J. Field Ornithol. 90(1):7–20, 2019 DOI: 10.1111/jofo.12283

Spatial and temporal factors associated with nest survival of Gray Flycatchers in managed ponderosa pine forests

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Received 19 October 2018; accepted 5 January 2019

ABSTRACT. Gray Flycatchers (*Empidonax wrightii*) breed in a variety of habitats in the arid and semi-arid regions of the western United States, but little is known about their breeding biology, especially in the northern portion of their range where they nest in ponderosa pine (*Pinus ponderosa*) forests. From May to July 2014 and 2015, we conducted surveys for singing male Gray Flycatchers along the eastern slope of the Cascade Range in Washington, U.S.A, monitored flycatcher nests, and quantified nest-site vegetation. We used a logistic-exposure model fit within a Bayesian framework to model the daily survival probability of flycatcher nests. During the 2 yr of our study, we monitored 141 nests, with 93% in ponderosa pines. Mean clutch size was 3.6 eggs and the mean number of young fledged per nest was 3.2. Predation accounted for 90% of failed nests. We found a positive association between daily nest survival and both nest height and distance of nest substrates from the nearest tree. Flycatchers that locate their nests higher above the ground and further from adjacent trees may be choosing the safest alternative because higher nests may be less exposed to terrestrial predators and nests in trees that are farther from other trees may be less exposed to arboreal predators such as jays (Corvidae) that may forage in patches with connected canopies. Nests in trees farther from other trees may also allow earlier detection of approaching predators and thus aid in nest defense.

RESUMEN. **Factores espaciales y temporales asociados con la supervivencia de nidos del mosquero *Empidonax wrightii* en bosques de *Pinus ponderosa*.**
Los mosqueros *Empidonax wrightii* anidan en varios hábitats en las regiones árida y semi-árida del oeste de los Estados Unidos. Se conoce poco sobre su biología reproductiva, especialmente en la porción norte de su rango donde anidan en bosques de *Pinus ponderosa*. De mayo a julio de 2014 y 2015, llevamos a cabo reconocimientos en búsqueda de machos cantando de *E. wrightii* a lo largo de la ladera este de la cordillera Cascade en Washington, EUA, dimos seguimiento a sus nidos y cuantificamos la vegetación del sitio de anidación. Utilizamos un modelo de exposición logística ajustado a un marco bayesiano para modelar la probabilidad de supervivencia diaria de los nidos de este mosquero. Durante los dos años de nuestro estudio, seguimos 141 nidos, 93% de estos en *P. ponderosa*. El tamaño medio de puesta fue de 3.6 huevos y la media de polluelos emancipados por nido fue de 3.2. La depredación fue la causal del 90% de los nidos fallidos. Encontramos una asociación positiva entre la supervivencia diaria del nido y ambos factores, la altura del nido y la distancia de los sustratos de anidación al árbol más cercano. Los mosqueros que ubican sus nidos a mayores alturas sobre el suelo y más lejos de árboles adyacentes podrían estar eligiendo la alternativa más segura porque los nidos más altos podrían estar menos expuestos a depredadores terrestres. Por su parte, los nidos en árboles que están más lejos de otros árboles podrían estar menos expuestos a depredadores arbóreos como urracas (Corvidae) que podrían forrajear en parches de bosque con doseles interconectados. Los nidos más lejos de otros árboles podrían también permitir una detección más temprana de depredadores que se acercan y con ello ayudar en la defensa del nido.

Key words: Bayesian framework, *Empidonax wrightii*, logistic-exposure model, nest height, period survival, *Pinus ponderosa*

Gray Flycatchers (*Empidonax wrightii*) are Neotropical migratory songbirds that breed in the arid and semi-arid regions of western North America, and winter primarily in Mexico and Baja California (Schlossberg and Sterling 2013). Gray Flycatchers nest in a diversity of habitats, including sagebrush (*Artemisia tridentata*) (Downes 2006), pinyon pine (*Pinus edulis*) – juniper (*Juniperus* sp.) (Goguen et al. 2005), ponderosa pine (*Pinus*

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ponderosa) – antelope bitterbrush (*Purshia tridentata*) (Cannings 1987), and open, mixed-conifer forests of ponderosa pine, white fir (*Abies concolor*), and incense cedar (*Calocedrus decurrens*) (Schlossberg and Sterling 2013). Historically, Gray Flycatchers occupied a core range that included Oregon, Nevada, Utah, Wyoming, Colorado, Arizona and New Mexico (Schlossberg and Sterling 2013). However, during the late 20th century their range expanded northward into central Washington and the Okanagan Valley of British Columbia (Lavers 1975). The first documented nesting in Washington occurred in a ponderosa pine forest in the Wenas Valley, Yakima County, in 1972 (Yaich and Larrison 1973).

The breeding biology and other aspects of the natural history of Gray Flycatchers have been little studied due to problems in differentiating them from other *Empidonax* flycatchers, the remoteness and patchy distribution of their breeding areas, and early nomenclatural confusion (Schlossberg and Sterling 2013). Studies in California (Johnson 1963), New Mexico (Goguen et al. 2005), and Utah (Russell and Woodbury 1941) have provided insights into Gray Flycatcher nest construction, nest-site characteristics, nest success, and breeding phenology. However, data collected in these studies were collected either from incidental observations or as part of larger avian community studies in areas of sagebrush, pinyon pine, juniper, and Jeffrey pine (*Pinus jeffreyi*). Gray Flycatchers use different habitat types and their life histories likely vary across their large breeding range (Sedgwick 1993).

Ponderosa pine forests of the inland northwest of the United States differ dramatically from historic conditions (Hessburg et al. 2005, Metlen and Fiedler 2006, Harrod et al. 2007). Historic forest conditions included fire-return intervals of 5–15 yr, average densities of 50 trees/ha, and average diameters at breast height (dbh) of 60–70 cm (Agee 1996, Gaines et al. 2007). Many of these forests were logged selectively (e.g., removal of the largest-diameter trees) prior to 1930 (Hessburg and Agee 2003) and routinely harvested thereafter due to their location at low elevations and relative ease of access. This, combined with an increased frequency of stand-replacing fires and a commensurate decline in low-intensity fires (i.e., fire suppression), has resulted in ponderosa pine forests now being stocked at 3–10 times their historic density and dominated by smaller trees that average 20–30 cm dbh (Harrod et al. 1999, Naficy et al. 2010). To reverse this trend, managers have implemented mechanical treatments throughout the interior west to increase fire resiliency (Agee and Skinner 2005). To conserve bird populations using ponderosa pine forests managed for timber production and where restoration involves forest management via mechanical treatments, information is needed about nesting success and habitat requirements of species that use these forests (Hazler et al. 2006, Kroll and Haufler 2010, Kozma and Kroll 2012). Therefore, detailed studies of the breeding biology of Gray Flycatchers in managed ponderosa pine forests are needed, including in the recently expanded northern portion of the range where the species has not been studied previously.

We began to study nest survival of Gray Flycatchers in managed ponderosa pine forests of the eastern Cascade Range, Washington, U.S.A, in 2014. Our objectives were to (1) document the density of their breeding territories and population demographic variables, e.g., clutch size, egg success, rates of nest parasitism by Brown-headed Cowbirds (*Molothrus ater*), and number of fledglings, (2) describe their nest-site characteristics, and (3) examine spatial and temporal factors associated with variation in daily nest survival rates at the nest and nest-patch scales.

METHODS

We conducted our study in the Wenas Valley, ~38 km northwest of Yakima, Washington (46°53′N, −120°48′W), along the eastern slope of the Cascade Range in Yakima and Kittitas counties, Washington, U.S.A, in 2014 and 2015. This area is characterized by hot, dry summers, with over 80% of the annual precipitation falling during winter (Wright and Agee 2004). Our study area consisted of gently sloping terrain on lands owned by the Washington Department of Natural Resources. We selected this study area because Gray Flycatchers were found to be abundant during previous studies of cavity-nesting birds in the same area (Kozma and Kroll 2010, 2012). Because our study area was located where ponderosa pine forest was adjacent to large lithosol areas (i.e., thinsoiled basalt formations containing primarily forbs and grasses), we could not randomly select plots because plots needed to consist of > 90% ponderosa pine to meet the objectives of our study. Therefore, we used aerial photographs to select five study plots, each ~20 ha of contiguous ponderosa pine forest. Mean distance between study plots was 1.68 km (range = 0.7–3.5 km) and all study plots had experienced timber harvest within the past 30 yr.

Overstory of the study plots was dominated by ponderosa pine, with Douglas-fir (*Pseudotsuga menziesii*) encountered only as scattered single trees and an understory dominated by antelope bitterbrush and wax currant (*Ribes cereum*). Overall, study plots were characterized as the "hot dry shrub/herb" (ponderosa pine/bitterbrush/bluebunch wheatgrass [*Pseudoroegneria spicata*]) vegetation type of Harrod et al. (1999). Elevation of plots ranged from 785 to 1010 m.

Territory density and nest monitoring. We began surveys for singing male Gray Flycatchers in late April or early May (~10 to 15 d after the first flycatchers were detected in the spring) using the spot-mapping procedure to estimate density of territories in each study plot (Christman 1984). We conducted two surveys on each plot, 9–14 d apart, and only surveyed on days with light winds (< 16 km/h) and no precipitation. Surveys were conducted between 08:00 and 12:00. During each survey, we walked four, equally spaced, parallel transects through each plot and used a GPS unit (62sc, Garmin Ltd., Olathe, KS) to mark locations of singing males. Although we did not color-band males, we were confident we could delineate individual territories by the recurrent use of singing perches by males and simultaneous identification of nearby territory holders (Kroll and Haufler 2007). We defined a territory as an area where a singing male was detected twice and where detections were within 80 m of each other, where a singing male was detected once and a confirmed nesting attempt was also documented, or where only a nesting attempt was documented. This allowed us to eliminate locations that were not identifiable as individual territories (Christman 1984). We calculated territory density as territories/km^2 and we included territories where singing males or nests were located outside the boundary of the study plot if they were within 50 m of the plot boundary.

We began nest searching during the second week of May in each year and continued until mid-July. We found nests by following adults carrying nest material or food, flushing adults from nests accidentally, and listening for adult scolding calls that are often given when observers are close to a nest (JMK, pers. observ.). We searched for and monitored nests on each plot 1–2 times per week and checked nests within 1–2 d of anticipated fledging to increase accuracy in assigning nest fates. We also monitored nests found outside the study-plot boundaries to increase our sample size of nests. We checked nests in 2014 using a nest-inspection system (TreeTop Peeper IV, Sandpiper Technologies, Inc., Manteca, CA; Kozma and Kroll 2010). In 2015, we removed the cavity probe from the TreeTop Peeper and replaced it with a smart cell phone (Samsung, Inc., Seoul, South Korea) mounted on an aluminum rod with the camera application set to "selfie mode." This allowed us to extend the cell phone up to and over nests and photo document the nest and contents with a handheld, Bluetooth, remote shutter release. When checking a nest, we recorded if adults were present, nest contents (e.g., clutch size, number of cowbird eggs or young, and number of nestlings), and nest fate. We determined a nest was deserted if no adults were observed for four or more consecutive checks and the contents of the nest remained unchanged. We assigned a fate of predated either if all nest contents disappeared before the anticipated fledge date (Liebezeit and George 2002) or nests were torn apart or damaged (Braden 1999). We considered nests containing only a cowbird nestling and no living flycatcher nestlings as failed. To confirm suspected fledging, we checked nests for the presence of fecal material in nest cups or on nest rims and searched the area surrounding nests for fledglings, parents carrying food, or parents giving scolding calls (Manolis et al. 2000, McCreedy and van Riper 2015). We also considered nests successful if young were in the nest 1–2 d prior to the expected fledge date because young are capable of force fledging at that time (JMK, pers. observ.). For successful nests, we estimated the number of fledglings as the number of young present during the prior nest visit. We calculated nest-initiation date (i.e., the day the first egg was laid) by backdating from the day of hatching or fledging, or from the age of young as estimated from feather development (Keyser et al. 2004) using a period length of 4 d for laying, 14 d for incubation, and 16 d for the nestling stage (Schlossberg and Sterling 2013). We calculated egg success by dividing the number of young fledged by the number of eggs laid (Murray 2000).

Vegetation sampling. We sampled nest-site habitat variables in July after most nest monitoring was completed. At each nest tree or shrub, we recorded nest height (measured to the nest rim), substrate species and height, tree dbh, nest orientation (direction the nest was facing in relation to the nest substrate), distance of nest from the trunk of the tree, and the distance of nest substrate to the nearest tree (> 10.2 cm dbh). We measured nest substrate and nest height either using the telescoping nest-inspection pole (graded in m and cm) or with a clinometer for trees taller than 11 m in height and nests more than 11 m above ground (Kozma 2012). We calculated the relative height of nests by dividing their height by the height of the nest substrate (Siegfried et al. 2010). We measured distance of nests from the trunk of the trees by extending the telescoping pole to the approximate center of the nest and measuring the distance between the trunk of the tree and the pole. We did not record estimates of nest concealment above or at the sides of the nest because we could not estimate concealment of nests high in trees (≥ 3.0 m) with the same level of accuracy as those located lower in trees or in shrubs.

We sampled patch-scale habitat variables in circles with radii of 2, 5, and 11.3 m centered on each nest (modified from James and Shugart 1970 and Martin et al. 1997). Within the 2-m circle, we estimated the percent cover of herbaceous plants (forbs and grasses). We used a spherical crown densiometer to measure percent canopy cover in the four cardinal directions at 2 m from the nest and then averaged the four estimates (Farnsworth and Simons 1999). We divided the 5-m circle into four quarters and visually estimated the percent cover of each shrub species, and measured the height of two random shrubs in each quarter. In the 11.3-m (0.04-ha) circle, we counted all trees and snags in four dbh classes (10.2 to < 25.4 cm, 25.4 to < 50.8 cm, 50.8 to < 76.2 cm, and ≥ 76.2 cm). We measured the height and dbh of the nearest canopy tree (> 10.2 cm dbh) in each of the four quadrants, and then averaged each of those values to determine a mean canopy height and mean canopy dbh for each nest patch.

Statistical analysis. We compared nest-site and patch-scale habitat characteristics between years using *t*-tests and found that only two nest-site variables, tree height and relative nest height (which were correlated), were different between years. Therefore, we pooled nests from both years to summarize nest-site and patch-scale habitat characteristics. We simplified tree and snag dbh classes into one category, all trees and snags ≥ 10.2-cm dbh, because the two largest dbh classes were virtually absent on the landscape. We used Rayleigh's test to determine if the orientation of nests clustered around a mean (Zar 1974, Braden 1999, Kozma 2014). We used a chi-square test to determine if nests were placed against the trunk of trees more frequently than away from the trunk on branches.

We used a logistic-exposure model fit within a Bayesian framework to model the daily survival probability of Gray Flycatcher nests (Shaffer 2004, Schmidt et al. 2010). We specified a multilevel structure that allowed us to incorporate the inherent nested design of nest-survival studies. The Bayesian framework supports inclusion of spatial and temporal covariates as fixed or random effects at different levels of nesting as appropriate and allows for the easy calculation of derived quantities, such as period survival (Kozma et al. 2017).

We denoted the interval survival of the observed nests as $y_{i,j}$, where $y_{i,j} = 1$ if nest i survives interval j, and $y_{i,j} = 0$ if nest i fails during interval j. The observed nest survival was assumed to follow a Bernoulli distribution, $y_{i,j} = Bern(\theta_{i,j})$, where $\theta_{i,j}$ is the probability that nest i survives interval j. The daily nest-survival probability for nest i during interval j is $s_{i,j}$ so $\theta_{i,j} = s_{i,j}^{t_{i,j}}$, where $t_{i,j}$ is the length of interval j for nest i. The daily nest survival is modeled as a function of covariates using a logit link function, $\text{logit}(s_{i,j}) = X\beta$, where X is the design matrix of the covariates of interest and β is the parameter vector.

We modeled daily survival as a function of 11 covariates. To account for temporal variation, we included two interval-specific covariates as fixed effects: nest stage (building, laying, incubation, and nestling; Kroll and Haufler 2009) and ordinal date as both a linear and quadratic effect (Grant et al. 2005, Kozma and Kroll 2010, 2012). Year, represented as a categorical variable, was included as a fixed effect, allowing the model intercept to vary by year. To account for spatial variation, we included nest height, distance of nests from trunks, distance of nest substrates to the nearest live tree, average shrub cover, total number of live trees within an 11.3-m radius circle, and orientation as fixed effects. We divided orientation into two orthogonal measurements, one showing north-south orientation and the other east-west orientation. For the north-south orientation, a value of 1 indicates due north orientation whereas a value of -1 indicates a due south orientation. A value of zero would indicate a due east or due west orientation. Likewise, for the east-west orientation measure, a value of 1 indicates due east orientation, a value of -1 indicates due west, and value of zero indicates due north or south orientation. We included study location as a random effect to help explain any unaccounted spatial variation. We chose these covariates because each has been associated with avian nest survival in previous studies (Martin and Roper 1988, Kelly 1993, Smith et al. 2005, Noa et al. 2007, Kozma and Kroll 2012). We centered and scaled nest height, distance to nearest tree, and ordinal date to have a mean of zero and a standard deviation of one.

The daily nest-survival probability model was:

$$\begin{aligned}\text{logit}(s_{i,j}) = {} & \alpha_0 + \gamma_{Location_i} + \tau_{Nest_i} + \alpha_1 \cdot 2015_i + \alpha_2 \cdot \text{Nest Height}_i + \alpha_3 \cdot \text{Nest Distance to Trunk}_i \\ & + \alpha_4 \cdot \text{Distance to Nearest Tree}_i + \alpha_5 \cdot \text{Average Shrub Cover}_i + \alpha_6 \cdot \text{Total Live Trees}_i + \\ & \alpha_7 \cdot \text{Orientation North-South}_i + \alpha_8 \cdot \text{Orientation East-West}_i + \alpha_9 \cdot \text{Ordinal Date}_{ij} + \\ & \alpha_{10} \cdot \text{Ordinal Date}^2_{ij} + \alpha_{11} \cdot \text{Laying}_{i,j} + \alpha_{12} \cdot \text{Incubation}_{i,j} + \alpha_{13} \cdot \text{Nestling}_{i,j}\end{aligned}$$

where 2015, Laying, Incubation, and Nestling are all indicator variables, taking the value of 1 if the argument is true and 0 otherwise, $\gamma_{Location_i}$ is a random intercept adjustment for each of the five locations, $\gamma_{Location_i} \sim N(0, \sigma^2_{Location})$, and τ_{Nest_i} is a random intercept adjustment for each of the 100 nests, $\tau_{Nest_i} \sim N(0, \sigma^2_{Nest})$. When summarizing the model, we calculated 90% credible intervals for coefficients and derived quantities because a 90% credible interval provides sufficient confidence around the estimates (Kroll et al. 2016, Kozma et al. 2017).

We used the mean coefficient estimates to calculate daily and period survival probabilities (the probabilities that a nest survives a single day in a given stage and the entire nesting period, respectively). We assumed that the typical nesting period of Gray Flycatchers consisted of 8 d in the nest-building stage, 4 d in the laying stage, 14 d in the incubation stage, and 16 d in the nestling stage, for a total nesting period of 42 d (JMK, pers. observ., Schlossberg and Sterling 2013). To approximate an ordinal date for each nest stage, we centered the full nesting period at the mean ordinal date for all nests and then calculated the median ordinal date for each individual stage. We used day 4.5 as the median for the build stage (median of days 1–8), day 10.5 as the median for the laying stage (median of days 9–12), day 19.5 as the median for the incubation stage (median of days 13–26), and day 34.5 as the median for the nestling stage (median of days 27–42). Centering the full nesting period (median of full period is day 21.5) on the mean ordinal date for all nests, which is ~166, we estimated the following ordinal dates for the medians of each stage: build = 149.5, laying = 155.5, incubation = 164.5, and nestling = 179.5. Placing these ordinal dates on the same scale as the centered and scaled values used in the model by subtracting the mean (166.1) and dividing by the standard deviation (19.7), we use these ordinal date covariate values to calculate survival probabilities: build = -0.843, laying = -0.539, incubation = -0.082, and nestling = 0.678. Using the coefficient estimates and the other nest specific covariates, we estimated the daily survival rate for nest *i* during the building stage as:

$$S_{i,Build} = logit^{-1}\left(\begin{array}{r}\alpha_0 + \gamma_{Location_i} + \tau_{Nest_i} + \alpha_1 \cdot 2015_i + \alpha_2 \cdot Nest\ Height_i + \alpha_3 \cdot Nest\ Distance\ to\ Trunk_i + \\ \alpha_4 \cdot Distance\ to\ Nearest\ Tree_i + \alpha_5 \cdot Average\ Shrub\ Cover_i + \alpha_6 \cdot Total\ Live\ Trees_i + \\ \alpha_7 \cdot Orientation\ North - South_i + \alpha_8 \cdot Orientation\ East - West_i + \alpha_9 \cdot -0.843 + \\ \alpha_{10} \cdot (-0.843)^2\end{array}\right)$$

where logit^{-1} $(x) = e^x/(1 + e^x)$. Daily survival rate estimates for the laying, incubation, and nestling stages follow from the same equation, with appropriate values replacing the ordinal date value.

Using the nest specific daily survival rates, we calculated the period survival probability, *P*, using the assumed stage lengths:

$$P_i = \left(s^8_{i,build}\right) \cdot \left(s^4_{i.laying}\right) \cdot \left(s^{14}_{i,incubation}\right) \cdot \left(s^{16}_{i,Nestling}\right)$$

We fit our model using JAGS (Plummer 2003) called from R (R Core Team, 2018) using the “jags” function from package R2jags (Su and Yajima 2015). We used a *N* (4,4) (mean, variance) prior distribution for the overall intercept coefficient, a *Uniform* (0.1,2) prior distribution for the random effect standard deviations, and an *N* (0,3) prior distribution for all other coefficients. We used a prior distribution centered at 4 for the overall intercept because daily nest-survival probabilities need to be sufficiently high for some nests to survive the full nesting period. Centering the prior distribution for the overall intercept at zero would mean that daily survival probabilities were near 0.5 (logit^{-1} (0) = 0.5), but using a daily survival probability of 0.5 over the course of a 42-d nesting period gives a period survival probability of nearly zero. Using a prior distribution centered at 4 and a relatively large variance allows the model to identify reasonable overall intercept values. We ran three Markov chains of length 200,000 with a burn-in period of 100,000 and 1/50 thinning. We assessed convergence using the Gelman-Rubin statistic (Gelman et al. 2004) and visual inspection of chains. All our coefficient estimates showed Gelman-Rubin statistics between 1.001 and 1.002, supporting our assumption of convergence. We provide our code for the nest-survival model (Appendix S1). A posterior predictive check (Appendix S2) to assess the model fit yielded no evidence for a lack of fit. We provide R code for the posterior predictive checks in Appendix S3 and nest-survival data to run the nest-survival model is available on request. Values are reported as means ± 1 SD.

RESULTS

Breeding density and nest monitoring. We began surveys for singing male Gray Flycatchers on 6 May 2014 and 28 April 2015. Mean territory density was 23.3 ± 9.9 territories/km^2 (95% CI: 10.9, 35.7; range = 12.5–36.4 territories/km^2) in 2014 and 33.8 ± 9.7 territories/km^2 (95% CI: 21.7, 45.9; range = 22.5–43.6 territories/km^2) in 2015, and we found no evidence of a difference between years (95% CI overlapped; Nakagawa and Cuthill 2007). Overall, a nesting attempt was confirmed for 74% of territories, and singing males were detected on two separate occasions for 26% of territories.

We monitored 141 Gray Flycatcher nests during 2014 and 2015. Peak nest initiation occurred during the last 2 weeks of May (Fig. 1), with the earliest nest initiated on 14 May. Mean clutch size across all years was 3.6 ± 0.6 eggs (range = 2–5 eggs, *N* = 99). Mean clutch size of nests prior to 21 June (3.9 ± 0.4 eggs; 95% CI: 3.8, 4.0; *N* = 65), the midpoint of the breeding period, was

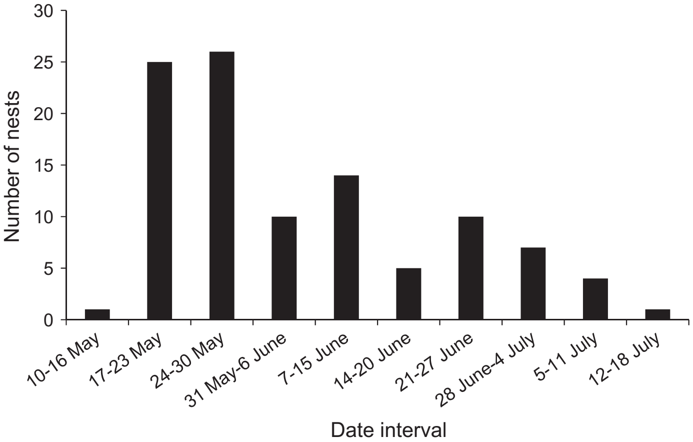

Fig. 1. Frequency at which nests were initiated by Gray Flycatchers by week along the eastern Cascade Range, Washington, USA, 2014–2015.

greater (95% CI did not overlap) than after 21 June (3.1 ± 0.6 eggs; 95% CI: 2.8, 3.3; $N = 20$). For successful nests, the mean number of young fledged was 3.2 ± 0.9 (range = 1–4, $N = 40$). Predation accounted for 90% of all nest failures, Brown-headed Cowbirds parasitized 7% of nests and accounted for only 3% of nest failures, 6% of nests failed due to unknown causes, and 1% of nests failed due to weather. Egg success was 0.3 (i.e., 30% of all eggs laid resulted in fledged young) and apparent nest success was 30%.

Nest-site characteristics. Gray Flycatchers nested in three plant species, with 93% of nests ($N = 132$) in ponderosa pines. Remaining nests were in antelope bitterbrush ($N = 8$) and Douglas-fir ($N = 1$). When placed in trees, we found no difference ($\chi^2_1 = 1.9$, $P = 0.17$) in the number of nests located on a limb against the trunk of trees ($N = 75$) versus away from the trunk ($N = 58$). Mean nest-tree dbh was 30.4 ± 12.5 cm (range = 3.8–78.5 cm, $N = 133$), mean nest-tree height was 13.9 ± 5.8 m (range = 1.1–35.7 m, $N = 133$), and mean nest height was 4.6 ± 2.8 m above ground (range = 0.7–13.3 m, $N = 131$). This resulted in a mean relative nest height of 0.34 ± 0.10 ($N = 131$). When nesting away from the trunk of trees, nests were a mean distance of 1.4 ± 0.9 m (range = 0.3–5.0 m, $N = 70$) from the trunk. Mean nest orientation was 19°, but the distribution did not differ from random ($N = 139$, $r = 0.12$, $z = 1.9$, $0.2 > P > 0.1$). Nest substrates and their closest adjacent tree were on average 5.7 ± 2.8 m (range = 0.7–17.6 m, $N = 141$) apart.

At the nest-patch scale, mean canopy cover was 39.0 ± 18.1% (range = 0–84.1%, $N = 141$), mean dbh of canopy trees was 33.9 ± 7.5 cm (range = 16.9–65.4 cm, $N = 139$), and mean height of canopy trees was 15.3 ± 3.6 m (range = 7.1–28.1 m, $N = 139$). Mean cover of herbaceous vegetation was 61.5 ± 25.3% (range = 0–99%, $N = 141$) and mean shrub cover was 15.6 ± 16.5% (range = 0–70%, $N = 141$), with a mean height of shrubs of 0.7 ± 0.4 m (range = 0.1–1.8 m, $N = 114$). Mean tree density was 104 ± 65 trees/ha (range = 0–300 trees/ha, $N = 141$).

Nest survival. We were able to use 100 of the 141 Gray Flycatcher nests we monitored to model nest survival. We were not able to use all nests because of unknown nest fates, data-collection errors, and missing vegetation measurements. Of the nests used, 61 (61%), 9 (9%), 19 (19%), and 11 (11%) were found during the building, laying, incubation, and nestling stages, respectively. The average number of visits to nests was 5.1 ± 2.6 (range = 1–12), and the average interval between visits was 4.1 ± 1.5 d (range = 1–10 d, $N = 510$ intervals).

At the nest level, we found evidence of a positive association between daily survival rate and distance to the nearest tree (coefficient estimate = 0.327; 90% CRI: 0.008, 0.647) as well as nest height (coefficient estimate = 0.318; 90% CRI: 0.023, 0.641) (Figs. 2 and 3). Credibility intervals for other covariates included 0 (Table 1). At the visit level, we found evidence of a negative association between daily survival rate and the laying (coefficient estimate = −1.034; 90% CRI: −1.897, −0.2) and incubation (coefficient estimate = −0.897; 90% CRI: −1.714, −0.136) stages compared to the building stage (Table 1). Daily survival probabilities were estimated to be 0.988 (90% CRI: 0.977, 0.996), 0.964 (90% CRI: 0.933, 0.985), 0.967 (90% CRI: 0.946, 0.982), and 0.972 (0.951, 0.986) for the building, laying, incubation, and nestling stages, respectively. As a result, and due to differences in stage duration, the estimated period survival rate was substantially lower during both incubation and nestling stages than the building stage (Fig. 4). Estimated standard deviations for plot (0.362; 90% CRI: 0.115, 0.904) and nest (0.593, 90% CRI: 0.142, 1.251) indicated variation at the study plot and nest level not accounted for by fixed effects (Table 1). We retained random effects in the model even though credible intervals contained zero for some plot random effects (Table 1).

DISCUSSION

Breeding density of Gray Flycatchers in our study area ranged from 23 to 34 territories/km^2, which is similar to densities reported in pinyon-juniper in Arizona (19–29 territories/km^2; LaRue 1994) and western juniper (*Juniperus occidentalis*) in Oregon (25 pairs/km^2; Friedmann et al. 1977). These results suggest that the breeding densities of Gray Flycatchers in managed ponderosa pine forests in Washington are similar to those in other habitats throughout their range.

Nest initiation in our study peaked during the last two weeks of May, with the earliest nest initiated on 14 May. Similarly, the earliest nest initiation dates reported in New Mexico and California were 12 May and 13 May, respectively (Goguen et al. 2005, Schlossberg and Sterling 2013). Our mean clutch size of 3.6 eggs was identical to that reported by Goguen et al. (2005) and similar to the mean clutch size of 3.47 eggs reported in northern Arizona (Schlossberg and Sterling 2013). As also noted by Goguen et al. (2005), we found that average clutch size declined after the midpoint of the nesting season. Given the

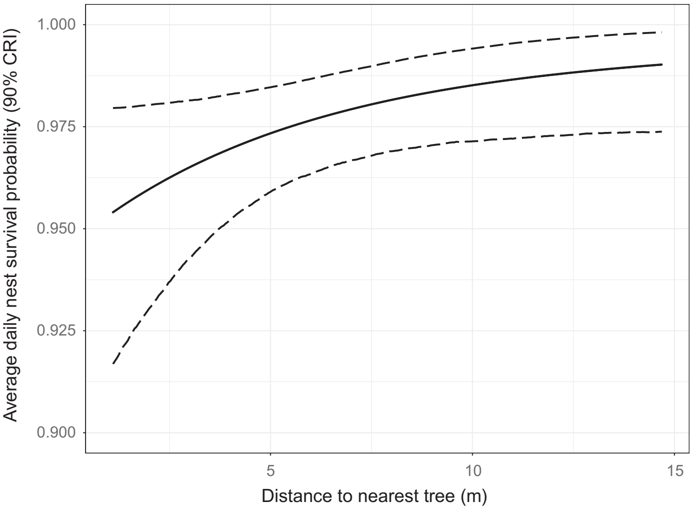

Fig. 2. Average daily nest-survival probability (and 90% CRI) across the range of nest distance to nearest tree values observed for Gray Flycatchers in the eastern Cascade Range, Washington, USA, 2014–2015. Calculated using assumed period durations (8 d for building, 4 d for laying, 14 d for incubation, and 16 d for the nestling period), period-specific median ordinal dates (149.5 for building, 155.5 for laying, 164.5 for incubation, and 179.5 for the nestling period), and average nest-level covariate values for the other covariates.

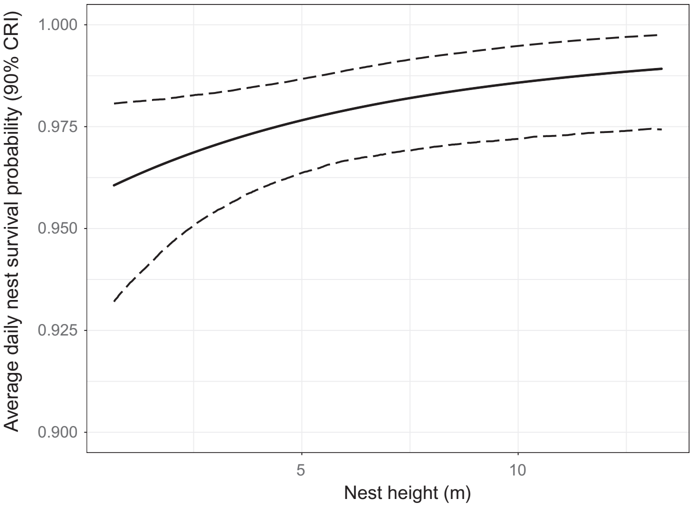

Fig. 3. Average daily nest-survival probability (and 90% CRI) across the range of nest heights observed for Gray Flycatchers in the eastern Cascade Range, Washington, USA, 2014–2015. Calculated using assumed period durations (8 d for building, 4 d for laying, 14 d for incubation, and 16 d for the nestling period), period-specific median ordinal dates (149.5 for building, 155.5 for laying, 164.5 for incubation, and 179.5 for the nestling period), and average nest-level covariate values for the other covariates.

Table 1. Parameter estimates (for fixed and random effects) from a multilevel nest-survival model for Gray Flycatchers in the eastern Cascade Range, Washington, USA, 2014–2015.

Parameter	Level	Mean	90% credibility interval
Intercept (fixed)	Nest	4.588	3.535, 5.744
Average shrub cover (fixed)	Nest	−0.010	−0.028, 0.009
Distance near tree (fixed)	Nest	0.327	0.008, 0.647
Nest distance to trunk (fixed)	Nest	−0.274	−0.549, 0.006
Nest height (fixed)	Nest	0.318	0.023, 0.641
Orientation East-West (fixed)	Nest	0.279	−0.138, 0.717
Orientation North-South (fixed)	Nest	−0.257	−0.628, 0.09
Total live trees (fixed)	Nest	0.019	−0.101, 0.142
Year 2015 (fixed)	Nest	−0.280	−0.851, 0.273
Ordinal date (fixed)	Visit	−0.097	−0.457, 0.259
Ordinal date^2 (fixed)	Visit	0.207	−0.068, 0.508
Laying (fixed)	Visit	−1.034	−1.897, −0.2
Incubation (fixed)	Visit	−0.897	−1.714, −0.136
Nestling (fixed)	Visit	−0.731	−1.773, 0.18
Location 1 (random)	Study plot	0.001	−0.463, 0.467
Location 2 (random)	Study plot	−0.080	−0.596, 0.361
Location 3 (random)	Study plot	0.066	−0.362, 0.557
Location 4 (random)	Study plot	−0.050	−0.56, 0.422
Location 5 (random)	Study plot	0.108	−0.312, 0.645
Location.sigma	Study plot	0.362	0.115, 0.904
Nest.sigma*	Nest	0.593	0.142, 1.251

*We present nest.sigma as a summary of nest-specific random effects due to the space requirement for means for each of 100 nests. These estimates are available from the corresponding author upon request.

high incidence of nest failure we observed, many of these later nests were likely re-nesting attempts following a predation event. Female Gray Flycatchers that experienced nest failure due to predation may have reduced clutch sizes for subsequent nesting attempts, a

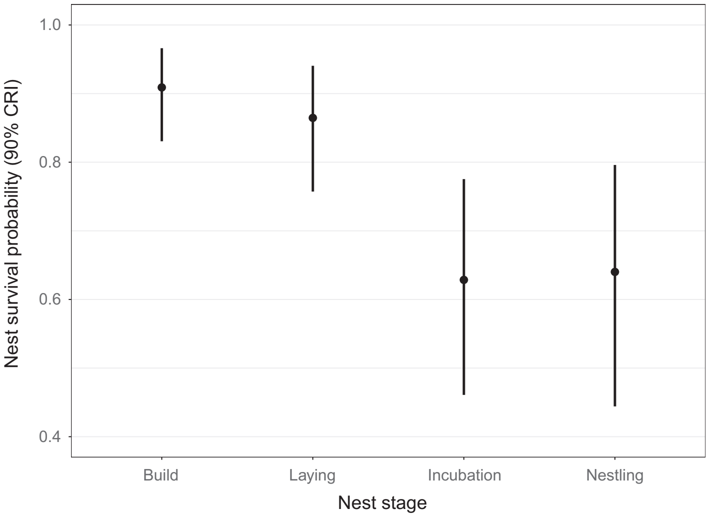

Fig. 4. Average period nest-survival probability (and 90% CRI) for Gray Flycatcher nests in the eastern Cascade Range, Washington, USA, 2014–2015. Calculated using assumed period durations (8 d for building, 4 d for laying, 14 d for incubation, and 16 d for the nestling period), period-specific median ordinal dates (149.5 for building, 155.5 for laying, 164.5 for incubation, and 179.5 for the nestling period), and average nest-level covariate values.

trend also observed in other passerines (Chalfoun and Martin 2010a, Morris et al. 2015) including the closely related Dusky Flycatcher (*Empidonax oberholseri*) (Kroll and Haufler 2007), because they perceive a higher risk of predation (Zanette et al. 2011). Alternatively, physiological limits may prevent females from laying normal clutches (3–4 eggs) because of the increased energetic demands of multiple nesting attempts (Goguen et al. 2005).

Parasitism of flycatcher nests by Brown-headed Cowbirds was low in our study despite cowbirds being common in our study area. Previous studies have also documented low rates of cowbird parasitism for both Gray Flycatchers (Friedmann et al. 1977, Goguen et al. 2005) and many congeners (Liebezeit and George 2002, Cain et al. 2003, Hazler et al. 2006). We sometimes observed adult flycatchers aggressively chasing female cowbirds from near nests, and other *Empidonax* flycatchers have also been found to act aggressively toward a model female cowbird presented near nests (Briskie et al. 1990, Uyehara and Narins 1995). Thus, aggressive responses to female cowbirds near nests, along with other behaviors we witnessed by flycatchers (e.g., males not singing near nests, and females sitting in nests before clutches were complete) may be effective counter adaptations to cowbird parasitism (Uyehara and Narins 1995, Banks and Martin 2001).

Gray Flycatchers built nests almost exclusively in conifers in our study; a finding documented throughout the flycatcher's range (Schlossberg and Sterling 2013). Shrubs were rarely used as nest sites even though antelope bitterbrush, the only shrub they used for nesting in our study, was common across our study area. We did not search for flycatcher nests outside of ponderosa pine stands, but saw and heard flycatchers singing in areas of pure bitterbrush. Thus, the importance of shrubs as nest substrates for Gray Flycatchers should be investigated further in areas where trees are absent.

Nests of Gray Flycatchers in trees tended to be oriented toward the north, a pattern also observed at other locations (Johnson 1963, Goguen et al. 2005). However, nest orientation did not influence nest survival in our study because predation was the primary source of nest failure. Because temperatures in our study area are highest from June to August, locating nests on the north-facing side of trees could confer thermal advantages to adults and nestlings by keeping nests cooler (Hartmann and Oring 2003, Mallord et al. 2007).

Birds should select nest sites that minimize predation risk because predation limits avian fitness (Latif et al. 2012). We found that daily nest survival increased as nest height increased. In our study area, Gray Flycatchers face a diverse assemblage of possible nest predators, including Steller's Jays (*Cyanocitta stelleri*), Clark's Nutcrackers (*Nucifraga columbiana*), Common Ravens (*Corvus corax*), Cooper's Hawks (*Accipiter cooperi*), American Kestrels (*Falco sparverius*), Northern Saw-whet Owls (*Aegolius acadicus*), golden-mantled ground squirrels (*Callospermophilus lateralis*), Douglas squirrels (*Tamiasciurus douglasii*), yellow-pine chipmunks (*Tamias amoenus*), long-tailed weasels (*Mustela frenata*), deer mice (*Peromyscus maniculatus*), gopher snakes (*Pituophis catenifer*), and striped whip snakes (*Masticophis taeniatus*) (Eichholz and Koenig 1992, Sieving and Willson 1998, Tomback 1998, Boarman and Heinrich 1999, Liebezeit and George 2002, Pietz and Granfors 2005, Richardson and Vander Wall 2007, Kroll and Haufler 2009, Lorenz and Fischer 2018). Almost half of these potential predators are primarily terrestrial (e.g., gopher snakes and long-tailed weasels) and venture into trees primarily to forage. Higher nests are likely safer from these predators because the farther a nest is from the ground, the greater the time and energy required for a terrestrial predator to find it (Schmidt 1999, Forstmeier and Weiss 2004). Higher nests may also be less visible to terrestrial predators because they are more obscured by branches and needles. This could explain why shrubs were rarely used when trees were present. However, nests located higher in trees are not safer from avian predators, especially jays and raptors (Rangen et al. 1999, Schmidt 1999).

We found that daily nest survival increased as the distance of nest trees to the nearest live tree increased. Nest trees located farther from adjacent trees may limit the ability of some predators to move between trees (e.g., mice, snakes, and smaller sciurids), especially if the canopies are not connected. In addition, predators such as Steller's Jays and Clark's Nutcrackers may select patches of trees to search because they can move through multiple tree canopies, resulting in more efficient foraging. Finally, Gray Flycatchers actively defend their nests and those that nest in trees further from another tree may be better able to detect approaching predators, which could provide advantages for nest defense (Murphy et al. 1997). On multiple occasions, we observed adult flycatchers successfully drive yellow-pine chipmunks down the trunk of nest trees to the ground. We also observed an adult flycatcher strike a male White-headed Woodpecker (*Dryobates albolarvatus*) in flight and drive it to the ground.

We observed a higher daily survival rate and higher period survival during the building stage than during the incubation and nestling stages. Increased activity at nests by incubating females and both sexes while feeding nestlings could make it easier for predators to find nests during these periods. The results of previous studies have shown that nest survival tends to decline with the onset of incubation (Filliater et al. 1994, Kroll and Haufler 2009, Kozma et al. 2017) and that nestling begging and adults feeding young increase the risk of nest predation (Haskell 1994, Martin et al. 2000, Muchai and du Plessis 2005). Nest survival may have been higher during the building stage, when females make multiple visits with nest material, because this stage is shorter in duration, increasing the probability that nests will survive that period. Although some nests in our study were torn apart during the building stage, possibly by corvids searching for eggs, others may have been discovered by predators during the building stage, but left undisturbed and visited again at a later date.

Gray Flycatcher nests are exposed to terrestrial and arboreal predators with varied search strategies. This exposure may limit the possibility of finding a safe nest site because all sites may be subject to similar predation risk (Filliater et al. 1994, Braden 1999). Gray Flycatchers that locate their nests higher above ground and farther from adjacent trees may be choosing the safest alternative because doing so reduces the risk of predation from terrestrial predators (~50% of the potential predator community) and may provide benefits to nest defense through earlier detection of approaching predators. Nests located in these "safer" locations may be built by females that experienced a prior nest loss due to predation, in other words, a "lose-switch" strategy (Chalfoun and Martin 2010b, Kearns and Rodewald 2013). Environments similar to our study area that do not provide the cues needed for flycatchers to predict the risk of predation due to diverse predator communities may require females to rely on past experience to select nest sites with a lower predation risk (Chalfoun and Martin 2010a). Studies of the characteristics of nest sites that are re-nesting attempts are needed to test this hypothesis.

ACKNOWLEDGMENTS

We thank K. Lucas for his assistance with developing the cell phone/nest monitoring setup and sampling vegetation at nest sites. The Washington Department of Natural Resources provided access to their land. Funding was provided by the Bureau of Indian Affairs.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Appendix S1. Code for the nest-survival model.

Appendix S2. Details of posterior predictive checks for Bayesian nest survival model.

Appendix S3. R code for the posterior predictive checks.