



Erratum: In the original publication of this article the Figure 4 caption was incorrect.
The caption was amended on 12 February 2025.

Avian Behavior, Ecology, and Evolution

Nest site selection of Dusky and Hammond's flycatchers over an elevational gradient

Selección de sitio de nidificación por el Papamoscas Matorralero y el Papamoscas de Hammond a través de un gradiente altitudinal

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ABSTRACT. Release from interspecific competition can lead to niche shifts and have positive fitness consequences. I studied two closely related and ecologically similar *Empidonax* species that breed across an elevational gradient in the southern Sierra Nevada, California: Dusky Flycatcher (*Empidonax oberholseri*) and Hammond's flycatcher (*E. hammondi*). The two species coexisted at low and moderate elevations but only Dusky Flycatchers occurred in high elevation forests. Where they co-occurred, Dusky Flycatchers nested primarily in shrubs but at high elevations they nested primarily in trees and snags. My objective was to examine whether ecological release from interspecific competition was responsible for the apparent niche shift in Dusky Flycatcher nests sites at high elevations where Hammond's Flycatchers do not occur. Both species nested higher and had higher nest survival at higher elevations. Dusky Flycatcher nest survival was higher when nesting in trees or snags compared to shrubs and Hammond's Flycatcher nest survival increased with increasing nest height. Upon closer inspection, Dusky Flycatchers did not occupy the nest site niche of Hammond's Flycatchers at high elevations. When nesting in trees, Dusky Flycatcher nests were much lower (mean = 4.3 m) than Hammond's Flycatcher nests (mean = 18.0 m). The observed distributions of these two species over the elevational gradient appeared to correspond to the habitat preferences of the two species, rather than interactions between the species and their preferred nesting locations. Should warming due to climate change trigger upslope range expansion, Hammond's Flycatchers' preferred nesting locations would not be available and they would likely incur fitness consequences. Increased vertical overlap in habitat use could lead to increased competitive interactions with Dusky Flycatchers. These results provide important findings related to the habitat requirements, species' ranges, and ecological niches of these two species and help us to better predict species' responses to climate change and inform conservation strategies.

RESUMEN. La liberación de la competencia interespecífica puede conducir a cambios en los nichos y tener consecuencias positivas para el fitness. Estudié dos especies de *Empidonax*, estrechamente relacionadas y ecológicamente similares, que se reproducen a lo largo de un gradiente altitudinal en la Sierra Nevada del sur de California: el Papamoscas Matorralero (*E. oberholseri*) y el Papamoscas de Hammond (*E. hammondi*). Las dos especies coexistieron en elevaciones bajas y moderadas, pero solo los papamoscas matorraleros se encontraron en los bosques de elevaciones altas. Donde coexistían, los papamoscas matorraleros nidificaban principalmente en arbustos, pero en elevaciones altas lo hacían principalmente en árboles y troncos muertos. Mi objetivo fue examinar si la liberación ecológica de la competencia interespecífica era responsable del aparente cambio de nicho en los sitios de nidificación del Papamoscas Matorralero en elevaciones altas, donde los papamoscas de Hammond no están presentes. Ambas especies nidificaron a mayor altura y tuvieron mayor supervivencia de nidos en elevaciones más altas. La supervivencia de los nidos del Papamoscas Matorralero fue mayor cuando nidificaba en árboles o troncos muertos en comparación con arbustos, y la supervivencia de los nidos del Papamoscas de Hammond se incrementó con la altura del nido. Al examinar más a fondo, los papamoscas matorraleros no ocuparon el nicho del sitio de nidificación de los papamoscas de Hammond en elevaciones altas. Al nidificar en árboles, los nidos del Papamoscas Matorralero estaban mucho más bajos (promedio = 4,3 m) que los nidos del papamoscas de Hammond (promedio = 18,0 m). Las distribuciones observadas de estas dos especies a lo largo del gradiente altitudinal parecieron corresponder a las preferencias de hábitat de cada especie, más que a interacciones entre las especies y sus ubicaciones preferidas para nidificar. Si el calentamiento provocado por el cambio climático desencadena una expansión altitudinal, las ubicaciones preferidas para nidificar del Papamoscas de Hammond podrían no estar disponibles y probablemente sufrirían consecuencias negativas para su fitness. Un aumento en la superposición vertical en el uso del hábitat podría llevar a un aumento de las interacciones competitivas con los papamoscas matorraleros. Estos resultados ofrecen hallazgos importantes relacionados con los requerimientos de hábitat, los rangos de distribución y los nichos ecológicos de estas dos especies y ayudan a prever mejor las respuestas de las especies al cambio climático e informar estrategias de conservación.

Key Words: *Dusky Flycatcher*; *ecological release*; *elevational gradient*; *Empidonax oberholseri*; *Empidonax hammondi*; *Hammond's Flycatcher*; *nest height*; *nest site selection*; *niche partitioning*

INTRODUCTION

Understanding factors that influence the coexistence of species is a central issue of ecology that has consequences for the maintenance of biodiversity in a changing world. Classical coexistence theories posit that each species inhabits a particular

niche involving a combination of abiotic and biotic factors. According to the competitive exclusion principle, two species cannot occupy the exact same niche in a habitat (Hardin 1960). Because of interspecific interactions, the realized niche of a species is smaller than its fundamental niche, at least when

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densities of the species are high (Bolnick et al. 2010, Valladares et al. 2015, Samplonius and Both 2019). An ecological opportunity occurs when selection acting on some ecologically important trait is relaxed (Des Roches et al. 2011). This can be the result of a reduction in competition, predation, or parasitism (Parent and Crespi 2009, Yoder et al. 2010, Des Roches et al. 2011). An ecological opportunity can lead to ecological release, i.e., expansion of the realized niche of a species where constraining interspecific interactions are reduced or removed and can occur either through evolutionary or ecological means (Herrmann et al. 2021). Ecological release can be expressed through density compensation, broadening of the niche through niche expansion, niche shifts, or niche expansion combined with niche shifts (Cox and Ricklefs 1977, Yoder et al. 2010, Herrmann et al. 2021).

Commonly hypothesized mechanisms to avoid niche overlap include habitat partitioning. In birds, the ecological consequences of habitat selection are often evaluated through nest site selection (Martin and Martin 2001). Nest sites can have important implications for reproductive success and birds may be sensitive to nest site overlap and competition for nest sites (Ye et al. 2019). Strong fitness costs are incurred by being similar in nest site selection because it can have fitness consequences and can influence nesting habitat choice (Martin 1996, Fontaine and Martin 2006). Because nest predation is usually the primary source of nest failure, predation risk can select against the coexistence of species that are similar in their nest sites (Martin 1993, 1996).

The availability of suitable nest sites may limit breeding density in birds (Brazill-Boast et al. 2010). Although not always the case, nest-site limitation has been found for secondary cavity-nesting birds and weak excavators (Brawn and Balda 1988, Holt and Martin 1997), and for seabirds such as penguins, gulls, and terns (Trivelpiece and Volkman 1979, Quintana and Yorio 1998). It is important to note that, although nest sites may be a crucial factor for reproduction, other factors may play important roles in limiting niche overlap (Ye et al. 2019).

Elevational gradients are useful systems in which to study life history variation because they allow observation of populations experiencing a considerable range of environmental conditions over a relatively small geographic area (Able and Noon 1976, Boyle et al. 2016). They are powerful “natural” experiments for testing ecological and evolutionary responses to both physiologically based and biotic factors such as competition, predation, parasitism, and habitat selection (Körner 2007, Boyle et al. 2016).

I studied two *Empidonax* congeners that breed across an elevational gradient in the southern Sierra Nevada in California, USA: Dusky Flycatcher (*Empidonax oberholseri*) and Hammond’s Flycatcher (*E. hammondi*). These morphologically similar insectivorous flycatchers maintain their reproductive isolation by behavioral means, including differences in vocalizations and aggressive displays, and through differences in general habitat preferences, foraging locations, and nesting habitat (Johnson 1963, Sedgwick 1994, Pereyra and Sedgwick 2020). The two species differ in habitat use, with Dusky Flycatchers found in open, brushy habitats, usually with some scattered trees (Pereyra and Sedgwick 2020), whereas Hammond’s

Flycatchers occur in mature conifer and mixed conifer forests, often with limited understory (Sedgwick 1994, Pereyra and Sedgwick 2020). The two species co-occur where their preferred habitats are found in a vegetational mosaic (Ashmole 1968, Beaver and Baldwin 1975). Hammond’s Flycatchers usually forage in the mid-canopy, higher than Dusky Flycatchers, which forage in brushy areas or from the lower levels of trees (Beaver and Baldwin 1975, Pereyra and Sedgwick 2020). They also differ in the location of their nests. Hammond’s Flycatchers have relatively narrow nesting habitat requirements, nesting exclusively in live, tall, large-diameter trees (Johnson 1966, Sakai and Noon 1991, Sedgwick 1994), whereas Dusky Flycatchers nest primarily in shrubs and small saplings within a few meters of the ground (Pereyra and Sedgwick 2020). Although not previously documented, Dusky Flycatchers nesting at high elevations in the Sierra Nevada, CA, USA, where Hammond’s Flycatchers do not co-occur, nest primarily in trees. This observed niche shift in nest site locations of Dusky Flycatchers is the focus of this paper.

My objective was to examine whether ecological release from interspecific competition is responsible for the observed niche shift in Dusky Flycatchers at high elevations. I hypothesized that (1) Dusky Flycatcher abundance would be higher in high elevation sites where Hammond’s Flycatchers do not occur, assuming other resource-partitioning differences such as habitat structure, food availability, predation risk, and abiotic conditions remain constant, (2) Dusky Flycatchers would broaden and/or shift their nesting niche where Hammond’s Flycatchers are not present, and (3) changes in niche breadth or niche shifts would have beneficial fitness consequences.

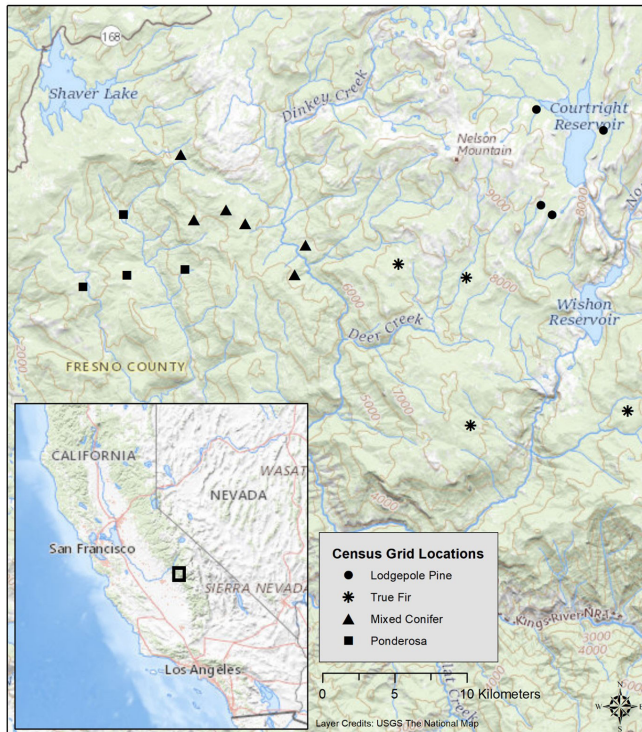
METHODS

Study sites

I studied Dusky and Hammond’s flycatchers in four forest types along a 1750-m elevational gradient in the High Sierra Ranger District of the Sierra National Forest on the western slope of the southern Sierra Nevada, California, USA (Fig. 1). Forest types in order of increasing elevation were ponderosa pine (*Pinus ponderosa*; elevation 1024–1372 m), mixed conifer (elevation 1707–2012 m), true fir (elevation 2170–2347 m), and lodgepole pine (*P. contorta*; elevation 2469–2774 m).

As part of a larger study examining the abundance and productivity of forest birds, I selected 18 study sites consisting of four replicate sites in each forest type, except for mixed conifer, where six sites were selected for a proposed extension of this study intended to look at forest management effects in mixed conifer forests. Of the six mixed-conifer sites, four were sampled each year on a rotating schedule, such that each site was sampled an equal number of years of the study. The four sites in each of the other forest types were sampled each year of the study. Dominant tree species in ponderosa pine sites included ponderosa pine, incense cedar (*Calocedrus decurrens*), and several hardwood species (mostly *Quercus* spp.). Mixed conifer sites included a mixture of primarily white fir (*Abies concolor*), incense cedar, sugar pine (*P. lambertiana*), ponderosa pine, and California black oak (*Quercus kelloggii*). True fir sites were dominated by white fir and red fir (*A. magnifica*), and lodgepole pine sites were made up almost exclusively of lodgepole pine, with a small component of red fir. All sites consisted of ≥ 60 ha of mature forest. Although

Fig. 1. Location of study sites (N = 18) in four forest types over an elevational gradient in the Sierra National Forest, Fresno County, California, USA.



sites within a forest type were intended to be replicates, natural heterogeneity in these steep, rugged mountains with variable topography resulted in all sites having some open rocky or brushy areas and small meadows or streams. No site had experienced recent major disturbance due to logging, fire, or other forest management.

Within each of the sites, a 40-ha plot was gridded at 50-m intervals to facilitate bird surveys and mapping and relocation of nests. Grids were laid out by establishing a baseline using a staff compass mounted on a Jacob staff to determine the horizontal direction of a line and a fiberglass surveyor measuring tape for distance. Parallel lines were then established by checking distances and directions to perpendicular points. Intersections were marked with a steel fencepost and a cap of PVC pipe marked with an alphanumeric code. Grid lines between markers were marked with flagging.

A 1000 m transect within the 40 ha plot was established to facilitate bird surveys. Grid markers along the line transects were painted blue and the corresponding markers 50-m on each side of the census lines were painted orange to help censusers determine the location of birds relative to the transect.

Fieldwork

From 1995 through 2002, field technicians censused birds on eight (1995) or 16 (1996–2002) study sites using a timed line transect method (Verner 1985). Observers walked at a rate of 50 m per 3 minutes, recording all birds detected within 50 m of the transect

line and those detected at unlimited distance. Each site was visited six times per season by 3–4 observers each year of the study. Because observer variability is the most common source of variation in bird counts (Verner and Milne 1989), efforts were taken to control for observer variability as follows. Observers were selected for proficiency in bird identification, especially by vocalizations, and were retained for as many years as possible. A total of seven observers surveyed birds over the eight years so that most observers were repeat observers for several years of the study. Prior to the beginning of the field season, observers completed two weeks of training to sharpen their skills and familiarize them with the details of the protocol, with additional training as they moved into higher forest types and encountered new species. All observers visited each site an equal number of times each year. Surveys were completed during the peak singing period for each forest type: 17 April through 16 May in ponderosa pine sites, 22 May through 15 June in mixed conifer sites, 5 June through 6 July in true fir sites, and 21 June through 25 July in lodgepole pine sites. The order of visits to sites and starting point were randomly selected, with the constraint that visits were evenly divided between the two starting points. Recording of birds began at 0700 PDT in all forest types except ponderosa pine, where counting began at 0730 PDT to account for shorter day lengths earlier in the season. The total count time was 60 minutes, plus the time needed to walk between segments of the transect line. Maximum end time was 0935 for ponderosa pine sites and 0830 for the other forest types.

Field crews located nests on all sites each year and monitored them every 3 to 4 days, until the nest failed or fledged young (Martin and Geupel 1993). For low nests, we checked contents directly. Higher nests were checked once a week using a mirror on a pole or a miniature video camera mounted on an extendable pole or accessed by climbing. These nests were checked on a second weekly visit by observing them from the ground, noting the presence and behavior of adults that provided clues as to the stage of the nest and its success or failure, such as copulatory behavior and adults carrying nesting material, bringing food to nestlings, or removing fecal pellets. For nests whose contents could be examined, the number of eggs and nestlings and the appearance of the nestlings (size, whether the eyes were closed, slits, or open, presence of down and pin feathers, and the extent of emergence of the remiges and rectrices), the presence of eggshell fragments, and the appearance of an empty nest (flattened, the presence of fecal droppings) were recorded. After the nest fledged or failed, we recorded elevation, nest substrate type (shrub, tree, or snag), nest height, substrate species, and substrate height.

Nests that fledged at least one young were considered successful. We assumed predation when eggs or nestlings too young to have fledged disappeared from the nest. For Hammond's Flycatcher nests too high to access that were observed from the ground, predation was assumed when no activity was observed ($n = 26$ nests) and when storms likely to have contributed to nest failure had not occurred in the days preceding the final nest check. Following fledging or failure, habitat data were collected at each nest site and included nest height (high nests were measured with a clinometer and meter tape or a hypsometer), substrate height and species, and the elevation at each nest was measured with an altimeter.

To characterize the forest types, habitat measurements were collected on 35 random plots on each of the 18 study sites (N = 630) from 1996 through 1999. Plot centers were located a random distance and direction from randomly selected grid markers, with random points at least 100 m apart and within 50 m of the edge of the gridded plot. Average maximum canopy height was recorded by measuring the height of a tree in the canopy that represented the average height of the top of the canopy within an 11.3-m diameter circle centered on the plot center. We measured canopy closure at the nearest tree, snag, shrub, and sapling to the plot center, using a concave spherical densiometer and averaging four readings taken at right angles to each other. To characterize understory habitat and shrub cover across forest types, we used a point intercept method (Caratti 2006). Ten-m transects were laid out in each compass direction from the plot center. We recorded “hits” of plant species on a rod (~15 cm diameter PVC pole) extended vertically from the ground every 0.5 m along the 4 transects. We included hits below 1.36 m in height or the height of the shrub canopy, whichever was higher. Percent cover was calculated as the number of points that included hits of any woody plant species divided by the total number of points measured (80).

Statistical analysis

The index of abundance for each forest type was calculated as total count per transect for detections within 50 m and to unlimited distance. For each species, the individual observations (counts of birds) are represented by y_{ijk} where i represented forest type, j represented the observer, and k was the site index. All observers visited all sites an equal number of times each year. We assumed a generalized linear mixed model (Dobson and Barnett 2018) where the log of the expected count was a linear model of habitat and observer with plot being a random effect. Specifically,

$$\log E(y_{ijk}|u_k) = \beta_{ij} + u_k \quad (1)$$

where β_{ij} is the effect of habitat i and observer j , u_k is the random effect of plot k with $u_k \sim N(0, \sigma^2)$, and y_{ijk} conditioned on the random effect u_k has a Poisson distribution with mean $\lambda_{ijk} = e^{\beta_{ij} + u_k}$. The model was fit using PROC GLIMMIX (SAS Institute 2022). Estimates for each habitat and observer were averaged over all observers to account for any heterogeneity among observers. That estimate in terms of mean number of birds per site for habitat i was

$$\hat{\lambda}_i = \exp\left(\frac{1}{7} \sum_{j=1}^7 \hat{\beta}_{ij}\right) \quad (2)$$

because there were 7 observers. Standard errors and confidence intervals were part of the output produced by PROC GLIMMIX. Estimates of the overdispersion parameter were near 1 for both species and the count variable. Differences in abundance among forest types were tested with Tukey’s Honestly Significant Difference test, controlling for experiment-wise error rates (SAS Institute 2022).

Differences in habitat variables at nest sites compared to random samples among forest types were tested using ANOVA (Proc Mixed, SAS Institute 2022), followed by Tukey’s Honestly Significant Difference test adjusted for all possible pairwise comparisons. Differences in nest height, relative nest height, and substrate height between bird species were tested using ANOVA (Proc Mixed, SAS Institute 2022), and correlation analysis was used to evaluate the relationship between nest height and elevation (Proc Corr, SAS Institute 2022). To characterize available habitat as it varied over elevation, I tested differences in canopy height, canopy closure, and percent shrub cover among forest types in the same manner.

I used the logistic exposure method (Shaffer 2004) to calculate daily nest survival rates across habitats both within and between bird species, and to examine whether nest survival varied with forest type, elevation, and nest height. To examine covariates potentially important to nest survival, I evaluated candidate models using AIC_c (Burnham and Anderson 2002). For Hammond’s Flycatchers, I evaluated all possible combinations of 2 variables, nest height and elevation, plus a null model, for a total of 4 models. In addition to these two variables, I added nest substrate as a variable in Dusky Flycatcher models, yielding a total of 8 models.

To calculate period nest success, I raised the daily survival rate based on the constant survival model to the power of the number of days in the nesting period (Shaffer and Thompson 2007). I used data from this study to determine the length of the nesting period, employing data from nests with complete information for a particular period rather than published values. For Dusky Flycatchers, the average duration incubation was 14.0 days (n = 152, SD = 1.2) and the nestling period averaged 17.3 days (n = 42, SD = 1.20). Average clutch size was 3.6 (n = 333, SD = 0.58), yielding a laying period of 2.6 days, and the number of days to complete a nesting cycle was 31.9 days, slightly lower than published values (Pereyra and Sedgwick 2020). For Hammond’s Flycatchers, average incubation period was 14.1 days (n = 49, SD = 0.53), average nestling period was 16.5 days (n = 15, SD = 1.19), average clutch size was 3.8 (n = 51, SD = 0.51), with a laying period of 2.8 days, and the total length of the nesting cycle was 33.4 days, again slightly lower than published values (Sedgwick 1994).

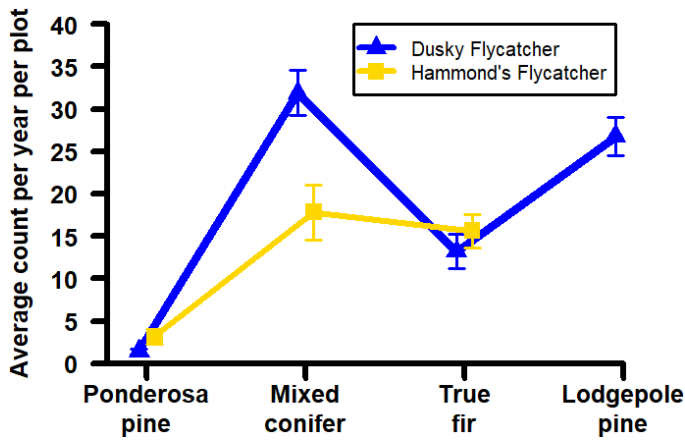
RESULTS

Abundance

Patterns for detections within 50 m and to unlimited distance were similar and results of statistical tests were the same for both species. Only results of detection within 50 m are presented here. Observer effects and the interaction between observer and forest type were significant (adj. $P < 0.001$ for all), suggesting significant observer variability.

Dusky Flycatcher abundance differed among forest types ($F_{3,588} = 17.18$, $P < 0.001$; Fig 2). Abundance was highest in the mixed conifer and lodgepole pine forest types and did not differ (adj. $P = 0.95$) between the two forest types. Both were significantly higher compared to both ponderosa pine and true fir habitats (all adj. $P < 0.02$). Hammond’s Flycatchers did not occur in high elevation lodgepole pine sites and relative abundance did not differ among the other three forest types ($F_{2,418} = 2.09$, $P = 0.12$; Fig. 2).

Fig. 2. Relative abundance of Dusky (*Empidonax oberholseri*) and Hammond's flycatchers (*E. hammondi*) in four forest types over an elevational gradient in the southern Sierra Nevada, California. Relative abundance was calculated as the total count per habitat per plot per year and is shown for detections within 50 m of the transect line. Error bars represent 1 standard error.



Nests

We located 450 Dusky Flycatcher and 130 Hammond's flycatcher nests (Fig. 3). Dusky Flycatchers generally nested in shrubs at low and moderate elevations, but in lodgepole pine habitat they switched to nesting in trees or snags (Fig. 3a). Dusky Flycatcher nests in snags ($n = 5$) were similar in nest height, substrate height, and relative height compared to those in trees and were combined with nests in trees for analysis. Dusky Flycatchers did not always nest in shrubs at lower elevations and sometimes nested in shrubs at upper elevations. Hammond's flycatchers nested exclusively in live, tall trees.

When nesting in shrubs, Dusky Flycatcher nest height averaged 0.9 m (SD = 2.6, $n = 334$). For nests in trees and snags, Dusky Flycatcher nests had an average height of 4.3 m (SD = 3.8, $n = 116$). Average nest height of Hammond's Flycatcher nests was 18.0 m (SD = 8.0, $n = 129$).

Nest height, relative nest height, and substrate height of Dusky Flycatchers nesting in trees and snags were all significantly lower compared to Hammond's Flycatcher nests (nest height: $F_{1,243} = 284.26$, $P < 0.01$; relative height: $F_{1,243} = 11.52$, $P < 0.01$; substrate height: $F_{1,244} = 273.09$, $P < 0.01$). Nest height increased with elevation for both species (Fig. 4; Dusky Flycatcher $r = 0.60$, $P < 0.01$, $n = 451$; Hammond's Flycatcher $r = 0.48$, $P < 0.01$, $n = 129$).

Nest survival

Daily nest survival increased with elevation for both species (Fig. 5). For Dusky Flycatchers, nest survival was significantly higher in lodgepole pine compared to mixed conifer habitat ($\chi^2 = 9.39$, $P < 0.001$) but not compared to true fir ($\chi^2 = 2.48$, $P = 0.12$). For Hammond's Flycatchers, nest survival was significantly higher in true fir compared to ponderosa pine habitat ($\chi^2 = 5.28$, $P = 0.02$) but not compared to mixed conifer habitat ($\chi^2 = 3.12$, $P = 0.08$). Period nesting success for Dusky Flycatchers increased from 31.5% in mixed conifer, to 37.6% in true fir, to 47.7% in lodgepole pine. For Hammond's Flycatchers, period nesting success increased from

Fig. 3. Sample sizes of Dusky (A; *Empidonax oberholseri*) and Hammond's flycatcher (B; *E. hammondi*) nests by forest type over an elevational gradient. Dusky Flycatcher nests in shrubs vs. trees or snags are also shown. All Hammond's Flycatcher nests were in trees.

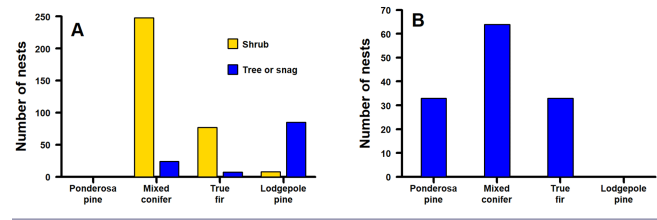
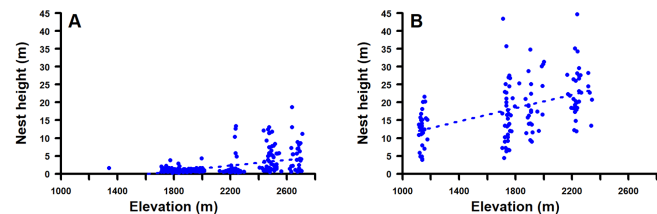


Fig. 4. Nest height increased with elevation for Dusky Flycatcher (A) and Hammond's Flycatcher (B).



27.2% in ponderosa pine to 33.7% in mixed conifer to 48.8% in true fir. Daily survival rates for Dusky and Hammond's flycatchers did not differ within the same forest type (mixed conifer: $\chi^2 = 0.42$, $P = 0.51$; true fir: $\chi^2 = 0.72$, $P = 0.39$).

Dusky Flycatcher nest survival increased with elevation and for nests in trees and snags (Table 1). A global model including all three variables was also competitive but 95% confidence intervals for nest height included 0 and the model with nest height alone was less supported than the null model, suggesting that nest height was an uninformative parameter (Arnold 2010). For Hammond's Flycatchers, nest survival increased with nest height and elevation.

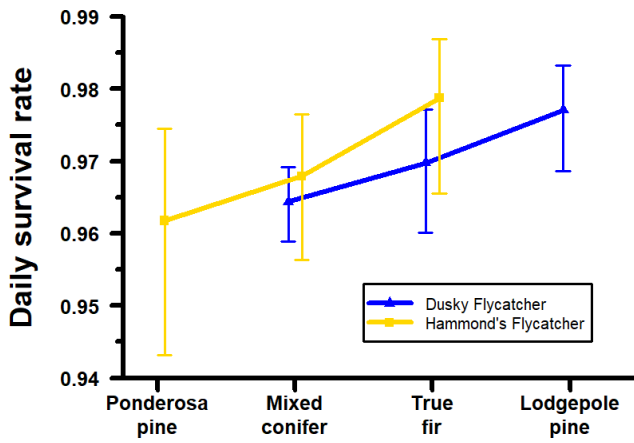
Habitat characteristics

The average maximum height of the tree canopy differed across forest types ($F_{3,619} = 63.47$, $P < 0.001$; Fig. 6a). True fir habitat had the tallest trees, with a mean of 38.05 m (SE = 0.95) and differed significantly from the other three forest types (all adj $P < 0.01$). Ponderosa pine and lodgepole pine had the shortest canopies (mean = 23.57 m, SE = 0.83 for ponderosa pine and mean = 25.50 m, SE = 0.50 for lodgepole pine). Compared to the average maximum canopy height, trees used for nesting by Hammond's Flycatchers were significantly taller (adj. $P < 0.001$ for ponderosa pine, mixed conifer and true fir).

Canopy closure differed across forest types ($F_{3,627} = 24.42$, $P < 0.01$). Canopy closure was highest in ponderosa pine and mixed conifer forests (adj. $P = 0.91$), lower in true fir (all adj. $P < 0.02$), and lowest in lodgepole pine (all adj. $P < 0.02$; Fig. 6b).

Shrub cover decreased with elevation (Fig. 6c), with the highest shrub cover in ponderosa pine habitat (all adj. $P < 0.001$), next highest in mixed conifer (all adj. $P < 0.001$), and the lowest in true

Fig. 5. Daily nest survival rates for Dusky (*Empidonax oberholseri*) and Hammond's flycatcher (*E. hammondi*) in four forest types along an elevation gradient in the southern Sierra Nevada, CA. Error bars represent 95% confidence intervals.



fir and lodgepole pine habitats (comparisons with ponderosa pine and mixed conifer adj. $P < 0.001$), which did not differ from each other (adj. $P = 0.17$).

DISCUSSION

Studies on closely related and/or ecologically similar species can reveal differences in realized niche space and interactions among species. I examined the consequences of coexistence for two *Empidonax* flycatchers. Specifically, I examined whether the observed shift in nesting substrate use in Dusky Flycatchers at high elevations was due to ecological release from competition where Hammond's Flycatchers do not occur. Results addressing my first hypothesis, that Dusky Flycatcher abundance would be higher in high elevation sites where they do not co-occur with Hammond's Flycatchers, were ambiguous. Dusky Flycatcher abundance increased in high elevation lodgepole pine compared to true fir habitat occurring at immediately lower elevations; however, abundance did not differ between mid-elevation mixed conifer and lodgepole pine habitat, representing weak evidence for ecological release. In accordance with my second hypothesis, I observed a niche shift in Dusky Flycatcher nest site selection, but no apparent broadening of the niche for this aspect of their ecology. This niche shift had fitness consequences that supported my third hypothesis: nest survival was higher for Dusky Flycatchers when nesting in trees or snags compared to shrubs and was higher at higher elevations.

A closer look at the nest sites used by Dusky Flycatchers reveals flaws in arguments for ecological release. Although Dusky Flycatchers switched to nesting in trees, they did not occupy the nest sites of Hammond's Flycatchers when nesting at high elevations. Dusky Flycatchers continued to nest much lower than Hammond's Flycatchers. When nesting in trees, Dusky Flycatcher nest height, nest substrate height, and relative height were all significantly lower compared to those attributes of Hammond's Flycatcher nests. They tended to nest on the lower

Table 1. Results of logistic exposure models examining the effects of elevation, nest height and nest substrate (shrub vs trees and snags) on Dusky (*Empidonax oberholseri*) and Hammond's flycatcher (*E. hammondi*) daily nest survival. Nest substrate was the same for all Hammond's Flycatcher nests and was not included in models. Nestht = nest height, Subcat = nest substrate (shrub vs. tree or snag). N_{eff} (effective sample size) for Dusky Flycatcher models was 7933 and for Hammond's Flycatcher models was 2479.

Model	AIC _c	k	Δ AIC _c	Akaike weight
Dusky Flycatcher				
Elevation Subcat	1673.08	3	0	0.515
Elevation Subcat Nestht	1674.95	4	1.876	0.202
Subcat	1674.97	2	1.895	0.200
Subcat Nestht	1676.96	3	3.881	0.074
Elevation	1681.89	2	8.808	0.006
Elevation Nestht	1683.72	3	10.647	0.003
Null	1686.82	1	12.746	0.001
Nestht	1687.42	2	14.345	0.000
Hammond's Flycatcher				
Nestht	501.51	2	0	0.65
Elevation Nestht	502.95	3	1.44	0.32
Elevation	508.25	2	6.74	0.02
Null	510.00	1	8.49	0.01

branches of smaller trees, not high in tall trees as Hammond's do. The nest site locations used in lodgepole pine habitat were not unique to high elevations; although less common, Dusky Flycatchers also occasionally nested low in small trees at lower elevations.

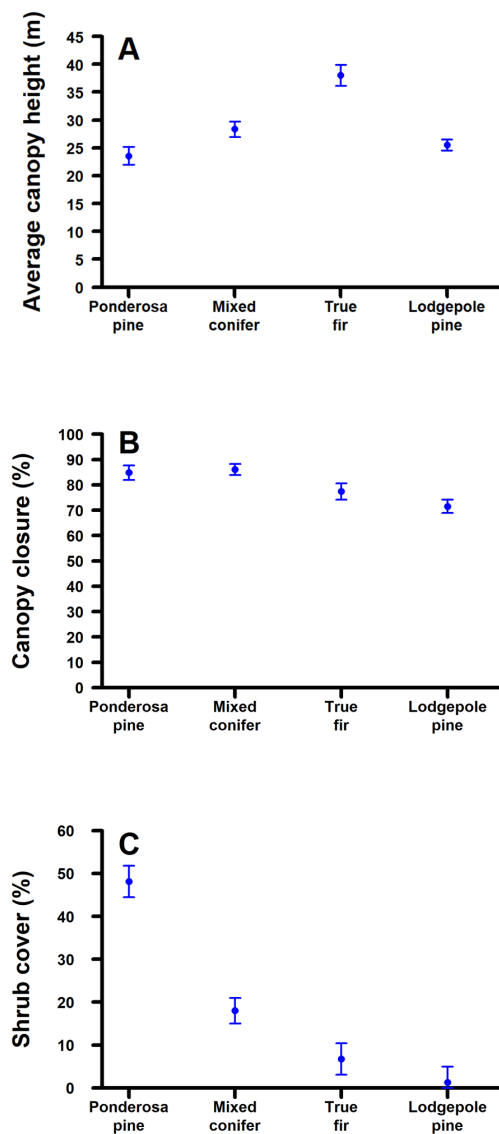
Dusky Flycatcher abundance was high in mixed conifer habitat where shrubs were abundant, decreased in true fir habitat, which was characterized by low shrub cover and large, tall trees, and increased in lodgepole pine habitat. Nesting success was higher at higher elevations and when nesting in trees. In high elevation lodgepole pine forest, characterized by low shrub cover and shorter trees, they switched from nesting primarily in shrubs to nesting in trees; Dusky Flycatchers appear to be taking advantage of available nesting substrates.

Hammond's Flycatchers reached their highest abundance in true fir forest, followed by mixed conifer. Nesting success increased with elevation and nest height. Trees used for nesting by Hammond's Flycatchers were among the tallest trees available. True fir forest most closely represents their preferred habitat, with the tallest tree canopies and an open understory (Sedgwick 1994). In mixed conifer, they found nest sites in the dense tree canopies with moderate tree height. They did not occur in high elevation lodgepole pine forests, likely because of the lack of the tall trees they prefer for nesting. Thus, the observed distributions of these two species over the four forest types appeared to correspond to the habitat preferences of the two species, rather than because of interactions between the species and their preferred nesting locations.

Nest placement is considered to be evolutionarily conservative (Martin 1993). As a group, flycatchers show a remarkable degree of uniformity in morphology, are uniform in their choice of

nesting habitat, show relatively slight geographic variation, and have limited ecological tolerance (Johnson 1966, Sakai and Noon 1991). Dusky Flycatchers were more variable in their nest site selection. They are considered well-adapted to the more extreme conditions of high elevations (Pereyra 2011) and there is evidence of northward range expansion (Campbell et al. 1997, Eckert 1998). Hammond's Flycatchers were selective in their nest site locations, always nesting high in tall, live trees, and in agreement with the findings of others (Johnson 1966, Sakai and Noon 1991, Sedgwick 1994). The variability in nest site location found in Dusky Flycatchers is more unexpected than the lack of variability in Hammond's Flycatchers and suggests adaptability to change and the ability to survive in Dusky Flycatchers.

Fig. 6. Average maximum height of the tree canopy (A), percent canopy closure (B), and percent shrub cover (C) over four forest types. Error bars represent 95% confidence intervals.



These two species, as well as other related and similar species in the *Empidonax* complex, are thought to be able to coexist largely because of vertical separation related to differences in their foraging locations, nest site placement, and general habitat preferences, as well as the associated differences in nest site placement seen here (Bent 1942, Johnson 1966, Beaver and Baldwin 1975, Sedgwick 1994, Pereyra and Sedgwick 2020). Reproductive isolation is also maintained by vocalizations and aggressive displays (Johnson 1963). Although nest site placement may have been important in avoiding competition in the past, it does not currently appear important to the coexistence of these two species.

Breeding at higher elevations appeared to be beneficial for both species. The root causes of this relationship are likely complex and are possibly related to changes in the abundance and diversity of nest predators, the availability of food resources, release from density-dependent predation, and abiotic conditions. Given that Hammond's Flycatchers have higher nesting success at high elevations, why do they not occur in high elevation lodgepole pine forests? Species' distributions and why species occur in one location and not in another are poorly understood and are likely influenced by complex, interacting factors (Jankowski et al. 2010). Range boundaries are influenced by abiotic factors that have physiologically based explanations. At high elevations, abiotic factors include the variability and unpredictability in weather patterns, a shorter growing season, lower plant productivity, shorter nesting season, and seasonal delays in insect emergence are all important. Biotic interactions also influence species' relationships and their dynamics that have important implications for predicting future distributions of species (Van der Putten et al. 2010, Jankowski et al. 2013, Wisz et al. 2013). Asymmetry of interspecific competition may affect both the distribution of species over elevational gradients and the relationship between a species' realized and fundamental niches (Jankowski et al. 2013). Species that breed over a wider elevational range, such as Dusky Flycatchers, may show more variability in life history traits and have better competitive abilities (Bears et al. 2008).

A general pattern of biological communities is that species richness decreases with increasing elevation (Able and Noon 1976). This is true for bird species, their predators, and the food resources upon which they rely. Hammond's Flycatchers are one of the species that drops out at higher elevations. Similarly, another closely related *Empidonax* species, the Pacific-slope Flycatcher (*E. difficilis*), which also occurs in our study area, is found at lower elevations but does not occur in lodgepole pine habitat (Author, unpublished data). Based on the results presented here, differences in habitat structure are likely an important factor in the distribution of Hammond's Flycatchers.

This was an observational study rather than a true experiment, and the results presented here do not represent hard tests of cause and effect. Such experiments are challenging but provide the best evidence for distinguishing between alternative hypotheses for the causes of species turnover along environmental gradients (Martin and Ghalambor 2023). Empirical studies do not always demonstrate competitive exclusion among species occupying similar niches and, in some settings, coexistence among multiple species has been observed (Neill et al. 2009, Hening and Nguyen

2020). For example, recent work on Darwin's finches showed broad niche overlap, with species overlapping more in diet than expected by chance (De Leon et al. 2014, Villegas et al. 2021). Taken together, the results of this study provide important findings related to the habitat requirements of these two species and suggest how they might respond to climate change.

Conservation implications

Conservation of species depends on understanding their breeding biology and identifying the habitat features that affect their ability to survive and reproduce (Martin 1992). Studying species that segregate along environmental gradients may help us understand and better predict species' responses to climate change. With the expected warming in montane landscapes, upslope range expansion may occur, if conditions permit. Should Hammond's Flycatchers move upslope they will likely find a lack of their preferred nest sites in tall trees and increased vertical overlap with Dusky Flycatchers, increasing the possibility of competitive interactions between the two species.

In light of the potential effects of climate change on the ability of species to survive and reproduce in a changing environment, it is necessary to understand the ecological constraints and consequences of elevational movements to predict current and future elevational ranges and potential threats to montane species. To do so, we need to focus attention on understanding the factors that affect the geographic ranges of species and how species interactions might shift with changes in climate in a dynamic world.

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Data Availability:

The data code that support the findings of this study are available in Forest Service Research Data Archive at <https://doi.org/10.2737/RDS-2024-0023>, reference number RDS-2024-0023.

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