) included 95% confidence limits that excluded zero (β = −0.03, SE = 0.11, 95% CI = −0.05 to −0.004), suggesting less forest fragmentation was beneficial for Spotted Owl survival (Fig. 1b). The model containing the log of the amount of edge habitat had 95% confidence limits just barely overlapping zero (β = 2.39, SE = 1.27, 95% CI = −0.09 to 4.88), suggesting that as predicted, certain amounts of edge habitat (up to some threshold) may improve survival. We combined the two best habitat covariates (lg_NUMP, MNN) *a posteriori*, and this two-factor model received slightly more support than each single factor model (ΔAIC_c = 0.00, AIC_c Wt. =
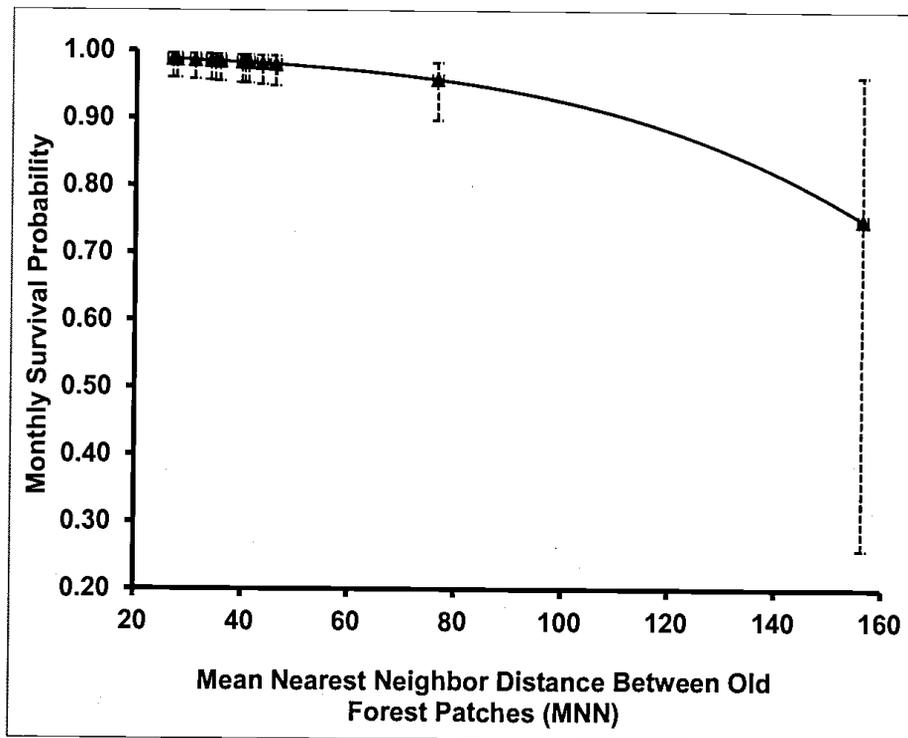
a)
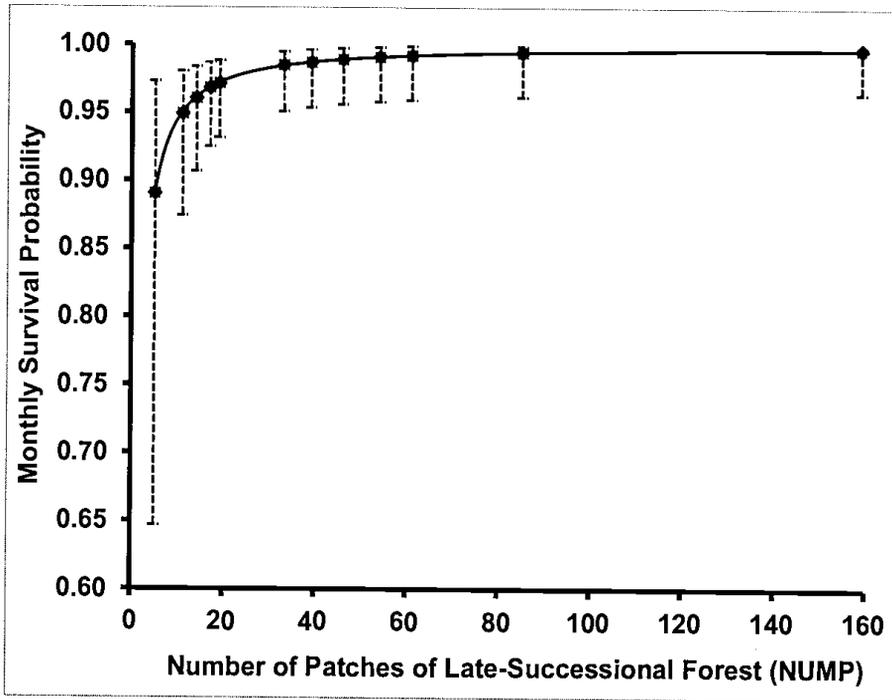
b)

Figure 1. Monthly survival rates from (a) the best model, $S(_{\text{lg\_NUMP}})$ plotted against the number of late-seral forest patches and (b) a competitive model $S(_{\text{MNN}})$ plotted against mean nearest neighbor distances (m) between late-seral forest patches within individual Northern Spotted Owl home ranges in southern Oregon, 2006–08.

Table 4. Model selection results for all competitive models (<2 AIC$_c$) from the analyses of annual and seasonal home-range size of Northern Spotted Owls in southern Oregon in relation to habitat characteristics within home ranges, 2006–08. Annual and seasonal estimates were based on analyses at the home-range scale (95% fixed kernel), and the core area scale was equal to the greater than average observation density contour. Models were ranked according to Akaike's Information Criterion adjusted for small sample size (AIC$_c$). The number of parameters (k), ΔAIC$_c$, AIC$_c$ weights (AIC$_c$ WT), and -2log likelihoods (-2log$L$) are given for all models. Models including the pseudo-threshold structure of covariates are designated as "lg" and the intercept-only model is included for comparison. See Table 1 for definitions of habitat covariate acronyms.

SEASON	MODEL	AIC$_C$	ΔAIC$_C$	AIC$_C$ WT	K	-2LOGL
Annual	lg_EDGE	146.06	0.00	0.97	4	131.4
	Intercept-only	157.63	11.58	0.00	3	148.2
Breeding	EDGE	172.78	0.00	1.00	4	159.8
	Intercept-only	195.47	22.69	0.00	3	186.8
Nonbreeding	EDGE	155.41	0.00	0.98	4	141.7
	Intercept-only	169.13	13.67	0.00	3	160.1
Core area	lg_EDGE	113.15	0.00	0.79	4	98.5
	Intercept-only	116.50	5.28	0.06	3	109.0

0.12). However, when combined in the same model the 95% confidence limits on the betas for both covariates included zero, although the direction of effects was still as predicted (lg_NUMP: β = 2.27, SE = 1.38, 95% CI = −0.44 to 4.989 and MNN: β = −0.02, SE = 0.01, 95% CI = −0.04 to 0.003).

We ran bootstrap procedures on our best models with covariates, S(lg_NUMP), S(MNN), and S(lg_EDGE), following Bishop et al. (2008). We used Program MARK to run 1000 replicate data sets for each individual covariate model (using mean values) by resampling our owl data with replacement based on site locations (pair status). Estimates of $\hat{c}$ for these models were all <1.0 (S(lg_NUMP) = 0.75, S(MNN) = 0.78, S(lg_EDGE) = 0.79) suggesting no serious dependence issues within our survival data.

Annual Home Ranges. The mean annual home-range size for all individual owls was 576 ha but there was considerable variability among individuals (n = 11, SE = 75, range = 192–894, 95% CI = 429–723). Annual home ranges were on average 120 ha larger for males (n = 6, $\bar{x}$ = 630, range = 376–892, 95% CI = 466–795) than for females (n = 5, $\bar{x}$ = 511, range = 192–894, 95% CI = 267–756), but there was a lot of overlap in annual home-range size between the sexes.

The best model for evaluating relationships between home-range size and habitat characteristics received strong support (AIC$_c$ wt. = 0.97; Table 4) and included the log structure of the amount of edge on annual home-range size (lg_EDGE). Annual home-range size increased in relation to increased amounts of edge with some evidence of a diminishing effect at the highest ranges of our data (β = 545.25, SE = 82.95, 95% CI = 382.7–707.8; Fig. 2).

Seasonal Home Ranges. The mean breeding season home-range size was 491 ha (n = 13, SE = 97, range = 279–1516, 95% CI = 301–680) and was slightly larger than the mean nonbreeding season home range (n = 12, $\bar{x}$ = 469, SE = 59, range = 158–838, 95% CI = 354–585). The 95% confidence limits overlapped extensively, so the differences were not significant.

There was a very strong effect of edge on both breeding and nonbreeding season home-range sizes (AIC$_c$ wt = 1.0 and 0.98, respectively; Table 4), and there was little support for any effect of other habitat covariates on seasonal home-range size. As predicted seasonal home-range size increased linearly in conjunction with the amount of edge (breeding season: β = 12.90, SE = 01.06, 95% CI = 10.82–14.98; nonbreeding season: β = 9.82, SE = 1.38, 95% CI = 7.11–12.52; Fig. 3).

Core Areas. Mean size of annual core areas was 94 ha and there was considerable variation in these areas of concentrated use (SE = 11, range = 20–125, 95% CI = 56–98). The best model indicated that core area size was positively correlated with the amount of edge in the core up to certain levels, where the additional increases in the amount of edge resulted in diminished increases in core area (lg_Edge: β = 77.66, SE = 18.19, 95% CI = 42–113; Fig. 4).
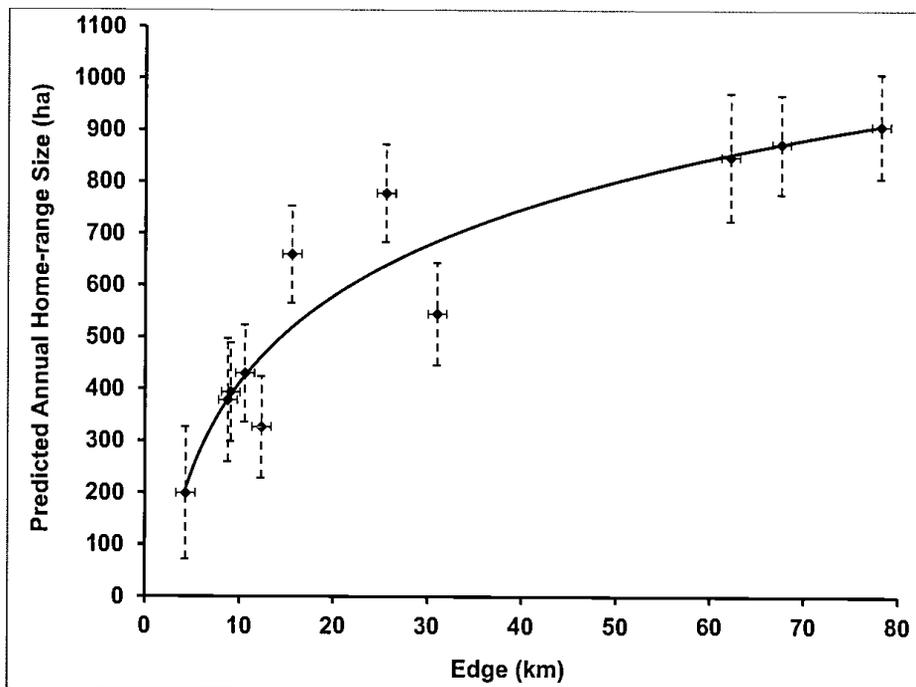
Figure 2. Annual home-range size estimates (ha) from the best model (HR_{lg_EDGE}) plotted against the amount of edge (km) between suitable and non-suitable habitat within 11 individual Northern Spotted Owl home ranges in southern Oregon, 2006–08.

DISCUSSION

Survival. Monthly survival rates ranged from 0.89–1.0, depending on the number of patches of late-seral forest (lg_NUMB) within the owls' annual home range, and these rates were comparable to those of Northern Spotted Owls in unburned forest in the South Cascades (Clark 2007). The amount of edge habitat (lg_EDGE) had a weaker, but similar, positive effect on survival, consistent with previous work on Spotted Owl survival in northern California (Franklin et al. 2000). The mean nearest neighbor distance between late-seral forest patches (lg_MNN) also had an important effect on survival, and both the number of older forest patches and the distance between them indicated a relationship between monthly survival and amount of fragmentation of late-successional forests. Several studies have attempted to relate annual survival to forest fragmentation, but none have found any significant effects (Olson et al. 2005, Dugger et al. 2005). However, increased fragmentation of old forest has been found to negatively affect annual occupancy rates of territories by Northern Spotted Owls in southern Oregon (Dugger et al. 2011). Franklin and Gutiérrez (2002) suggested that a better understanding of the effects of forest fragmentation and heterogeneity on Spotted Owl life-history traits was needed, and they emphasized that

fragmentation and habitat loss can have different effects when considered separately. The researchers also expressed the importance of quantifying the amount or pattern of fragmentation beyond which reproduction, survival, or fitness began to decline. Although this type of threshold has been determined regarding the quantity of late-seral forest beneficial to Spotted Owl demographics (Lande 1988, Bart and Forsman 1992, Gutiérrez 1994), these thresholds have not been determined for the configuration of late-successional forests.

Although the amount of late-seral forest near the core of Spotted Owl territories influenced the annual survival of Spotted Owls in southern Oregon (Olson et al. 2004, Dugger et al. 2005), it did not influence monthly survival rates at the home-range scale in our study. These other studies also investigated relationships at the home-range scale, and concluded little or no effect of the amount of old forest on survival beyond what was observed at core areas near the nest tree (Olson et al. 2004, Dugger et al. 2005); these findings were consistent with our results. However, sample size in our study was relatively small ($n = 15$), so we may have lacked the statistical power to find associations between survival and the amount of late-seral forest at the home-range scale. In addition, the mean percentage of late-seral forest within
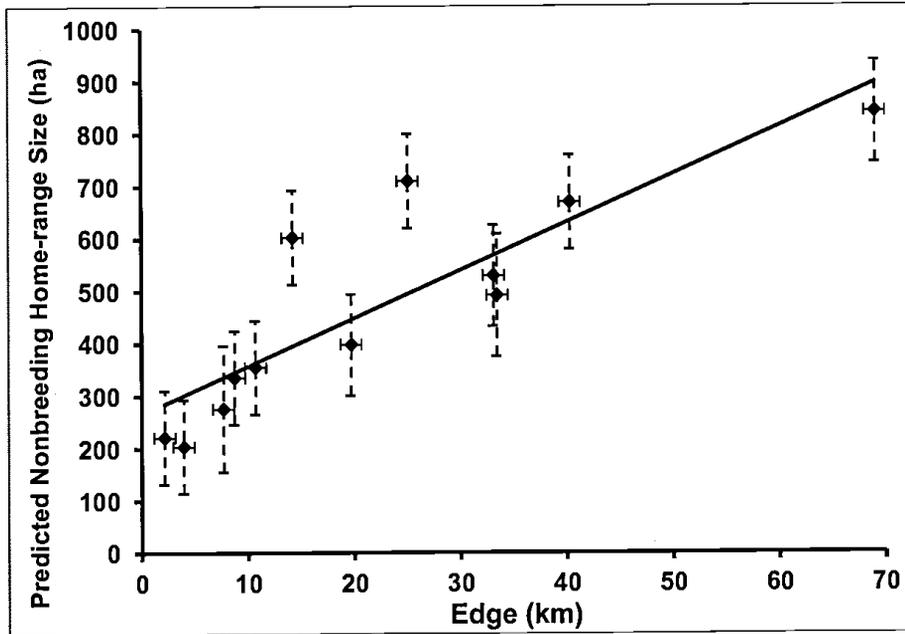
a)
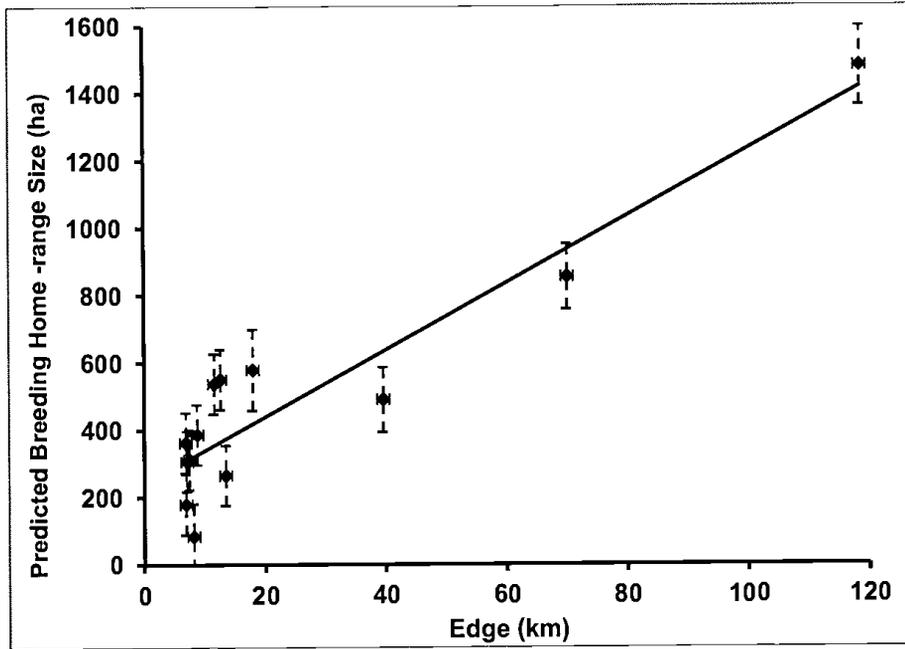
b)

Figure 3.   Home-range size estimates from the best model best model (HR_{EDGE}) plotted against the amount of edge (km) for (a) 13 Northern Spotted Owls during the breeding season and (b) 12 Northern Spotted Owls from the nonbreeding season during 2006–08 in the Siskiyou Mountains of Oregon.

individual home ranges in our study was high (mean = 71.7%), although the range among territories was quite variable (range = 48–88). This might suggest that most of the birds in our study had home ranges that included enough late-seral forest to exceed some

required threshold for survival ($\geq50\%$). This would be consistent with another study from southern Oregon where survival rates begin to level off when the amount of habitat at the core was made up of 40–60% old forest, and few increases in survival were
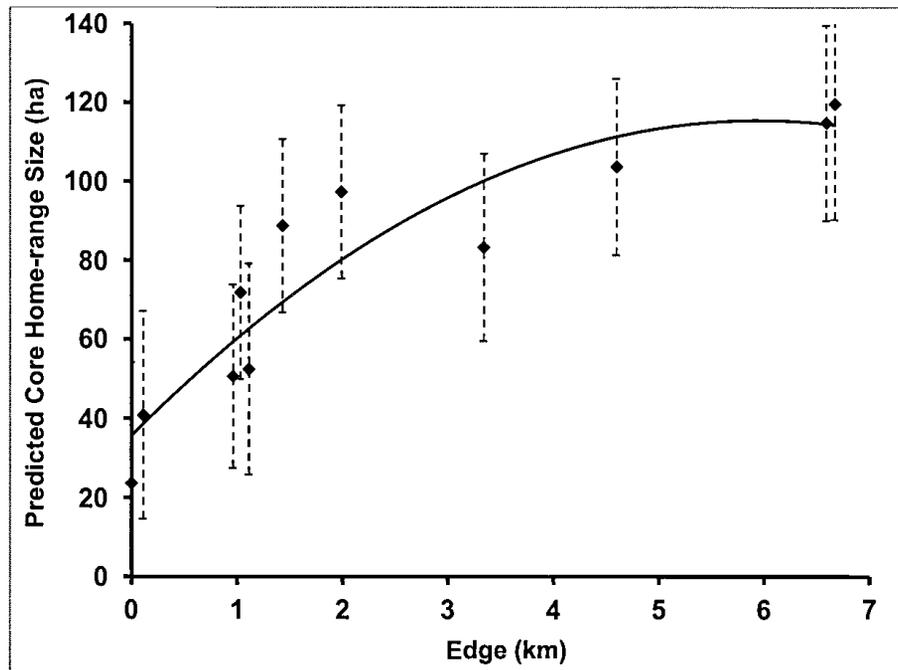
Figure 4.　Estimates of core area size from the best model (HR_{lg_EDGE}) for 11 Northern Spotted Owls plotted against the amount of edge (km) from 2006–08 in the Siskiyou Mountains of Oregon.

gained with old forest amounts >70% (Dugger et al. 2005).

Large backpack transmitters (20–24 g) have been linked to decreased reproductive rates of Northern Spotted Owls, but they have not been shown to negatively influence survival (Paton et al. 1991, Foster et al. 1992). To decrease the potential effect of the instrument package on owl vital rates, we chose smaller (5 g) backpack transmitters and do not think they contributed to the lower survival rates of owls in this study.

Finally, although Spotted Owl detection rates (Olson et al. 2005), occupancy (Kelly et al. 2003, Olson et al. 2005, Dugger et al. 2011), survival and recruitment (Forsman et al. 2011), and reproductive success (Olson et al. 2004, Anthony et al. 2006) have all been negatively associated with the detection of Barred Owls adjacent to Spotted Owl territories, we found no influence of Barred Owls on Spotted Owl survival in this study. However, it is difficult to link detections of Barred Owls during the breeding season to monthly survival rates, so it's likely our Barred Owl covariate was not measured on a fine enough temporal scale to model monthly survival rates of Spotted Owls.

Home-range Size. As expected, the mean home-range size of Northern Spotted Owls in this study reflected the trend of smaller home ranges in the

southern portion of the subspecies' range (Carey et al. 1990, Zabel et al. 1995, Clark 2007). The smaller home ranges in the southern portion of the Northern Spotted Owls' distribution are likely related to the more abundant and diverse prey base available to the owls in these regions (Carey et al. 1992, Zabel et al. 1995). However, we found little evidence for seasonal differences in home-range size in this study, which is in contrast to most previous work suggesting that Northern Spotted Owls generally have larger home ranges during the nonbreeding season than the breeding season (Glenn et al. 2004, Clark 2007, Hamer et al. 2007). Difficult travel resulting in limited access to telemetry stations during the winter months may have contributed to an underestimation of nonbreeding-season home ranges in this study. In addition, two owls in this study had breeding home-range sizes substantially larger than nonbreeding home-range size, and given our small overall sample sizes, these individuals had a strong effect on the seasonal means.

The amount of edge was the best indicator of annual, breeding, and nonbreeding home-range sizes as well as the size of core use areas. Home-range size increased in linear and log-linear fashions in relation to increased amounts of edge between suitable habitat (old forest, mature forest, pole/young stands) and non-habitat, which was a measure of

increased fragmentation of forest habitat for the species. This was consistent with our predictions as well as results from another study in southwestern Oregon (Clark 2007). The inclusion of more prey-rich edge habitats within the home range may provide an energetic benefit to Spotted Owls; however, these edges increase the amount of fragmentation within the landscape and their lack of cover might expose owls to a higher risk of predation by Great Horned Owls (*Bubo virginianus*), Northern Goshawks (*Accipiter gentilis*), and Red-tailed Hawks (*Buteo jamaicensis*; Forsman et al. 1984, Carey et al. 1990). They also increase the distance an owl must travel to acquire prey, which may result in the need for increased home-range size, at least up to a point. Carey and Peeler (1995) equated fragmentation with the loss of a preferred prey species that occurred in high densities in the Oregon Coast Range. Furthermore, Spotted Owls cannot indefinitely expand their home range without a significant reduction in fitness. Thus, the loss of fitness associated with fragmentation and the resulting home-range expansion must somehow be offset by the increased energy gained in procuring food sources at greater distance from the site center. Amount of edge was highly and positively correlated with the number of patches of old forest found within the nonbreeding ($r = -0.61$, $P = <0.05$) and annual ($r = -0.83$, $P = <0.05$) home ranges of owls in our study (Schilling 2009), which would be expected as more fragmented patches of late-seral forest would increase the amount of edge on the landscape.

Similar to our results for survival, home-range size was not related to the amount of late-seral stage forest as we predicted. However, the proportions of late-seral forest in annual home ranges were high in our study area (48%–88%) and negatively correlated ($r = -0.75$, $P = <0.05$) with the amount of edge (Schilling 2009), which means that there is less edge habitat in home ranges with high amounts of late-seral forest. Because the amount of late-seral forest was high ($\bar{x} = 72\%$ in annual home ranges) it is possible that a fitness threshold has been reached on our study area for most of our birds and additional amounts of late-seral forest are not beneficial to increasing survival and reproduction.

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