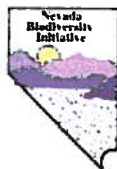# Avian Nest-site Selection and Nesting Success in Sierra Nevada Aspen

Final Report: 2003-2006

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SUMMARY

With the 2006 breeding season, fieldwork was completed for the fifth year of the Avian Use, Nest-site Selection, and Nesting Success in Sierra Nevada Aspen Project. The initial phase of the project, which was initiated in 2002 and focused on bird-habitat relationships using point counts, was completed in 2004. Results from this phase were summarized in a 2004 Final Report to NDSL and in Richardson and Heath (2004). The second phase, which was initiated in 2003 and focused on habitat factors related to nest site selection, nesting success, and nest predators, was completed in 2006 and is summarized here, predominately in the form of two manuscripts, modified chapters from Richardson's (2007) Ph.D. dissertation submitted for publication as companion pieces to the peer-reviewed journal *the Auk*. Data from this project have been published in three peer-reviewed scientific journals thus far (Richardson 2003, Richardson and Heath 2004, Richardson and VanderWall 2007). Including the two manuscripts that follow, four papers incorporating data from this project are currently in review (Richardson *In Review*, Richardson et al. *In review-a*, Richardson et al. *In review-c, b*), and one paper is currently in preparation (McCreedy et al. *In preparation*). I anticipate several additional papers to incorporate the results from this important study.

INTRODUCTION

Quaking aspen (*Populus tremuloides*) holds special ecological value as one of the very few species of hardwood trees that thrive in the mountains of the western United States, and it is essentially the only species of hardwood tree found in the Sierra Nevada east of the crest. The importance of aspen to birds and other wildlife in western North America has long been appreciated by biologists (Salt 1957, Flack 1976, DeByle 1985b). Many studies from this region have demonstrated that aspen habitats typically support much greater diversity, richness, and abundance of birds than adjacent conifer-dominated or mixed aspen-conifer habitats (Flack 1976, Winternitz 1980, Finch and Reynolds 1988, Mills et al. 2000, Rumble et al. 2001, Griffis-Kyle and Beier 2003). Further, recent work in the eastern Sierras suggests that aspen supports greater bird diversity than other types of riparian habitat (Heath and Ballard 2003, Figure 1).

Several bird species have shown a strong affinity with aspen, including Northern Goshawk (*Accipiter gentilis*), Red-naped and Red-breasted Sapsuckers (*Sphyrapicus nuchalis/ruber*), Dusky Flycatcher (*Empidonax oberholseri*), Warbling Vireo
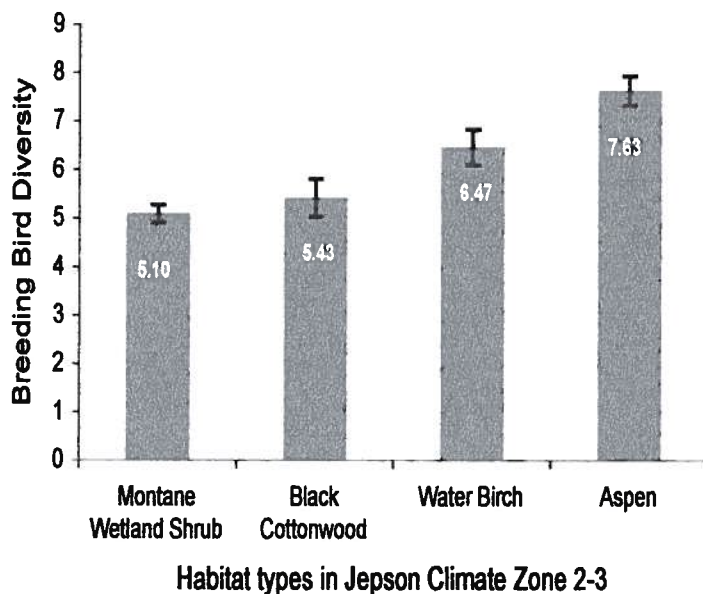

Figure 1. Breeding Bird Diversity in the eastern Sierra Nevada by riparian habitat type. Aspen BBD > all other habitats (*P*<0.02) (adapted from Heath and Ballard 2003).

(*Vireo gilvus*), Swainson's Thrush (*Catharus ustulatus*), and MacGillivray's Warbler (*Oporornis tolmiei*)(Salt 1957, Flack 1976, Finch and Reynolds 1988, Heath and Ballard 2003).

The obvious benefits to birds breeding in aspen stands are many, and principally affect nesting success through differences in the availability and quality of resources such as food or nest sites as well as the pressures of nest predation (Figure 2). Ground-nesting birds benefit from an exceedingly thick herbaceous layer and deep leaf litter, which aids in potential for nest concealment (Flack 1976, DeByle 1985b). Both primary and secondary cavity nesters benefit from aspen's susceptibility to heart rot and an associated abundance of cavity-bearing trees (DeByle 1985b, Daily et al. 1993). It is highly likely that one of the main benefits to all birds breeding in aspen stands is the increased abundance and diversity of invertebrate prey (Winternitz 1980). Refuge from nest predators primarily associated with conifers may also benefit birds nesting in the interior of larger stands (Sieving and Willson 1998, Willson et al. 2003).

Despite these benefits, this habitat may become greatly reduced for birds in the foreseeable future. Because western aspen primarily reproduce through vegetative suckering, generally following a disturbance of some kind, whole stands may succumb to conifer succession within a few hundred years if no disturbance occurs (e.g. fire suppression). Much of the aspen in the western United States is threatened in this manner, and much, if not most, of the historic aspen coverage in western states has already been lost (Mueggler 1988, Kay 1997, Bartos and Campbell Jr 1998, Bartos 2001), with an estimated 60% decline in aspen dominated-landscapes on National Forest

System lands in Utah alone (Bartos and Campbell Jr 1998). The current extent and

condition of aspen in the Sierra Nevada mountains of California and Nevada has yet
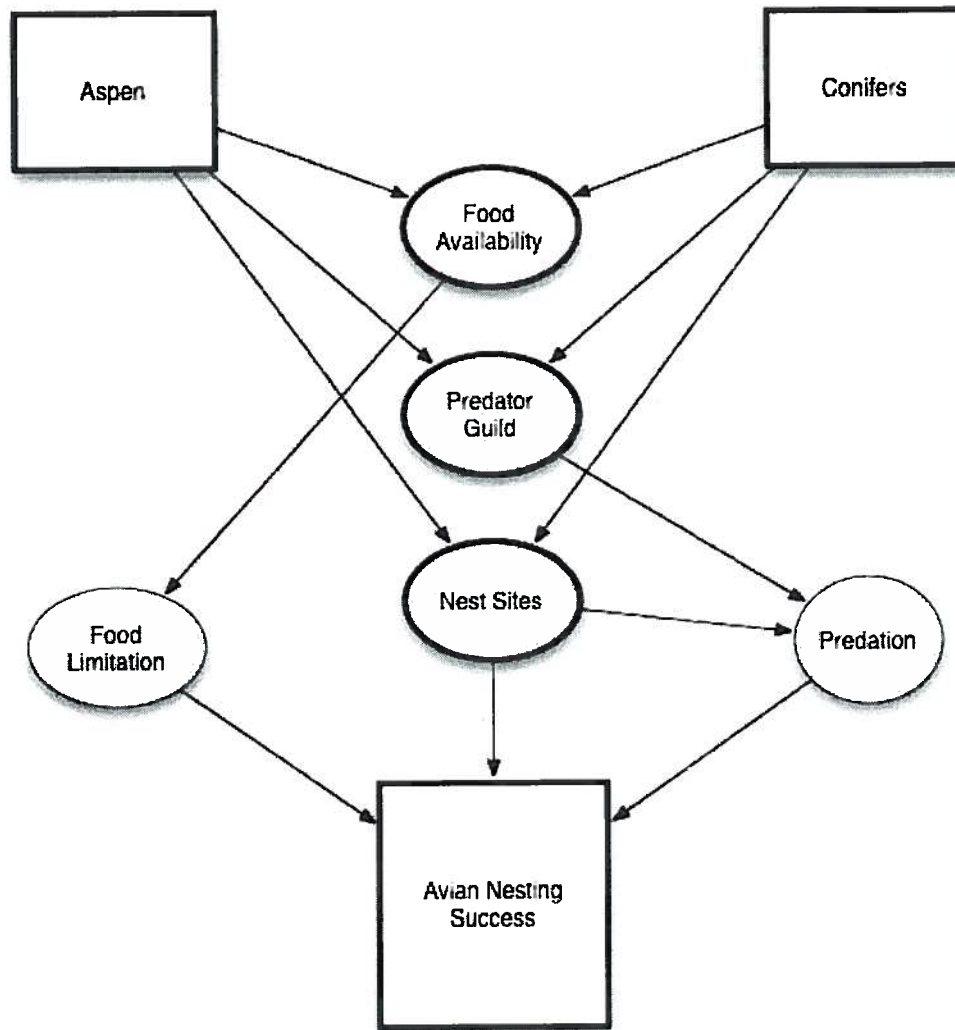
Figure 2. Conceptual model of indirect effects of aspen and conifer vegetation types on avian nesting success.

to be fully inventoried (Burton 2000). However, results from aspen stand condition

inventories on three National Forests across the Sierra Nevada indicate that the majority

of the stands found there are subject to the same factors implicated in the decline of aspen

in the Rocky Mountains and Intermountain West (Rich et al. 2001). Under current fire

regimes and without active management (livestock fencing, conifer thinning, etc.), most

small stands in the Sierra will be displaced by conifers (Rich et al. 2001). Due to reduced

aspen regeneration and accelerated succession of aspen to conifers in the Sierra, land

managers throughout the Sierra (including BLM, Lassen National Park, California Dept.

of Fish and Game, Lake Tahoe Nevada State Park, and at least seven USFS Ranger

Districts) have begun to investigate and engage in active aspen habitat management

(livestock fencing, conifer thinning, etc.; Burton 2002). These management actions will

have direct and indirect consequences on the birds utilizing the aspen vegetation type

(Figure 3).
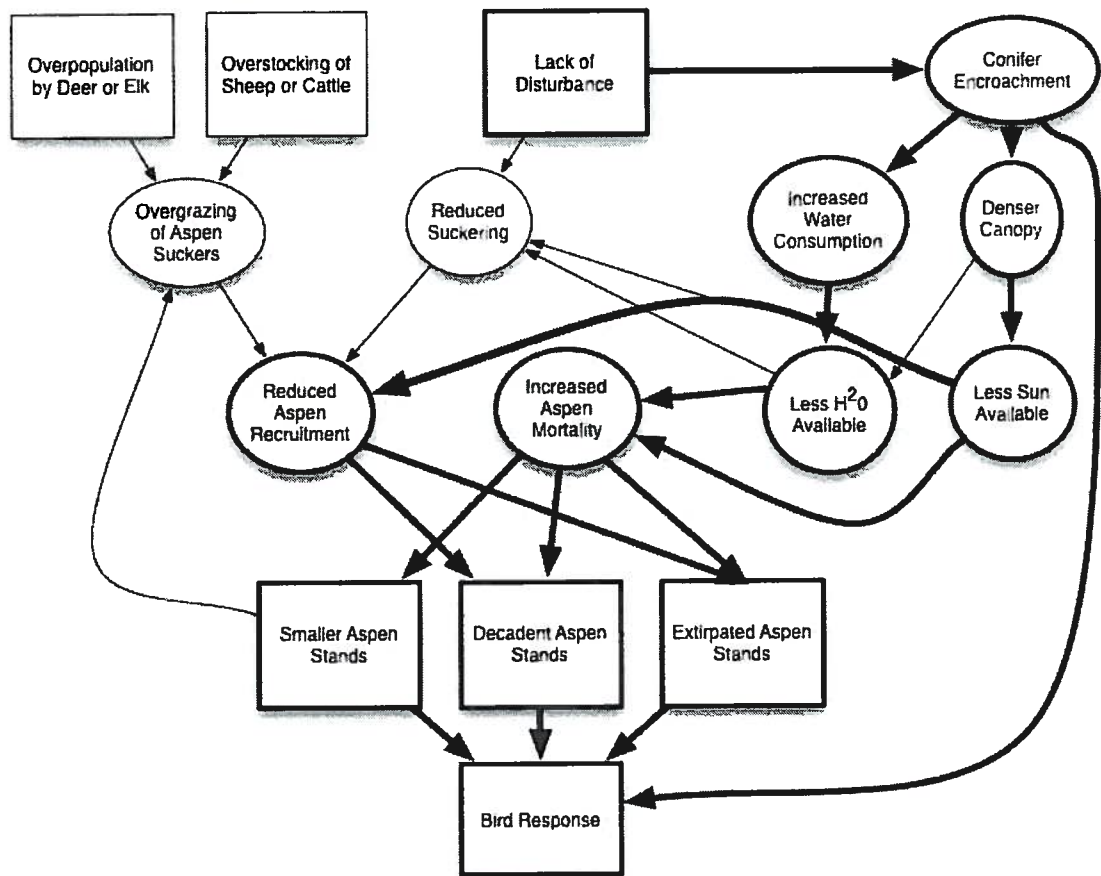
Figure 3. Conceptual model of the main threats to aspen in California and Nevada and their principal effects.

In light of the threatened status of aspen habitat, it is important to highlight the documented population declines and tenuous status of some aspen-associated bird species in the west. Western Warbling Vireo population declines are well documented (Gardali (Gardali et al. 2000, Gardali and Jaramillo 2001, Ballard et al. 2003) et al. 2000, Ballard et al. 2003), and Swainson's Thrushes are declining or have been extirpated from much of their historic breeding range in the Sierra Nevada (Verner and Boss 1980, Gaines 1988, Siegel and DeSante 1999). Northern Goshawk is a California Bird Species of Special Concern and a United States Forest Service, Region 5 Sensitive Species. Clearly, the losses incurred on both aspen and associated bird species warrant a more thorough investigation into the relationship between aspen, conifer encroachment, and the bird communities affected.

I conducted evaluations of avian use, nest-site selection, and nesting success among birds breeding in mixed aspen forests of the eastern slope of the Sierra Nevada mountains, California and Nevada, from 2002-2006. Specific questions addressed in this report are: (1) what are the preferred nest-site characteristics among birds breeding in aspen, and is nest-site selection affected by conifer density?, and (2) what are the important nest-site characteristics affecting nest predation among birds breeding in aspen, and in particular, does conifer density around the nest affect nest success?

SITE DESCRIPTION AND METHODS

Site Description

Study sites were selected to meet a number of criteria. The focus of this phase of the study addressed the effects of conifer encroachment on nest-site selection and nesting success. Thus, an attempt was made prior to the 2003 field season to locate the largest, purest aspen stands, but that were bordered by conifers on at least one side. Nest-searching plots were selected based on size and maturity of stand, apparent productivity, slope, and access considerations. Each contained areas of relatively pure aspen and various levels of conifer encroachment. Plots were located approximately 1950-2400 m elevation and 7.5 –14.5 ha in area. Several plots were purposefully placed within the boundaries of Lake Tahoe Nevada State Park to provide park managers with data and recommendations based on our findings. In 2003 these nest monitoring plots were established at the Fallen Leaf Lake Road, Logan House Creek, Glenbrook Creek, Marlette Basin, and Tunnel Creek sites (Figure 4). Due to budget constraints, the Fallen Leaf Lake Road site was not monitored in 2005.

Nest Monitoring

Nest searching began as soon as access permitted, typically between 20 May and 1 June, depending upon the site, and lasted until breeding activity declined in late August of each year. All nests were monitored to completion. BRRC biologists conducted all nest monitoring, following specific guidelines in Martin and Geupel (1993) and the BBIRD protocol (Martin et al. 1997). Special care was taken to minimize disturbance to the adults and nest site and human-induced predation probability. Nests of all species
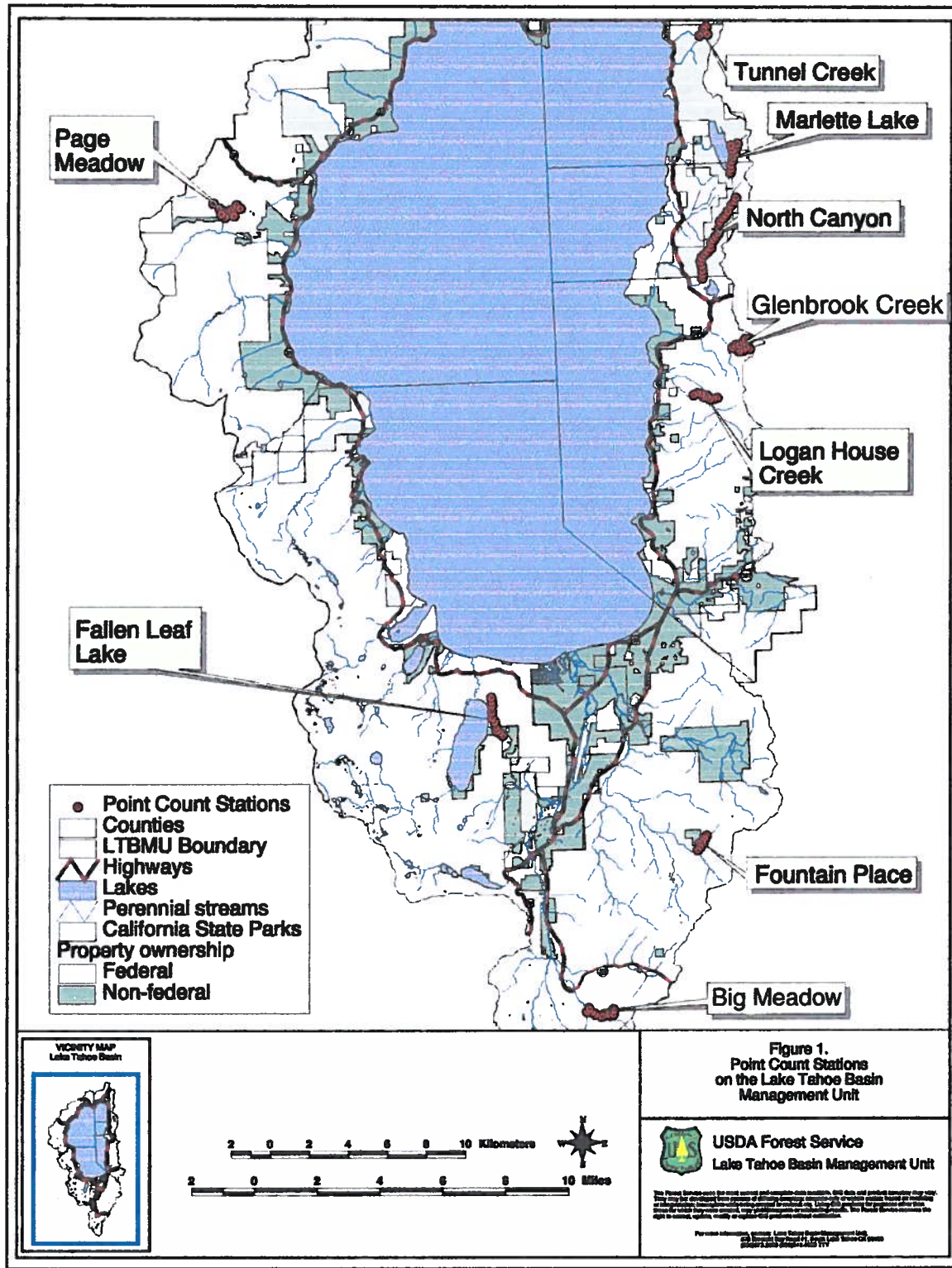
Figure 4. Study Area, Tahoe Basin

were located at all stages (construction, egg laying, incubation, and nestling). Nest outcomes were determined by checking nests every 1 - 4 days until completion, typically every other day. In 2005, six nests at the Logan House Creek site were monitored to completion with remote surveillance cameras. Incidences of parasitism by Brown-headed Cowbirds were noted, though parasitism rates were very low. Telescoping mirror poles were used to check the contents of high nests when possible. Nests of species such as Western Wood-Pewee (*Contopus sordidulus*), Warbling Vireo, and American Robin (*Turdus migratorius*) often remained unreachable due to height. For such nests parental, nestling, or fledgling behavior, or disturbance to the nest and other evidence were used to determine nest status and outcomes. All nest monitoring data were recorded and entered in a format compatible with the BBIRD program of the Fish and Wildlife Service Cooperative Unit at the University of Montana (Martin et al. 1997). Basic measurements of the nest and nest substrate were also recorded after outcome was determined. See Martin et al. (1997) for a complete list of data variables.

Nest Plot Vegetation Assessments

BRRC biologists conducted nest vegetation assessments at all nest locations, for which at least one egg was laid. Soon after the nesting attempt terminated, we measured the nest substrate and surrounding vegetation patch of each nest. A slightly modified version of the BBIRD method for vegetation measurements was used (Martin et al. 1997), which included a section for forb cover and average forb height by species. The basic units for vegetation sampling were a 5-meter radius plot (for shrubs, forbs and ground cover) and an 11.3-meter radius plot (for trees) centered on the nest. For cavity nesters and nests above 10 meters, detailed forb and shrub data were not taken. In 2004

all conifers within 60 meters of all nests and nest monitoring plot boundaries were

mapped and described by species and three height categories ($\geq$ 5m, $\geq$ 10m, and $\geq$ 20m),

a total of 6756 conifer trees. From these data we were able to calculate conifer densities

by species and height within variable-radius plots around each nest. For a detailed

description of BBIRD measurements and estimations used see Martin et al. (1997).

Statistical Analyses

Nest Monitoring

Nest success calculations were limited to nests with known outcome, which were

observed with at least one egg or young. Thus, all apparently abandoned nests cannot be

used for these analyses. Nest success was calculated using Program MARK (White and

Burnham 1999), which allows for more complex and realistic models of nest survival rate

that include covariates that vary by individual, nest stage, time, etc.(Dinsmore et al. 2002,

Rotella et al. 2004). Important parameters were assessed via AIC model selection

(Akaike 1973, Burnham and Anderson 1998). Of the hundreds of potential parameters

and covariates from the vegetation assessments, we selected those that were believed to

have a potential impact on nesting success based on *a priori* hypotheses. Additional

details are outlined in the second of the two following manuscripts.

Nest Site Selection

We investigated nest-site preferences with respect to canopy cover,

canopy height, nest orientation, tree density, and conifer density. For tree nesting species

(Western Wood-Pewee, Warbling Vireo, and American Robin), we additionally

examined nest tree height and diameter at breast height (dbh). For ground and shrub

nesters (Dusky Flycatcher and Oregon Junco (*Junco hymalis thurberi*)), we additionally examined shrub cover and forb cover. We investigated preferences using univariate comparisons, blocked by study site, of nests and the random, non-use sites. Nest tree species preference among arboreal nesting species was analyzed at two scales by comparing tree species use relative to availability at the territory scale (non-use, approximately 30 m), and availability adjacent to the nest tree (11.3 m radius). Additional details are outlined in the following manuscript.

Personnel

All aspects of fieldwork, project design and set-up, and data analysis were conducted by BRRC Research Associate and project director Will Richardson, with guidance from Program Director, Dennis Murphy. Nest monitoring was conducted by Will Richardson and BRRC field biologists Wendy Beard, Kevin Crouch, Jennifer Knight, Dacey Mercer, Eric Nolte, Alicia Rodrian, Ingrid Verhoeckx, and Neal Walker. Point counts were primarily conducted by Will Richardson, with assistance from Eric Nolte and Kristie Nelson. Assistance with statistical analyses was provided by UNR professors George Fernandez and Jim Sedinger.

NEST SUCCESS AND NEST SITE SELECTION

Between 2003-2006, 853 avian nests of 36 species were found and monitored. Determination of nest status proved difficult for many species, as mean nest height over the two year years was 815 ± 338 cm (range = 40-1900 cm) for Western Wood-Pewee and 937 ± 484 cm (range: 70-2150 cm) for Warbling Vireo. We had many nests over 15 m high. During 2005-2006, this effort was focused on five species: Western Wood-

Pewee, Dusky Flycatcher, Warbling Vireo, American Robin, and Oregon Junco. I selected these five species because they each had sufficient sample sizes (across the four years, these five species provided 492 active nests for hypothesis testing) and nested in open cup nests, making them more susceptible to predation (Martin and Li 1992). Additionally, their nest locations collectively represented the major vegetation strata of interest: canopy, shrub, and ground. Results for these five species are summarized in great detail in the following two manuscripts.

In 2005, attempts were made to use video surveillance techniques to positively identify the dominant nest predators of aspen-breeding birds. However, none of the nests monitored with cameras was depredated, a highly improbable outcome, statistically speaking. This result led to an investigation of potential camera-effects on nest predation, which has been submitted for publication to the Journal of Wildlife Management (Richardson et al. *In review-a*).

AVIAN NEST-SITE SELECTION IN SIERRA NEVADA ASPEN STANDS

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Abstract

Selection of nest-sites is critical to reproductive success in birds. Recent research has shown that conifer density surrounding nests of birds breeding in mixed aspen stands was negatively correlated with models of nest success. We examined nest-site selection among five species of passerines breeding in mixed aspen stands of the Sierra Nevada mountains, to determine if nest-sites were chosen relative to conifer density. We also examined nest-site selection relative to two previously published, non-competing hypotheses (the *potential prey-site* and *nest-concealment hypotheses*), and a third, non-competing hypothesis, which we introduce here: the *predator-barrier hypothesis*. We found little evidence to suggest that birds nesting in aspen select nest placements relative to conifer density, although we found strong evidence for selection of aspen for use as nest trees among arboreal nesters. For many cases, the potentially adaptive benefits of nest-site preferences were clearly linked to nest success based on models published elsewhere, and we found evidence supporting nest-site selection consistent with predictions of all three hypotheses. In several cases, nest-site preferences were theoretically consistent with, but not empirically linked to, increased nest success. Several apparent nest-site preferences could not be readily explained.

INTRODUCTION

Selection of nest-sites is critical to reproductive success in passerine birds. Discovery of a passerine nest by a predator typically results in complete failure of that reproductive effort. Indeed, survival of a clutch of eggs to fledging may depend more on the location of the nest than any other factor, including food provisioning and parental behavior; thus, there is strong selective pressure exerted on birds to deter nest predators by selecting nest-sites that are less likely to be discovered or are inaccessible to predators (Collias and Collias 1984). The selection of a nest-site can be examined on three spatial scales: (1) nest-site (that is, the immediate vicinity of the nest), (2) nest patch (characteristics of the habitat patch surrounding the nest), and (3) landscape or stand-level characteristics. The three scales address different but somewhat overlapping factors relating to structural support, control of egg and nestling temperature, shelter from predators and weather, and availability of nesting material and food resources. Of these considerations, the need for security from predators is likely to exert the greatest influence on nest-site selection at all three scales (Collias and Collias 1984).

At nest-site and nest patch scales, two primary hypotheses have been proposed to explain nest-site selection as it relates to predation. The *nest-concealment hypothesis* predicts that increased density of vegetation at the nest-site level impedes detection of nests by potential nest predators and therefore lowers predation risk (Martin 1993b). Increased vegetation around the nest-site can also impede foraging or even locomotion of small mammalian nest predators (Bowman and Harris 1980, Holway 1991), and can help conceal activity of adult birds as they travel to and from their nests (Holway 1991, Kelly 1993). The *nest-concealment hypothesis* predicts that birds should preferentially select

well-concealed nest placements, and that nest concealment and increased density of vegetation should positively affect nest survival. Support for this hypothesis has been equivocal (reviews by Martin 1992a, Burhans and Thompson III 1998). The *potential prey-site hypothesis* predicts that search efficiency of a predator decreases as the number of potential nest-sites increases at the nest patch scale (Bowman and Harris 1980, Martin and Roper 1988, Martin 1993b); therefore, birds that select sites with greater numbers of potential nest-sites immediately surrounding their nests should have higher nest success, which should, in turn, promote this strategy of nest-site selection. Support for the *potential prey-site hypothesis* also has been inconsistent (Martin and Roper 1988, Kelly 1993, Martin 1993b, Steele 1993, Liebezeit and George 2002).

We propose a third hypothesis, *the predator-barrier hypothesis,* for birds that utilize substrates that prevent or seriously impede predator access. Many species of birds exploit substrates that effectively cannot be reached by nest predators. Examples include species that nest on predator-free islands, on sheer cliffs, or among thorny plants. Among passerines and woodpeckers, smooth bark has been demonstrated to decrease or prevent nest predation by snakes, putatively explaining increased nesting success for a number of bird species (Rudolph et al. 1990, Hooge et al. 1999, Saenz et al. 1999, Mullin and Cooper 2002). Recent experiments have shown that chipmunks cannot climb the smooth bark of aspen trees (Richardson and VanderWall 2007), suggesting that aspen bark may act as an impediment or barrier to small mammalian nest predators. Thus, the *predator-barrier hypothesis* predicts that arboreal nesting birds should preferentially select aspen trees for placement of their nests, and that within a given species nests in aspen should have higher nest success than those in conifer trees or low shrubs. Among ground-

nesting species, birds should preferentially place nests in areas of dense vegetation. None of these hypotheses relevant to the nest-site and nest patch scales is mutually-exclusive.

A stand-level perspective of nest-site selection assumes that birds actively avoid high densities of nest predators by simply nesting elsewhere (Fontaine and Martin 2006, Siepielski 2006). Studies from throughout western North America have shown consistently higher densities of birds in pure aspen stands than in either coniferous forest types or mixed aspen-conifer stands (Finch and Reynolds 1988, Mills et al. 2000, Rumble et al. 2001, Griffis-Kyle and Beier 2003, Richardson and Heath 2004). This may be due, in part, to higher densities of predators, and therefore higher predation rates, where conifers dominate. Studies from Canada and Alaska have shown that risk of nest predation from *Tamiasciurus* squirrels is higher in coniferous habitats than deciduous habitats (Sieving and Willson 1998), suggesting that nest success may decrease as cone-bearing trees and *Tamiasciurus* reach higher densities (Sieving and Willson 1998, Willson et al. 2003). In the central Rocky Mountains, Struemph (2000) found that most birds had higher nesting success in pure aspen stands than in nearby mixed or coniferous forests. Such stand-level dynamics might be expected to scale down to the nest patch scale. Steller's Jays (*Cyanocitta stelleri*) may reach highest densities at the border of coniferous and deciduous forest (Sieving and Willson 1998), and in mixed conifer-aspen forests of the Sierra Nevada, both douglas squirrel and Steller's Jay presence were positively correlated with density of fir (*Abies*) trees (TWR, unpub. data). As conifers encroach into aspen forests, nest predators associated with conifers are likely to increase in the interdigitated aspen, either numerically or in terms of space use. Because nest-site selection is a response to predation pressures, we expect birds nesting in aspen forests to

select preferentially those locations that minimize risk of nest predation by nesting in areas of lower than average conifer densities.

We examined nest-site characteristics and preferences among cup-nesting birds breeding in mature aspen forests in the Sierra Nevada, California and Nevada: Specifically, we sought to (1) examine nest placement relative to vegetation available within the aspen stands, and immediately adjacent to actual nest locations, (2) examine nest placement relative to conifer density, and (3) determine if apparent nest-site preferences conform to predictions of the *nest-concealment, potential prey-site*, and *predator-barrier hypotheses* and are adaptive based on models of nest success from this study system (Richardson 2007).

METHODS

Nest monitoring and vegetation assessments

Data were collected from 2003-2006, at five large aspen stands in the Lake Tahoe basin, California and Nevada. Study sites were approximately 7.5 – 14.5 ha in area, corresponding to the size of the aspen stands. Four sites were located at approximately 2400m in the Carson Range on the east side of the basin, and the fifth was at approximately 1950m, on the southwest side of Lake Tahoe. The lower elevation site was not monitored in 2005 due to a budget shortfall. Dominant shrubs included *Symphoricarpos, Ribes*, and young aspen and conifers. Each site contained areas of relatively pure aspen, typically associated with lush herbaceous ground vegetation, and areas of high conifer density. Each site was bounded by conifer forest on at least one side, and sites were encroached to varying degrees by a mix of Jeffrey and lodgepole pine (*Pinus jeffreyi* and *P. contorta*) and red and white fir (*Abies magnifica* and *A. concolor*).

Nests were located and monitored following Martin and Geupel (1993), minimizing human-induced predation probability and disturbance to the adults and nest-site, and visited every 2-4 days until nest completion. Efforts were focused on five open-cup nesting species that were both common and spanned the vertical gradient of nesting substrates: Western Wood-Pewee (*Contopus sordidulus*), Dusky Flycatcher (*Empidonax oberholseri*), Warbling Vireo (*Vireo gilvus*), American Robin (*Turdus migratorius*), and Oregon Junco (*Junco hyemalis thurberi*). Only nests known to have contained at least one egg were considered for these analyses. We conducted nest-site assessments after the completion of nest cycles following a modified BBIRD protocol (Martin et al. 1997). Canopy height, nest plant height, and nest height were either measured directly or with a clinometer. Plant diameter at breast height (dbh) was measured directly with a diameter tape. Percent canopy cover was estimated using average counts from a spherical densiometer. We made ocular estimates of lateral, above nest, and below nest concealment. Nests with average concealment scores greater than 50% were considered well-concealed, while nests with average concealment scores less than 30% were considered conspicuous. Ocular estimates of percent shrub and herbaceous cover were estimated within a 5 m radius of each ground or shrub nest. All trees within 11.3 m of each nest were recorded to species and according to three size-classes: 8-23 cm, 23-38 cm, and > 38 cm dbh. To establish the extent of conifer encroachment relative to each nest, UTM coordinates were mapped for nest locations and every coniferous tree (>5m in height) within 60 m of the plot boundaries. Trees surveyed were identified to species and assigned to one of three height categories (5-10 m, 10-20 m, >20 m). Densities of fir and pine, according to size class, were then obtained within 25 m and 50 m of each nest,

using GIS. We then used principal components analysis to reduce these measures, along with the conifer densities at the 11.3m radius scale, into a biologically meaningful index of conifer density. Non-use nest-site vegetation assessments were conducted at 35 random points (simulating five ground nests and 30 tree nests) within each nest plot, following the same protocol for nest-sites. Non-use sites were located at (ground) or nearest to (tree) a point 30 m distant in a randomly selected direction from randomly selected nests.

Data Analysis

For all five species, we investigated nest-site preferences with respect to canopy cover, canopy height, nest orientation, tree density, and conifer density. For tree nesting species (Western Wood-Pewee, Warbling Vireo, and American Robin), we additionally examined nest tree height and diameter at breast height (dbh). Random trees were restricted to aspens for comparisons of tree size preference by Western Wood-Pewee and Warbling Vireo, due to their strong preference for that species. For ground and shrub nesters (Dusky Flycatcher and Oregon Junco), we additionally examined shrub cover and forb cover. We investigated preferences using univariate comparisons, blocked by study site, of nests and the random, non-use sites. Nest tree species preference among arboreal nesting species was analyzed at two scales by comparing tree species use relative to availability at the territory scale (non-use, approximately 30 m), and availability adjacent to the nest tree (11.3 m radius), using Fisher's Exact Test. All statistical tests were performed in Program R, version 2.4.1 (RDCT 2006); and, nest orientations were examined with Rayleigh's Tests as implemented in the statistical package "Circular" (Agostinelli and Lund 2006). Means are reported with associated standard deviations.

<p style="text-align:center">RESULTS</p>

We found 492 active nests of the five focal species: Western Wood-Pewee (n = 87),

Dusky Flycatcher (n = 54), Warbling Vireo (n = 152), American Robin (n = 115), Oregon

Junco (n = 84). Only one species, Western Wood-Pewee, appeared to select nest-sites

relative to conifer density (Table 1). Nest orientation was random with respect to

compass bearing for all but one species, Oregon Junco (Figs. 1 and 2).

Western Wood-Pewee

Western Wood-Pewee nests typically were very conspicuous (mean concealment

score = 27 ± 25 %), located from one to several meters from the tree bole on dead,

horizontal limbs, often secured to a horizontal fork in the branch. These locations

generally were adjacent to, and often oriented towards, small openings in the mid-story

and canopy, as reflected by their preference for less canopy cover ($F_{3,261} = 4.87$, $P =$

0.028) and fewer small trees within 11.3 m of the nest tree ($F_{3,261} = 10.33$, $P = 0.001$;

Table 1). Nest orientation, however, was random with respect to compass bearing (Fig.

1). Mean nest height was 815 ± 338 cm (range = 40-1900 cm), with little overlap with

Dusky Flycatcher nests (Fig. 3). Mean nest plant height was 1856 ± 499 cm, which was

significantly higher than the mean height of non-use aspen trees ($F_{3,229} = 31.33$, $P <$

0.001; Table 1), and mean nest plant dbh was 32.0 ± 10.2 cm. Wood-pewees selected

trees that were taller than random for either their nest tree, nest patch (canopy height:

$F_{3,261} = 4.46$, $P = 0.036$), or both, but due to collinearity between nest tree height and

small tree density (8-23 cm dbh, r = -0.28, $P < 0.001$) and nest tree height and canopy

height (r = 0.56, $P < 0.001$), we could not disentangle those apparent preferences.

Canopy height and small tree density were also significantly correlated for this species (r

= -0.32, $P < 0.001$). Eighty-six nests (98.9%) were located in aspen, and one nest was placed in a western juniper (*Juniperus occidentalis*). This preference for aspen was disproportionate to the number of aspen available at the nest-site and territory scales ($P < 0.001$; Table 2). Because wood-pewees selected for larger trees, many of the smaller aspen trees considered to be "available" actually may have been unsuitable as nest-sites; therefore, the preference for nesting in aspen may be even more pronounced than our data suggest. Despite the clear preference for placing nests in aspen, Western Wood-Pewees selected nest-sites that had greater densities of conifers than non-use sites ($F_{3,261} = 7.37$, $P = 0.007$; Table 1).

Dusky Flycatcher

Dusky Flycatchers were absent from the low elevation site. Early-season nest structures were often completed a week or more before nest lining and clutch initiation, and in several instances nests were relocated before to clutch initiation. Dusky Flycatcher nest height ranged from 25 to 1800 cm (mean = 293 ± 392 cm), though slightly over half (52%) were placed 0.25-1.25 m above the ground (Fig. 3, median height = 120 cm). These nests typically were in heavily browsed, shrubby aspen or placed in low shrubs such as *Ribes* (n = 9), *Artemisia* (n = 2), *Salix* (n = 1), or *Symphoricarpos* (n = 1). One nest was placed on the underside of a fallen log, supported by peeling bark. An additional 31% of nests were placed in slightly taller aspen saplings, and the remaining nests above 5 m (17%) were all in large diameter aspen (Table 2). Nests in aspen saplings or trees were placed in vertically oriented crotches where branches met the bole of the tree. Despite universal placement of tree nests in aspen, this preference was not significantly different from species availability at the nest-site ($P =$

0.143) and territory scales ($P = 0.221$; Table 2), due to insufficient statistical power. Approximately 30% (n = 16) of Dusky Flycatcher nests were in trees > 10 cm dbh. Nest-site selection was non-random with respect to canopy height (lower; $F_{2,194} = 4.97$, $P = 0.027$), shrub cover (greater; $F_{2,194} = 5.84$, $P = 0.017$), and forb cover (less; $F_{2,194} = 17.38$, $P < 0.001$; Table 1); however, because significant collinearity was detected between shrub cover and forb cover (r = -0.26, $P < 0.001$), the apparent preference for less herbaceous cover may simply reflect a preference for greater shrub cover, or vice versa. Overall mean concealment score was 43 ± 26 % for Dusky Flycatcher nests.

Warbling Vireo

Early-season nest building efforts by this species were particularly general and indecisive with regards to site; vireos often initiated multiple nests concurrently, and shuttled nest-building material back and forth between several partially completed nests, before ultimately settling on a nest-site. This behavior was seldom observed after the first month of each breeding season. Mean nest height for vireos was 937 ± 484 cm (range: 70-2150 cm). Most vireo nests were placed high in the canopy, typically well away from the center of the tree, in the densest foliage of the crown (mean concealment score = 59 ± 22 %). Nest height and nest tree height, therefore, were highly correlated (r = 0.83, $P < 0.001$). Mean nest tree height was 1447 ± 654 cm (range: 197-2900 cm), although use was skewed towards taller trees (Fig. 4). Mean nest plant dbh was 24.7 ± 13.9 cm (range: 2-65 cm). Nests were located in trees that were smaller in diameter than unused aspens ($F_{3,271} = 4.25$, $P = 0.040$), although vireos exploited a wide range of tree sizes (Fig. 4). Nest locations also had reduced densities of large trees (>38 cm dbh), although this difference was only marginally significant ($F_{3,326} = 3.36$, $P = 0.068$).

Furthermore, we found significant site interactions with this effect, suggesting that this relationship was only significant for the site with the highest density of large trees. Warbling Vireo nests were almost exclusively placed in aspen at these study sites (99.3% of nests), although one nest was placed in a lodgepole pine. This preference for aspen was disproportionate to the number of aspen available at the nest-site and territory scales ($P < 0.001$; Table 2).

American Robin

Consistent with the known plasticity in nest placement among American Robins (Howell 1942, Sallabanks and James 1999), robins used a wide variety of nest-sites in our study, and nest placement was nearly completely random with respect to the nest-site and habitat variables examined (Table 1). Despite this variation, robin nests often were placed high in aspens, flush against the bole where a lateral branch formed a crotch. Nest height and nest tree height were highly correlated (r = 0.69, $P < 0.001$). Mean nest height was 702 ± 535 cm (range: 10-2400 cm). Mean nest tree height was 1331 ± 798 cm (range: 57-3400 cm) and mean nest plant dbh was 24.1 ± 13.3 cm (range: 4-86 cm). Nest trees were smaller in diameter than randomly chosen trees ($F_{3,256}$ = 8.97, $P = 0.003$), although this comparison was not significant when restricted to aspens. The overall mean concealment score for American Robin was 48 ± 22 %. Post-hoc comparisons found no evidence of seasonal shifts in species use or nest height for robins (*cf.* Howell 1942, Savard and Falls 1981, Warkentin et al. 2003). We had insufficient data to examine statistically any seasonal shifts in nest tree species use, but mean clutch initiation date was almost identical for conifers (15 June ± 6 days, n=6) and deciduous trees (16 June ± 15 days, n=109), with conifer use essentially limited to the peak of the breeding season.

Clutch initiation date explained almost none of the variation in nest height (simple linear regression; $r^2 = 0.003$, $F_{1,112} = 0.302$, $P = 0.538$), and orientation was random (Fig. 1, $P = 0.683$). Robin nest tree selection was proportional to species availability at the nest-site scale, but showed a marginally significant preference for aspen at the territory scale ($P = 0.052$; Table 2). One hundred and seven robin nests (93%) were placed in aspen. Three nests each were placed in small white and red fir (mean plant height, 349 ± 152 cm; mean nest height, 227 ± 94 cm), and two nests were placed in mountain alder (*Alnus incana*; mean plant height, 525 ± 35 cm; mean nest height, 285 ± 35 cm).

Oregon Junco

Junco nests were universally well-concealed (mean concealment score = 87 ± 16 %) and placed in small depressions in the ground, under overhanging leaf litter or herbaceous growth, often in rodent burrows or under an overhanging shrub stem that had collected litter. These overhangs typically were oriented downslope. As most of the study area had a western aspect (mean aspect at junco nests = 262°), this circumstance led to a significant correlation between aspect and orientation of nest openings (Fig. 2; mean nest orientation = 248°, circular $R = 0.33$, $P = 0.006$). Junco nests were often found in small clearings and openings in the canopy. These openings typically had no trees within 11.3 m and no measurable canopy (recorded as 0 for canopy height and canopy cover). Such openings greatly lowered the average values for canopy cover, canopy height, and density of mid-sized trees. Canopy cover, which was correlated with both canopy height ($r = 0.26$, $P < 0.001$) and tree density (23-38 cm dbh, $r = 0.34$, $P < 0.001$), was, thus, probably the best indicator of nest-site preference. Additionally, there was less shrub cover at junco nests than non-use sites. In several instances, two active junco nests were

located within 10-15 m of one another; we were unable to determine whether these cases represented adjacent territories or polygamy.

DISCUSSION

Nest-site selection for individual species was largely consistent with general trends reported elsewhere (see reviews in Sedgwick 1993a, Bemis and Rising 1999, Sallabanks and James 1999, Gardali and Ballard 2000, Nolan Jr. et al. 2002). The potentially adaptive benefits of nest-site preferences were clearly linked to nest success (Richardson et al. *In review-c*), and we found evidence of nest-site selection consistent the *nest-concealment, potential prey-site,* and *predator-barrier hypotheses* (Table 3). While we did not quantify concealment relative to availability, the fact that Warbling Vireos placed their nests in dense foliage of outer tree crowns, and the relatively high mean concealment scores for this species, was consistent with the positive relationship between concealment and survival (Richardson 2007), and supports the *nest-concealment hypothesis*. Consistent with this preference, Smith et al. (2005) found that Warbling Vireo nest success was higher in nests placed towards the periphery of tree foliage, and suggested that the small diameters of supporting branches might limit access by Douglas squirrels, consistent with the *predator-barrier hypothesis*. The apparent preference for somewhat infrequent tall yet smaller-diameter trees by Warbling Vireos may be related to avoidance of the sparse canopies found in the largest diameter aspen at these sites, many of which were extremely old and decadent. Also, due to the increased height/dbh ratio of forest-interior aspen (Ek 1974, King 1981), vireos may select for nest trees located away from open edges; however, distance to open edge was not measured, and many vireo nests were found adjacent to forest openings or edges (TWR, pers. obs.).

In several cases, nest-site preferences were theoretically consistent with, but not empirically linked to, increased nest success. For example, Western Wood-Pewee had strong preferences regarding nest tree and canopy height, canopy cover, and tree density surrounding the nest. Behavioral observations suggest that a preference for nesting adjacent to small openings in the mid-story may facilitate simultaneous foraging and nest vigilance, especially during egg laying and nestling periods. Tall, self-pruning aspen provided the larger dead limbs favored by wood-pewees, and conspicuous nest placement may provide the birds clear views of the nest from the surrounding area as well as a clear view of incoming threats while at the nest. These are all important elements that likely facilitate the aggressive nest defense for which this species is known, yet none of these factors was important for predicting wood-pewee nest survival at these sites (Richardson 2007).

We found that Dusky Flycatchers selected nest-sites with higher shrub densities than would be expected at random, consistent with the *potential prey-site hypothesis*, yet shrub cover was not an important predictor of nest success at our sites (Richardson et al. *In review-c*). Successful shrub-nesting Dusky Flycatchers were found in areas with slightly higher than mean surrounding shrub cover, but this difference was not significant. We found little variation in shrub cover among Dusky Flycatchers, and this lack of variation certainly reduced our ability to detect a relationship between shrub cover and nest survival. One seemingly contradictory result is not easily explained; we found that Oregon Junco nests were placed in locations that had lower than random shrub cover, a result that does not conform to the predictions of any of our hypotheses, yet shrub cover had a positive relationship with junco nest success (Richardson et al. *In review-c*).

We found strong evidence for selection of aspen as nest trees among arboreal nesters. Nest placement is often evolutionarily conservative for many passerines (Martin 1993b), and Warbling Vireo is associated with the genus *Populus* throughout its range (Gardali and Ballard 2000). However, the preferences observed at our sites were not reflections of genetic constraints. All five study species range widely over diverse vegetation and habitat types across the west (Western Wood-Pewee, Dusky Flycatcher) or North America (Warbling Vireo, American Robin, Dark-eyed Junco (*J. hyemalis*)), and all might be considered habitat generalists to varying degrees. Additionally, the four species of arboreal nesters commonly place nests in conifers adjacent to aspen stands in this study (TWR pers. obs.) and throughout western North America (Kelly 1993, Sedgwick 1993b, Curson et al. 1996, Chace et al. 1997, Liebezeit and George 2002, 2003, Warkentin et al. 2003, Dobbs 2005, Smith et al. 2005). As widespread generalists, these species are likely to encounter highly variable nest-site selection pressures throughout their respective ranges, and nest-site preferences should reflect adaptation to local conditions to varying degrees, depending on gene flow from adjacent habitats (Willson and Gende 2000). Indeed, Warkentin et al. (2003) found that American Robin in central Nevada used aspen less frequently, and pines more frequently, than expected by chance. Slightly north of our study area, Smith et al. (2005) reported finding Warbling Vireo nests in aspen and lodgepole pine with approximately equal frequency, although they did not quantify availability of tree species. Thus, the apparent preferences toward aspen found in our study are likely the result of local adaptations.

At these study sites, birds locating their nests in mature aspen potentially experience dual benefits in terms of predation. Because aspen is the most abundant tree

species at these sites, it provides the most potential nest-sites for predators to search, making it difficult for predators to become efficient, as predicted by the *potential prey-site hypothesis*. Additionally, the smooth bark of aspen may also provide a barrier or impediment to mammalian nest predators such as sciurid rodents, consistent with the *predator-barrier hypothesis* (Richardson and VanderWall 2007). These advantages were supported at these sites by higher proportional nesting success in aspen for all arboreal nesters and positive relationships between nest height and nest survival in robins and nest plant diameter and nest survival in Dusky Flycatcher (Richardson et al. *In review-c*). Slightly north of our study area, Smith et al. (2005) found higher nest success among Warbling Vireos nesting in aspen versus lodgepole pine. However, this difference was not statistically significant, and no distinction was made between predation and other causes of failure. At our sites the *potential prey-site* and *predator-barrier hypotheses* were non-competing, because aspen was the most abundant species of tree available. Future study may be able to assess the relative importance of these two hypotheses by examining nest-site selection in habitat where aspen are outnumbered by conifers.

Why Dusky Flycatchers were absent from the low-elevation study site is unclear. The site appeared to provide suitable habitat, and the species was found < 1.5 km away, at the same elevation and in similar vegetation, all of which was part of one large complex of aspen stands (TWR, unpub. data). However, this site was a relatively young aspen stand, with a high density of smaller trees. It also had the lowest canopy, on average, and a high density of breeding Western Wood-Pewees. Why more Dusky Flycatchers did not nest in aspen trees is also uncertain. This is an important question, as nesting in aspen trees could have clear fitness benefits for this species (Richardson and

VanderWall 2007, Richardson 2007). Martin (1993) suggested that nest placement is often evolutionarily conservative and therefore may be constrained by evolved preferences over a large geographic area. Stereotypy of nest placement in low shrubs among Dusky Flycatchers may be simply an adaptive trait from adjacent habitats or on a regional scale. However, this species has shown considerable plasticity in nest placement across the species' range (Sedgwick 1993a), and nests in large trees have been reported in other studies (Liebezeit and George 2002, Dobbs 2005).

An alternative explanation may be that nest placement by Dusky Flycatchers is constrained due to interspecific competition, as suggested by regularly observed agonistic interactions between the two species of flycatchers. Western Wood-Pewees were both numerically and behaviorally dominant over Dusky Flycatchers at our study sites, although often there was considerable apparent overlap in territories between the species. Though circumstantial, Dusky Flycatcher density consistently was highest at the study site with the lowest wood-pewee density. Most of this site comprised mature, tall aspen and may have allowed for greater vertical partitioning of niches. Beaver and Baldwin (1975) found Hammond's Flycatcher (*E. hammondi*) territories overlapping with those of Western Wood-Pewee in Colorado "only in tall, well shaded aspen forest." As Fig. 3 demonstrates, we found very little overlap in nest height between the two species. Foraging behavior was not quantified in our study, but Western Wood-Pewees and Dusky Flycatchers were observed to partition the forest vertically for foraging as well as nesting. Beaver and Baldwin (1975) contended that territories of two flycatcher species could overlap only if they had very little overlap in prey size. They found Hammond's Flycatchers nesting high in aspen ("above 30 ft and on the main stem") where territories

overlapped with wood-pewees, but believed that the two species were sufficiently

morphologically distinct that they did not compete for food (Beaver and Baldwin 1975).

Dusky Flycatchers, however, are larger than Hammond's Flycatchers in terms of bill

morphology and general dimensions (Johnson 1963, Pyle 1997). Thus, their prey size

may overlap with Western Wood-Pewees sufficiently that the dominant wood-pewees

maintain interspecific territories within the middle and upper strata of the forest. More

study is required to determine whether Dusky Flycatcher nest placement in aspen stands

is determined by genetic constraints or interspecific competition.

We found no preference for nest orientation relative to compass bearing for the

four shrub and tree nesting species. Others have found significant nest orientation

preference for Warbling Vireo nesting in non-aspen (Walsberg 1981, Smith et al. 2005)

and American Robin in the Great Basin (Warkentin et al. 2003, but see review by

Sallabanks and James 1999). However, Smith et al. (2005) also found that vireo nests in

aspen demonstrated no orientation preference. Steep and varied topography at the study

sites complicated effects of aspect on insolation, and our study sites were largely closed-

canopy. Therefore, the potential thermal benefits of being on one side of an individual

tree canopy would be greatly diminished by the canopy of adjacent trees. Despite being

closed, a heavy canopy of aspen provides protection from storms (Pereyra and Morton

2001), while leaf flutter provides spatially uniform insolation in the understory (Rodden

and Pearcy 1993) and thus more spatially uniform temperature (Smith et al. 2005).

Oregon Junco showed a preference for nest orientation, but this was a byproduct of slope

aspect, as nest entrances almost always faced downhill. While nesting on a slope may

increase risk of predation in some systems (Whittingham et al. 2002), it is typical for

juncos (Nolan Jr. et al. 2002). At our study sites, nesting on slopes increased the opportunity for highly cryptic nest-sites located beneath leaf litter, with the added benefit of shelter from harsh environmental conditions. Late spring snowfalls are a regular occurrence in the Sierra Nevada, and snow, sleet, or hail may fall at any time during the summer. The preference by juncos for snow-bearing roofs over their nests was noted by Hanford (1913), who found two nests built inside discarded tin cans, successfully sheltering eggs and young, respectively, from several inches of snow.

We found little evidence to suggest that birds nesting in aspen select nest placements relative to conifer density. The only species that exhibited nest placement that was non-random with respect to conifer density, Western Wood-Pewee, placed their nests at higher than random densities of conifers. This was opposite our prediction based on assumed differences in predation pressure. All four shrub and tree nesting species, including Western Wood-Pewees, demonstrated evidence of reduced nesting success related to higher densities of conifers immediately surrounding the nest (Richardson et al. *In review-c*). However, three of these species also demonstrated a positive relationship between nest survival and conifer densities at larger scales. It is possible that our overall measure of conifer density may be correlated with other landscape features not considered here. For example, conifer density at three of the study sites was highest not outside the edge of the aspen stands, but along watercourses running through the sites. Moisture conditions have been important for predicting nesting locations at the patch scale in other shrub and tree nesting birds, such as thrushes (Dilger 1956, Martin and Roper 1988), though possible mechanisms for such a preference by an arboreal flycatcher are unknown. Such landscape features may affect nest-site selection as it relates to

different suites of predators, availability of resources, microclimate, nest parasitism, or a combination of these factors.

Fontaine and Martin (2006) were able to experimentally link habitat choice by forest birds with varying densities of nest predators, and at least one study has been able to demonstrate that nest selection preferences had clearly adaptive benefits (Martin 1998). However, observational studies often have been unable to demonstrate direct avoidance of high densities of predators (Møller 1988, Willson et al. 2003, Siepielski 2006) or clearly link adaptiveness of nest-site preferences with nest success (Kelly 1993, Filliater et al. 1994, Pribil 1998, Misenhelter and Rotenberry 2000, Chase 2002, Liebezeit and George 2002). Aside from the correlative nature of observational studies, many confounding variables make such analyses difficult. For example, where preferred territory or nest-sites are limited, sub-optimal sites will be selected by subordinate males, and inexperienced breeders may be more likely to settle in high-risk areas. Such scenarios might lead to misidentification of nest-site preferences. Post-hoc analyses of nest site characteristics and egg-laying dates failed to reveal whether pair quality was associated with nest site characteristics in our study. Alternatively, if most birds are able to select optimal nest-sites, lack of variability will hinder detection of survival benefits conferred by nest-site choices. Additionally, trade-offs between nest-site selection and other factors may exist. When selecting a territory or nest site, individual birds must balance considerations of nest predation against other factors related to nest success and fecundity, such as resource availability (Martin 1995, Turner and McCarty 1997), territory defense (Fontaine and Martin 2006), parasitism (Tewksbury et al. 2002), risk of predation on adults (Burhans and Thompson III 2001), and microclimate (Walsberg

1981, 1985). Finally, annual variation in the environment may allow for the selection of

a variety of nest sites to be adaptive over time at any given locale (Wray II and Whitmore

1979), and adaptations over large spatial scales may dilute selective benefits at smaller

scales (Martin 1993b). Because aspen forests constitute a very small proportion of the

landscape in the Sierra Nevada, and because our study species nest widely in adjacent

vegetation types, gene flow may be swamping the birds' ability to adapt to localized

conditions found in aspen in the Sierra.

Table 1. Nest site preferences among five species of birds breeding in mixed-aspen forests of the central Sierra Nevada, 2003-2006.

Based on univariate comparisons, blocked by study site, of nests and random, non-use sites (see Methods). Differences reported for p

≤ 0.1. Bold print denotes $p < 0.05$. Blanks indicate that no comparison was made. n.d. = no difference $(p > 0.1)$

	Canopy Cover	Canopy Height	Tree Density[a]	Conifer Density	Nest Tree DBH	Nest Tree Height	Shrub Cover	Forb Cover
Western Wood-Pewee (n = 117)	**less** 0.028	**higher** 0.036	**fewer**[b] 0.001	**greater** 0.007	n.d.	**taller**[c] <0.001		
Dusky Flycatcher (n = 54)	n.d.	**lower** 0.027	n.d.	n.d.			**greater** 0.017	**less** <0.001
Warbling Vireo (n = 152)	n.d	n.d.	fewer[d] 0.068	n.d.	**smaller**[c] 0.040	n.d.		
American Robin (n = 115)	n.d.	n.d.	n.d.	n.d.	**smaller** 0.003	n.d.		
Oregon Junco (n = 84)	**less** 0.044	**lower** 0.018	fewer[e] 0.058	n.d.			less 0.079	n.d.

[a] Tested independently for 8-23 cm, 23-38 cm, and >38 cm dbh size classes.
[b] 8-23 cm dbh (all trees: fewer, $F_{3,261} = 9.89$, p = 0.002)
[c] Due to nest plant species preference, non-use tree sample restricted to aspens
[d] >38 cm dbh (all trees: n.d.)
[e] 23-38 cm dbh (all trees: n.d.)

Table 2. Nest tree species preference of arboreal cup-nesting birds breeding in mixed-aspen forests of the central Sierra Nevada, 2003-2006. Nest site trees were those available within 11.3 m of nests. Additionally, approximately 30 random, non-use trees were sampled at each study site (see methods). *P*-values refer to Fisher's Exact Test of Probability, comparing tree species use relative to availability.

	Nest Tree		Nest Site			Random		
	Aspen	Non-aspen	Aspen	Non-aspen	*P*	Aspen	Non-aspen	*P*
Western Wood-Pewee	86	1	1718	355	< 0.001	127	22	< 0.001
Dusky Flycatcher[a]	16	0	325	56	0.143[b]	102	17	0.221[b]
Warbling Vireo	151	1	3470	661	< 0.001	127	22	< 0.001
American Robin	107	8	2844	298	0.419	127	22	0.052

[a] Restricted to tree nests (nest plant height > 5 m).

[b] Lack of significance attributable to insufficient sample size; every tree-nesting Dusky Flycatcher placed its nest in aspen.

Table 3. Evidence of support from nest site preference (this study) and models of nest success (Richardson et al. *In review-c*) for three non-competing nest site selection hypotheses, among five species of birds nesting in aspen forests of the central Sierra Nevada. Format = nest site preference / nest success. + = positive support (apparent nest site preference or patterns of nest survival conformed to predictions of hypothesis) , 0 = neutral or mixed evidence, - = negative support.

	Hypothesis		
Species	Nest-Concealment	Potential Prey-Site	Predator-Barrier
Western Wood-Pewee	- / +	+ / 0[a]	+ / 0[a]
Dusky Flycatcher	0 / 0	0 / 0	- / +
Warbling Vireo	+ / +	+ / 0[a]	+ / 0[a]
American Robin	0 / +	0 / 0[a]	0 / 0[a]
Oregon Junco	+ / +	- / +	0 / +

[a] Specific predictions of hypothesis not tested due to consistency of nest placement

Fig. 1. Nest orientation among four species of shrub- and tree-nesting birds in aspen forests of the Sierra Nevada, California and Nevada. Bold arrows indicate mean direction, which was not significantly different from random for any species (Rayleigh's test; $p > 0.05$). Pooled mean $= 218°$.

Fig. 2. Directional relationship between slope aspect and nest orientation for Oregon Juncos nesting in aspen forests of the Sierra Nevada, California and Nevada. Bold arrows indicate mean direction (slope $= 262°$, nest $= 248°$) Circular $r = 0.33$, $p = 0.006$, $n = 84$.

Fig. 3. Frequency of heights of two species of flycatcher nests from mature aspen forests of the Sierra Nevada, California and Nevada.

Fig. 4. Frequency of dbh and heights of nest trees of 152 Warbling Vireo nests and 126 non-use aspen trees from aspen forests of the Sierra Nevada mountains, California and Nevada. Note apparent preference for taller yet smaller diameter trees. Skewness for nest plant height $= -0.30$.

Figure 1.

Figure 2.

Nest Orientation

Slope Aspect
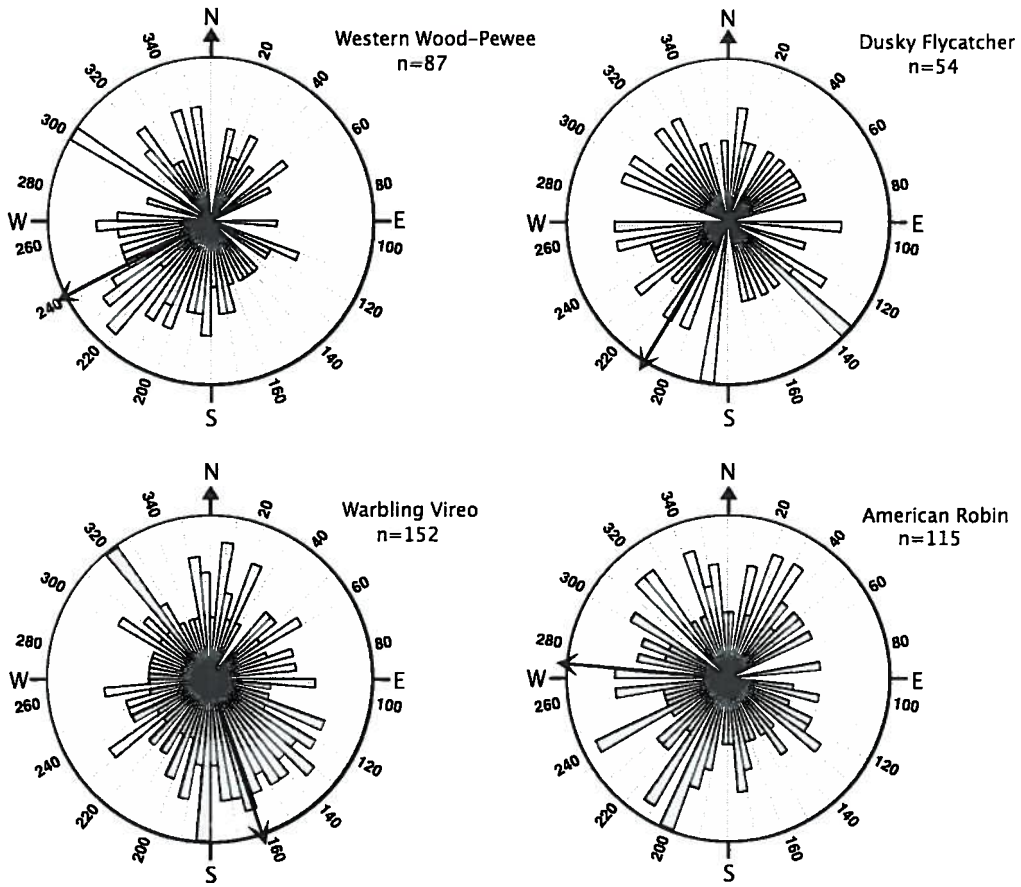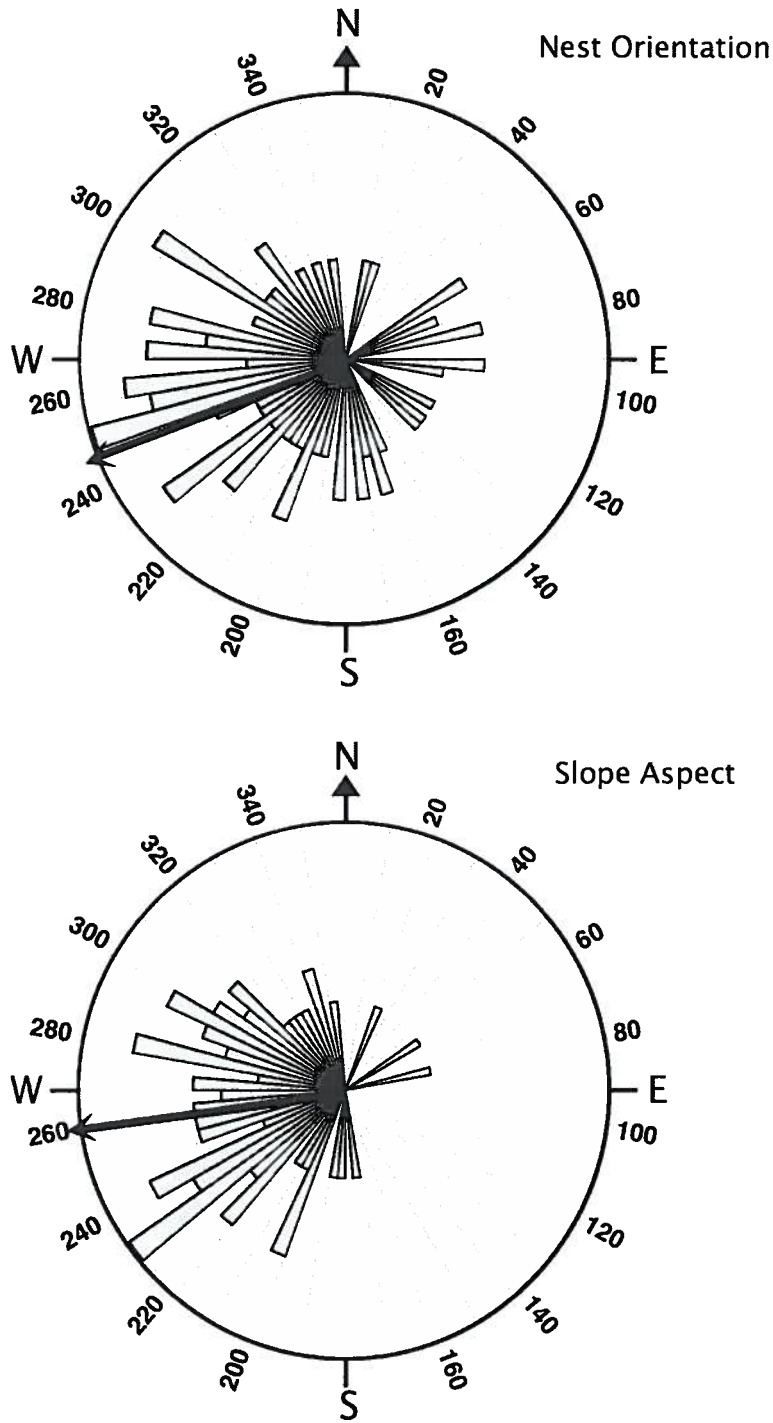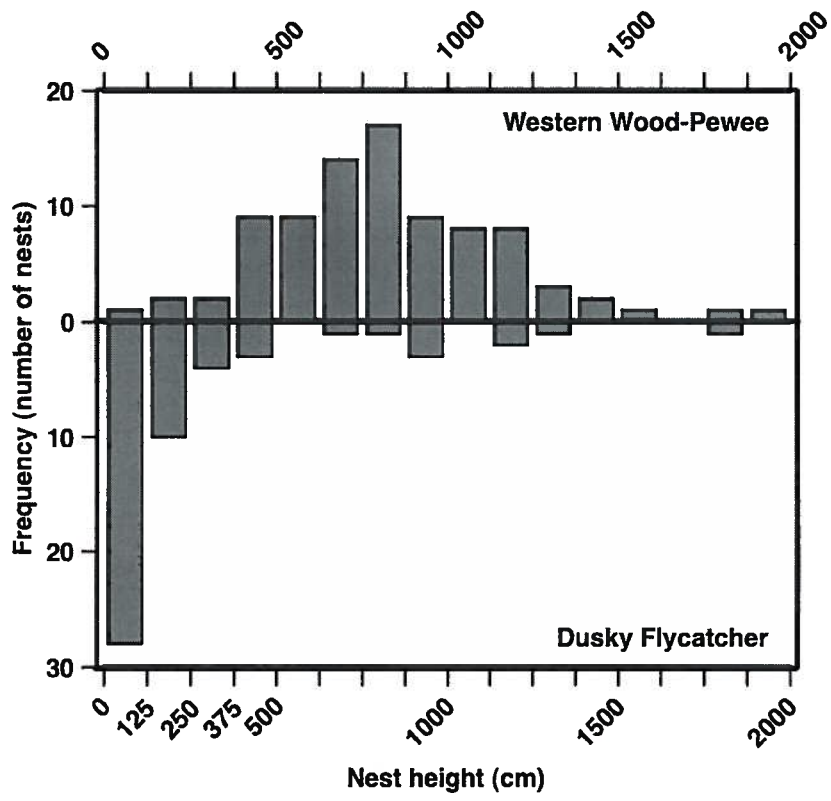
Figure 3.

Figure 4.
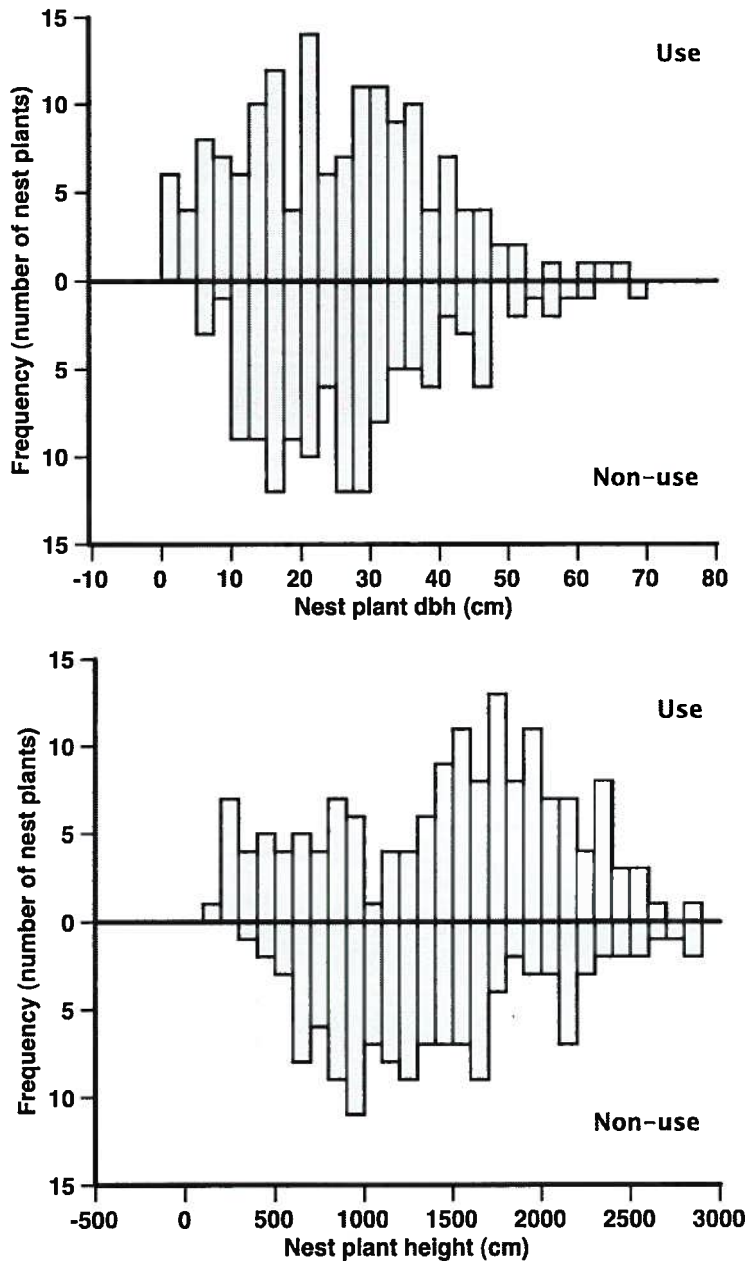
Appendix. Descriptive statistics of nest site characteristics among random, non-use sites and five species of birds breeding in mixed-aspen forests of the central Sierra Nevada, 2003-2006. Median values for nest plant measurements are in parentheses.

	Canopy Cover (%)	Canopy Height (m)	Nest Tree DBH (cm)	Nest Tree Height (cm)	Shrub Cover (%)	Forb Cover (%)
Non-use sites (n = 181)						
Minimum	9	7	5	375	0	3
Maximum	98	35	131	3650	80	98
Mean	74	19	30 (27)	1425 (1325)	17	67
Mean (aspen trees only)			27	1361		
Standard Deviation	19	6	19	679	17	25
Western Wood-Pewee (n = 117)						
Minimum	5	9	10	625	0	0
Maximum	99	33	61	3300	60	95
Mean	69	19	32 (31)	1856 (1825)	17	55
Standard Deviation	22	4	10	499	16	27

Dusky Flycatcher (n = 54)

Minimum	0	6	1	46	1	4
Maximum	98	29	46	2900	70	95
Mean	74	18	10 (3)	562 (230)	23	52
Standard Deviation	26	5	12	710	20	27

Warbling Vireo (n = 152)

Minimum	18	5	1	197	0	5
Maximum	98	30	65	2900	75	97
Mean	72	18	25 (24)	1447 (1550)	19	55
Standard Deviation	19	5	14	654	15	25

American Robin (n = 115)

Minimum	0	7	4	57	0	2
Maximum	98	34	86	3400	80	95
Mean	75	19	24 (24)	1331 (1300)	22	54
Standard Deviation	20	6	13	798	18	27

Oregon Junco (n = 84)

Minimum	1	0	N/A	N/A	0	5
Maximum	97	28	N/A	N/A	45	98
Mean	71	18	N/A	N/A	14	63
Standard Deviation	24	6	N/A	N/A	12	24

EFFECTS OF CONIFERS ON AVIAN NEST SUCCESS IN SIERRA NEVADA ASPEN

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Abstract

Numerous recent studies have demonstrated positive associations between important nest predators and coniferous vegetation. We attempted to determine the important habitat and nest site characteristics that influence nest predation for birds breeding in mixed aspen stands, which may serve as refugia from such predators in the conifer-dominated landscape of western North America. Best performing models of nest success demonstrated that conifer density near nests was negatively correlated with nest success for four of five species. Among arboreal nesters, nests located in aspen trees were disproportionately successful, and Dusky Flycatcher (*Empidonax oberholseri*) nests placed in aspen trees were less likely to be depredated than those placed in shrubs. We found relatively high nest success in of four of five species examined at these sites, suggesting that the habitat supported successful breeding of open-cup nesting passerines in general. Promoting larger and purer aspen forests may allow passerines to escape predation related to conifer-associated predators and therefore have the greatest impact on aspen's ability to provide source populations of insectivorous birds in western North American forests.

INTRODUCTION

Among cup-nesting passerine birds, nest predation typically is the leading cause of nest failure (Lack 1954, Nice 1957, Ricklefs 1969, Martin 1992a, b, 1993a), and Martin (1993b) calculated that predation accounts for 80% of nest failures on average. Because nest predation typically does not occur evenly across all nests, habitat and nest site characteristics that influence nest predation can be important factors determining reproductive success. Indeed, survival of a clutch of eggs to fledging may depend more on the location of the nest than any other factor, including food provisioning and parental behavior. Thus, there is a strong selective pressure exerted on birds to attempt to select nest sites that are less likely to be discovered or are inaccessible to predators (Collias and Collias 1984).

The landscape of predation risk can be examined on three spatial scales: (1) nest site (the immediate vicinity of the nest), (2) nest patch (characteristics of the habitat patch surrounding the nest), and (3) landscape or stand-level characteristics. Habitat and nest site characteristics at all three scales can relate directly to effects of different but overlapping factors relating to predation: from (1) likelihood of detection given a predator in the vicinity of the nest, to (2) likelihood of predators searching in a given area based on search image, density of potential nest sites, structural complexity of vegetation, etc., to (3) density and diversity of predator home ranges overlapping breeding territories. However, because identities of principal nest predators, and the habitat, space use, and foraging strategies of those predators, are seldom known for most study systems, attempts to link habitat and nest site characteristics to nesting success have produced mixed results.

Recent work by (Griffis-Kyle and Beier 2003) failed to find area or isolation effects on bird species richness and abundance breeding in small aspen stands distributed within a ponderosa pine matrix in Arizona (but see Hollenbeck 2006). These findings led Griffis-Kyle and Beier (2003) to conclude that "several small stands of aspen can be at least as valuable as…a single stand of the same total size" and that due to the potential benefits of forest insect consumption and the potential contribution of these stands as source populations, "several small stands may be more valuable than fewer, large stands." However, because several potentially important nest predators found in aspen are associated with coniferous vegetation types, area effects on nest success may exist where aspen occur within a matrix of conifer forest. In Montana, Tewksbury et al. (1998) found density of *Tamiasciurus* squirrels to increase with percent conifer forest cover at the 1 km scale. Studies from Canada and Alaska have shown that risk of nest predation from *Tamiasciurus* squirrels is higher in coniferous habitats than deciduous habitats (Sieving and Willson 1998) and suggest that nest success may decrease as cone-bearing trees and *Tamiasciurus* reach higher densities (Sieving and Willson 1998, Willson et al. 2003). In boreal aspen mixed-wood forests, Song and Hannon (1999) found nest predation highest along edges associated with conifers and attributed the difference to habitat preferences of *Tamiasciurus* squirrels and corvids. In the Sierra Nevada mountains of California, Cain III et al. (2003, 2006) also found that distance to coniferous forest edge were negatively correlated with Douglas Squirrel (*T. douglasii*) activity and both Dusky Flycatcher (*Empidonax oberholseri*) and Yellow Warbler (*Dendroica petechia*) nest failure. Steller's Jays (*Cyanocitta stelleri*) may reach their highest densities at the border of coniferous and deciduous forest (Sieving and Willson

1998), and in mixed conifer-aspen forests of the Sierra Nevada, both Douglas Squirrel and Steller's Jay presence were positively correlated with density of fir (*Abies*) trees (TWR, unpub. data). As conifers encroach into aspen forests, nest predators associated with conifers are likely to increase in the aspen, either numerically or in terms of space use. Larger, purer aspen forests may provide refugia from these predators, and thus are more likely to act as source populations for insectivorous birds.

We attempted to determine the important habitat and nest site characteristics that influence nest predation for birds breeding in aspen stands of the Sierra Nevada Mountains of California and Nevada. Specifically, we predicted that increased conifer density around bird nests would lead to reduced nesting success. Additionally, recent work has demonstrated that the smooth bark surface of aspen trees may provide a barrier to nest predation from small mammalian nest predators (Richardson and VanderWall 2007). Thus, we hypothesized that arboreal nesting species would have greater proportional nesting success in aspen versus non-aspen nest trees. Further, we hypothesized that nest plant height and DBH would demonstrate positive linear or negative exponential relationships with nesting success for these species.

METHODS

Nest Monitoring and Vegetation Assessments

Data were collected during 2003-2006, at five large aspen stands in the Lake Tahoe basin, California and Nevada. Study sites were approximately 7.5 – 14.5 ha in area, corresponding to the size of the aspen stands. Four sites were located at approximately 2400 m elevation in the Carson Range on the east side of the basin, and the fifth was at approximately 1950 m elevation, on the southwest side of Lake Tahoe.

The lower elevation site was not monitored in 2005 due to a budget shortfall. Dominant shrubs included *Symphoricarpos*, *Ribes*, and young aspen and conifers. Each site contained areas of relatively pure aspen, typically associated with lush herbaceous ground vegetation, and areas of high conifer density. Each site was bounded by conifer forest on at least one side, and sites were encroached to varying degrees by a mix of Jeffrey and lodgepole pine (*Pinus jeffreyi* and *contorta*), and red and white fir (*A. magnifica* and *concolor*).

We located and monitored nests following Martin and Geupel (1993), minimizing human-induced predation probability and disturbance to the adults and nest site. Briefly, we located nests through observation of adult behavior and systematic searches, and visited each nest, to determine contents and status, every 2-4 days until nest completion. In 2005-2006, nest monitoring efforts were focused on five species: Western Wood-Pewee (*Contopus sordidulus*), Dusky Flycatcher, Warbling Vireo (*Vireo gilvus*), American Robin (*Turdus migratorius*), and Oregon Junco (*Junco hyemalis thurberi*). Nest chronology data were used to plan additional visits on likely hatching and fledging days. Nest fates were assigned based on nest appearance and other forensic evidence at or below the nest (remains of eggs or nestlings, fecal matter), presence of recently fledged young on the territory, nest chronology, and parental behaviors. In the absence of other cues, we assumed successful fledging if the nest was active within two days of the predicted fledging date.

After completion of nest cycles, we conducted measurements of nest substrate and vegetation immediately surrounding each nest site following a modified BBIRD protocol (Martin et al. 1997) Canopy height, nest plant height, and nest height were either

measured directly or with a clinometer. Percent canopy cover was estimated using average counts from a spherical densiometer. We made ocular estimates of lateral, above nest, and below nest concealment and estimated or directly measured the distance from the nest to the foliage edge. Percent shrub and herbaceous cover were estimated within a 5m radius of each ground or shrub nest, and all trees within 11.3m of each nest were recorded to species and assigned to one of three size-classes: 8-23cm, 23-38, and > 38 cm dbh. To establish the extent of conifer encroachment relative to each nest, UTM coordinates were mapped for nest locations and every coniferous tree (>5m in height) within 60 m of the plot boundaries. Trees surveyed were identified to species and assigned to one of three height categories (5-10m, 10-20m, >20m). Densities of fir and pine, in each size class, were then estimated within 25m and 50m buffers of each nest, using GIS. Douglas squirrel territories are centered around a mature cone-bearing tree and typically less than 1 ha in size (Smith 1968, 1981), thus by mapping every conifer within 60 m of nests, we captured the centers of most territories of squirrels potentially depredating bird nests on study plots. Trees surveyed were identified to species and assigned to one of three height categories (5-10 m, 10-20 m, >20 m).

Data Analysis

For the five focal species, we used Program MARK (White and Burnham 1999) to estimate nest survival and assess hypotheses about factors affecting nesting success. Because our principal interest was in factors influencing predation, we excluded nests that failed due to other factors (e.g. parasitism, weather) from analyses. Parasitized nests that failed due to predation or fledged at least one host young were included, however. Models were built in a series of steps that used both *a priori* and exploratory components

to test *a priori* hypotheses, using the logit-link function and bias-corrected Akaike's Information Criterion (AIC_c, Burnham and Anderson 1998). We used single-predictor exploratory models to select the best-fit parameter out of those that quantified the same habitat or nest site feature. For example, nest concealment was measured above the nest, below the nest, and laterally from the four cardinal directions. From these, we ran models exploring the fit of above-nest concealment, below-nest concealment, average lateral concealment, and average overall concealment. Unless different measures had opposing effects, we then restricted further models incorporating "concealment" to those with the measure that had the best fit. For nest plant variables describing DBH or height, where we predicted a non-linear effect, we applied the same exploratory approach to examine transformed values describing quadratic, exponential, or inverse exponential forms of those variables. Site, nest phase (laying+incubation or nestling), nest initiation date, and year effects were also included in models. All covariates were standardized within Program MARK. See Appendix for a complete list of parameters and definitions used in the analyses. Overdispersion factors were estimated according to Hazler (2004), by dividing the deviance of the most general model by its degrees of freedom, but were found to be < 1 for each focal species. Thus, we considered unadjusted AIC_c values to represent valid estimates of model fit. Models within $\Delta AIC_c \leq 4$ were considered to have some support and were used to produce model-averaged estimates of survival and parameter coefficients and weights of evidence for the importance of individual variables.

Sample sizes were insufficient to examine categorical effects of nest plant species on nest survival. Therefore, we pooled nest fates of 12 arboreal cup-nesting species for nests that either fledged or were depredated: Mourning Dove (*Zenaida macroura*, n=1),

Calliope Hummingbird (*Stellula calliope*, n=10), Western Wood-Pewee (n=86), Dusky

Flycatcher (for nests ≥ 5m height, n = 16), Warbling Vireo (n=138), Clark's Nutcracker

(*Nucifraga columbiana*, n=1), American Robin (n=114), Yellow-rumped Warbler

(*Dendroica coronata*, n=15), Western Tanager (*Piranga ludoviciana*, n=3), Black-headed

Grosbeak (*Pheucticus melanocephalus*, n=1), Pine Grosbeak (*Pinicola enuncleator*, n =

1), Cassin's Finch (*Carpodacus cassinii*, n=7). Ratios of fledged versus depredated nests

were then examined according to nest tree species (aspen versus non-aspen) using

Fisher's Exact test in Program R (ver. 2.4.1, R Development Core Team 2006).

RESULTS

During 2003-2006, we found and monitored 843 avian nests of 36 species. For

nests of focal species that contained at least one egg (n=492), nest predation accounted

for approximately 45% of nest fates and 91% of all nest failures (Fig. 1). Of nests that

either fledged or were depredated, Western Wood-Pewee (n=86), Dusky Flycatcher

(n=52), Warbling Vireo (n=138), American Robin (n=114), and Oregon Junco (n=80)

provided sufficient sample sizes for hypothesis testing.

Model results

For no species did a single model best describe probability of nesting success

(Table 1). Nest phase (laying and incubation phase versus nestling phase) was an

important predictor of daily nest survival rates (DSR) for all species (Table 1), with DSR

consistently higher during the laying and incubation phase (Table 2), though this effect

was less pronounced in Warbling Vireo (Table 2c, 3c). Estimated DSR was relatively

high for four of five species (Table 2). Juncos had the highest nest survival probability

(68.9 %, Table 2e), and Dusky Flycatchers had the lowest (24.7%, Table 2b). Year

effects were important for three species (Table 3a,b,e), including the two low-nesting

species, however these effects were not consistent across species. Site effects and date

effects did not contribute to the best models for any species.

Western Wood-Pewee

Five competing models best approximated DSR for Western Wood-Pewee (Table

1a). Nest phase and year effects were incorporated in all of the best models.

Concealment above the nest was positively correlated with DSR, although the 95% CI

slightly overlapped zero (Table 3a). Density of 10 m conifers within 50 m of the nest

was positively correlated with DSR, although the density of 10 m conifers within 20 m of

the nest and the density of large-diameter conifers within 11.3 m of the nest were both

negatively correlated with DSR.

Dusky Flycatcher

Two competing models best approximated DSR for Dusky Flycatcher; each

included nest phase and year effects, and the density of small trees within 11.3 m of the

nest (Table 1b). Small tree density was negatively correlated with DSR (Table 3b).

These two models were separated from all others by their inclusion of the inverse of

DBH (DBH^{-1}). Figure 2 illustrates the relationship between DBH and estimated DSR.

The density of ≥ 5 m tall conifer trees within 20 m of the nest was also negatively

correlated with DSR, but the 95% CI for the parameter linking DSR to density of conifers

substantially overlapped zero (Table 3b).

Warbling Vireo

The best three competing models for Warbling Vireo DSR all incorporated

opposing concealment and conifer effects (Table 1c). Lateral concealment had a positive

relationship with DSR, while concealment below the nest had a negative relationship with DSR (Table 3c). Likewise, density of 20 m firs within 50 m of the nest had a positive relationship with DSR, while density of large conifers within 11.3 m of the nest had a negative relationship with DSR (Table 3c). Nest phase explained some variation in daily nest survival (Table 1c), but less than for the other species. Distance to edge of foliage was positively related to DSR, but a substantial portion of the 95% CI for the parameter linking distance to edge overlapped zero (Table 3c).

American Robin

Eleven weakly-differentiated models best approximated DSR for American Robin (Table 1d). Standardized beta coefficients for each parameter likewise demonstrated weak effects of explanatory variables (Table 3d). Nonetheless, these models each had significantly more explanatory power than the null model (Table 1d). These 11 models all included nest phase and density of 23-38 cm dbh trees within 11.3 m of the nest, which had a negative relationship with DSR (Table 3d). Density of 20 m fir trees within 20 m of the nest was negatively correlated with DSR (Table 3d) and was incorporated in the four most competitive models (Table 1d). Lateral concealment and distance from foliage edge were both positively correlated to DSR, although the 95% CI for distance from edge slightly overlapped zero. Nest height was not correlated with concealment in robins and was positively correlated with robin nest DSR, although its 95% CI also overlapped zero slightly. Density of small aspen within 11.3 m of the nest had a weakly positive relationship with DSR, however this parameter received little support (Table 3d).

Oregon Junco

Five models best approximated DSR for Oregon Junco nests (Table 1e), all of which included nest phase, year effects, and shrub cover. The latter parameter was positively correlated with nest survival, as was forb cover (Table 3e). However, the number of aspen shrub stems was negatively correlated with DSR of junco nests. The density of 20m conifer trees within 50m of the nest demonstrated a positive relationship with DSR; however, a substantial portion of the 95% CI for the parameter estimate overlapped zero, and this parameter was only weakly supported by model selection (Table 3e).

Nest Tree Species

For the 12 species of arboreal cup-nesting birds, pooled proportional nesting success was significantly higher for nests placed in aspen versus non-aspen trees (p = 0.009, Table 4).

DISCUSSION

The high nest success of four of five species at these sites exceeded the rate believed necessary to sustain migrant birds with 2-3 nesting attempts per season (~ 35-40%, Donovan and Thompson III 2001), and suggests that these sites supported successful breeding of open-cup nesting passerines in general. However, overall nest success of Dusky Flycatcher was relatively low (24.7%), far below that reported for this species breeding in aspen or mixed-aspen in Oregon (49%, Heltzel and Earnst 2006), Montana and Idaho (54.1%, Carle 2006), and Utah (40%, Dobbs 2005). Aspen is not a novel habitat for Dusky Flycatcher, but availability of suitable shrubs for nesting may be relatively low in the taller, more mature stands used for this study (Richardson et al. *In*

review-b). Thus, placing nests in the few patches of low shrubs that exist leads to high cumulative density of nests in that substrate and therefore increases predation risk due to the greater efficiency of foraging nest predators (Martin and Roper 1988, Martin 1993b). Stereotypy of nest placement in low shrubs, possibly an adaptive trait from adjacent habitats or on a regional scale, or due to interspecific competition with Western Wood-Pewees (Richardson et al. *In review-b*), may be leading to poor reproductive success at these sites. Additionally, year effects were very strong for Dusky Flycatcher (apparent nesting success: 2003-4, 25%; 2005-6, 80%), and our low overall estimate of nesting success may reflect an average that included two reproductive seasons that were poor for reasons unrelated to vegetation.

Nest Concealment

Studies of the importance of nest concealment have been somewhat equivocal (see Burhans and Thompson III 1998), but a review by Martin (1992a) found that improved nest concealment typically leads to decreased rates of predation for most species. Nest site characteristics relating directly to nest concealment were important factors influencing DSR for all three arboreal-nesting species in this study. This suggests that greater nest concealment may reduce nest detectability, and nest predation, by predators relying on visual cues. At these sites such predators likely include three species of *Accipiter*, several species of owl (Strigiformes), Steller's Jay, and Clark's Nutcracker (*Nucifraga columbiana*), but not Douglas Squirrel, which are believed to rely on olfactory cues to find nests (Pelech 1999). The importance of above-nest concealment for Western Wood-Pewee is also consistent with avian nest predation.

It has been suggested that nest concealment may interfere with nest defense, or that selecting sites that offer greater concealment may impose other, maladaptive costs, particularly among larger birds that select conspicuous nest locations (Götmark et al. 1995, Cresswell 1997, Weidinger 2002). Thus, it was not expected that concealment would positively influence DSR for robins and wood-pewees, as nests of both species tend to be conspicuous, these species apparently opting for a strategy of nest defense over concealment (Weidinger 2002). However, positive relationships between nest concealment and nest survival have been found for another species of *Turdus* thrush (Hatchwell et al. 1996) and other large tyrannid flycatchers (Murphy 1983). The negative relationship between below-nest concealment and DSR for Warbling Vireo was surprising, especially in light of the positive relationship with lateral concealment. This suggests that vireo nest defense may be facilitated by either seeing below the nest, or having a clear escape route (Götmark et al. 1995, Kilgo et al. 1996, Burhans and Thompson III 2001). Alternatively, selecting for less concealment below the nest may be adaptive for adult survival for the same reasons, and may co-vary with other habitat and nest-site features associated with successful breeders.

Direct measures of nest concealment were not important factors influencing junco nest survival. As a ground nesting species, juncos likely experience most predation from small mammals, for which visual concealment is less effective. Instead, successful junco nests had higher densities of ground cover in the vicinity of the nest, both shrubs and forbs, which may act to impede foraging or even locomotion of small mammalian nest predators (Bowman and Harris 1980, Holway 1991), provide more potential nest sites for

a predator to search (Martin and Roper 1988, Martin 1993b), and help conceal activity of adult birds as they travel to and from the nest (Holway 1991, Kelly 1993).

Accessibility of nests in aspen

Among arboreal nesters, nests located in aspen were disproportionately successful. Birds locating their nests in mature aspen experience dual benefits in terms of predation. Because aspen is the most abundant tree species at these sites, it provides the most potential nest sites for predators to search, making it difficult for predators to become efficient (Martin and Roper 1988, Martin 1993b). Additionally, the smooth bark of aspen may also provide a barrier or impediment to mammalian nest predators such as sciurid rodents (Richardson and VanderWall 2007). This is supported by the positive linear relationship between nest height and DSR in robins and the very strong threshold effect found with Dusky Flycatcher DSR and nest plant diameter. While the majority of Dusky Flycatchers at these sites nest in low shrubs (Richardson et al. *In review-b*), nesting in larger diameter aspen has clear reproductive benefits, likely due to release from predation by chipmunks, a frequent nest predator of this species (Liebezeit and George 2002). It has been established that chipmunks cannot climb aspen trees (Richardson and VanderWall 2007), and the smooth bark and lack of cover found on mature aspen may impede or discourage foraging by slightly larger mammalian nest predators as well. *Tamiasciurus* squirrels are important nest predators in forests of western North America (Martin 1988, 1993a, b, Sieving and Willson 1998, Martin and Joron 2003, Willson et al. 2003, Siepielski 2006), and have been observed making systematic searches for bird nests through the canopy in deciduous trees (Uphoff 1990). It is notable that during this study

Douglas Squirrels were never observed in the canopy of a mature aspen tree despite their occurrence at all five study sites.

Conifer Density

Several studies have shown a positive relationship between apparent predator density, space use, or activity and predation rates on bird nests (Schmidt et al. 2001, Cain III et al. 2003, Schmidt and Ostfeld 2003b, a, Cain III et al. 2006), while others have shown no relationship (Peterson et al. 2004, Mahon and Martin 2006). Because one can expect a positive numerical or functional relationship between conifer density and conifer-associated nest predators in deciduous forests (Sieving and Willson 1998, Willson et al. 2003), we predicted that increased conifer density would increase nest predation among birds nesting in aspen stands. Negative relationships between conifer density and nest DSR received support for four of five species. Strongest support was found among the arboreal nesting species, and all negative relationships with DSR corresponded to conifer density measured at the smaller scales (within 11.3 m or 20 m of nests). However, three species also showed positive relationships between DSR and conifer density when measured at the largest scale (50 m), although support for this effect was very weak for Oregon Junco (95% CI of the estimate overlapped zero significantly). These apparently conflicting results are difficult to interpret. Nonetheless, we offer two possible explanations for these patterns.

First, both bird use (Richardson and Heath 2004, TWR pers. obs.) and density of nests of all species (TWR pers. obs.) appears to be highest at these sites away from the coniferous ecotone. In particular, Western Wood-Pewees and Warbling Vireos nest in somewhat similar locations within trees, and vireos often place their nests within 10-20 m

of wood-pewee nests (Richardson et al. *In review-b*). Agonistic interaction of wood-pewees towards vireos was observed regularly in these circumstances, especially early in the nest cycle (TWR, pers. obs). Nesting at high densities or in association with aggressive heterospecifics may have benefits related to nest defense, but it is possible that increases in bird use or nest density may be positively related to nest predation in two ways. Increased agonistic interaction at higher densities could lead to greater disturbance at the nest and reduced incubation, brooding, or feeding by one or both parents, which could, in turn, increase predation rates due to increased nest activity (Martin et al. 2000, Tewksbury et al. 2002), longer nest cycles, reduced nest vigilance, or a combination of factors. Additionally, predators may demonstrate a functional response in foraging effort or behavior to increased nest density, particularly where multiple species place their nests in similar contexts (Martin 1988, 1993b, Hoi and Winkler 1994, Schmidt and Whelan 1998, Roos 2002).

Secondly, Tewksbury et al. (2006) found support for an additive predation model in which vegetation and land use patterns affect rates of nest predation differently at different scales. Thus, it is possible that conifer density at the 50m scale may be correlated with other landscape features not considered here. These features may affect predation as it relates to different suites of predators, availability of resources, microclimate, brood parasitism, or a combination of these factors. For example, conifer density at three of the study sites was highest along watercourses running through the sites, not outside the edge of the aspen stands. Additionally, frequency of nest parastism exhibited a pattern correlated to conifer density at these sites (TWR, unpub. data). Two of the species exhibiting positive relationships with conifers at the 50m scale were

regular hosts of Brown-headed Cowbird (*Molothrus ater*) parasitism (Warbling Vireo, 16 of 151 nests (10.6%) and Oregon Junco, 15 of 84 nests (17.9%)), and the density of large conifers at the 50m scale was significantly lower in parasitized nests for both Warbling Vireo (5A20, t = 5.35, df = 128, p < 0.001) and Oregon Junco (5AL20, t = 3.36, df = 71, p = 0.001). These apparent rates of parasitism were too low to investigate whether or not parasitism increased predation for these two species; also, because most vireo nests were inaccessible (median height = 10m), the rate of parasitism among vireo nests that were depredated is likely to be underestimated. However, parasitism could be positively correlated with increases in predation in two fundamental ways. First, cowbirds have been demonstrated to be significant predators of eggs and nestlings, putatively destroying nests to facilitate renesting attempts by hosts and therefore increase parasitism opportunities (Arcese et al. 1992, Arcese et al. 1996). Thus, where parasitism occurs, one can expect additional nest predation by cowbirds, particularly during incubation. Second, Ortega (1998, Table 7.6) found that parasitized nests are more likely to fail than non-parasitized nests, in most species. The noisy and intense begging behavior of cowbird young may increase predation rates at parasitized nests (Haskell 1994, Dearborn 1999), and Tewksbury et al. (2002) showed that increased parasitism may lead to increases in nest predation as birds modify behaviors to try to balance opposing selective forces related to parasitism and predation. The above explanations are purely speculative, but increased nest activity and increased cowbird predation are both consistent with the weaker nest phase effect found in Warbling Vireo. Further investigation into scale-dependent effects of conifer density and its effects on nest density, parasitism, and predation is warranted for these species and this system as a whole.

None of the aspen stands in this study were large enough or pure enough to be completely free of conifer-associated predators. Indeed, this may be the case throughout the Sierra Nevada. As a result, this study may have lacked sufficient scale to detect consistent patterns of conifer effects at these interfaces. For example, Cain et al. (2006) found evidence that survival of Dusky Flycatcher nests in Sierra Nevada meadows were affected by activity levels of chipmunks and Douglas Squirrels at the 200m scale, but not the 100m scale. In the central Rocky Mountains, Struemph (2000) found that most birds had higher nesting success in pure aspen than in nearby mixed or coniferous forests. Additionally, a rich guild of nest predators may have obscured the importance of conifer encroachment on nest predation by diluting the effects of predators associated with conifers (Filliater et al. 1994). Video surveillance of nests failed to identify principal nest predators (TWR, unpub. data), but nests at these sites were variously subjected to a large, diverse suite of potential nest predators that included accipiters, owls, corvids, sciurid, cricetid, and zapodid rodents, mustelids, raccoons (*Procyon lotor*), bears (*Ursus americanus*), and reptiles. Perhaps it is no coincidence that the ground-nesting Oregon Juncos, which were subjected to the largest suite of nest predators, were the only species that did not exhibit an increase in predation associated with conifer density at any scale.

In summary, this study is the first to investigate the effects of conifer encroachment on the nesting success of birds breeding in aspen. Evidence that aspen may provide refugia from conifer-associated predators, and that avian nesting success is high in Sierra Nevada aspen, is consistent with the numerous findings of high avian nesting success (Carle 2006, Heltzel and Earnst 2006), species richness (Flack 1976, Finch and Reynolds 1988, Griffis-Kyle and Beier 2003, Richardson and Heath 2004),

abundance (Salt 1957, Flack 1976, Finch and Reynolds 1988, Griffis-Kyle and Beier 2003, Richardson and Heath 2004), and diversity (Flack 1976, Rumble et al. 2001, Heath and Ballard 2003, Hollenbeck 2006) in aspen from the Sierra Nevada and throughout western North America. Conifer encroachment has been established as the principal threat to the sustainability of aspen in the Sierra Nevada (Shepperd et al. 2006) and one of the primary threats to aspen in the western United States as a whole (Bartos and Campbell Jr 1998). Because encroachment into aspen stands by conifers has negative impacts on herbaceous ground cover (Harper 1973, Korb and Ranker 2001), stand moisture (DeByle 1985a), insect abundance (Schimpf and MacMahon 1985), and bird species richness, abundance, and nesting success, removal of conifers not only helps to ensure the long-term persistence of the stand itself, it can be a critical factor in the preservation of the stand's ecological function. Therefore, promoting larger and purer aspen stands may have the greatest impact on aspen's ability to provide source populations of insectivorous birds in the conifer-dominated landscape of western North American forests.

Table 1. Highest ranking ($\Delta AIC_c \leq 4$) and null models for predicting daily nest survival for five species of passerines breeding in aspen forests of central Sierra Nevada Mountains, California and Nevada, USA, 2003–2006. Deviance, Akaike's Information Criterion scores adjusted for small sample size (AIC_c), ΔAIC_c, AIC_c weights (ω), and number of parameters (k). Models ranked according to AIC_c from best to worst approximating model. Sample sizes refer to number of nests.

Model[a]	ΔAIC_c	Deviance	ω	k
A. Western Wood-Pewee (n = 86)				
Phase + Year + conG38 + AB + 2AL10 + 5AL10	0.00	231.51	0.45	9
Phase + Year + conG38 + AB + 5AL10	1.89	235.42	0.17	8
Phase + Year + conG38 + AB	2.35	237.88	0.14	7
Phase + Year + AB + 2AL10 + 5AL10	2.45	235.97	0.13	8
Phase + Year + 2AL10 + 5AL10	2.73	238.27	0.11	7
Null	14.98	262.56	0.00	1
B. Dusky Flycatcher (n = 52)				
Phase + Year + DBH^{-1} + trees8	0.00	169.44	0.69	7
Phase + Year + DBH^{-1} + trees8 + 2AL5	1.63	169.04	0.31	8
Null	29.85	211.37	0.00	1
C. Warbling Vireo (n = 138)				
BE + X4 + conG38 + 5A20	0.00	455.44	0.39	5

BE + X4 + conG38 + 5A20 + Phase	0.28	453.71	0.34	6
BE + X4 + conG38 + 5A20 + Edge	0.76	454.19	0.27	6
Null	23.30	486.76	0.00	1

D. American Robin (n = 114)

Phase + treesG23 + X4 + 2A20	0.00	382.98	0.20	5
Phase + treesG23 + X4 + Edge + 2A20	0.40	381.38	0.17	6
Phase + treesG23 + X4 + 2A20 + HT	0.80	381.77	0.14	6
Phase + treesG23 + X4 + Edge + 2A20 + HT	1.05	380.01	0.12	7
Phase + treesG23 + X4	1.56	386.55	0.09	4
Phase + treesG23 + X4 + Edge + as8	2.16	383.13	0.07	6
Phase + treesG23 + X4 + HT	2.51	385.50	0.06	5
Phase + treesG23 + X4 + Edge	2.66	385.65	0.05	5
Phase + treesG23 + X4 + Edge + HT	3.52	384.50	0.04	6
Phase + treesG23	3.67	390.67	0.03	3
Phase + treesG23 + Edge	3.87	388.86	0.03	4
Null	17.11	408.11	0.00	1

E. Oregon Junco (n = 80)

Phase + Year + Shrcov + Forbcov + Shras	0.00	255.47	0.50	8
Phase + Year + Shrcov + Forbcov + Shras + 5AL20	1.68	255.13	0.21	9
Phase + Year + Shrcov + Forbcov	2.61	260.11	0.13	7
Phase + Year + Shrcov	3.57	263.08	0.08	6
Phase + Year + Shrcov + Forbcov + 5AL20	3.94	259.41	0.07	8
Null	23.04	292.60	0.00	1

[a] See Appendix for parameter definitions

Table 2. Model-averaged daily survival rate estimates (DSR), standard error (SE), and 95% confidence intervals, and period survival probabilities (ϕ) for five species of passerines nesting in aspen forests of central Sierra Nevada Mountains, California and Nevada, USA, 2003–2006. Sample sizes refer to number of nests.

Nest Phase (days)	DSR	SE	95% CI [a]	Period ϕ
A. Western Wood-Pewee (n = 86)				
Laying+Incubation (18)	0.9875	0.0048	0.9734 - 0.9942	0.8179
Nestling (16)	0.9642	0.1227	0.9305 - 0.9820	0.5589
Total nest period (34)	0.9766	0.0603	0.8584 - 1.0948	0.4457
B. Dusky Flycatcher (n = 52)				
Laying+Incubation (19)	0.9797	0.0101	0.9470 - 0.9923	0.7197
Nestling (16)	0.9389	0.0295	0.8486 - 0.9768	0.3647
Total nest period (35)	0.9610	0.0190	0.9238 - 0.9982	0.2468
C. Warbling Vireo (n = 138)				
Laying+Incubation (16)	0.9819	0.0031	0.9747 - 0.9870	0.7460
Nestling (15)	0.9795	0.0041	0.9698 - 0.9861	0.7327
Total nest period (31)	0.9807	0.0036	0.9737 - 0.9877	0.5466
D. American Robin (n = 114)				
Laying+Incubation (16)	0.9864	0.0029	0.9807 - 0.9920	0.8029
Nestling (13)	0.9617	0.0068	0.9457 - 0.9730	0.6016

Total nest period (29)	0.9753	0.0047	0.9662 - 0.9844	0.4831

E. Oregon Junco (n = 80)

Laying+Incubation (16)	0.9927	0.0031	0.9867 - 0.9988	0.8899
Nestling (11)	0.9770	0.0087	0.9522 - 0.9891	0.7743
Total nest period (27)	0.9863	0.0054	0.9758 - 0.9968	0.6891

[a] Individual Phase CIs from Program MARK output. Total nest period CIs calculated from DSR and SE.

Table 3. Weights of evidence, model-averaged standardized coefficient estimates (β), standard errors (SE), and 95% confidence intervals for variables included in best-approximating models ($\Delta AIC_c \leq 4$) for daily nest survival for five species of passerines nesting in aspen forests of central Sierra Nevada Mountains, California and Nevada, USA, 2003–2006. Sample sizes refer to number of nests.

Parameter[a]	Weights of Evidence	$\hat{\beta}$	SE	LCI	UCI
A. Western Wood-Pewee (n = 86)					
Phase[b]	1.00				
Year	1.00				
AB	0.89	0.4229	0.2221	-0.1247	0.8583 [c]
5AL10	0.86	0.6077	0.2667	0.0850	1.1303
conG38	0.76	-0.4627	0.1865	-0.8283	-0.0972
2AL10	0.69	-0.6085	0.0259	-1.1160	-0.1010
B. Dusky Flycatcher (n = 52)					
Phase[b]	1.00				
Year	1.00				
trees8	1.00	-0.4092	0.1166	-0.6377	-0.1807
DBH[-1]	1.00	-0.3902	0.1024	-0.5909	-0.1895
2AL5	0.31	-0.0186	0.0279	-0.0733	0.0362 [d]
C. Warbling Vireo (n = 138)					
BE	1.00	-0.6500	0.1518	-0.9475	-0.3525

5A20	1.00	0.5551	0.1940	0.1749	0.9352
X4	1.00	0.4183	0.1431	0.1378	0.6989
conG38	1.00	-0.3452	0.1070	-0.5550	-0.1354
Phase[b]	0.34				
Edge	0.27	0.1374	0.1276	-0.1127	0.3874[d]

D. American Robin (n = 114)

Phase[b]	1.00				
treesG23	1.00	-0.0292	0.0065	-0.0419	-0.0165
X4	0.94	0.0197	0.0072	0.0055	0.0339
2A20	0.63	-0.0141	0.0038	-0.0216	-0.0066
Edge	0.48	0.0084	0.0044	-0.0002	0.0170[c]
Height	0.35	0.0052	0.0028	-0.0003	0.0108[c]
as8	0.07	0.0014	0.0006	0.0003	0.0025

E. Oregon Junco (n = 80)

Phase[b]	1.00				
Year	1.00				
Shrcov	1.00	0.7159	0.2909	0.1458	1.2860
Forbcov	0.92	0.3315	0.1866	-0.3417	0.6972[c]
Shras	0.71	-0.4236	0.1933	-0.8025	-0.0447
5AL20	0.28	0.1410	0.2084	-0.2675	0.5498[d]

[a] See Appendix for parameter definitions

[b] For each species DSR was higher during the laying and incubation phase

[c] Minor portion of 95% CI overlaps zero

[d] Substantial portion of 95% CI overlaps zero

Table 4. Proportional nesting success of 12 arboreal cup-nesting species using aspen and non-aspen nest trees in aspen forests of central Sierra Nevada Mountains, California and Nevada, USA, 2003–2006. Numbers represent total numbers of nests per cell (Fisher's exact test; p = 0.009)

Nest Tree Species	Fledged Young	Depredated	Total	% Successful
Aspen	202	168	370	54.6
Non-aspen	6	17	23	26.1

Figure Captions:

Figure 1. Nest fates for five focal species, excluding potential abandonment prior to laying. Nest predation accounts for 90.9% of all failures. "Cowbird" includes nests that fledged only cowbird young. "Other" includes failure due to weather, desertion of eggs or young, structural failure of the nest without predation, and falling debris from canopy.

Figure 2. Negative exponential relationship between nest plant diameter breast height (DBH) and model-averaged daily survival rate (DSR) estimates for Dusky Flycatchers nesting in aspen forests of central Sierra Nevada Mountains, California and Nevada, USA, 2003–2006.
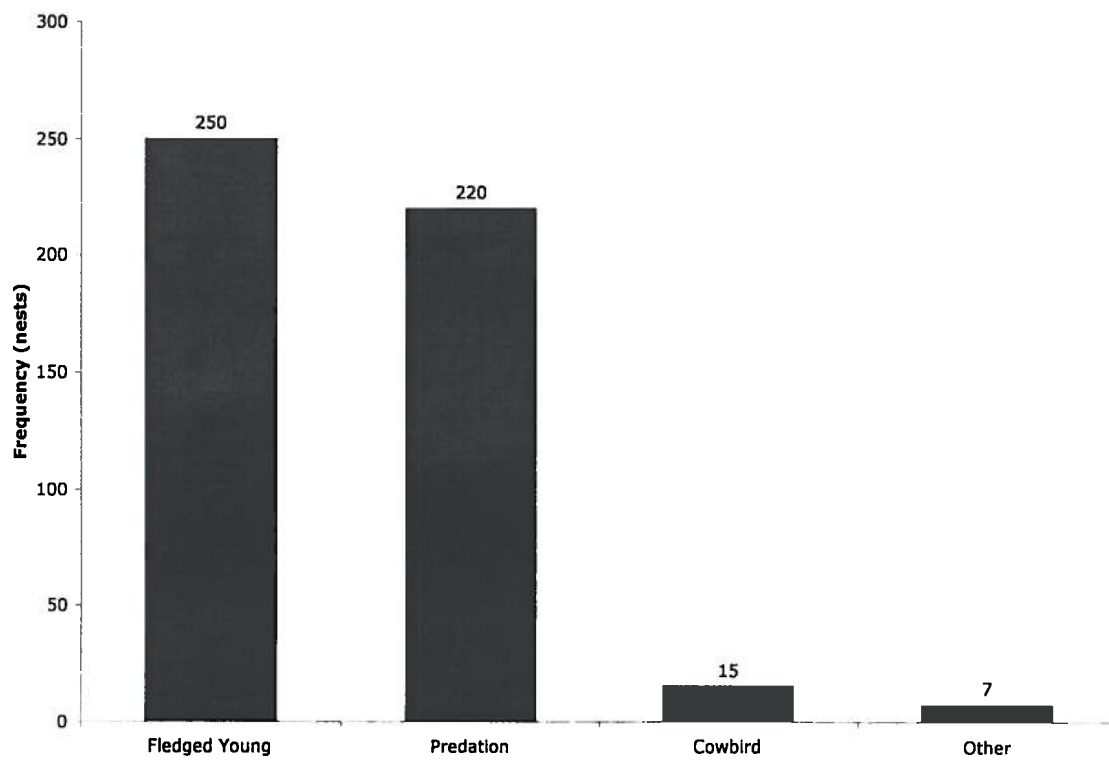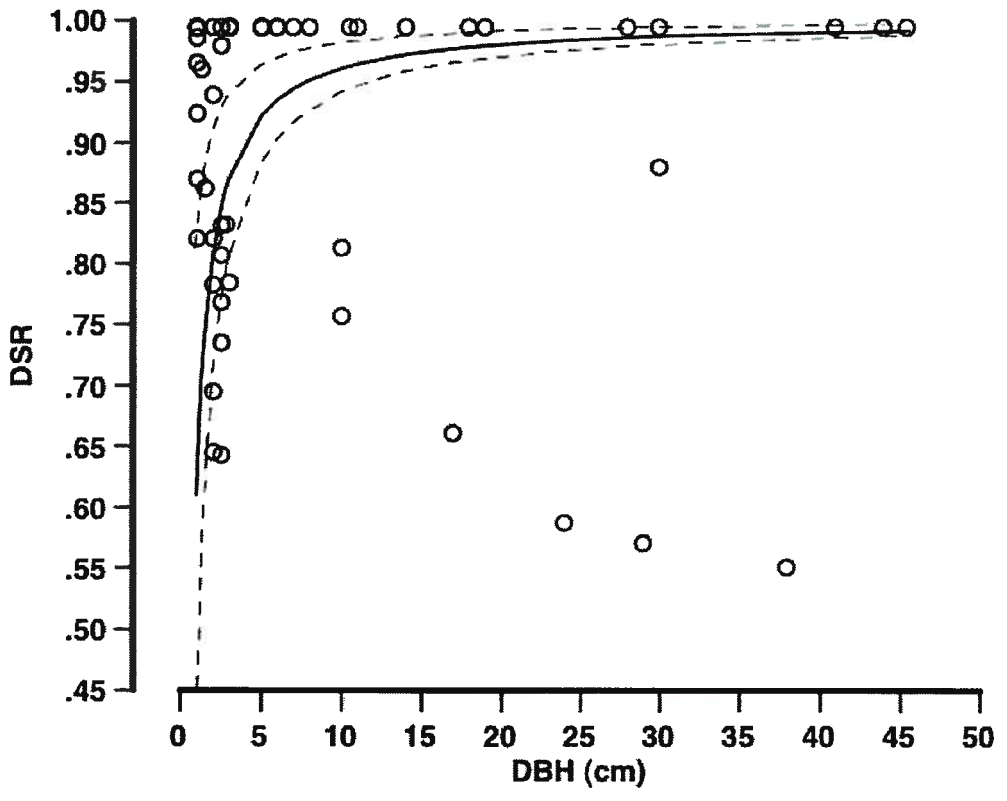
Figure 1.

Figure 2.

Appendix. Parameter definitions from model selection in Program Mark.

Parameter	Definition
.	Unparameterized model
phase	Nesting phase (laying + incubation, nestling)
t	Day
year	Year
jda	Julian date of first egg
ab	Index of concealment of nest from above
be	Index of concealment of nest from below
X4	Index of lateral concealment of nest
X6	Index of overall concealment of nest
edge	Distance from edge of foliage
plantht	Height of nest plant
htfrgrd	Height of nest from ground
dbh	Diameter at breast height of nest plant
5al20	Density of $\geq$ 20 m-tall conifer trees within 50 m of nest
5al10	Density of $\geq$ 10 m-tall conifer trees within 50 m of nest
5al5	Density of $\geq$ 5 m-tall conifer trees within 50 m of nest
5a20	Density of $\geq$ 20 m-tall *Abies* trees within 50 m of nest
5a10	Density of $\geq$ 10 m-tall *Abies* trees within 50 m of nest
5a5	Density of $\geq$ 5 m-tall *Abies* trees within 50 m of nest

5p20 Density of $\geq$ 20 m-tall *Pinus* trees within 50 m of nest

5p10 Density of $\geq$ 10 m-tall *Pinus* trees within 50 m of nest

5p5 Density of $\geq$ 5 m-tall *Pinus* trees within 50 m of nest

2al20 Density of $\geq$ 20 m-tall conifer trees within 20 m of nest

2al10 Density of $\geq$ 10 m-tall conifer trees within 20 m of nest

2al5 Density of $\geq$ 5 m-tall conifer trees within 20 m of nest

2a20 Density of $\geq$ 20 m-tall *Abies* trees within 20 m of nest

2a10 Density of $\geq$ 10 m-tall *Abies* trees within 20 m of nest

2a5 Density of $\geq$ 5 m-tall *Abies* trees within 20 m of nest

2p20 Density of $\geq$ 20 m-tall *Pinus* trees within 20 m of nest

2p10 Density of $\geq$ 10 m-tall *Pinus* trees within 20 m of nest

2p5 Density of $\geq$ 5 m-tall *Pinus* trees within 20 m of nest

asL8 Density of < 8 cm dbh aspen within 11.3 m of nest

as8 Density of 8-23 cm dbh aspen within 11.3 m of nest

as23 Density of 23-38 cm dbh aspen within 11.3 of nest

asG38 Density of >38 cm dbh aspen within 11.3 of nest

con8 Density of 8-23 cm dbh conifers within 11.3 m of nest

con23 Density of 23-38 cm dbh conifers within 11.3 of nest

conG38 Density of >38 cm dbh conifers within 11.3 of nest

trees8 Density of 8-23 cm dbh trees within 11.3 m of nest

trees23 Density of 23-38 cm dbh trees within 11.3 of nest

treesG38 Density of >38 cm dbh trees within 11.3 of nest

shrcov Absolute percentage of 11.3 m plot covered by shrubs

Appendix (cont'd).

Parameter	Definition
forbcov	Absolute percentage of 11.3 m plot covered by herbaceous ground cover
cancov	Canopy cover (mean of four densiometer readings)
canht	Average maximum canopy height
shras	Total number of shrub-class aspen stems within 11.3 m of nest
shrrib	Total number of *Ribes* stems within 11.3 m of nest
shrsyro	Total number of *Symphoricarpos* stems within 11.3 m of nest
shrtot	Total number of shrub stems within 11.3 m of nest

CONCLUSIONS and MANAGEMENT RECOMMENDATIONS

Conifer encroachment is the greatest threat to aspen stand survival and condition throughout much of the Sierra Nevada (Shepperd et al. 2006). Through a synthesis of observational studies and experiments, I have shown that the encroachment of conifers into aspen forests may have direct and indirect negative effects on the breeding birds that use these habitats. Encroachment into aspen stands by conifers has negative impacts on herbaceous cover (Harper 1973, Korb and Ranker 2001), stand moisture (DeByle 1985a), insect abundance (Schimpf and MacMahon 1985), and bird species richness and abundance, and near-nest conifer density was negatively correlated with nest success. Removal of conifers not only helps to ensure long-term persistence of the stand itself, it can be a critical factor in the preservation of the stand's ecological function. Conifer removal in at-risk stands, performed outside of the avian breeding season, may increase bird species richness and abundance and increase the ability of the stands to provide source populations of insectivorous birds. Any successful management plan designed to maintain or improve the purity, area, and function of mature aspen stands will almost certainly have positive effects on aspen-breeding bird population levels.

Efforts should be made to manage aspen stands for a healthy herbaceous understory community. Herbaceous cover was an important habitat variable in almost every model of Richardson and Heath (2003). It is unclear whether herbaceous cover provides direct benefits to aspen-breeding birds or if it is merely associated with hidden factors that we failed to measure or parameterize (e.g. moisture, abundance of invertebrates). Regardless, herbaceous cover was often highly positively correlated with a high percentage of aspen in the canopy and negatively correlated with a coniferous

overstory. The herbaceous community experiences significant decreases in species richness and diversity with succession to conifer in the canopy (Harper 1973, Korb and Ranker 2001), and Harper (1973) found that understory production decreased by 50% where the canopy was composed of a high percentage of conifers (>50%). At many sites, release from conifer encroachment through thinning or natural disturbance may be all that is required to stimulate herbaceous growth by increasing both available moisture and sunlight needed by these plants. However, aspen stands are often very wet or in a riparian context, and Potter (1998) considered the Quaking Aspen/Corn Lily (*Veratrum californicum*) plant association to be one of the more fragile habitats in the Sierra Nevada. Thus, any conifer-thinning treatment must consider its impact on the soil and its seedbank as well as local hydrological considerations. Finally, excessive livestock grazing in aspen stands can degrade the quality of herbaceous cover, alter the hydrological conditions that allow for a vigorous herbaceous understory, and limit aspen regeneration (Bartos and Campbell Jr 1998).

I found evidence suggesting that aspen stands, and aspen trees in particular, may provide refugia from conifer-associated nest predators. Further, I found evidence that aspen stands supported successful breeding of open-cup nesting passerines in general. Thus, land managers should strive for maximum stand size and purity (ie. removal of *all* conifers) whenever possible. Larger, purer stands are likely to support higher bird abundance, bird species richness, and nesting success than smaller, conifer-encroached stands. Efforts should also be made to increase the age complexity, and regeneration of aspen habitats at the landscape scale to ensure long-term persistence of aspen in the Sierra Nevada. However, land managers must consider the immediate effects of these

actions on bird populations. For example, clear-cutting aspen to promote vegetative regeneration would have an immediate negative impact on most aspen-breeding birds. Repopulation of the stand might be swift for many species, but woodpeckers and other cavity nesters, canopy nesters such as Warbling Vireo, and some forest-interior ground nesting species may not be able to re-colonize the stand for over ten years following treatment (Scott and Crouch 1998). A mosaic of age classes on the landscape should ensure that mature stands are available as refugia for these species.

An added difficulty in conservation planning for aspen explicitly is the wide variety of ecological roles aspen can play, depending on the environmental context. For example, what are the differences between seral and climax aspen communities in terms of importance to breeding birds? Wherever aspen occurs, it is likely to be a keystone species, especially in terms of its effect on local soil, hydrology, and vascular plants, but also birds and other wildlife. Certain generalizations would likely apply to any management guidelines for bird conservation (e.g. herbaceous cover is good for birds in Sierra Nevada aspen stands). However, because of aspen's ecological valence, management actions should always be locally prescriptive and not based solely on regional or broader-scale generalizations.

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