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NEST SURVIVAL OF WESTERN BLUEBIRDS USING TREE CAVITIES IN MANAGED PONDEROSA PINE FORESTS OF CENTRAL WASHINGTON

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Abstract. We examined the association of temporal and spatial factors with nest survival of Western Bluebirds (*Sialia mexicana*) nesting in tree cavities in ponderosa pine (*Pinus ponderosa*) forests along the east slope of the Cascade Mountains, Washington. All study areas were managed for timber production through planned harvests or postfire salvage logging. Bluebirds laid a mean clutch of 5.3 ± 0.1 (SE) eggs ($n = 131$), and successful nests fledged an average of 4.5 ± 0.2 young ($n = 85$). Using a model-selection framework, we found that nest survival was a function of clutch size and treatment and that there was a quadratic effect of nest age. Daily survival rates decreased after the onset of incubation, then increased through the nestling period, and were higher for clutches with ≥5 eggs and in stands that were burned and salvaged. Survivorship over the entire period for clutches ($n =$ 131 nests) with ≤4, 5, and ≥6 eggs was 0.39 (95% CI: 0.11, 0.65), 0.61 (95% CI: 0.34, 0.80), and 0.71 (95% CI: 0.46, 0.85), respectively. Vegetation variables associated with nest sites did not significantly affect nest survival. Predation accounted for the most nest failures (34% of nests). We suggest that parental defense of nests accounts for the quadratic effect of nest age, with adult bluebirds defending nests more aggressively as nestlings approach fledging, and that bluebirds laying larger clutches are older, more experienced birds, resulting in greater nest survival.

Key words: *cavity-nesting bird, clutch size, nest survival, ponderosa pine,* Sialia mexicana, *forest burns, Western Bluebird.*

Supervivencia de Nidos de *Sialia mexicana* que Utilizan Cavidades en Bosques Manejados de

Resumen. Examinamos la asociación entre factores espaciales y temporales con la supervivencia de nidos de individuos de *Sialia mexicana* que anidan en cavidades de pino ponderosa (*Pinus ponderosa*) en bosques que se encuentran a lo largo de la ladera este de las montañas Cascade en Washington. Todas las áreas de estudio fueron manejadas para la producción de madera a través de cosechas programadas o por cortes de aprovechamiento después de incendios. Los individuos de *S. mexicana* tuvieron una puesta promedio de 5.3 ± 0.1 (EE) huevos ($n =$ 131) y los nidos exitosos produjeron en promedio 4.5 ± 0.2 volantones ($n = 85$). Utilizando una aproximación de selección de modelos, encontramos que la supervivencia de los nidos estuvo en función del tamaño de la puesta y del tratamiento, y que hubo un efecto cuadrático de la edad del nido. Las tasas de supervivencia diaria de los nidos disminuyeron después del inicio de la incubación, luego aumentaron durante el periodo de pichones y fueron mayores para nidos con puestas de más de 5 huevos y en parches de bosque que fueron quemados y reaprovechados. La supervivencia a lo largo de todo el periodo para las puestas ($n = 131$ nidos) con ≤4, 5 y ≥6 huevos fue de 0.39 (95% IC: 0.11, 0.65), 0.61 (95% IC: 0.34, 0.80) y 0.71 (95% IC: 0.46, 0.85), respectivamente. Las variables de vegetación asociadas a los sitios de anidación no afectaron significativamente la supervivencia de los nidos. La depredación dio cuenta de la mayoría de los fracasos de nidos (34% de los nidos). Sugerimos que la defensa parental puede estar dando cuenta del efecto cuadrático de la edad del nido, ya que los padres defienden el nido más agresivamente a medida que se acerca el momento en que los polluelos abandonarán el nido. Además, que los individuos con puestas mayores son de mayor edad y con más experiencia, lo que resulta en una supervivencia de nidos mayor.

INTRODUCTION

The Western Bluebird (*Sialia mexicana*) is a secondary-cavity-nesting thrush that breeds in semi-open habitats throughout much of western North America (Guinan et al. 2008). Nest cavities and low perches from which the birds hunt insects in an open understory are habitat components critical to the species (Germaine and Germaine 2002). Ponderosa pine (*Pinus ponderosa*) forests provide these requirements, and constitute one of the Western Bluebird's typical habitats (Cunningham et al. 1980, Saab and Dudley 1998, Haggard and Gaines 2001).

Historically, the Western Bluebird was more common in Washington west of the Cascade crest than to the east (Herlugson 1978), but today it is more abundant in the eastern Cascades. The decline of Western Bluebird populations in western

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Washington and some other parts of the range is attributed to competition with the European Starling (*Sturnus vulgaris*) for cavities, “sanitation” of logged forest by removal of snags and defective live trees, and habitat loss due to increased urbanization and higher forest densities resulting from decades of fire suppression (Herlugson 1978, Germaine and Germaine 2002, Keyser et al. 2004). It is important to understand the response of breeding Western Bluebirds to the various factors shaping their habitat, including management of forests for timber harvest. Thus, our goal is to investigate how the Western Bluebird’s breeding success and nest-site characteristics are related to current forest-management practices.

The propensity for all three species of bluebirds to use artificial nest boxes has made them a frequent focus of study, particularly in investigations of reproductive success (Brawn and Balda 1988, Fiehler et al. 2006, Etterson et al. 2007) and demography (Keyser et al. 2004, Citta and Lindberg 2007). Unfortunately, information obtained from nest-box studies may not accurately represent nests in natural cavities (Purcell et al. 1997), and only a few studies have estimated the reproductive success and other life-history traits of Western Bluebirds using natural cavities (Brawn 1987, Li and Martin 1991, Purcell et al. 1997, Wightman and Germaine 2006). Finally, although the characteristics of habitat where Western Bluebirds nest in natural cavities have been widely investigated (Zarnowitz and Manuwal 1985, Horton and Mannan 1988, Schreiber and deCalesta 1992, Arsenault 2004), we found only one study in Arizona that examined the relationship between characteristics of nest sites in natural cavities and the Western Bluebird’s nest survival (Wightman and Germaine 2006).

Considerable research has recently been directed toward evaluating the influence of vegetation, habitat, and nest-site selection on avian nest survival and reproductive success (Davis 2005, Peak 2007, Brown and Collopy 2008, Bullock and Buehler 2008). However, confusion persists over whether a nest’s mortality is influenced by its site’s characteristics (Schmidt and Whelan 1999). Although some studies have found that characteristics such as nest concealment (Rangen et al. 1999, Smith et al. 2007), vegetation density (Easton and Martin 2002, Schill and Yahner 2009), and nest height (Burhans et al. 2002, Noa et al. 2007, Brown and Collopy 2008) influence nest survival, others have found no such relationship (Rodewald and Yahner 2001, Bonnot et al. 2008, Kus et al. 2008). Because the majority of studies investigating this relationship have focused on open-cup nests of passerines, it is important to evaluate this relationship further with nests in cavities.

Our objectives were to (1) examine the temporal and spatial factors associated with variation in the daily survival rate of Western Bluebird nests and (2) document nest-initiation dates, clutch size, egg success (percentage of eggs resulting in fledged young), and fledging rates of Western Bluebirds in natural tree cavities. We predict that nests located in higher cavities will have higher daily survival rates (Li and Martin 1991) and, because bluebirds can be aggressive toward potential nest predators (Guinan et al. 2008; JMK, unpubl. data), we predict that daily survival rates will increase as the young approach fledging, according to the offspring-value hypothesis (Onnebrink and Curio 1991, Tryjanowski and Golawski 2004).

METHODS

STUDY AREA

We conducted our study along the eastern slope of the Cascade Mountains within southern Kittitas, Yakima, and northern Klickitat counties, Washington (Fig. 1). The eastern slope of the Cascades has a complex topography (Everett et al. 2000) and is characterized by hot, dry summers, with over 80% of the annual precipitation falling during winter (Wright and Agee 2004). Our study sites were located in the Okanogan–Wenatchee National Forest and on lands owned by the Washington Department of Natural Resources, Western Pacific Timber Company, and one private landowner. We selected 18 sites as part of a study investigating nest-site selection of cavity-nesting birds, including the Western Bluebird, Hairy Woodpecker (*Picoides villosus*), White-headed Woodpecker (*P. albolarvatus*), and Northern Flicker (*Colaptes auratus*)

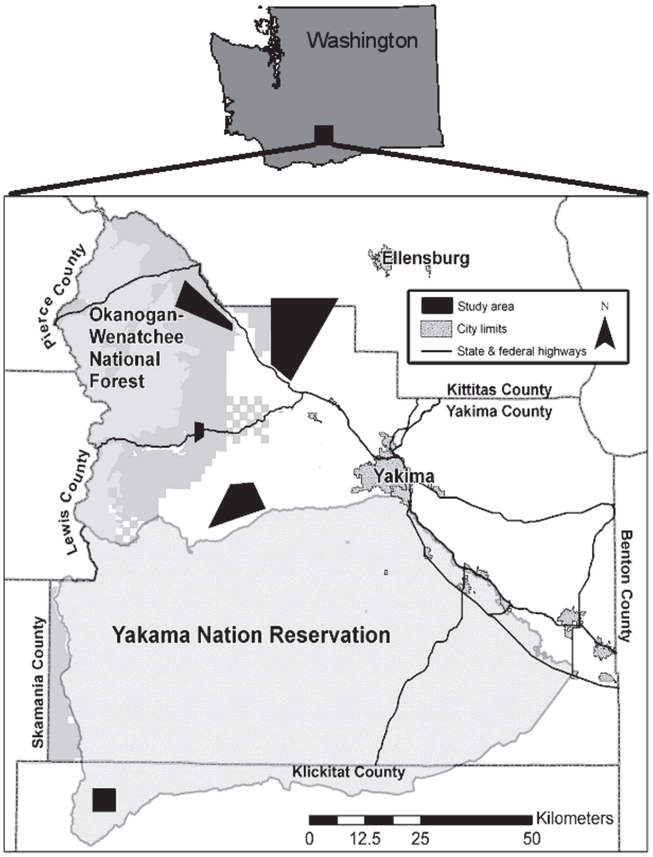

FIGURE 1. Areas searched for nests of Western Bluebirds within Kittitas, Yakima, and Klickitat counties, Washington, 2005–2008.

(Kozma 2009). Sites comprised approximately 660 ha of ponderosa pine or mixed-conifer habitats dominated by ponderosa pine, and no sites were harvested or salvage logged after they were included in the study.

The overstory of the study sites was dominated by ponderosa pine with a small component of Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), grand fir (*Abies grandis*), and quaking aspen (*Populus tremuloides*), depending upon elevation and topography. The understory was dominated by snowbrush ceanothus (*Ceanothus velutinus*), antelope bitterbrush (*Purshia tridentata*), snowberry (*Symphoricarpos alba*), and Douglas spirea (*Spirea douglasii*). Overall, the sites were characterized as a mixture of the "hot dry shrub/herb" (ponderosa pine/bitterbrush/bluebunch wheatgrass [*Agropyron spicatum*]) and "warm dry shrub/herb" (Douglas-fir/bitterbrush/bluebunch wheatgrass) vegetation types of Harrod et al. (1999). All study areas were in managed forests from which timber had been harvested within the past 15 years. Nine of these stands burned 1–9 years before our study and had some degree of salvage logging (hereafter referred to as burned-salvaged). The remaining nine stands were unburned and experienced management for trees of uneven ages by thinning or shelterwood harvest (hereafter referred to as unburned-harvested). Elevation of sites ranged from 560 to 1180 m.

NEST SEARCHING AND MONITORING

From 2005 to 2008, we searched for Western Bluebird nests from mid-April to mid-June. Because of time constraints, we searched only a subset of the 18 sites each year. Sites monitored within a given year were searched at least once every 7–10 days, resulting in approximately equal search effort at each site. We located nests by checking cavities in which we knew bluebirds to have nested in previous years and by following adults carrying nesting material or food to new or previously unknown cavities. We recorded the location of each nest with a hand-held GPS reader. We inspected cavities with a Tree Top Peeper IV nest-inspection system (Sandpiper Technologies, Inc., Manteca, CA). When checking a nest, we recorded the date, time, nesting stage, clutch size, number of young, and an estimate of the nest's age (determined by the date incubation started if known or feather development of young). We checked each nest at least once a week until we determined its fate.

We considered a nest successful if we observed fledglings near the cavity or if the cavity was occupied by young of known age that were within 2 days of fledging (18–20 days old). We recorded nests as depredated if all eggs or young were gone before the anticipated time of fledging (Kozma and Mathews 1997). We calculated nest-initiation dates (day the first egg was laid) by backdating from the day of hatching, assuming that incubation began on the day the last egg was laid and that one egg was laid each day (Keyser et al. 2004). We calculated egg success by dividing the number of young fledged by the number of eggs laid (Murray 2000).

VEGETATION SAMPLING

We sampled vegetation characteristics in the vicinity of the nest after cavities were vacated. At each nest tree or snag we recorded microhabitat variables that included cavity height, tree or snag height, diameter at breast height (dbh), tree or snag species, and canopy cover. Using a spherical crown densiometer at the base of the nest tree or snag, we measured canopy cover in the four cardinal directions then averaged the four estimates (Farnsworth and Simons 1999).

We sampled macrohabitat in circles of radii of 2, 5, and 11.3 m centered on each nest tree or snag (modified from James and Shugart 1970). Within the 2-m circle, we visually estimated the percent cover of bare ground, rock, grass, forbs, litter, and woody debris so that the total of all variables equaled 100%. Within the 5-m circle, we visually estimated the percent cover of each species of shrub and recorded the shrubs' average height. Within the 11.3-m circle (0.04 ha), we tallied trees and snags in three categories of dbh (25.4–50.7 cm, 50.8–76.1 cm, and ≥76.2 cm) and measured slope and aspect. After vegetation sampling was completed, the nest tree or snag was permanently marked with a numbered aluminum tag on the side opposite the cavity.

STATISTICAL ANALYSIS

We used an information-theoretic framework (Burnham and Anderson 2002) to evaluate support for 15 candidate models of survival of Western Bluebird nests. We fit models in a two-stage process. First, we fit six models with factors that influenced temporal variation in survival, including age of the nest, date when the nest was initiated, and nest stage (i.e., laying, incubation, or nestling; Grant et al. 2005). We also examined quadratic effects of nest age and date, as well as a constant-survival model (the Mayfield model). We then used the best model from this first stage as a base model to examine nine additional models that included spatial factors such as differences in habitat characteristics, clutch size (Leech and Leonard 1997, Martin et al. 2000, Kroll and Haufler 2009), and treatment (burned-salvaged or unburned-harvested). We considered the following habitat characteristics: cavity height (m), percent shrub cover, total stems (sum of all trees and snags ≥25.4 cm dbh), herbaceous cover (percent cover of forbs and grasses), and dbh of the nest tree or snag.

We used the logistic-exposure method (Shaffer 2004) to model daily nest survival. The logistic-exposure model estimates daily nest survival as a logistic function of the values of independent covariates on a given day. The logistic-exposure method differs from traditional estimators of nest survival, such as the Mayfield estimator (Mayfield 1961, 1975) in that it treats intervals between visits to the nest rather than the entire nesting attempt, as one sample. The two assumptions of this model are that nest fates are independent of each other (i.e., the fate of a nest is not influenced by the fate of other nests) and that daily survival probabilities are equivalent if two nest-days have equal values of explanatory covariates. In this analysis, each interval between visits to a nest was treated as one observation. We then calculated three period-survival rates as the product of daily survival rates during the egg-laying, incubation, and nestling periods (Shaffer and Thompson 2007). We defined the lengths of each period as 6 days for egg laying (starting from the day the first egg was laid), 13 days for incubation, and 21 days for nestling (Keyser et al. 2004; Guinan et al. 2008), summing to a 40-day nesting period. We fit nest-survival models with PROC GENMOD (SAS/STAT version 9.1, SDS Institute, Cary, NC) by using a logit-link function.

We examined the fit of the global model (the model with all covariates included in the analysis) by means of the goodness-of-fit test of Hosmer and Lemeshow (2000). We identified models with the most support by using Akaike's information criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). We computed Akaike weights (w_i) for each model, where w_i represents the probability of a model being the best approximating model of those in the candidate set (Burnham and Anderson 2002). Effective sample size (n) was calculated as the total number of days that nests were known to survive plus the total number of intervals in which a failure occurred (Rotella et al. 2004). We examined confidence intervals for parameter estimates and graphed fitted values as a function of the independent covariates (Hosmer and Lemeshow 2000).

Because in some years samples were small, to summarize demographic data we pooled nests from all years (Barber et al. 2001). We calculated descriptive statistics including mean, standard error (SE), and 95% confidence intervals (CI) with SYSTAT version 8.0 (SPSS, Chicago). All statistical tests were based on comparisons between 95% confidence intervals (i.e., equivalent to conducting a test at $\alpha = 0.05$) (Nakagawa and Cuthill 2007). Values are reported as means ± SE.

RESULTS

We monitored 154 Western Bluebird nesting attempts from 2005 to 2008. Of these, we had sufficient data on 131 (13 in 2005, 19 in 2006, 36 in 2007, and 63 in 2008) to be used in the analysis of nest survival (effective sample size = 3276). Of these 131 nests, 76, 42, and 13 were found during the building or egg-laying, incubation, and nestling stages, respectively. Of the nests with clutches of ≤4 eggs, 65% fledged at least one young. Similarly, the fledging rate was 66% for clutches with five eggs, while clutches with ≥6 eggs achieved a rate of 71%. The mean interval between nest visits was 5.9 ± 0.1 days ($n = 600$). The global model fit the data adequately ($\chi^2 = 9.23$, df = 8, $P = 0.32$).

The best model from the first stage of the logistic-exposure analysis included a quadratic effect of nest age ($w_i = 0.51$). The most supported model in the second stage of the analysis included an effect of clutch size (Tables 1 and 2). Ninety-five percent confidence intervals for both age terms in the base model did not include zero (Table 2). Daily survival rates began to decrease after the onset of incubation, declined until the young were between 4 and 6 days old, and then increased, while nest survival was positively associated with clutch size (Fig. 2). Survivorship estimated over the entire 40-day nesting cycle for clutches with ≤4, 5, and ≥6 eggs was 0.39 (95% CI: 0.11, 0.65), 0.61 (95% CI: 0.34, 0.80), and 0.71 (95% CI: 0.46, 0.85), respectively (Fig. 3). The daily survival rate of clutches with ≥6 eggs was higher than that of clutches with ≤4 or 5 eggs. Some support existed for a model with a habitat effect (Tables 1 and 2), with daily nest-survival rates in burned-salvaged plots being higher than in unburned-harvested plots. All other models were ranked below the base model with a

TABLE 1. Model-selection results for 12 logistic-exposure models of daily survival rate of Western Bluebird nests along the east slope of the Cascade Mountains, Washington, 2005–2008 (effective sample size = 3276). All models contain quadratic nest age as a base effect (see Methods).

Model[a]	log *L*	*K*	ΔAIC_c	w_i
Clutch size[b]	−151.26	5	0.00	0.38
Treatment	−152.79	4	1.07	0.22
Nest age^2	−154.81	3	3.10	0.08
Cavity height (m)	−153.83	4	3.15	0.08
Shrub cover (%)	−154.22	4	3.92	0.05
Total stems	−154.38	4	4.24	0.05
Herb cover (%)	−154.44	4	4.36	0.04
Diameter at breast height (cm)	−154.68	4	4.84	0.03
Nesting attempt	−154.81	4	5.10	0.03
Global	−147.01	12	5.51	0.02
Mayfield	−159.92	1	9.33	0.00
Nest age	−159.75	2	10.98	0.00

[a] The model parameter "treatment" refers to burned and salvaged or unburned and harvested forest, "nest age^2" is the quadratic effect of nest age, "total stems" refers to number of trees and snags ≥25.4 cm dbh within 11.3 m of the nest tree or snag, "nesting attempt" distinguishes between first and second attempts, and "Mayfield" represents constant daily survival.

[b] Lowest value of $AIC_c = 312.53$.

TABLE 2. Parameter estimates for the best two models of daily survival of Western Bluebird nests along the east slope of the Cascade Mountains, Washington, 2005–2008 (effective sample size = 3276).

Parameter	Estimate	95% confidence limits
Intercept[a]	6.862	5.142, 8.582
Nest age	−0.244	−0.410, −0.078
Nest age^2	0.006	0.002, 0.009
Clutch size (≤4 eggs)	−1.019	−1.747, −0.291
Clutch size (5 eggs)	−0.328	−1.027, 0.371
Intercept[b]	5.996	4.283, 7.709
Nest age	−0.239	−0.405, −0.073
Nest age^2	0.005	0.002, 0.009
Habitat	0.656	0.040, 1.272

[a] Intercept represents a clutch size ≥6 eggs.

[b] Intercept represents habitat that was burned and then salvage logged.

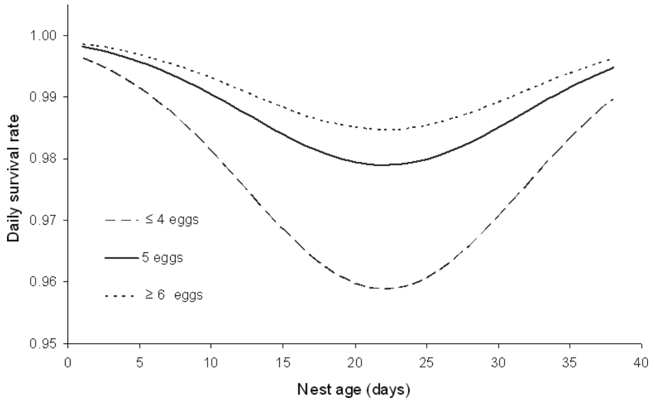

FIGURE 2. Daily survival rate of Western Bluebird nests as a function of nest age and clutch size in managed ponderosa pine stands along the east slope of the Cascade Mountains, Washington, 2005–2008.

quadratic effect of nest age (Table 1), indicating that they received no support in the analysis.

Western Bluebirds initiated nests during two peak periods (Fig. 4). Initiation of first nesting attempts peaked during mid-May, that of second attempts in mid to late June. The mean size of all clutches was 5.3 ± 0.1 eggs (*n* = 131). The mean size of first clutches (5.6 ± 0.1 eggs; 95% CI: 5.34, 5.86; range 2–8; *n* = 65) was significantly greater (95% CI did not overlap) than that of second clutches (5.0 ± 0.1 eggs; 95% CI: 4.76, 5.21; range 3–6; *n* = 57). For all successful nests, the mean number of young fledged was 4.5 ± 0.2 (range 1–7, *n* = 80). The mean number of young fledged per successful first nesting attempts (5.0 ± 0.2 young; 95% CI: 4.62, 5.38; range 2–7; *n* = 45) was significantly greater (95% CI did not overlap) than the mean for successful second attempts (3.9 ± 0.2 young; 95% CI: 3.42, 4.34; range 1–6; *n* = 34). Egg success was 0.53 (*n* = 130), i.e., 53% of all eggs laid resulted in fledged young.

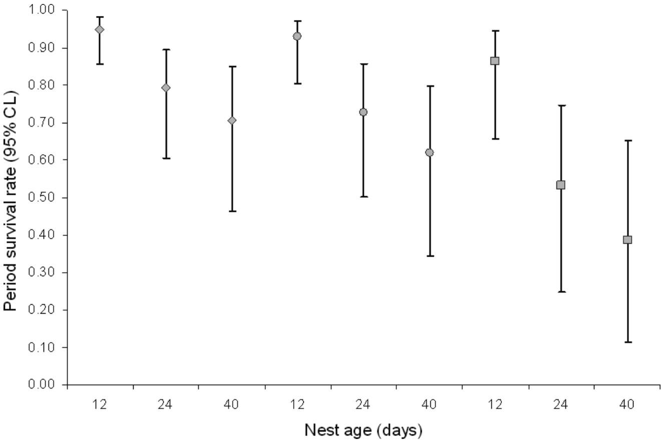

FIGURE 3. Survival rates of Western Bluebird nests with ≥6 eggs (diamonds, left three points), 5 eggs (circles, center three points), and ≤4 eggs (squares, right three points) over 12, 24, and 40 days in managed forests of ponderosa pine along the east slope of the Cascade Mountains, Washington, 2005–2008.

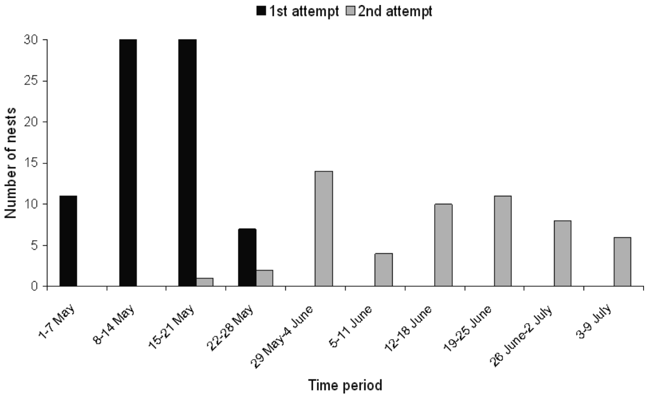

FIGURE 4. Number of first and second nests Western Bluebirds initiated by week in managed forests of ponderosa pine along the east slope Cascade Mountains, Washington, 2005–2008.

DISCUSSION

Our study is the first in Washington to document survival of Western Bluebird nests in natural tree cavities. Much of the detailed information regarding the nesting ecology and reproductive success of the Western Bluebird has resulted from studies using nest boxes (Brawn 1987, Mock 1991, Purcell et al. 1997, Dickinson 2004, Keyser et al. 2004, Fiehler et al. 2006, Etterson et al. 2007, but see Li and Martin 1991, Purcell et al. 1997, Germaine and Germaine 2002, Saab et al. 2007). Although these nest-box studies presented estimates of nest survival by methods that assume constant survival within each nest stage (e.g., Mayfield method) and then related these estimates to differences in treatment or causes of nest failure, our approach of modeling daily nest-survival rates accommodated the inclusion of biological factors in the nest-survival models. This approach generates more biologically meaningful estimates of survival and provides better understanding of possible mechanisms underlying demographic patterns (Dinsmore et al. 2002, Grant et al. 2005).

Contrary to our prediction, none of the micro- or macrohabitat characteristics associated with Western Bluebird nests, including nest height, influenced nest survival. Instead, temporal factors affected nest survival the most, a pattern also observed for other cavity nesters, including the Black-backed Woodpecker (*Picoides arcticus*) in South Dakota (Bonnot et al. 2008) and Yellow-bellied Sapsucker (*Sphyrapicus varius*) in Ontario, Canada (Tozer et al. 2009). Our results differ from those of Wightman and Germaine (2006) in Arizona, where ground-cover variables (e.g., grasses, forbs, and bare ground) and densities of ponderosa pine and Gambel Oak (*Quercus gambelii*) were best at predicting survival of Western Bluebird nests. However, the models of Wightman and Germaine (2006) did not include temporal effects, only habitat variables.

The model with a quadratic effect of nest age explained the most temporal variation in daily rates of survival of Western Bluebirds nests in natural cavities. We found no support for a constant rate. Daily survivorship of bluebird nests varied throughout the nesting period and was lowest when the chicks were ~4–6 days old. During the egg-laying period, adults spend little time at the nest cavity aside from the time the female is in the cavity laying eggs. The adults' lack of activity at or near the cavity entrance during egg laying could account in fewer predators being attracted to the cavity, resulting in the high daily survival rates during this period. As incubation begins, the male brings food to the incubating female (Guinan et al. 2008), and the female also leaves and returns to the cavity to forage, resulting in a decrease in daily nest survival through incubation, presumably due to the increased activity alerting predators to the presence of the nest. When the eggs hatch, activity increases further as adults begin feeding the young. It is at this point that daily survival rates are lowest. We believe that the increase in daily survival rates after this point is due to an increase in nest defense by both sexes (Guinan et al. 2008). During the laying stage, we rarely observed adults attending cavities, and during the incubation stage, we inspected cavities with little aggressive response from parent bluebirds other than warning calls. The intensity of nest defense increased through the nestling phase as the young aged and the adults' investment in the brood increased, with one or both adults aggressively calling, bill-snapping, and dive-bombing us during nest checks, behavior we also observed toward yellow pine chipmunks (*Tamias amoenus*), a potential nest predator. This pattern accords with the offspring-value hypothesis (Tryjanowski and Golawski 2004) and supports our earlier prediction that daily survival rates should increase as the young approach fledging. As chicks get older, the time available for renesting diminishes (Montgomerie and Weatherhead 1988), especially at higher elevations and in years when heavy snowfall delays first nest attempts (JMK, unpubl. data). Western Bluebirds may maximize their fitness by becoming increasingly aggressive as their chicks age and chances to renest diminish. Increased aggression during the nestling stage has been observed in many species of birds, including terns (Whitman and Leonard 2000), passerines (Kozma and Mathews 1995, Pavel and Bureš 2001), and owls (Galeotti et al. 2000). However, because we visited most bluebird nests repeatedly, the increased nest defense we witnessed could be due to positive reinforcement, parent birds being rewarded by observers retreating after nest checks with no harm to the nest contents (Knight and Temple 1986, although see Montgomerie and Weatherhead 1988). Therefore, variation in the bluebird's nest defense with respect to the nest stage needs further investigation.

We found a significant positive association between clutch size and nest-survival rates. We offer two explanations for this pattern. First, bluebirds with larger clutches may defend cavities more aggressively because larger clutches, and consequently larger broods, may be perceived as having higher reproductive value than smaller clutches or broods (Montgomerie and Weatherhead 1988). However, previous reports of the relationship between intensity of nest defense and clutch or brood size have been inconclusive, with some studies finding defense intensity increasing with clutch or brood size (Wiklund 1990, Olendorf and Robinson 2000, Rytkönen 2002) and others finding no relationship (Galeotti et al. 2000, Palestis 2005, Fisher and Wiebe 2006). Second, birds with larger clutches could be older and more experienced, resulting in greater reproductive success (Williams and Christians 2003). Keyser et al. (2004) found that clutch size, number of eggs hatched, and number of young fledged increased with a female Western Bluebird's age. Although we did not measure nest defense directly or know the age of nesting adults, increased nest defense, more experienced adults, or both, could explain the higher daily survival rates of larger clutches.

The third variable that contributed to explaining daily nest-survival rates was habitat, with daily survival rates being higher at burned-salvaged sites. Although we are unsure of the true effect of habitat because of the confounding effects of harvest and habitat type (i.e., were differences due to salvage logging or to the fire itself?), we offer two hypotheses for the higher daily survival rates at burned-salvaged sites. First, nest predators may be fewer at the burned-salvaged sites. The abundance of small mammals, which are common predators of cavity-nesting birds, is often lower after forest fires and is thought to rebound around 4 years after a fire (Saab et al. 2004). This potential reduction in cavity-nest predators was thought to result in higher nesting success of cavity-nesting birds in recent burned forests (Saab and Vierling 2001, Saab et al. 2007). Second, the abundance of small mammals in unburned-harvested forest may have been elevated. Populations of small mammals, such as deer mice (*Peromyscus maniculatus*) and chipmunks (*Tamias* spp.), have been shown to be higher in unburned forests where silviculture (e.g., thinning) reduced stem densities (Sullivan and Klenner 2000, Carey 2001, Klenner and Sullivan 2009). Because these factors may be acting alone or in concert, further investigation into differences in daily survival rates between burned and unburned, and harvested and unharvested, ponderosa pine forests is warranted.

Except for clutches of ≤4 eggs, survivorship (0.61 and 0.71) of Western Bluebird nests over the entire cycle was high, which is common for cavity-nesting birds (Martin 1993, 1995). We found nest survivorship to be higher than reported for Western Bluebirds using nest boxes and natural cavities in California (Mayfield success of 0.59 and 0.29, respectively; Purcell et al. 1997), similar to that of bluebirds using natural cavities in central Arizona (Mayfield success of 0.67; Li and Martin 1991) and partially salvage-logged burned forest in western Idaho (0.65; Saab et al. 2007), and slightly lower than that of bluebirds using natural cavities in restored ponderosa pine forests in northwestern Arizona (Mayfield success of 0.75; Germaine and Germaine 2002).

The vital rates of the Western Bluebirds we studied are comparable to those reported by other studies in the western

United States. Mean clutch size was similar to that of Western Bluebirds nesting in boxes or natural cavities in Arizona, California, and Oregon (Germaine and Germaine 2002, Keyser et al. 2004, Fiehler et al. 2006). Keyser et al. (2004) demonstrated, as did we, that average clutch size decreased from first to second nest attempts. The mean number of young fledged per nest we observed was higher than that of bluebirds using cavities in Arizona (2.8–4.1 young per nest; Germaine and Germaine 2002) but nearly identical to that of bluebirds using boxes in vineyards in California (4.6–4.7 young per nest; Fiehler et al. 2006). We found that the number of chicks fledged per successful nest declined significantly from first to second clutches. In contrast, for bluebirds nesting in boxes in western Oregon, Keyser et al. (2004) found a nonsignificant trend toward an increase in number of chicks fledged from first clutches to third clutches. The mesic habitat of western Oregon may result in arthropod prey being more available to bluebirds when they are feeding young during second and third nesting attempts. The lack of summer rain and high temperatures in our study area cause ground vegetation to die back when many bluebirds are initiating second clutches, which could affect food supplies for nestlings as the invertebrates that feed on this vegetation become scarce, resulting in fewer fledged young.

Predation was the main cause of failure of the Western Bluebird nests we studied. On the basis of various factors, we believe that most predation of bluebird nests was by small mammals, although other nest predators, such as the gopher snake (*Pituophis catenifer*), short-tailed weasel (*Mustela erminea*), and black bear (*Ursus americanus*), undoubtedly accounted for a small number of nest failures. The most common mammalian predators in our study area that can easily enter cavities include the yellow pine chipmunk, Douglas squirrel (*Tamiasciurus douglasii*), and mice (*Peromyscus* spp.). These species or genera are arboreal and documented as nest predators (Reitsma et al. 1990, Craig 1998, Pietz and Granfors 2000, Fontaine and Martin 2006). Because these mammals are mostly diurnal it is conceivable that they were attracted to nests by increased parental activity at cavities when the young hatched (Martin et al. 2000). We have also observed yellow pine chipmunks, Douglas squirrels, and northern flying squirrels (*Glaucomys sabrinus*, also a potential nest predator; Bradley and Marzluff 2003) actively denning in cavities. Therefore, some nests may have failed through competition for cavities (Schmidt et al. 2001, Lawler and Edwards 2002). We acknowledge the potential shortfalls of inferring predators from nest remains (Larivière 1999) and therefore recommend further study to positively identify the predators of Western Bluebird nests.

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