

FACTORS AFFECTING NEST SURVIVAL OF THREE SPECIES OF MIGRANT  
SONGBIRDS IN THE GREATER YELLOWSTONE ECOSYSTEM

by

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May, 2006

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## ABSTRACT

In the Greater Yellowstone Ecosystem (GYE), spatial patterns of habitat types and human land uses create an overlap between high-intensity human disturbance and productive habitat types at low elevations. This overlap suggests concern for species such as Neotropical Migrant songbirds, whose populations may depend on the productivity of individuals breeding in low-elevation habitats. We examined patterns of nest survival of three songbird species within the GYE to determine the relative importance of covariates of interest at nest-, patch-, and landscape-level spatial scales to nest survival. We hypothesized that covariates at several spatial scales would be important to nest survival and that broad-scale characteristics of the surrounding landscape would have the strongest spatial-level influence on nest survival. From 1997 to 1999 we located and monitored 233 nests of Dusky Flycatchers (*Empidonax oberholserii*), 129 nests of Warbling Vireos (*Vireo gilvus*), and 290 nests of Yellow Warblers (*Dendroica petechia*) in aspen and cottonwood habitats across southwestern Montana and adjoining portions of Idaho. We found that covariates at multiple spatial scales were important to the nest survival of all three species and that landscape-level variables had the strongest spatial-level effects on the nest survival of Dusky Flycatchers and Yellow Warblers. For all three songbird species, higher substrates appeared to provide the most favorable nesting habitat and date and parasitism status were important variables in the model suites. Variation in the nest survival of Dusky Flycatchers was influenced by all spatial-level covariates, while the variation in nest survival of Yellow Warblers was influenced primarily by surrounding home density. Warbling Vireos appeared to be an edge species in the GYE, and their nest survival was influenced by smaller-scale covariates. Overall, our results emphasize variation in species' responses to surrounding habitat and land use features. We suggest that future studies should evaluate both a variety of species and a variety of habitat and land use features in order to determine how surrounding habitat and anthropogenic factors influence songbird communities.

## FACTORS AFFECTING NEST SURVIVAL OF THREE SPECIES OF MIGRANT SONGBIRDS IN THE GREATER YELLOWSTONE ECOSYSTEM

### Introduction

The Greater Yellowstone Ecosystem is a landscape characterized by extensive ecological and anthropogenic variation. A broad elevational gradient creates variable climates, topographies, and habitats ranging from high-elevation coniferous forests, mid-elevation shrublands, and riparian lowlands. Deciduous habitats present at lower elevations, such as aspen and cottonwoods, are sources of high net primary productivity and species richness. This is in contrast to higher elevation habitats, which are less productive (Hansen and Rotella 2002a). Land use in the GYE also comprises a spatial gradient, with reserves and national parks at higher elevations and private lands at lower elevations (Hansen and Rotella 2001). These patterns of variability in habitat types and land use create an overlap of private lands with key productive habitats at low elevations. This overlap may threaten species whose breeding populations depend on the productivity of low-elevation deciduous habitats, such as Neotropical migrant songbirds (Hansen and Rotella 2002b).

Over the past several decades, human influences have experienced a notable transition in the GYE. The presence of remote areas and natural amenities has been a strong predictor of demographic change, resulting in high rates of human population growth and accelerated expansion of development and agricultural land uses (Ingram and Lewandrowski 1999, Rasker and Hansen 2000). These land uses may threaten songbird populations by favoring high densities and altered abundances of nest predators and

brood parasites. In other ecosystems, nest predation and the abundance of predators has been shown to increase in proximity to development and agriculture (Ammon and Stacey 1997, Haskell et al. 2001, Chalfoun et al. 2002). Also, Brown-headed Cowbirds (*Molothrus ater*) frequent areas near agricultural and residential land use (Yamasaki et al. 2000, Hansen and Rotella 2002a, Tewksbury et al. 2002), and high parasitism rates have been found near agricultural edges (Ford et al. 2001). Based on this evidence, populations of migrant songbirds in proximity to low-elevation development and agriculture in the GYE are hypothesized to experience poor breeding success due to high rates of predation and brood parasitism.

Due to nationwide concerns for declining populations of songbird species, many studies have evaluated habitat suitability for breeding songbird populations across a broad range of North American landscapes and habitats. Estimates of reproductive output, an important component of the population growth rate of r-selected species (Lebreton and Clobert 1991, Sæther and Bakke 2000), are often used to determine how characteristics of these different landscapes and habitats affect songbird populations.

Studies have used estimates of nest survival to examine the effects of individual habitat features on songbird reproductive output at several spatial scales. Temporal effects may also influence nest survival as surrounding vegetation and predator communities change throughout the nesting season (Grant et al. 2005). Characteristics of a nest site such as a nest's degree of concealment, surrounding vegetation, and height from the ground may influence the ability of predators and brood parasites to locate a nest (Martin 1993, Burhans 1997). Predators and brood parasites may be further

influenced by the size of the patch of habitat surrounding a nest, which can affect their ability to penetrate a habitat patch and search the enclosed vegetation for individual nests (Robinson et al. 1995, Tewksbury et al. 1998, Chalfoun et al. 2002). In the GYE, the broader spatial scale that distinguishes the surrounding landscape is characterized by an elevational gradient of differences in climate severity, soils, fire frequency, and net primary productivity across habitat types. The expansion of human land use at low elevations favors the presence of brood parasites and many species of predators, which spread throughout their home ranges to impact nest survival in surrounding areas (Rothstein et al. 1984, Thompson 1994, Marzluff et al. 2004). The presence of expanding human land uses such as agriculture and rural residential development may thus dominate the spatial gradient in the GYE by causing high rates of nest failure in low-elevation deciduous habitats regardless of habitat features at local spatial scales.

Studies evaluating songbird nest survival in different regions and for different study species have reported equivocal results regarding which aspects of the surrounding habitat are important to nest survival and whether the effects of different variables are positive or negative. One possible explanation for this variation is that, though studies often relate the effects of variables at individual spatial scales to nest survival, few studies have considered how variables measured at multiple scales act together. This occurs despite evidence indicating that nest survival is likely influenced across many scales (Tewksbury et al. 1998, Thompson et al. 2002, Peak et al. 2004). It is important for studies to consider variables at multiple scales because, while several spatial scales may contribute to the nest survival of a species, the importance of features at one scale may

depend upon features at another scale (Chalfoun et al. 2002, Thompson et al. 2002). If multiple scales are not considered together, the importance of some variables may be missed or interpreted outside of their larger context.

Many fragmentation studies have demonstrated that predators and brood parasites are influenced most strongly by fragmentation at the landscape scale, as opposed to smaller scales (Donovan et al. 1997, Chalfoun et al. 2002, Stephens et al. 2003). Also, theoretical models suggest that effects at smaller scales are dependent on the context of the larger landscape (Thompson et al. 2002). This evidence suggests that the larger-scale context of the landscape will have the most prominent effects on nest survival compared with smaller-scale effects, and that this larger context may determine patterns of influence of variables at smaller spatial scales.

Given the rapid rate of change in human populations and land use in the GYE (Hansen et al. 2002) and the concern for populations of Neotropical migrant songbirds at low-elevation habitats (Hansen and Rotella 2002b), this study was designed to evaluate how nest survival is influenced by different variables at nest-level, patch-level, landscape-level, and temporal scales. We hypothesize that variables from multiple spatial scales will combine to influence nest survival, and that variables describing broad-scale characteristics of the overall landscape will be the primary drivers of nest survival in the GYE. Our goal is to provide insights into how habitat and land use gradients affect songbird breeding productivity in the GYE and how the landscape context influences the effects of smaller spatial scale features on nest survival.

Based on results of previous studies of songbird nest-survival, we developed a variety of hypotheses and predictions regarding relationships between nest survival and environmental covariates measured at various scales (see METHODS). We use an information-theoretic approach to evaluate the relative importance of nest-site, patch-level, landscape-level, and temporal effects on the nest survival of three songbird species in the GYE (Akaike 1973). A suite of *a priori* and exploratory models is used to test these hypotheses and show how effects at different scales combine to influence nest survival.

## METHODS

### Data Collection

Data were collected from 1997-1999 across southwestern Montana and adjoining portions of Idaho. Throughout the study area, riparian habitat occurs along the upper Gallatin, Madison, and Henry's Forks watersheds, all of which originate in Yellowstone National Park. Lowlands are characterized by deciduous forests and fertile soils, while coniferous forests and grasslands distinguish uplands. Land ownership varies from private lands at lower elevations to public lands at higher elevations. Types of land use include reserves and national forests on public lands and grazing, residential development, and other agricultural land uses on private lands. Human activity and disturbance are at their highest intensities at lower elevations.

We chose to analyze the nests of three common nesting songbirds in the GYE: Dusky Flycatchers (*Empidonax oberholseri*), Warbling Vireos (*Vireo gilvus*), and Yellow Warblers (*Dendroica petechia*). These species were selected because they share several desirable life history traits, including (1) each species builds open-cup nests and is susceptible to predation and parasitism by Brown-headed Cowbirds, which should also make them susceptible to the land use and habitat gradients characteristic of the GYE; (2) the species vary in their typical nest placements both within the canopy and sub-canopy and throughout the landscape such that, in combination, they allow comparisons of patterns across a broad range of conditions and habitat settings; and (3) the three species were abundant enough in the study area that sufficient samples could be gathered for these analyses.

Nest searching began each year in mid-May and continued through the end of July. Eleven plots in aspen and five plots in cottonwood were searched at a range of distances from surrounding land use. Cottonwood plots were present at low elevations (1,320 - 1,397 m) whereas aspen plots were present at mid (1,664 - 1,724 m) and high (2,042 - 2,140 m) elevations. Several of these plots were in close proximity, but all plots were separated by at least 20 m of open habitat. These locations were selected to achieve representations of a large, variable portion of the landscape gradient in the GYE.

Each nest was monitored until it successfully fledged young, or failed. Characteristics hypothesized to be potentially relevant to nest survival were measured at each nest, plot, and for the surrounding landscape. Different variables were selected and compared at each spatial scale to determine which variables at which spatial scales are important to nest survival. Variables measured at the scale of nest site were nest height and nest substrate height (nest substrate height was included as an index of the vegetative structure immediately surrounding the nest). At the patch-level scale, areas of plots were estimated from remotely-sensed imagery. Areas of contiguous cottonwood stands were difficult to measure, but plot areas were included for those nests that were present in cottonwood stands to keep the model suites consistent between species. The small plot areas in cottonwood stands reflect the narrow widths of the long, contiguous patches of habitat. At a landscape scale, the elevation of each nesting plot was derived from digital elevation models and parent material from soil atlases, and densities of homes were measured at radii of 1, 3, and 6 km from each plot.

### Model Justification and Model-Building Strategy

Nest survival analyses have only recently developed methods that allow models of daily survival rate to incorporate multiple covariates. As such, only a sparse and often equivocal base of literature was available to suggest how covariates of interest might combine to influence nest survival. To evaluate our *a priori* hypotheses while incorporating these exploratory combinations of covariates, we constructed a model suite based on *a priori* ideas that merged both *a priori* and exploratory components. While this somewhat lessened the strength of inference we were able to make from our model suite, it allowed us to address covariates and hypotheses that are relatively unexplored in newer nest survival analyses while still testing *a priori* hypotheses of biological interest.

Our merged model suite was built in a series of steps that used both *a priori* and exploratory components to evaluate *a priori* ideas: (1) single-predictor *a priori* models were constructed to assess hypotheses of how each covariate relates to nest survival; (2) single-predictor exploratory models were evaluated to select the best approximating functional form of several continuous covariates; (3) *a priori* models that combined covariates at the level of spatial scale tested hypotheses about the importance of variables from each spatial scale to nest survival; (4) based on results from the model suite, several exploratory interactions were tested for each species; and (5) the best models in the overall suite were combined with interactions that were supported by the model suite and then adjusted until a best approximating model was obtained. These five steps are described in detail below.

(1) Covariate Predictions. We formulated several predictions that described how key environmental variables in the GYE relate to the daily survival rates of Dusky Flycatchers, Warbling Vireos, and Yellow Warblers. These predictions were based on available evidence from twenty-seven previous studies of songbird nest survival that considered how one or more of the covariates we measured affect both songbirds in general and the three species in this study (Table 1). Each of these studies evaluated daily survival rate in relation to one or more habitat and/or temporal variables in this study, and together they provide evidence that nest survival is likely affected by variables operating at a variety of spatial and temporal scales. Based on this literature, we hypothesized that several features measured at these different scales may be important to nest survival in the GYE. Each of these features was evaluated independently in a set of linear single-predictor *a priori* models that were used to address our hypotheses of how each variable in this study affects the nest survival of Dusky Flycatchers, Warbling Vireos, and Yellow Warblers in the GYE.

Table 1. Twenty-seven previous studies of songbird nest survival, predation rates, or parasitism rates and the effects of nest-level, patch-level, landscape-level, and temporal scales on daily survival rate. The ‘Songbirds’ column provides results from studies of songbird species not examined in this study, while the other studies are specific to Dusky Flycatchers, Warbling Vireos, and/or Yellow Warblers. Each study found effects of one or more covariates that were either positive (+), negative (-), or neutral (0).

<b>Scale</b>	<b>Covariate</b>	<b>Songbirds</b>		<b>Dusky Flycatchers</b>	
<b>Nest</b>	Nest Height	Best and Stauffer 1960	0	Wilson and Cooper 1998	+
		Briskie et al. 1990	-	Banks and Martin 2001	0
		Martin 1993	-		
	Nest Substrate Height and/or Concealment	Best and Stauffer 1960	0	Kelly 1993	+
		Hahn and Hatfield 1995	+	Banks and Martin 2001	0
		Burhans 1997	+	Liebezeit and George 2002	0
		Martin and Roper 1988	+		
		Wilson and Cooper 1998	+		
		Uyehara and Whitfield 2000	+		
	<b>Patch</b>	Stand Area	Paton 1994	+	Tewksbury et al. 1998
Hoover et al. 1995			+	Liebezeit and George 2002	+
Tewksbury et al. 1998			0		
Friesen et al. 1999			0		
Zanette and Jenkins 2000			0		
<b>Landscape</b>	Development	Tewksbury et al. 1998	-	Tewksbury et al. 1998	-
		Hansen and Rotella 2001	-		
		Marzluff 2001	-		
		Phillips et al. 2005	-		
<b>Temporal</b>	Seasonal Date	Winter 1999	0		
		Grant et al. 2005	-		

Table 1 cont'd.

Scale	Covariate	Warbling Vireos		Yellow Warblers	
<b>Nest</b>	Nest Height	Ward and Smith 2000	0	Goosen and Sealy 1982	0
		Banks and Martin 2001	0	Briskie et al. 1990	-
		Ortega and Ortega 2003	0	Hanski et al. 1996	0
				Ortega and Ortega 2000	0
				Banks and Martin 2001	0
	Nest Substrate Height and/or Concealment	Banks and Martin 2001	0	Hanski et al. 1996	0
		Ortega and Ortega 2003	0	Banks and Martin 2001	0
<b>Patch</b>	Stand Area	Tewksbury et al. 1998	0	Tewksbury et al. 1998	0
<b>Landscape</b>	Development	Tewksbury et al. 1998	-	Tewksbury et al. 1998	-
				Hansen and Rotella 2002b	-
<b>Temporal</b>	Seasonal Date			Briskie et al. 1990	+

At the nest-level scale, studies of several songbird species have suggested a negative relationship between nest height and daily survival rate (Briskie et al. 1990, Martin 1993). Of studies that have examined Dusky Flycatchers, Warbling Vireos, or Yellow Warblers, most have found no relationship between nest height and daily survival rate (Ortega and Ortega 2000, Banks and Martin 2001, Ortega and Ortega 2003), though one study found a positive relationship between nest height and Dusky Flycatcher nest survival (Wilson and Cooper 1998) and another study found a negative relationship between nest height and Yellow Warbler nest survival (Briskie et al. 1990). There is some evidence for a positive relationship between nest substrate height and/or concealment and daily survival rate for several songbird species (Martin and Roper 1988, Wilson and Cooper 1998, Uyehara and Whitfield 2000), and two studies have found

positive relationships between nest concealment and the daily survival rate of Dusky Flycatcher nests (Kelly 1993, Liebezeit and George 2002), though no studies have found relationships between concealment and nest survival for Warbling Vireos or Yellow Warblers (Hanski et al. 1996, Banks and Martin 2001, Ortega and Ortega 2003). Based on this evidence, we predict a positive relationship between nest height and nest survival for Dusky Flycatchers and a negative relationship between nest height and nest survival of Yellow Warblers and Warbling Vireos. Nest substrate height is expected to have a positive relationship with nest survival for all three species.

Analyses of the effects of patch area on daily survival rate have produced equivocal results, as many studies have found no relationship between the size of a patch and daily survival rate (Friesen et al. 1999, Tewksbury et al. 1998, Zquette and Jenkins 2000) while others have found positive relationships between these variables (Paton 1994, Hoover et al. 1995). Of studies examining the effects of patch area on Dusky Flycatcher nest survival, one found a positive relationship between patch area and nest survival (Liebezeit and George 2002), while another found no relationship (Wilson and Cooper 1998). The only study that examined patch size in relation to Warbling Vireo and Yellow Warbler nest survival found no relationship between these variables (Tewksbury et al. 1998). Given this evidence, we chose to predict a positive relationship between patch size and nest survival for all species in this study.

All studies evaluating the effects of residential development on nest survival have concluded that high densities of homes have a negative effect on nest survival, both for songbirds in general (Tewksbury et al. 1998, Hansen and Rotella 2001, Phillips et al.

2005) and for the three species in this study (Tewksbury et al. 1998, Hansen and Rotella 2002b). The effects of elevation on nest survival are relatively unstudied, however, given the effects of steep elevational gradients in the GYE on songbird densities (Hansen and Rotella 2002a) nest survival is expected to increase with elevation.

Few studies have examined how seasonal date affects the daily survival rate of songbird nests, though several recent studies have included seasonal date in nest survival analyses and have found effects of date (Winter 1999, Grant et al. 2005). As abundances and densities of predators and brood parasites may change throughout the nesting season we expect daily survival rate to change with seasonal date, but due to a lack of evidence we do not predict directions for this change.

A final predictor (parasitism) was included in these analyses to address whether nest survival differed between parasitized and unparasitized nests. A difference in survival between parasitized and unparasitized nests may indicate that either parasitized nests are more likely to fail because they are parasitized or because unknown characteristics of these nests make them more susceptible to failure.

(2) Functional Relationships. We evaluated a set of exploratory models that addressed the possibility that, for several continuous covariates, the relationship between the log odds of daily survival rate and these covariates may have been nonlinear (Anderson and Burnham 2002). No previous data were available for making *a priori* predictions about the possible shapes of these curves for individual species, so we considered possible nonlinearities using single-predictor exploratory models. Several biologically reasonable functional relationships such as quadratic ( $\hat{\beta}_0 + \hat{\beta}_1 x_1 + \hat{\beta}_2 x_1^2$ ),

inverse ( $\hat{\beta}_0 + \hat{\beta}_1 x_1^{-1}$ ), and exponential ( $\hat{\beta}_0 + \hat{\beta}_1 \exp(x_1)$ ) transformations of the data (Neter et al. 1996) were performed for these continuous covariates, and all modified relationships were evaluated in the model suite. Functional relationships were only examined for those continuous predictors that were measured at each nest (nest height, nest substrate height, and date) as we did not believe that our sample size ( $n = 16$  plots) for those continuous covariates measured at each plot (elevation, home density, and patch area) was large enough to estimate nonlinear relationships between the log odds and the continuous covariates.

This set of exploratory nonlinear models evaluated several different functional versions of nest height, nest substrate height, and date (inverse and exponential relationships were tested for nest height and nest substrate height, while a quadratic relationship was tested for date). Additionally, the set of single-predictor *a priori* models described in step 1 included three nested counts of home density at 1, 3, and 6 km from the nesting plots. Because incorporating several functional versions of nest height, nest substrate height, and date or several nested versions of home density in a single model would be redundant, only the version of each variable that best described the daily survival rate of each species was used in all models containing more than one predictor. As such, the best versions of nest height, nest substrate height, home density and date were selected in an exploratory fashion after viewing modeling results from the sets of single-predictor models evaluated for each species. These versions used were allowed to differ between species and were incorporated in the set of 14 *a priori* scale-effects models and all further exploratory models described below.

(3) Scale-Level Hypotheses. Given our predictions about how each covariate influences nest survival we made further predictions about the importance of variables measured at each spatial scale to nest survival. Most of the variables evaluated in this study fit into categories of spatial scale: nest-site (nest height, nest substrate height), patch (patch area), and broad-scale variables that describe characteristics of the larger landscape (home density, elevation; hereafter ‘landscape-level variables’). Elevation was included as a landscape-level effect because, due to the known elevational gradients of habitat types and land use in the GYE, elevation is believed to act as a surrogate for unmeasured variables exerting broad-level effects on nest survival. These effects may include changes in predator communities, vegetation structures, climate, and prey availabilities.

To test our predictions regarding scale-level effects, we evaluated 14 *a priori* models with multiple additive effects. These models were constructed to compare the importance of effects of (1) variables from several spatial scales with variables from fewer spatial scales, and (2) landscape-level effects with smaller-scale effects. To make these comparisons, we additively combined all predictors within each of the three spatial scales and then built these models at the level of scale (Table 2). In this manner, (1) each of the three spatial scales was modeled individually, (2) each individual scale was paired in all possible combinations with other scales, and (3) all three scales were combined together in a single model. All of the predictors in these models were combined additively, and this yielded a total of seven models. As any of these relationships may vary with time, temporal effects (date, year) were additively included in each of these

seven models. Also, because parasitism did not fit within any of the three spatial scales, the seven above models were duplicated and parasitism was additively included in each one. This yielded a total of 14 *a priori* models with multiple additive predictors. Several of these models contained correlated variables (nest height and nest substrate height, or elevation and homes), and therefore the stability of the betas for these models was examined before results from these models were evaluated (Neter et al. 1996).

Table 2. The set of 14 *a priori* models constructed at the level of spatial scale. Covariates are Nest, Patch, Landscape, Parasitism, and Time, each representing an additive combination of all covariates within that scale: Nest (nest height + nest substrate height), Patch (stand area), Landscape (home density + elevation), Parasitism (whether the nest was parasitized), and Time (seasonal date + year).

<b>Multi-Scale Models</b>		
	<b>Spatial Scale + Time</b>	<b>Spatial Scale + Parasitism + Time</b>
<b>One Spatial Scale</b>	Nest + Time	Nest + Parasitism + Time
	Patch + Time	Patch + Parasitism + Time
	Landscape + Time	Landscape + Parasitism + Time
<b>Two Spatial Scales</b>	Nest + Patch + Time	Nest + Patch + Parasitism + Time
	Nest + Landscape + Time	Nest + Landscape + Parasitism + Time
	Patch + Landscape + Time	Patch + Landscape + Parasitism + Time
<b>Three Spatial Scales</b>	Nest + Patch + Landscape + Time	Nest + Patch + Landscape + Parasitism + Time

We believe that landscape-level effects such as elevational, habitat, and land use gradients determine the larger context for the distribution of predators and brood parasites throughout the landscape. Hence, we predict that landscape-scale variables will exert the strongest effects on nest survival compared with variables measured at smaller spatial scales. Smaller-scale patch- and nest-level variables are believed to influence the ability of predators and brood parasites to locate an individual nest, and while these effects are subject to the context of the larger landscape they are also expected to act in conjunction with broad-scale variables to determine patterns of influence on nest survival throughout

the GYE. Based on these ideas, we hypothesize that daily survival rate will be influenced by effects at multiple spatial scales, with landscape-level effects maintaining the strongest importance on daily survival rate for all three species.

Comparing across the three species in this study, we expect the hypothesis that multiple spatial-scale effects will influence daily survival rate to be true for all species. However, the importance of different landscape-level effects and the presence and magnitude of smaller-scale effects may vary between species. Evidence was not available to suggest which covariates might be the most important to each species given competing spatial scales, so we made no predictions of species-specific differences in importances of spatial-level variables. However, given the life histories of the three study species (Ehrlich et al. 1988) we hypothesize that results for Dusky Flycatchers and Warbling Vireos may be relatively similar, while results for Yellow Warblers may be different from those of the other two. Dusky Flycatchers and Warbling Vireos are fly-catching species that, compared to Yellow Warblers, nest higher off the ground and mainly in aspen habitat. The Yellow Warbler, in contrast, is a gleaning species that nests closer to the ground and mainly in cottonwood habitat, but is present in both aspen and cottonwood habitats in the GYE. Also, because Yellow Warblers nest across a broader elevational gradient compared with the other two species, their nest sites are surrounded by more variable densities of human land uses (such as residential development). This may provide a stronger response in Yellow Warbler nest survival to surrounding landscape-level effects.

(4) Interactions. Interactions were evaluated in a set of exploratory models, and each interaction model was comprised of only the interaction and its additive components. Predictors were selected for inclusion in interaction models based on confidence intervals and model-selection results from the rest of the model suite, hence these models were exploratory. These interaction models were compared with corresponding nested additive models. If the model containing the interaction received more support than its corresponding nested model (Burnham and Anderson 2002) then the interaction was added in an exploratory fashion to the best models in the overall suite (step 5). All possible interactions were not evaluated. Rather, only a few biologically reasonable combinations were explored. A different set of interaction models was evaluated for each species.

(5) Exploratory Modifications of Best Models. Because covariates in the *a priori* models were grouped at the level of scale, there were many intermediate combinations of covariates which represent hypotheses that we did not evaluate in our *a priori* models. While we believed that these hypotheses were of biological interest, our ability to evaluate these hypotheses in an *a priori* fashion was limited because (1) previous research cannot provide us with enough certainty to formulate *a priori* hypotheses that describe exactly how our covariates will combine to influence nest survival, and (2) it was necessary to keep the suite of models to a reasonable size (Anderson and Burnham 2002). Hence, we used exploratory analyses to modify our best models and generate intermediate hypotheses that described which specific covariates were important to the daily survival rates of each species in our study. We recognize that our strength of

inference from these models is limited, and we expect that these exploratory models will outcompete our *a priori* models in the model suites. We chose to separately compare our exploratory and *a priori* models when evaluating support for our hypotheses, and use our exploratory models to generate hypotheses about specific relationships between covariates in our dataset.

### Statistical Analyses

Maximum likelihood estimates of daily survival rates were obtained using generalized linear models (McCullagh and Nelder 1989). A logit link function was used to model the relationship between the binomially distributed response and covariates of interest. The probability that a nest survived from day  $i$  to day  $i+1$  (daily survival rate),  $\theta_i$ , was modeled as  $\exp(\beta_o + \sum_j \beta_j x_{ji}) / (1 + \exp(\beta_o + \sum_j \beta_j x_{ji}))$  where  $x_{ji}$  is the value of a covariate,  $j$ , on day  $i$  (Rotella et al. 2004). Because the probability of surviving each interval was a function of the probability of surviving each day, parameter values could be assigned to models that incorporated covariates varying by time, by group, and by nest. These likelihood-based equations also allowed observation intervals to vary in length and did not make assumptions about when nest failure occurs during an observation interval (Dinsmore et al. 2002).

Parameters of continuous covariates were estimated from standardized data. All land use variables were scaled per unit area, and dummy (indicator) variables were used to model discrete covariates such as year of study or a nest's parasitism status. The effective sample size for these models was equal to the number of days that all nests survived plus the number of intervals that ended in failure (Rotella et al. 2004).

Estimations of daily survival rate were carried out using PROC NLMIXED in SAS as described by Rotella et al. (2004). The best-supported models were selected based on Akaike's information criterion adjusted for sample size,  $AIC_c$ , and  $AIC_c$  model weights (Burnham and Anderson 2002). Model averaging was performed to address model selection uncertainty and to test predictions about relationships between individual variables and daily survival rate. Model-averaged parameter estimates and their standard errors were calculated using Akaike model weights (Burnham and Anderson 2002). Goodness of fit for the most general model and for the best model in each suite was assessed using an unweighted sum of squares of the Kernel-smoothed model residuals and PROC IML in SAS, as described by Sturdivant et al. (In Press). Though these analyses assumed that nest fates were independent, available methods do not yet allow estimations of overdispersion and we were not able to estimate overdispersion of the nest survival data (Dinsmore et al. 2002). Additionally, no random effects were considered, and spatial and temporal autocorrelations may be present in the data that our models were unable to account for.

To assess whether the data supported effects of each covariate of interest on daily survival rate we examined the confidence intervals of model-averaged parameter estimates to determine the extent to which they overlapped zero. The presence or absence of each variable in the best model was also considered, as were parameter estimates from the best model. If a variable was present in the best model and parameter estimates and confidence intervals from the best model and from model averaging did not overlap zero, then the relationship of the variable to daily survival rate was considered to be different

from zero. If the confidence intervals of either parameter estimate overlapped zero, caution was used when interpreting results in keeping with the amount to which the interval overlapped zero. Weights of evidence for each predictor were used to gauge the relative importance of each variable in the model suites, and model weights were used to gauge the importance of each model in the models suites (Burnham and Anderson 2002).

## RESULTS

### Overview: Data Summary and Organization of Results

#### Data Summary

We located and monitored a total of 652 nests of Dusky Flycatchers, Warbling Vireos, and Yellow Warblers in high-elevation aspen habitat (2,042 - 2,140 m), mid-elevation aspen habitat (1,664 - 1,725 m), and low-elevation cottonwood habitat (1,320 - 1,397 m). Nests of each species varied in their locations across the landscape which provided us with a broad representation of the elevational gradient in the GYE. Each species also differed in their nesting locations within the canopy. We provide Box and Whisker plots (Tukey 1977) to illustrate the different ranges of covariates measured for each species (Appendix A). Also, relative magnitudes of effects of each covariate on the daily survival rates of each species are illustrated in Figure 1. These magnitudes are discussed within the results for covariate relationships for each species.

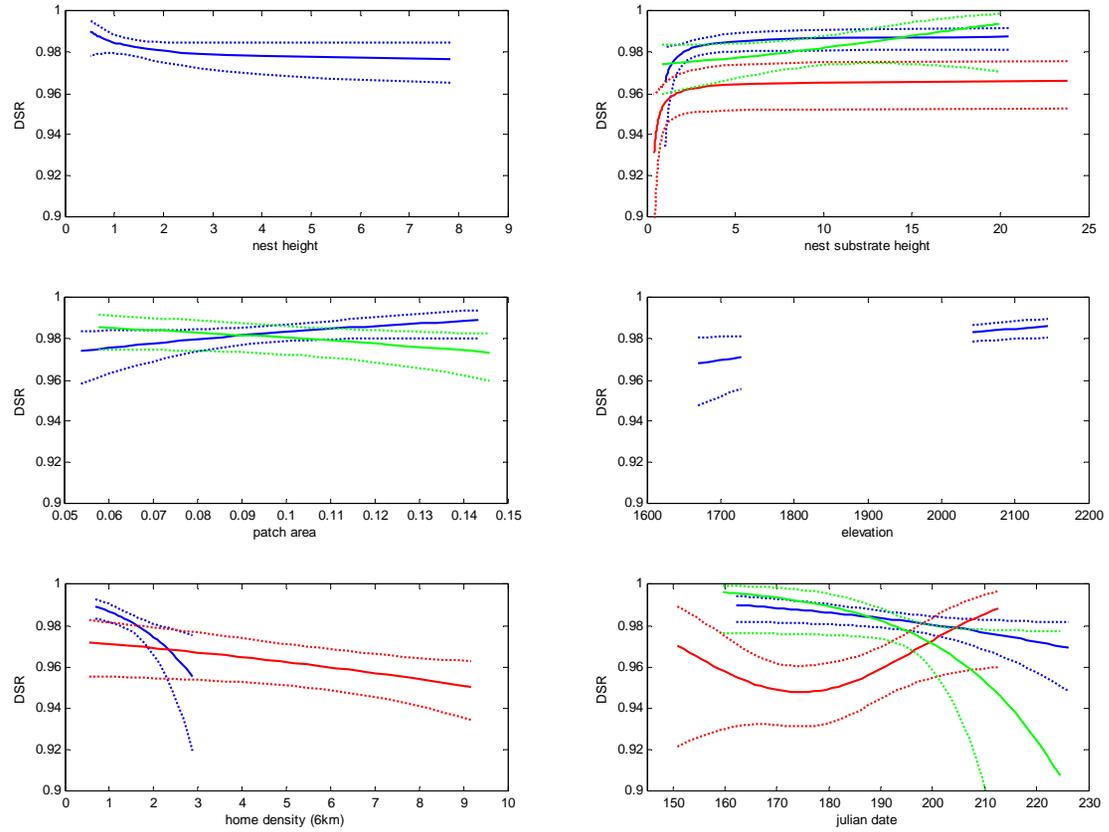


Figure 1. Comparisons of the relative magnitudes of effects of each continuous covariate on daily survival rate. Plots are constructed using the best models of daily survival rate for Dusky Flycatchers (blue), Warbling Vireos (green), and Yellow Warblers (red). Only estimates from covariates that were present in the best models are shown. These estimates assume that all other covariates are at their mean values and that nests are not parasitized by Brown-headed Cowbirds.

Pearson correlation coefficients and associated p-values are presented for each species in Appendix B. For Dusky Flycatchers, high correlations ( $r > 0.5$ ) were present between patch area and home density at 6 km from the nesting plot ( $r = 0.6763$ ;  $n=1718$ ;  $p < 0.0001$ ) and between nest height and nest substrate height ( $r = 0.8246$ ;  $n=1718$ ;  $p < 0.0001$ ). Warbling Vireos had a moderate correlation between elevation and home density at 6 km ( $r = -0.5713$ ,  $n = 809$ ;  $p < 0.0001$ ). There was also a correlation between elevation and home density at 6 km in the Yellow Warbler data ( $r = -0.9109$ ,  $n = 1231$ ,  $p < 0.0001$ ), as well as a correlation between nest height and nest substrate height ( $r = 0.84364$ ;  $n = 1231$ ;  $p < 0.0001$ ). Beta estimates from models containing correlated covariates did not appear to fluctuate.

Goodness of fit analyses were performed for the best and most complex models of daily survival rate for all three species. For Dusky Flycatchers, the calculated statistic and moments using the cubic kernel and a bandwidth of 0 for both the most complex model ( $P = 0.901$ ) and the best model ( $P = 0.890$ ) had corresponding high p-values, and hence we were unable to reject the null hypothesis that these models fit the data. For Warbling Vireos, results from the most complex model ( $P = 0.851$ ) and from the best model ( $P = 0.821$ ) again failed to reject the null hypothesis that these models fit the data. Finally, results from the most complex model ( $P = 0.803$ ) and from the best model ( $P = 0.817$ ) describing Yellow Warbler daily survival rate again had high corresponding p-values, and failed to reject the null hypothesis that these models fit the data.

## Organization

We present modeling results according to the 5 steps outlined in METHODS. Steps 1 and 2 were combined in RESULTS because covariate relationships were best described using the version of each covariate that received the greatest support from the model suite. Steps 4 and 5 were also combined because interactions that received support were incorporated into exploratory models. Results from model averaging are presented to describe covariate hypotheses, and model-averaged parameter estimates were calculated using all models in each species' models suite that had weight. These parameters were estimated from standardized covariates, and hence magnitudes of changes in daily survival rate with each covariate are discussed using graphical representations and not parameter estimates. Once model selection results are reported to indicate the functional form of each variable that was used, model selection results for scale-level hypotheses and exploratory modeling are presented.

## Dusky Flycatchers

### General Results

We monitored 233 Dusky Flycatcher nests in 11 aspen plots, which provided a total of 1,718 observation intervals and an effective sample size of 4801. The study plots varied in size from 0.05 to 0.14 km<sup>2</sup> and were present in 3 mid- (1,664 - 1,725 m) and 8 high-elevation (2,042 - 2,140 m) plots. Nests were initiated from early June to early August and the number of nests per plot ranged from 1 to 21 per year. The interval from the day that the first egg was laid to fledging averaged 34 days (mean = 34.422, SE = 0.134). Brown-headed Cowbirds parasitized 9% of Dusky Flycatcher nests in the study.

### Summary of Model-Selection Results

The best supported *a priori* model of daily survival rate was the most general model ( $\Delta AIC_c = 3.32$ ), and provided evidence that all of the covariates we examined were related to daily survival rate. The best exploratory model of daily survival rate was nearly identical to the best *a priori* model and contained all covariates except year ( $\Delta AIC_c = 0.00$ ). The best model in the suite accounted for 65% of the model weight (Table 3). Models that included parasitism status and landscape effects received support throughout the model suite, and there was evidence for effects of all spatial-level variables (Appendix C).

Table 3. Model selection results for the best models of daily survival rate for Dusky Flycatchers. Models  $\leq 10 \Delta AIC_c$  are shown. Models are designated either EX for exploratory or AP for *a priori*. Names of spatial and temporal scales represent additive combinations of all variables within that spatial scale: Nest ( $NestHt^{-1} + NestSubstHt^{-1}$ ), Patch (stand area), Landscape (home density + elevation), and Time (date + year).  $AIC_c$  adjusted for sample size was used to select the best models, and  $w_i$  is the weight of evidence for each model given the other models in the suite.

<b>Dusky Flycatchers</b>				
(n=4801)				
Model	$k$	$AIC_c$	$\Delta AIC_c$	$w_i$
EX: Nest + Patch + Landscape + Parasitism + Date	8	750.554	0.000	0.650
AP: Nest + Patch + Landscape + Parasitism + Time	10	753.879	3.324	0.123
AP: Patch + Landscape + Parasitism + Time	8	754.304	3.750	0.100
AP: Nest + Landscape + Parasitism + Time	9	755.483	4.929	0.055
AP: Landscape + Parasitism + Time	7	756.051	5.496	0.042
AP: Nest + Patch + Landscape + Time	9	759.923	9.368	0.006
AP: $B_0$	1	769.397	18.843	0.000

### Covariate Relationships and Predictions

Evaluation of single-predictor models indicated that nest height and nest substrate height were best represented by inverse functional forms ( $NestHt^{-1}$  and

$NestSubstHt^{-1}$ , see Appendix C). Thus, these functional versions were used in all further modeling of nest-level variables.

Model-averaged parameter estimates (Table 4) suggested that daily survival rate decreased with  $NestHt^{-1}$  ( $\hat{\beta} = 0.2963$ , 95% CI = -0.0806, 0.6731) and increased with  $NestSubstHt^{-1}$  ( $\hat{\beta} = -0.3507$ , 95% CI = -0.6888, -0.0125). Parameter estimates from the best model (Table 5) provided similar results, as daily survival rate appeared to decline with  $NestHt^{-1}$  ( $\hat{\beta} = 0.2883$ , 95% CI = -0.0851, 0.6616) and increase with  $NestSubstHt^{-1}$  ( $\hat{\beta} = -0.3466$ , 95% CI = -0.6828, -0.0104). These parameter estimates indicated that daily survival rate dropped off when a nest was in low substrates, and increased when a nest was close to the ground. Although the confidence intervals for  $NestHt^{-1}$  slightly overlapped zero, this is likely due to modest precision of the estimates. The bulk of the confidence intervals fell to one side of zero, indicating a high degree of confidence in the signs of the estimated coefficients. These results provide support for our hypothesis that daily survival rate increases with nest substrate height, but they do not support our hypothesis that daily survival rate increases with nest height.

Table 4. Model-averaged parameter estimates for individual covariates, and their 95% confidence intervals. Estimates were obtained from all models in the suite that had weight.

<b>Dusky Flycatchers</b>				
Covariate	Model-Averaged Parameter Estimate	SE	95% LCI	95% UCI
$B_0$	4.0497	0.1478	3.7600	4.3394
$NestHt^{-1}$	0.2963	0.1923	-0.0806	0.6731
$NestSubstHt^{-1}$	-0.3507	0.1725	-0.6888	-0.0125
Patch Area	0.3159	0.1800	-0.0369	0.6686
Home Density (6 km)	-0.4685	0.1681	-0.7979	-0.1391
Elevation	0.2534	0.1133	0.0313	0.4756
Date	-0.2368	0.1091	-0.4507	-0.0230

1997	-0.1621	0.2570	-0.6658	0.3417
1998	-0.1302	0.2431	-0.6066	0.3463
Parasitism	-0.9573	0.2979	-1.5411	-0.3734

Table 5. Parameter estimates from the best model of daily survival rate for Dusky Flycatchers.

<b>Dusky Flycatchers</b>				
<u>Covariate</u>	<u>Estimate</u>	<u>SE</u>	<u>95% LCI</u>	<u>95% UCI</u>
$B_0$	4.0353	0.1179	3.8041	4.2666
$NestHt^{-1}$	0.2883	0.1904	-0.0851	0.6616
$NestSubstHt^{-1}$	-0.3466	0.1714	-0.6828	-0.0104
Patch Area	0.3128	0.1790	-0.0384	0.6640
Home Density (6km)	-0.4872	0.1615	-0.8039	-0.1704
Elevation	0.2588	0.1114	0.0404	0.4772
Date	-0.2348	0.1075	-0.4457	-0.0240
Parasitism	-0.9445	0.2945	-1.5221	-0.3670

At the patch-level scale, the model-averaged parameter estimate for patch area ( $\hat{\beta} = 0.3159$ , 95% CI = -0.0369, 0.6686) and the parameter estimate from the best model ( $\hat{\beta} = 0.3128$ , 95% CI = -0.0384, 0.6640) indicated that daily survival rate increased with patch area. The confidence intervals for these estimates had only a slight overlap with zero, and these results provide support for our hypothesis that daily survival rate increases with patch area.

Variables at broader spatial scales also entered the best models. A model that incorporated home density measured within 6 km of the nesting plots ( $\Delta AIC_c = 12.74$ ) received more support compared with models that considered home density at shorter radii (3 km:  $\Delta AIC_c = 13.82$ ; 1 km:  $\Delta AIC_c = 17.99$ ) from the nesting plots. Measures of home density at a 6 km radius from the nesting plots were thus used in all further modeling of this variable. The model-averaged parameter estimate for home density at 6

km ( $\hat{\beta} = -0.4685$ , 95% CI = -0.7979, -0.1391) and the parameter estimate for home density from the best model ( $\hat{\beta} = -0.4872$ , 95% CI = -0.8039, -0.1704) both indicated a negative relationship between home density and daily survival rate. Also measured at a broad spatial scale, elevation was positively related to daily survival rate according to both the model-averaged parameter estimate ( $\hat{\beta} = 0.2534$ , 95% CI = 0.0313, 0.4756) and the parameter estimate from the best model ( $\hat{\beta} = 0.2588$ , 95% CI = 0.0404, 0.4772). These estimates for home density and elevation support our hypotheses that daily survival rate declines when a nest is surrounded by higher densities of homes and increases with elevation.

Of the non spatial-level variables evaluated in this model suite, date and parasitism appeared to be related to variation in daily survival rate but there was little difference in daily survival rate between years. Model-averaged parameter estimates ( $\hat{\beta} = -0.2368$ , 95% CI = -0.4507, -0.0230) and parameter estimates from the best model ( $\hat{\beta} = -0.2348$ , 95% CI = -0.4457, -0.0240) indicated that daily survival rate declined with date. Also, parasitized nests had a lower daily survival rate compared with unparasitized nests according to both model-averaged parameter estimates ( $\hat{\beta} = -0.9573$ , 95% CI = -1.5411, -0.3734) and parameter estimates from the best model ( $\hat{\beta} = -0.9445$ , 95% CI = -1.5221, -0.3670). These results support our hypothesis that daily survival rate is lower for parasitized nests than for unparasitized nests. Year appeared to have little influence on daily survival rate as the confidence intervals for the model-averaged parameter estimates

overlapped zero substantially ( $\hat{\beta}_{1997} = -0.1621$ , 95% CI = -0.6658, 0.3417;  $\hat{\beta}_{1998} = -0.1302$ , 95% CI = -0.6066, 0.3463), and as year was not present in the best model.

Dusky Flycatchers were the only species whose daily survival rate was influenced by nest height and elevation. The magnitude of the effect of nest substrate height on Dusky Flycatcher daily survival rate was similar to that of Yellow Warblers, and less than that of Warbling Vireos in higher nest substrates (Figure 1). Daily survival rate changed with patch area with a similar magnitude compared with Warbling Vireos, though the daily survival rate of Dusky Flycatchers increased in larger patches while the daily survival rate of Yellow Warblers declined in larger patches. The decline in the daily survival rate of nests of Dusky Flycatchers with increasing home density was sharper compared with that of Yellow Warblers, and the magnitude of the effect of date on Dusky Flycatcher daily survival rate was gradual compared with effects of date on the other two species. The difference between the daily survival rates of parasitized nests ( $DSR_{para} = 0.9565$ , 95% CI = 0.9281, 0.9740) and unparasitized nests ( $DSR_{unpara} = 0.9826$ , 95% CI = 0.9782, 0.9862) of Dusky Flycatchers was greater than those for the other two species.

#### Scale Selection: Landscape Effects Hypothesis

Model-averaged parameter estimates and parameter estimates from the best model (described above) supported effects of landscape-level variables on nest survival. Landscape-level variables received consistent support throughout the model suite (Appendix B), and both elevation and home density were present in the top 6 models ( $\Delta AIC_c < 10$ ) which had a combined model weight of 0.976 (Table 6). In the set of 14 *a priori* scale-level models, models with landscape-level variables received stronger

support than models without landscape-level variables (Appendix B). We compared  $\Delta AIC_c$  scores from only those models that contained the parasitism variable because models without parasitism were not well supported by the data. Among models that contained covariates from only one spatial scale, a model with only landscape-level variables ( $\Delta AIC_c = 5.50$ ) received more support than models with only patch- ( $\Delta AIC_c = 14.52$ ) or nest-level variables ( $\Delta AIC_c = 10.80$ ). Of models incorporating two spatial scales, a model with landscape- and nest-level variables ( $\Delta AIC_c = 4.93$ ) and a model with landscape- and patch-level variables ( $\Delta AIC_c = 3.75$ ) both received more support than a model with nest- and patch-level variables ( $\Delta AIC_c = 11.90$ ).

Weights of evidence for each group of predictors (Table 6) were higher for landscape-level variables ( $w_i = 0.979$ ) than for nest- ( $w_i = 0.840$ ) or patch-level variables ( $w_i = 0.883$ ). Of the individual spatial-level predictors, weights of evidence also indicated that home density ( $w_i = 0.987$ ) and elevation ( $w_i = 0.979$ ) were the most important spatial-level variables within the model suite.

Table 6. Weights of evidence for each individual covariate and for each scale in the Dusky Flycatcher model suite. These weights were obtained by summing the weights of evidence of all models containing each covariate, or all of the covariates within a spatial scale.

<b>Weights of Evidence: Dusky Flycatchers</b>			
<u>Covariate</u>	<u><math>w_i</math></u>	<u>Scale</u>	<u><math>w_i</math></u>
<i>NestSubstHr<sup>-1</sup></i>	0.847	Nest ( <i>NestSubstHr<sup>-1</sup></i> + <i>NestHr<sup>-1</sup></i> )	0.840
<i>NestHr<sup>-1</sup></i>	0.840	Patch (Stand Area)	0.883
Patch Area	0.883	Landscape (Home Density (6 km) + Elevation)	0.979
Home Density (6 km)	0.987	Temporal (Date + Year)	0.334
Elevation	0.979		
Date	0.988		
1997	0.334		
1998	0.334		
Parasitism	0.980		

### Scale Selection: Multiple-Scale Effects Hypothesis

Model-averaged parameter estimates and parameter estimates from the best model (described above) supported effects of nest height, nest substrate height, patch area, home density, and elevation on nest survival. This supports the hypothesis that effects at several spatial scales are important to nest survival.

The set of 14 *a priori* scale-level models also provides evidence for the hypothesis that nest survival is influenced by multiple spatial scales. Models that incorporated both landscape- and patch-level spatial scales ( $\Delta\text{AIC}_c = 3.75$ ) and landscape- and nest-level spatial scales ( $\Delta\text{AIC}_c = 4.93$ ) received more support than models of landscape-level effects alone ( $\Delta\text{AIC}_c = 5.50$ ), of patch effects alone ( $\Delta\text{AIC}_c = 14.52$ ) and of nest effects alone ( $\Delta\text{AIC}_c = 10.80$ ). A model of nest- and patch-level scales ( $\Delta\text{AIC}_c = 11.90$ ) received little support because this model did not contain landscape-level effects. The best in the set of 14 *a priori* models ( $\Delta\text{AIC}_c = 3.32$ ) contained effects of all three spatial scales.

### Exploratory Interactions and Modifications of Best Models

No interactions received support in the model suite. The best and only exploratory model ( $\Delta\text{AIC}_c = 0$ ) (Figure 1) included effects of nest-, patch-, and landscape-level spatial scales and only differed from the best *a priori* model ( $\Delta\text{AIC}_c = 0$ ) in that year of the study was not present in the model. This exploratory model supports the hypothesis that multiple scale effects are important to nest survival. Additionally, this model contributed a large model weight ( $w_i = 0.65$ ) both to results for the landscape effects hypothesis and to results for the multiple-scale effects hypothesis.

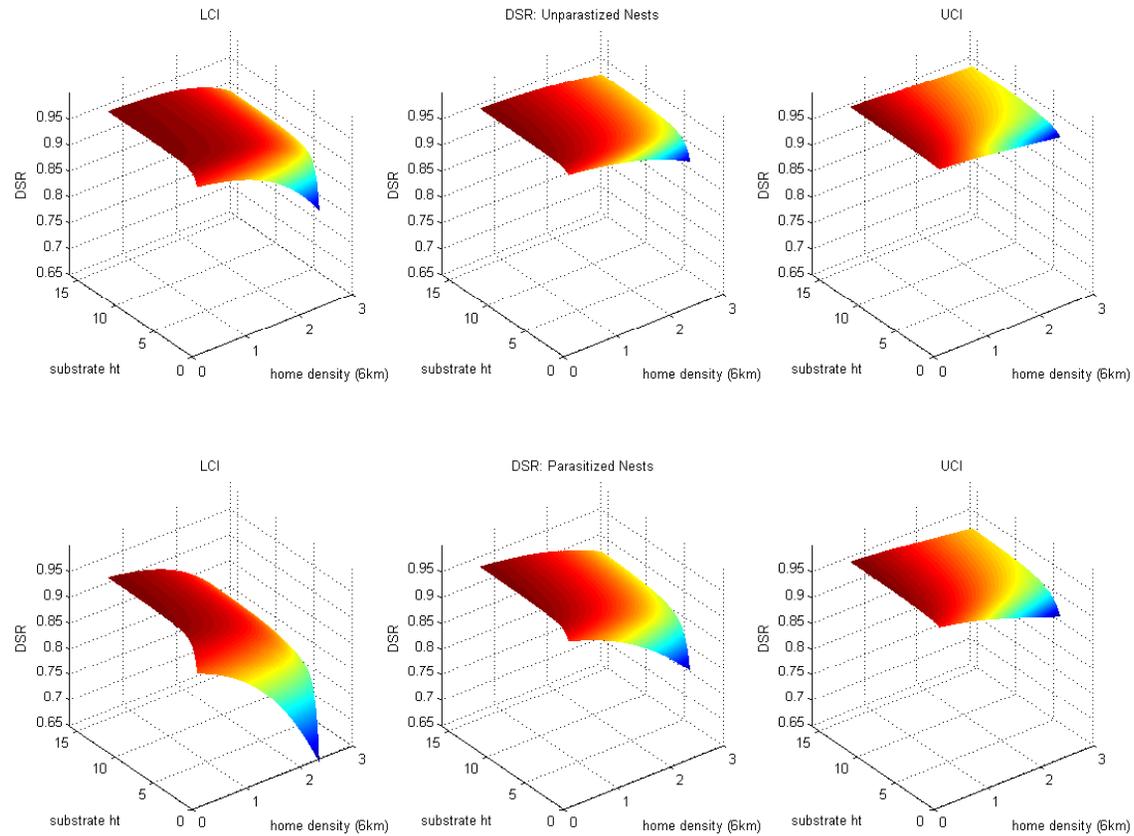


Figure 2. Changes in daily survival rate (DSR) of Dusky Flycatcher nests with parasitism, nest substrate height (substrate ht), and home density at a 6 km radius from the nesting plots. Lower (LCI) and upper (UCI) confidence intervals are shown as additional tiles. These estimates of daily survival rate are based on parameter estimates from the best model of daily survival rate for Dusky Flycatchers.

## Warbling Vireos

### General Results

Observers monitored 129 nests of Warbling Vireos in 3 low-elevation (1,320 - 1,396 m) cottonwood plots, 3 mid-elevation (1,664 - 1,725 m) aspen plots, and 8 high-elevation (2,042 - 2,140 m) aspen plots. This provided a total of 809 observation intervals and an effective sample size of 2,357. The nesting plots varied in size from 0.05 to 0.14 km<sup>2</sup> and the number of nests on one plot in a given year ranged from 1 to 11. Nests were initiated from mid-June to late July and the nesting interval averaged 29 days from the day the first egg was laid to fledging (mean = 29.575, SE = 0.300). Brown-headed Cowbirds parasitized 30% of Warbling Vireo nests in the study.

### Summary of Model-Selection Results

The best *a priori* model of daily survival rate included effects of nest height, nest substrate height, patch area, parasitism, date, and year of study ( $\Delta AIC_c = 1.066$ ). The best exploratory model was similar to the best *a priori* model, but without effects of nest height and year of study ( $\Delta AIC_c = 0$ ). Nest substrate height, patch area, parasitism, and date were present in the best *a priori* and exploratory models throughout the model suite. There was also some evidence in the model suite for an effect of elevation ( $\Delta AIC_c > 0.343$ ) and for an interaction between nest substrate height and date ( $\Delta AIC_c > 0.343$ ) (Appendix C). The best model accounted for 13% of the model weight, and the best 15 models ( $\Delta AIC_c < 4$ ) accounted for 91% of the model weight (Table 7).

Table 7. Model selection results for the best models of daily survival rate for Warbling Vireos. Models  $\leq 4 \Delta AIC_c$  are shown. Models are designated either EX for exploratory or AP for *a priori*. Names of spatial and temporal scales represent additive combinations of all variables within that spatial scale: Nest (nest height + nest substrate height), Patch (stand area), Landscape (home density + elevation), and Time (date + year).  $AIC_c$  adjusted for sample size ( $AIC_c$ ) was used to select the best models, and  $w_i$  is the weight of evidence for each model given the other models in the suite.

<b>Warbling Vireos</b>				
(n=2253)				
Model	$k$	$AIC_c$	$\Delta AIC_c$	$w_i$
EX: expNestSubstHt + Patch + Parasitism + Date	5	396.821	0	0.13
EX: expNestSubstHt + Patch + Parasitism + Date + Date*expNestSubstHt	6	397.113	0.292	0.112
EX: expNestSubstHt + Patch + Elevation + Parasitism + Time + Date* expNestSubstHt	9	397.164	0.343	0.109
EX: expNestSubstHt + Date + expNestSubstHt *Date	4	397.823	1.002	0.078
EX: expNestSubstHt + Date	3	397.856	1.035	0.077
AP: Nest + Patch + Parasitism + Time	8	397.887	1.066	0.076
AP: Patch + Parasitism + Time	6	398.032	1.211	0.071
EX: expNestSubstHt + Patch + Elevation + Parasitism + Date + Date*expNestSubstHt	7	398.612	1.791	0.053
EX: Nest Substrate Height + Elevation + Parasitism + Date + Date*expNestSubstHt	6	399.157	2.336	0.04
EX: Nest + Patch + Elevation + Parasitism + Time + Date*expNestSubstHt	10	399.18	2.359	0.04
AP: Nest + Parasitism + Time	7	399.475	2.654	0.034
AP: Nest + Time	6	399.612	2.791	0.032
AP: Nest + Patch + Time	7	399.647	2.826	0.032
AP: Date	2	400.497	3.676	0.021
AP: Nest + Patch + Landscape + Parasitism + Time	10	400.742	3.921	0.018
AP: B <sub>0</sub>	1	417.505	20.684	0.000

### Covariate Relationships and Predictions

Model-selection results from single-predictor models indicated that nest height was best represented by an inverse functional form ( $NestHt^{-1}$ ) while nest substrate height

was best represented by an exponential functional form ( $\exp NestSubstHt$ ) (Appendix C).

These functional versions were used in all further modeling of nest-level variables.

Model-averaged parameter estimates (Table 8) suggested that daily survival rate decreased with  $NestHt^{-1}$  ( $\hat{\beta} = -0.0458$ , 95% CI = -0.2928, 0.2011), but as the bulk of this confidence interval overlapped zero we cannot confidently conclude that the sign of this estimate was negative. Thus, this result does not provide support for our hypothesis that daily survival rate would decline with nest height.

Table 8. Model-averaged parameter estimates for individual covariates, and their 95% confidence intervals. Estimates were obtained from all models in the suite that had weight.

<b>Warbling Vireos</b>				
<u>Covariate</u>	<u>Model-Averaged Parameter Estimate</u>	<u>SE</u>	<u>95% LCI</u>	<u>95% UCI</u>
$B_0$	3.8470	0.2357	3.3851	4.3090
$NestHt^{-1}$	-0.0458	0.1260	-0.2928	0.2011
$\exp NestSubstHt$	0.4141	0.2326	-0.0418	0.8700
Patch Area	-0.2459	0.1447	-0.5295	0.0377
Home Density (6 km)	0.0570	0.1685	-0.2732	0.3873
Elevation	0.1432	0.1473	-0.1456	0.4320
Date	-0.6491	0.1863	-1.0142	-0.2840
1997	-0.0066	0.3839	-0.7590	0.7459
1998	0.6306	0.3222	-0.0009	1.2620
Parasitism	-0.5894	0.3375	-1.2509	0.0721

Both the model-averaged parameter estimate ( $\hat{\beta} = 0.4141$ , 95% CI = -0.0418, 0.8700) (Table 8) and the parameter estimate from the best model ( $\hat{\beta} = 0.3593$ , 95% CI = -0.0837, 0.8023) (Table 9) supported a positive relationship between  $\exp NestSubstHt$  and daily survival rate. The confidence intervals for the parameter estimates of  $\exp NestSubstHt$  overlapped zero slightly, but as the majority of these intervals lay above zero we are confident that  $\exp NestSubstHt$  had a positive relationship with daily survival

rate. These parameter estimates support our hypothesis that daily survival rate increased with nest substrate height.

Table 9. Parameter estimates from the best models of daily survival rate for Warbling Vireos.

Warbling Vireos				
<u>Covariate</u>	<u>Estimate</u>	<u>SE</u>	<u>95% LCI</u>	<u>95% UCI</u>
B0	3.9225	0.1827	3.6339	4.3511
<i>expNestSubstHt</i>	0.3593	0.2257	-0.0837	0.8023
Patch Area	-0.2480	0.1407	-0.5242	0.0281
Date	-0.6299	0.1435	-0.9116	-0.3482
Parasitism	-0.5862	0.3115	-1.1977	0.0253

The model-averaged parameter estimate for patch area ( $\hat{\beta} = -0.2459$ , 95% CI = -0.5295, 0.0377) suggested a decline in daily survival rate with increasing patch area, and the parameter estimate from the best model supported this relationship ( $\hat{\beta} = -0.2480$ , 95% CI = -0.5242, 0.0281). This result was contrary to our hypothesis, which expected daily survival rate to decline as patch area decreased.

Models that incorporated broad-scale variables received little support in the Warbling Vireo model suite. Single-predictor models of home density at 1 km ( $\Delta\text{AIC}_c = 22.56$ ), 3 km ( $\Delta\text{AIC}_c = 22.67$ ), and 6 km ( $\Delta\text{AIC}_c = 22.68$ ) from the nesting plots received less support than a model of constant daily survival rate ( $\Delta\text{AIC}_c = 20.68$ ). Because a measure of home density at 6 km from the nesting plots was the best version of home density for Dusky Flycatchers and Yellow Warblers, home density at 6 km was used in all further modeling of Warbling Vireo nest survival to keep the three model suites consistent.

The model-averaged parameter estimate for home density at 6 km indicated a positive relationship between home density and daily survival rate ( $\hat{\beta} = 0.0570$ , 95% CI = -0.2732, 0.3873). The confidence interval for this estimate had a substantial overlap with zero, and this result did not support our hypothesis that daily survival rate declines with increasing home density.

Similarly, the confidence interval from the model-averaged parameter estimate for elevation overlapped zero substantially ( $\hat{\beta} = 0.1432$ , 95% CI = -0.1456, 0.4320), and elevation was not present in the best model. The model-averaged parameter estimate for elevation suggested a positive relationship between elevation and daily survival rate, which agreed with our hypothesis, but this estimate did not provide a great deal of confidence of this relationship.

Model-averaged parameter estimates suggested that there was little difference between daily survival rates in 1997 and 1999 ( $\hat{\beta}_{1997} = -0.0066$ , 95% CI = -0.7590, 0.7459) though daily survival rates in 1998 may have been higher than those in the other two years ( $\hat{\beta}_{1998} = 0.6306$ , 95% CI = -0.0009, 1.2620). Date was present in the best model ( $\hat{\beta} = -0.6299$ , 95% CI = -0.9116, -0.3482), and both this estimate and the model-averaged parameter estimate for date ( $\hat{\beta} = -0.6491$ , 95% CI = -1.0142, -0.2840) indicated that daily survival rate declined as the season progressed. Parasitism was present in the best model ( $\hat{\beta} = -0.5862$ , 95% CI = -1.1977, 0.0253), and model-averaged parameter estimates ( $\hat{\beta} = -0.5894$ , 95% CI = -1.2509, 0.0721) supported a negative effect of parasitism on daily survival rate. These estimates agreed with our hypothesis

that daily survival rate is lower in parasitized nests. These results are equivocal, and it is uncertain whether nest- or patch-level variables are more important to nest survival.

Nests of Warbling Vireos exhibited a gradual increase in daily survival rate with increasing nest substrate height (Figure 1), and this effect had a stronger magnitude for nests in higher substrates compared with the other two species. The magnitude of the effect of patch area on daily survival rate was similar to that of Dusky Flycatchers, except that the daily survival rates of nests of Warbling Vireos declined with increasing patch size while the daily survival rates of nests of Dusky Flycatchers increased with increasing patch size. Date had an extremely strong influence on daily survival rate of Warbling Vireos compared with the other two species. The difference in daily survival rates of parasitized ( $DSR_{para} = 0.9657$ , 95% CI = 0.9516, 0.9757) and unparasitized ( $DSR_{unpara} = 0.9806$ , 95% CI = 0.9725, 0.9863) nests of Warbling Vireos was less than that of Dusky Flycatchers, and similar to that of Yellow Warblers.

#### Scale Selection: Landscape Effects Hypothesis

Results from the model suite did not support the hypothesis that landscape-level effects have the strongest spatial-level influence on daily survival rate. In the set of 14 *a priori* scale-level models, models with landscape-level effects received consistently less support than models without landscape-level effects (Appendix C). An effect of home density was not supported by the model suite and parameter estimates did not support an effect of home density that was different from zero. The weight of evidence for home density ( $w_i = 0.075$ ) (Table 10) did not support home density as an important variable in the model suite. There was some evidence for an effect of elevation in the best models

( $\Delta AIC_c < 2$ ) but this variable was weaker than effects at the nest- and patch-level spatial scales according to both model weights (Table 10) and scale-selection results (Appendix C).

Table 10. Weights of evidence for each individual covariate and for groups of covariates in the Warbling Vireo model suite. These weights were obtained by summing the weights of evidence of all models containing each covariate, or all of the covariates within a spatial scale.

<b>Weights of Evidence: Warbling Vireos</b>			
<u>Covariate</u>	<u><math>w_i</math></u>	<u>Scale</u>	<u><math>w_i</math></u>
<i>expNestSubstHt</i>	0.857	Nest ( <i>NestHt<sup>l</sup></i> + <i>expNestSubstHt</i> )	0.264
<i>NestHt<sup>l</sup></i>	0.264	Patch (Patch Area)	0.663
Stand Area	0.663	Landscape (Home Density (6 km) + Elevation)	0.075
Home Density (6 km)	0.075	Temporal (Date + Year)	0.472
Elevation	0.331		
Date	0.994		
1997	0.472		
1998	0.472		
Parasitism	0.685		

In the set of 14 *a priori* scale-level models, a model with only nest-level variables ( $\Delta AIC_c = 2.79$ ) received more support than a model with only patch-level variables ( $\Delta AIC_c = 5.59$ ) when nest parasitism status was not present in the models (Appendix C). When parasitism status was included in the models, a model of patch-level variables ( $\Delta AIC_c = 1.21$ ) received more support than a model with nest-level variables ( $\Delta AIC_c = 2.65$ ). The weight of evidence for nest-level variables ( $w_i = 0.26$ ) was less than the weight of evidence for patch-level variables ( $w_i = 0.66$ ). However, the weight of evidence for *expNestSubstHt* ( $w_i = 0.86$ ) had the highest weight of evidence of any individual spatial-level variable (Table 10).

### Scale Selection: Multiple-Scale Effects Hypothesis

Model-averaged parameter estimates and parameter estimates from the best model (described above) supported effects of nest substrate height and patch area on nest survival. There was also some evidence for an effect of elevation, though this result was less confident. These results provided support for the hypothesis that nest survival of Warbling Vireos is influenced by effects at more than one spatial scale.

In the set of 14 *a priori* models of spatial scale effects, we present  $AIC_c$  scores from models that contained the parasitism variable, as models without parasitism received less support. A model containing both nest- and patch-level effects ( $\Delta AIC_c = 1.07$ ) received more support than a model of nest- ( $\Delta AIC_c = 2.65$ ) or patch-level effects ( $\Delta AIC_c = 1.21$ ) alone (Appendix C). Landscape-level effects received little support in these models, but results for patch- and nest-level variables provide support for effects at these two spatial scales.

### Exploratory Interactions and Modifications of Best Models

An interaction between nest substrate height and date was supported by the model suite, and this interaction was included in several exploratory models. The best exploratory model of Warbling Vireo nest survival ( $\Delta AIC_c = 0$ ) included effects of nest substrate height, patch area, parasitism, and date (Figure 2) and had a model weight of 0.13 (Table 9). Six additional exploratory models ( $\Delta AIC_c < 2$ ) contained effects of both nest substrate height and patch area, and these models provided support for the multiple-scale effects hypothesis. Six exploratory models contained the interaction between nest

substrate height and date ( $\Delta AIC_c < 3$ ), and four exploratory models contained an effect of elevation ( $\Delta AIC_c < 3$ ).

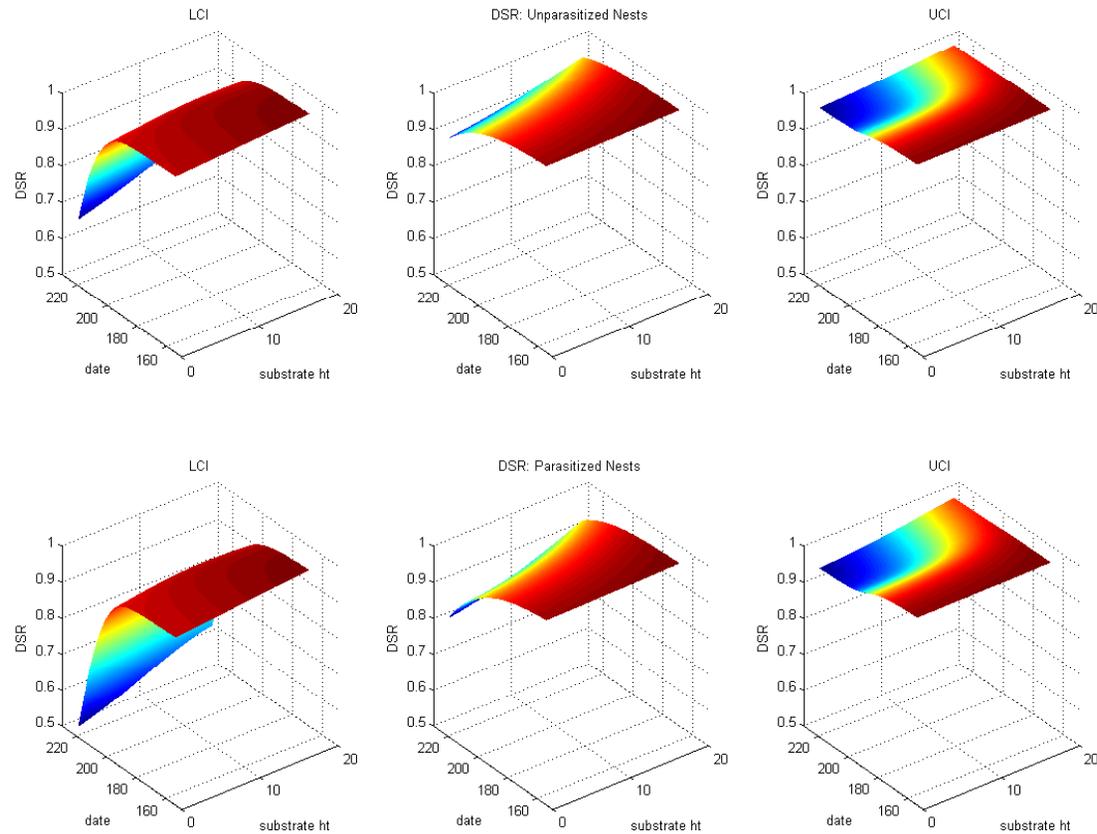


Figure 3. Changes in daily survival rate (DSR) of Warbling Vireos with parasitism, julian date (date), and nest substrate height (substrate ht). Lower (LCI) and upper (UCI) confidence intervals are shown as additional tiles. These estimates of daily survival rate are based on parameter estimates from the best model of daily survival rate for Warbling Vireos.

## Yellow Warblers

### General Results

Nests of Yellow Warblers were located in five low-elevation cottonwood plots (1,320 - 1,397 m), one mid-elevation aspen plot (1,664 m) and seven high-elevation aspen plots (2,042 - 2,109 m). These plots ranged in size from 0.04 to 0.14 km<sup>2</sup> and the number of nests per plot varied from 1 to 26 in a given year. Nest searchers located 290 nests, which provided a total of 1,231 observation intervals and an effective sample size of 3,293. Nests were initiated from early June to late July and the nesting interval averaged 24 (mean = 24.351, SE = 1.226) days for nests in the study. Brown-headed Cowbirds parasitized 39% of nests in the study.

### Summary of Model-Selection Results

The best *a priori* model of daily survival rate included home density, elevation, nest parasitism status, date, and year of study ( $\Delta\text{AIC}_c = 3.624$ ). The best exploratory model included effects of nest substrate height, home density, date, nest parasitism status, and an interaction between nest substrate height and date ( $\Delta\text{AIC}_c = 0$ ). The best model in the suite accounted for 26% of the model weight (Table 11). Models that included parasitism status, date, and home density were received support throughout the model suite (Appendix D).

Table 11. Model selection results for the best models of daily survival rate for Yellow Warblers. Models  $\leq 4$   $\Delta AIC_c$  are shown. Models are designated either EX for exploratory or AP for *a priori*. Names of spatial and temporal scales represent additive combinations of all variables within that spatial scale: Nest ( $NestHt^{-1}$  +  $NestSubstHt^{-1}$ ), Patch (stand area), Landscape (home density + elevation), and Time (date + date<sup>2</sup> + year).  $AIC_c$  adjusted for sample size was used to select the best models, and  $w_i$  is the weight of evidence for each model given the other models in the suite.

<b>Yellow Warblers</b>				
(n=3149)				
Model	$k$	$AIC_c$	$\Delta AIC_c$	$w_i$
EX: $NestSubstHt^{-1}$ + Home Density + Date + Date <sup>2</sup> + Parasitism + $NestSubstHt^{-1}$ *Date <sup>2</sup>	7	915.079	0	0.262
EX: Home Density + Parasitism + Date + Date <sup>2</sup>	5	915.275	0.197	0.237
EX: $NestSubstHt^{-1}$ + Home Density + Parasitism + Time + $NestSubstHt^{-1}$ *Date	9	917.368	2.289	0.083
EX: Home Density + Date	4	917.826	2.747	0.066
EX: Home Density*Date	5	918.359	3.281	0.051
AP: Landscape + Parasitism + Time	8	918.702	3.624	0.043
AP: B <sub>0</sub>	1	927.780	12.701	0

### Covariate Relationships and Predictions

The set of single-predictor exploratory models of Yellow Warbler daily survival rate indicated that, as with Dusky Flycatchers, nest height and nest substrate height were best represented by inverse functional forms ( $NestHt^{-1}$  and  $NestSubstHt^{-1}$ , see Appendix B). These functional versions were used in all further modeling of nest-level variables.

The model-averaged parameter estimate for  $NestHt^{-1}$  ( $\hat{\beta} = 0.0215$ , 95% CI = -0.2770, 0.3200) (Table 12) was close to zero, and the confidence interval for this estimate overlapped zero substantially. This estimate, as well as the absence of  $NestHt^{-1}$  in the best model, suggested that nest height was not important to the daily survival rate of Yellow Warblers in this study. Our hypothesis that daily survival rate would decline with nest height was not supported, and no relationship between nest height and daily survival rate

was inferred from these results.  $NestSubstHt^{-1}$  was present in the best model, and the parameter estimate from the best model (Table 13) indicated a negative relationship between  $NestSubstHt^{-1}$  and daily survival rate ( $\hat{\beta} = -0.1858$ , 95% CI = -0.3733, 0.0017). The confidence intervals for both this estimate and for the model-averaged parameter estimate ( $\hat{\beta} = -0.1775$ , 95% CI = -0.3736, 0.0185) overlapped zero only slightly, and these estimates indicated that nest substrate height contributed to the daily survival rate of Yellow Warblers. The inverse functional form of the nest substrate height variable supports our hypothesis that daily survival rate increased with nest substrate height, however, the interaction between nest substrate height and date in our exploratory models (Table 11) indicated that this relationship changed with the nesting season. Daily survival rate increased with nest substrate height in the middle of the nesting season, but declined with nest substrate height early and late in the nesting season.

Table 12. Model-averaged parameter estimates for individual covariates, and their 95% confidence intervals. Estimates were obtained from all models in the suite that had weight.

<b>Yellow Warblers</b>				
<u>Covariate</u>	<u>Model-Averaged Parameter Estimate</u>	<u>SE</u>	<u>95% LCI</u>	<u>95% UCI</u>
$B_0$	3.0154	0.1991	2.6252	3.4055
$NestHt^{-1}$	0.0215	0.1523	-0.2770	0.3200
$NestSubstHt^{-1}$	-0.1775	0.1000	-0.3736	0.0185
Plot Area	-0.0251	0.0892	-0.2000	0.1498
Home Density (6 km)	-0.2593	0.1311	-0.5163	-0.0023
Elevation	-0.0977	0.2321	-0.5527	0.3573
Date	0.1800	0.0948	-0.0058	0.3657
Date <sup>2</sup>	0.1288	0.0803	-0.0285	0.2861
1997	0.2081	0.2246	-0.2321	0.6483
1998	0.2614	0.1921	-0.1152	0.6380
Parasitism	-0.3663	0.1752	-0.7097	-0.0229

Table 13. Parameter estimates from the best models of daily survival rate for Yellow Warblers.

<b>Yellow Warblers</b>				
<u>Covariate</u>	<u>Estimate</u>	<u>SE</u>	<u>95% LCI</u>	<u>95% UCI</u>
B0	3.1265	0.1279	2.8755	3.3775
<i>NestSubstHr<sup>-1</sup></i>	-0.1858	0.0956	-0.3733	0.0017
Home Density	-0.2122	0.1047	-0.4176	-0.0068
Date	0.1746	0.0934	-0.0086	0.3577
Date <sup>2</sup>	0.1374	0.0785	-0.0166	0.2914
Parasitism	-0.3594	0.1720	-0.6968	-0.0219
<i>NestSubstHr<sup>-1</sup>*Date<sup>2</sup></i>	0.1368	0.0827	-0.0254	0.2991

Plot area was not present in any of the best models of Yellow Warbler daily survival rate. A model-averaged parameter estimate for plot area was close to zero, and the confidence intervals for this estimate overlapped zero substantially ( $\hat{\beta} = -0.0251$ , 95% CI = -0.2000, 0.1498). This result suggested that plot area was not closely related to variation in daily survival rate, which did not support our hypothesis that plot area was positively related to daily survival rate.

A model of home density at 6 km from the nesting plots ( $\Delta AIC_c = 5.08$ ) received more support than models of home density at 3 km ( $\Delta AIC_c = 3.67$ ) or 1 km ( $\Delta AIC_c = 7.68$ ) from the nesting plots. A model-averaged parameter estimate for home density suggested a negative relationship between home density and daily survival rate ( $\hat{\beta} = -0.2593$ , 95% CI = -0.5163, -0.0023) as did the parameter estimate from the best model ( $\hat{\beta} = -0.2122$ , 95% CI = -0.4176, -0.0068), and this supports our hypothesis that daily survival rate declines with increasing densities of homes. Elevation was not present in the best model, and the model-averaged parameter estimate for elevation was close to zero ( $\hat{\beta} = -0.0977$ , 95% CI = -0.5527, 0.3573) and had a confidence interval that moderately

overlapped zero. This result did not indicate a confident positive or negative relationship between elevation and daily survival rate, and hence did not support our hypothesis that daily survival rate would increase with elevation.

The set of single-predictor exploratory models indicated that date was best represented by a quadratic functional form,  $\text{date} + \text{date}^2$  (Appendix D). This functional version of date was used in all further models that incorporated date as a predictor. Model-averaged parameter estimates for these variables indicated a positive quadratic relationship between date and daily survival rate ( $\hat{\beta}_{\text{date}} = 0.1800$ , 95% CI = -0.0058, 0.3657;  $\hat{\beta}_{\text{date}^2} = 0.1288$ , 95% CI = -0.0285, 0.2861), as did parameter estimates from the best model ( $\hat{\beta}_{\text{date}} = 0.1746$ , 95% CI = -0.0086, 0.3577,  $\hat{\beta}_{\text{date}^2} = 0.1374$ , 95% CI = -0.0166, 0.2914). Because the bulk of these confidence intervals were above zero, we were confident that the sign of this relationship was positive.

Parasitism was also present in the best model, and model-averaged parameter estimates ( $\hat{\beta} = -0.3663$ , 95% CI = -0.7097, -0.0229) and parameter estimates from the best model ( $\hat{\beta} = -0.3594$ , 95% CI = -0.6968, -0.0219) supported a negative relationship between parasitism and daily survival rate. This agreed with our hypothesis that daily survival rate would be lower in nests that were parasitized by Brown-headed Cowbirds. Year was not present in the best model, and model-averaged parameter estimates indicated that there was little difference in daily survival rate between years ( $\hat{\beta}_{1997} = 0.2081$ , 95% CI = -0.2321, 0.6483;  $\hat{\beta}_{1998} = 0.2614$ , 95% CI = -0.1152, 0.6380).

The magnitude of the effect of nest substrate height on the daily survival rate of nests of Yellow Warblers was similar to that of Dusky Flycatchers (Figure 1). The daily survival rate of Yellow Warblers declined more gradually with increasing home densities compared with Dusky Flycatchers. Date had a relatively strong effect on Yellow Warbler daily survival rate compared with the other two species. The difference between the daily survival rate of parasitized ( $DSR_{para} = 0.9409$ , 95% CI = 0.9228, 0.9549) and unparasitized ( $DSR_{unpara} = 0.9580$ , 95% CI = 0.9466, 0.9670) nests of Yellow Warblers was similar to that of Warbling Vireos and much less than that of Dusky Flycatchers.

#### Scale Selection: Landscape Effects Hypothesis

The model-averaged parameter estimates and parameter estimates from the best model (described above) supported the hypothesis that landscape-level effects contributed to nest survival. Landscape-level effects were consistently supported by the model suite (Appendix D) and home density was present in the top 6 models ( $\Delta AIC_c < 4$ ) which had a combined model weight of 0.74 (Table 11).

Throughout the set of 14 *a priori* scale-level models, landscape-level effects received more support compared with effects at other spatial scales (Appendix D). We present  $\Delta AIC_c$  scores from only those models that contained the parasitism variable, as models that did not contain parasitism received less support. Of models considering only one spatial scale, a model of landscape-level effects ( $\Delta AIC_c = 3.62$ ) received more support than a model of nest-level effects ( $\Delta AIC_c = 4.532$ ) or a model of plot-level effects ( $\Delta AIC_c = 4.703$ ). A model of two spatial scales that included nest- and plot-level effects

( $\Delta AIC_c = 6.50$ ) received less support than a model of nest- and landscape-level effects ( $\Delta AIC_c = 3.05$ ) and a model of plot- and landscape-level effects ( $\Delta AIC_c = 1.889$ ).

Weights of evidence for each predictor (Table 14) indicated strong support for home density as an important predictor in the model suite. Home density had the largest weight of evidence of any spatial-level variable ( $w_i = 0.897$ ). Additionally, the weight of evidence for the group of landscape-level variables ( $w_i = 0.133$ ) was greater than the weight of evidence for nest- ( $w_i = 0.026$ ) or patch-level ( $w_i = 0.030$ ) variables.

Table 14. Weights of evidence for each individual covariate and for groups of covariates in the Yellow Warbler model suite. These weights were obtained by summing the weights of evidence of all models containing each covariate, or all of the covariates within a spatial scale.

<b>Weights of Evidence: Yellow Warblers</b>			
<u>Covariate</u>	<u><math>w_i</math></u>	<u>Scale</u>	<u><math>w_i</math></u>
<i>NestSubstHt</i> <sup>-1</sup>	0.469	Nest ( <i>NestHt</i> <sup>-1</sup> + exp <i>NestSubstHt</i> )	0.026
<i>NestHt</i> <sup>-1</sup>	0.027	Patch (Patch Area)	0.030
Plot Area	0.030	Landscape (Home Density (6 km) + Elevation)	0.133
Home Density (6 km)	0.897	Temporal (Date + Year)	0.227
Elevation	0.139		
Date	0.908		
Date <sup>2</sup>	0.908		
1997	0.227		
1998	0.227		
Parasitism	0.754		

### Scale Selection: Multiple-Scale Effects Hypothesis

Effects of nest substrate height and home density were supported by model-averaged parameter estimates and parameter estimates from the best model (described above). These results provide support for the hypothesis that effects at several spatial scales are important to Yellow Warbler nest survival.

In the set of 14 *a priori* models, models with the parasitism variable received more support than models without parasitism (Appendix D), hence we present  $\Delta AIC_c$  scores from models that contained parasitism. The best model in this set contained only landscape-level variables ( $\Delta AIC_c = 3.62$ ). However, models with both plot- and landscape-level variables ( $\Delta AIC_c = 5.51$ ) and nest- and landscape-level variables ( $\Delta AIC_c = 6.67$ ) received support as well. These models did not provide strong support for the multiple-scale effects hypothesis, though they did not indicate that nest- and patch-level scales were unimportant to variation in daily survival rate.

#### Exploratory Interactions and Modifications of Best Models

The best in the Yellow Warbler model suite ( $\Delta AIC_c = 0$ ) contained effects of  $NestSubstHt^{-1}$ , home density, date, and parasitism, as well as an interaction between  $NestSubstHt^{-1}$  and date (Figure 3). This model accounted for 26% of the total model weight (Table 11). The second best model in the suite ( $\Delta AIC_c = 0.197$ ) contained effects of home density, parasitism, and date and accounted for 24% of the total model weight (Table 11). These exploratory results provide some support for the multiple-scale effects hypothesis, but they also support the hypothesis that home density is the single, most important variable to daily survival rate of Yellow Warblers given the other variables in these models.

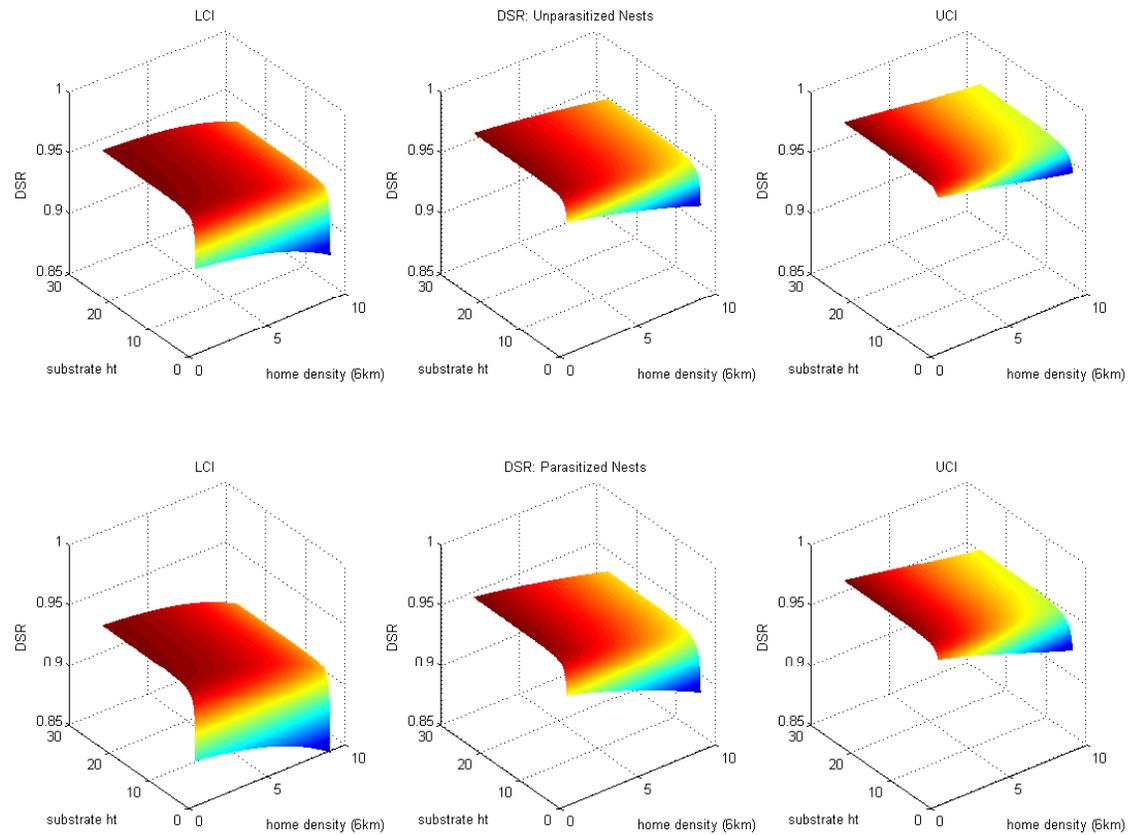


Figure 4. Changes in daily survival rate (DSR) of Yellow Warbler nests with parasitism, nest substrate height (substrate ht), and home density at a 6 km radius from the nesting plots. Lower (LCI) and upper (UCI) confidence intervals are shown as additional tiles. These estimates of daily survival rate are based on parameter estimates from the best model of daily survival rate for Yellow Warblers.

## DISCUSSION

This study is unique in its use of likelihood-based methods to (1) evaluate the relative importance of variables measured at nest-, patch-, and landscape-level spatial scales on nest survival data, and (2) compare these results among several songbird species. Many studies that emphasize the importance of multiple spatial scales have evaluated abundance data (Martin et al. 2006, Smith and Wachob 2006) rather than variation in a vital rate. Also, recent studies of nest survival have not compared the effects of local spatial scales with landscape-level scales (Donovan et al. 1997, Tewksbury et al. 1998, Peak et al. 2004, but see Hoover et al. 1995). We found effects of variables at more than one spatial scale for all three species as well as consistent effects of nest substrate height, date and parasitism. Landscape-level variables had the strongest spatial-level effects on daily survival rates of both Dusky Flycatchers and Yellow Warblers. Also of interest were the many differences between species, which seemed to suggest a gradient of species' responses to surrounding spatial characteristics at all scales. Below, we evaluate and compare results for each species and discuss interpretations of modeling results.

Several similarities were apparent between the three study species, including evidence for a positive effect of nest substrate height. Previous analyses of nests of Dusky Flycatchers, Warbling Vireos, and Yellow Warblers have found evidence relating nest concealment to daily survival rate, but these studies have not found or looked for a relationship between nest substrate height and daily survival rate (Banks and Martin 2001, Liebezeit and George 2002, Ortega and Ortega 2003). Our results indicate that nest

substrate height is an important predictor of daily survival rate for all three of these species. Both Dusky Flycatchers and Yellow Warblers expressed an inverse relationship between nest substrate height and daily survival rate, which indicated that daily survival rate dropped off when a nest was located in low substrates and increased gradually when a nest was located in higher substrates (Figures 1, 3). The evidence for an interaction between nest substrate height and date in the Yellow Warbler model suite, however, also suggested that the slope of the relationship between daily survival rate and nest substrate height changed with date. While higher nest substrates were favorable in the middle of the nesting season, lower nest substrates were favorable early and late in the nesting season. However, higher substrates provided a more consistent nesting habitat for this species, as well as high nest survival during some of the nesting season. Thus, taller nest substrates promoted high and/or consistent nest survival for both Dusky Flycatchers and Yellow Warblers. For Warbling Vireos, the relationship between nest substrate height and daily survival rate exhibited an exponential functional form, which indicated a gradual increase in daily survival rate as nest substrate height increased (Figure 2). Thus, for all three songbird species, higher substrates appeared to provide the most favorable nesting habitat.

We suggest that a possible reason that our study detected an effect of nest substrate height may be our use of functional relationships, which have not been evaluated for this covariate in previous studies. Also, our study was conducted in a region characterized by highly variable gradients and different habitat types compared with previous studies, and these factors may influence the context for nest substrate height to

influence daily survival rates. Our finding that nest substrate height is important to daily survival rate may indicate that nest substrate height acts as an index for nest concealment and/or for the accessibility of a nest to predators. The canopy may provide a more variable substrate for predators to search through compared with the understory (Martin 1988), or it may simply provide available nesting sites that are high enough off the ground that they are inaccessible to some predators. The difference we found in the functional relationships between species may be due to the range of nest substrate heights used by these species (Appendix A). Warbling Vireos tended to nest in higher substrates, and thus may not experience a notable decline in daily survival rate in lower substrates across the range of the data. Additionally, a decline in nest survival in lower nest substrates may be indicative that the lower vegetation is affected by grazing, which occurred on many of the nesting plots. Whether one or more of these effects is the cause of the observed decline in nest survival in low substrates is uncertain, and further study is needed.

We found differences in the daily survival rates of parasitized and unparasitized nests for all three species. Estimates from the best models (assuming all other covariates were at their mean values) indicated that Dusky Flycatchers had the largest difference between daily survival rates of parasitized and unparasitized nests (Table 5) while Warbling Vireos (Table 9) and Yellow Warblers (Table 13) had smaller differences. These results may be due to species-specific sensitivities to parasitism (Briskie et al. 1990, Banks and Martin 2001) or to differences between the surrounding characteristics of parasitized and unparasitized nests (Hahn and Hatfield 2000, Thompson et al. 2000,

Uyehara and Whitfield 2000). Because Dusky Flycatchers and Warbling Vireos had similar life history traits and were fairly sympatric in the study area, the observed differences in rates of parasitism for these two species may be due to host activity and behavior (Banks and Martin 2001). Yellow Warblers likely had a high rate of parasitism due to their close proximity to development and agriculture, in addition to the species' own vulnerability to parasitism (Lowther et al. 1999). High rates of parasitism on any of these species may also be due to a nest's proximity to a roost site or other landscape feature (Thompson and Dijak 2000), but we did not have measures of these features in this study. These results indicate that parasitism causes nest failures for all three species in this study, and that it is important for studies to consider parasitism as a response in order to discern what influences rates of parasitism in the GYE and how the effects of parasitism might be mediated.

Date was a strong predictor of the daily survival rates of all three species. Daily survival rate declined with date for Dusky Flycatchers and Warbling Vireos but showed a quadratic relationship for Yellow Warblers. These relationships may reflect changes in predator communities with the nesting season (Grant et al. 2005), but may also be indicative of changes in weather, nest age (Winter 1999), and vegetation structure. The magnitudes and shapes of the effect of date varied with species, though the decline of daily survival rate with date appeared to be strongest for Warbling Vireos (Figure 2). Our results indicate that it is important for future studies to consider changes in nest survival with date and the possible shapes of this relationship. Also, because we found an

interaction of nest substrate height with date, it may be necessary to consider date in order to detect effects of some habitat-level variables.

Because Dusky Flycatchers, Warbling Vireos, and Yellow Warblers nested in different locations both within the canopy and across the landscape, natural differences in the ranges of measured covariates are apparent for each species (Appendix A). Some of these differences may have influenced the effect of each covariate that we detected the daily survival rate of each species, and/or the shape of the effect of each covariate on daily survival rate. For nest-level variables, the ranges of covariate values were fairly similar between species. Patch areas, however, were similar for Dusky Flycatchers and Warbling Vireos but were much smaller for Yellow Warblers. This was an artifact of the measurement of plot areas instead of patch areas for the cottonwood stands, and may have made it less likely that plot area would be important to the daily survival rates of Yellow Warblers. At the landscape scale, differences in the ranges of elevations and home densities between the three species reflect differences in their nesting locations across the landscape. Hence, we only infer whether a species is influenced by those gradients of home density or elevation that its nests were in proximity to within the portion of the landscape that was considered in this study. Date had similar ranges for all species, though Yellow Warblers began nesting a few days earlier than Dusky Flycatchers or Warbling Vireos. Parasitism rates were higher for nests of Warbling Vireos and Yellow Warblers compared with nests of Dusky Flycatchers, and because only 9% nests of Dusky Flycatcher were parasitized this may have affected our ability to infer an effect of parasitism on this species.

Our results do not support the hypothesis that Dusky Flycatchers and Warbling Vireos respond similarly to surrounding influences on nest survival. Warbling Vireos' lack of response to variation in home density and to changes in elevation, combined with their higher nest survival in smaller patches of habitat, suggests that they may be an edge species in the GYE and that they are relatively resistant to human infringement. This is supported by some available literature, which has found high densities of Warbling Vireos in proximity to urban areas (Gardali and Ballard 2000). Dusky Flycatchers, in contrast, exhibited strong sensitivity to low densities of homes and appeared to nest more successfully in larger patches of habitat. Also, the substantially higher rate of parasitism experienced by Warbling Vireos compared with Dusky Flycatchers suggests that the causes of nest failures for these two species may be very different. While Warbling Vireos may experience a comparatively higher rate of nest failure due to brood parasitism, predation is likely the major cause of nest failure for Dusky Flycatchers (Cain and Morrison 2003). Dusky Flycatchers also appeared to be an extremely sensitive species compared with Warbling Vireos, as they were influenced by all variables in the model suite except for year. Dusky Flycatchers were the only species influenced by nest height, which may be due to a combination of their nesting locations throughout the landscape and to the suite of predators to which they are vulnerable. Also, because both of these species nested primarily in higher-elevation aspen stands, they only experienced a small gradient of surrounding human disturbance. We would infer from our results that, if home densities and other disturbances in proximity to these aspen stands were to

increase, the nest survival of Dusky Flycatchers nest survival would decline more substantially compared with that of Warbling Vireos.

Yellow Warblers were somewhat similar to Dusky Flycatchers, as home density was the most important predictor of daily survival rate for both of these species. Comparing the relationship between home density and daily survival rate for these two species, the slope relating Yellow Warbler daily survival rate to home density was more gradual than the slope for Dusky Flycatchers (Figures 1, 3). This suggests that Dusky Flycatchers are more sensitive to increasing densities of surrounding homes compared with Yellow Warblers. This pattern also suggests that Yellow Warblers' relative resistance to high home densities combined with their comparatively shorter nesting interval may facilitate their ability to nest successfully at low elevations. However, increasingly high densities of homes did cause the nest survival of Yellow Warblers to decline, and the ability of this species to maintain its populations in proximity to as many as 10 homes/km<sup>2</sup> while subject to comparatively high rates of parasitism is uncertain.

Interestingly, though Yellow Warblers were present across a broad elevational gradient this species was not strongly affected by changes in elevation. This suggests that the nest survival of songbird species may be increasingly independent of landscape location as mechanisms of surrounding disturbances such as residential development become increasingly strong. Also, the presence of surrounding residential development at lower elevations appeared to be vastly more influential to nest survival compared with all other variables in the Yellow Warbler model suite. An overwhelmingly strong influence is further suggested by the weaker evidence in support of the multiple-scale effects

hypothesis for Yellow Warblers. Though one variable at the nest-level scale, nest substrate height, was a good predictor of daily survival rate, this variable was vastly out competed by home density in the model suite. The mechanisms of surrounding home density may be having such a strong impact on Yellow Warbler nest survival that once home density is considered in a model little variation remains for variables such as nest substrate height to explain.

We found support for the multiple-scale effects hypothesis for all three species. Dusky Flycatchers were affected by variables at the nest-, patch-, and landscape-level scales, while Warbling Vireos were affected by variables at the nest- and patch-level scales and Yellow Warblers appeared to be influenced by variables at both the nest- and landscape-level scales. Nest substrate height had an effect on the daily survival rates of all three species, however most other spatial-level effects varied between species. Had we measured additional variables such as nest concealment, vegetation characteristics of the aspen and cottonwood stands, fragmentation of the surrounding landscape, and densities of surrounding agriculture such as crops and cattle we would likely have been able to expand our multiple-scale results. Our decision to include plausible functional relationships for several continuous variables in each model suite was important to the multiple-scale effects hypothesis, as this increased support for several covariates in the model suites and likely helped bring out effects of some of these covariates in the best models. Results from our evaluation of the multiple-scale effects hypothesis indicate that the responses of different species to surrounding features at different spatial scales are variable, as is the relative importance of features at each scale to each species. This

variability emphasizes a need for future studies to evaluate both a variety of species and of predictors in order to determine how surrounding habitat and anthropogenic factors influence the populations of a community of songbirds. Additionally, future studies should consider measures of the same variables at different spatial scales. Due to logistic constraints of working with an existing dataset, we were unable to compare the same features at different spatial scales, and this may have confounded our multiple-scale results. However, some features could not be measured at larger or smaller scales, such as home density and nest height, and many of the scale-level comparisons that we made were of features inherent to a particular spatial scale.

Model suites for both Dusky Flycatchers and Yellow Warblers supported the landscape-effects hypothesis. The sensitivity of these species to homes and other land uses may reflect their nesting locations throughout the landscape as well as their life history traits (Sedgwick 1993, Lowther et al. 1999). Dusky Flycatchers exhibited a greater sensitivity to homes and elevation compared with Yellow Warblers, despite a smaller range of home densities in proximity to aspen habitat. Both of these species showed a stronger sensitivity to homes compared with elevation, which may indicate that nest survival is more sensitive to the presence of land use than to a nest's location within the landscape. The presence of elevation in the best model of Dusky Flycatcher nest survival suggests that there may be additional unmeasured landscape-level variables affecting this species for which elevation acts as a surrogate. Similarly, home density may act as a surrogate for features such as the presence of agriculture or grazing, human disturbances, roads, exotic species, changes in vegetation structure, and other

anthropogenic influences. Hence, home density may not have a direct impact on the nest survival of songbird species in the GYE. Our results suggest that not all songbird species within the GYE are dominated by landscape-level effects, and that different species aren't necessarily influenced by the same landscape-level effects.

We also hypothesized that the broad-scale landscape context might influence which smaller-scale effects are important to nest survival (Chalfoun et al. 2002, Thompson et al. 2002). However, there was no support for interactions between landscape-level effects and smaller-scale effects in models for any species in this study. This suggests that the broad- and local-scale effects that we measured were independent.

Our inability to account for a possible lack of independence in our data due to spatial or temporal autocorrelation may have resulted in the overfitting of our models and in conclusions that are spurious to our dataset (Burnham and Anderson 2002). Several of the stands in these analyses were in close proximity, and individual nest observations may not have been completely independent throughout space and time. However, we were able to run goodness of fit on our models to determine that they fit the data, and we had a large overall sample size. We also took care not to run too many models on the data for each species. Overall, we are confident that inferences can be made from our modeling results and that our models provide a useful description of effects of features in the GYE on rates of nest survival of these three species.

### Management Implications

Because nest substrate height was important to the daily survival rates of all three species, there may be some opportunity for local-scale vegetation management to

improve songbird nesting habitat in the GYE. In other ecosystems, studies have measured declines in native vegetation and surrounding cover in proximity to development (Miller et al. 2003). Stands of aspen and cottonwoods that are not in proximity to high densities of homes may have higher nest survival rates in proximity to high densities of homes due to a lack of desirable vegetative cover. A decline in nest survival in low nest substrates may be indicative of a need to provide dense and variable substrates for these species to nest in. Dense, diverse substrates not only increase species diversity (MacArthur and MacArthur 1961) but may help decrease rates of nest predation (Martin 1988).

Songbird species that are sensitive to land use, such as Dusky Flycatchers, may also respond to management for larger patches of aspen and cottonwood stands. Several studies have indicated that, for interconnected songbird populations that have high rates of dispersal, maintaining several large ‘source’ habitats is essential (Robinson et al. 1995, Donovan et al. 1995). Additionally, in the western United States the landscape is more naturally fragmented than in the east (Tewksbury et al. 1998) and species may have higher rates of dispersal (Sallabanks et al. 1999). This could be useful to managers, as conserving large patches of source habitat far from development may have a stronger effect on the growth of the overall population.

Development may have a stronger effect on songbird communities compared with agriculture or forestry because it results in the permanent conversion of portions of the landscape into dissimilar and unnatural habitat (Marzluff and Ewing 2001). Homes within a landscape are an index for the loss of native vegetation, the presence of exotic species, the restriction of dispersal, and for higher densities of predators and brood

parasites. The effects of development on songbird populations may be mitigated by managing the matrix surrounding fragments of habitat (Marzluff and Ewing 2001). Encouraging native vegetation in the surrounding matrix may aid dispersal of species and help reduce the impact of the presence of homes. Future studies in the GYE should investigate the differential effects of management practices regarding homes, such as dispersed housing versus clustered housing, and consider these effects at the landscape scale.

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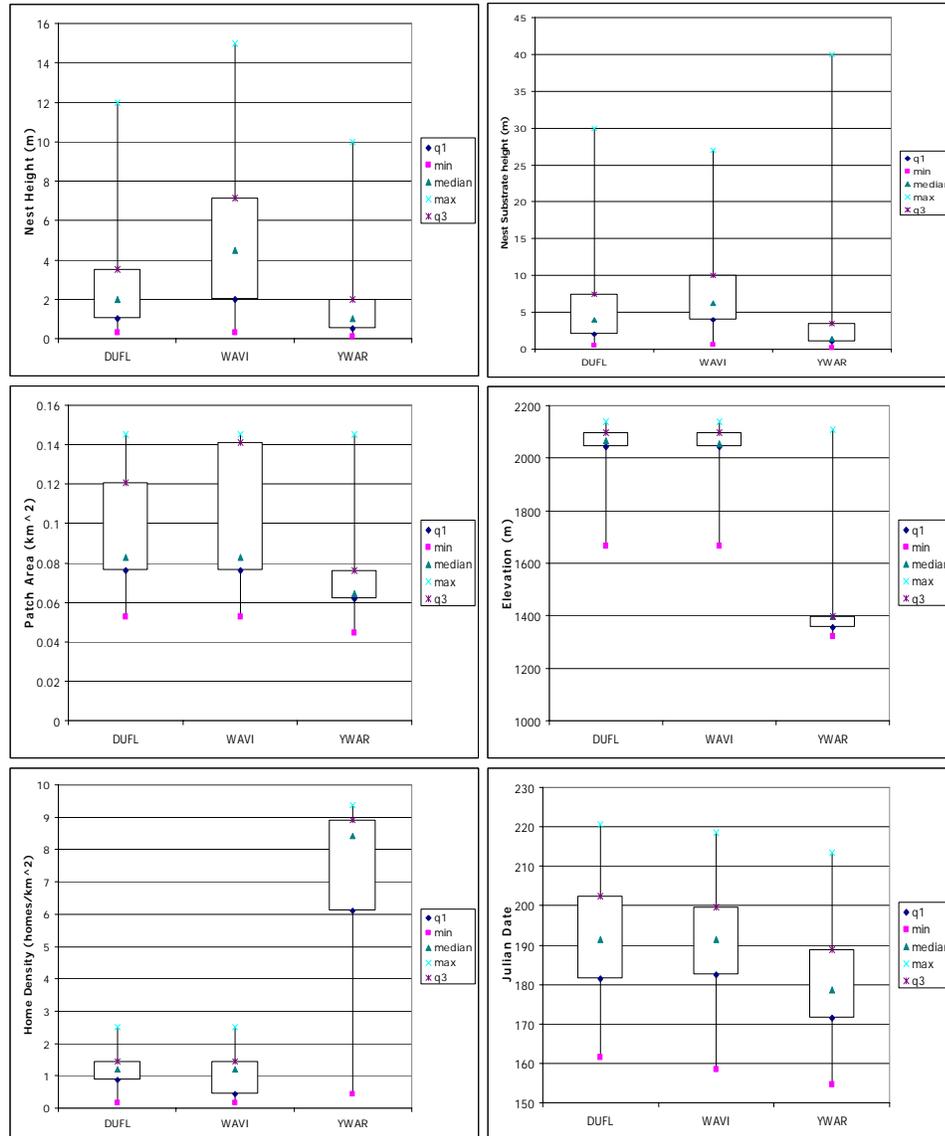
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APPENDICES

APPENDIX A

BOX AND WHISKER PLOTS

Box and Whisker plots of the seven continuous covariates (nest height, nest substrate height, patch area, elevation, home density, and julian date) measured in this study. Q1 = first quartile, min = minimum value, median = median, max = maximum value, q3 = third quartile.



APPENDIX B

PEARSON CORRELATION COEFFICIENTS

Pearson correlation coefficients (*r*) and associated p-values for covariates in the Dusky Flycatcher model suite. N = 1718.

	<b>Elevation</b>	<b>Home Density (6 km)</b>	<i>Nest Height</i> <sup>-1</sup>	<b>Patch Area</b>	<b>Date</b>	<b>Parasitism</b>	<i>Nest Substrate Height</i> <sup>-1</sup>	<b>1997</b>	<b>1998</b>	<b>1999</b>
<b>Elevation</b>	<b>1.0000</b>	-0.1051	-0.3692	-0.4154	0.2760	0.0217	-0.3813	-0.1064	-0.0306	0.1193
		<0.0001	<0.0001	<0.0001	<0.0001	0.3685	<0.0001	<0.0001	0.2045	<0.0001
<b>Home Density (6 km)</b>		<b>1.0000</b>	0.2134	0.6763	-0.1022	-0.0180	0.2338	0.0753	-0.0075	-0.0578
			<0.0001	<0.0001	<0.0001	0.4570	<0.0001	0.0018	0.7571	0.0166
<i>Nest Height</i> <sup>-1</sup>			<b>1.0000</b>	0.2711	-0.1211	0.0421	0.8246	0.1592	0.1035	-0.2314
				<0.0001	<0.0001	0.0813	<0.0001	<0.0001	<0.0001	<0.0001
<b>Patch Area</b>				<b>1.0000</b>	-0.1081	-0.1154	0.2965	0.0716	0.0066	-0.0674
					<0.0001	<0.0001	<0.0001	0.0030	0.7852	0.0052
<b>Date</b>					<b>1.0000</b>	-0.1521	-0.0898	-0.2219	0.2327	-0.0224
						<0.0001	0.0002	<0.0001	<0.0001	0.3542
<b>Parasitism</b>						<b>1.0000</b>	0.0951	0.1548	-0.0121	-0.1218
							<0.0001	<0.0001	0.6167	<0.0001
<i>Nest Substrate Height</i> <sup>-1</sup>							<b>1.0000</b>	0.0931	0.1112	-0.1816
								0.0001	<0.0001	<0.0001
<b>1997</b>								<b>1.0000</b>	-0.3652	-0.5244
									<0.0001	<0.0001
<b>1998</b>									<b>1.0000</b>	-0.6012
										<0.0001
<b>1999</b>										<b>1.0000</b>

Pearson correlation coefficients (*r*) and associated p-values for covariates in the Warbling Vireo model suite. N = 809.

	<b>Elevation</b>	<b>Home Density (6 km)</b>	<i>Nest Height</i> <sup>-1</sup>	<b>Patch Area</b>	<b>Date</b>	<b>Parasitism</b>	<i>expNest Substrate Height</i>	<b>1997</b>	<b>1998</b>	<b>1999</b>
<b>Elevation</b>	<b>1.0000</b>	-0.5713	0.0437	-0.1737	0.1958	-0.1915	-0.1480	-0.1160	-0.0225	0.1353
<b>Home Density (6 km)</b>		<0.0001	0.2140	<0.0001	<0.0001	<0.0001	<0.0001	0.0009	0.5231	0.0001
<i>Nest Height</i> <sup>-1</sup>		<b>1.0000</b>	0.0378	0.1875	-0.1715	0.1775	-0.1190	0.0598	-0.0030	-0.0544
<b>Patch Area</b>			0.2828	<0.0001	<0.0001	<0.0001	0.0007	0.0894	0.9319	0.1221
<b>Date</b>			<b>1.0000</b>	-0.0845	0.0862	0.2892	-0.3657	-0.0181	0.1468	-0.1367
<b>Parasitism</b>				0.0162	0.0142	<0.0001	<0.0001	0.6066	<0.0001	<0.0001
<i>expNest Substrate Height</i>				<b>1.0000</b>	-0.1207	-0.2005	0.0838	0.1025	-0.0799	-0.0148
<b>1997</b>					0.0006	<0.0001	0.0171	0.0035	0.0231	0.6740
<b>1998</b>					<b>1.0000</b>	-0.1287	-0.1144	-0.4896	0.3523	0.1017
<b>1999</b>						0.0002	0.0011	<0.0001	<0.0001	0.0038
						<b>1.0000</b>	-0.1955	0.0410	0.1014	-0.1459
							0.2439	0.0039	<0.0001	
							<b>1.0000</b>	0.2114	-0.1939	0.0000
							<0.0001	<0.0001	0.9991	
							<b>1.0000</b>	-0.5091	-0.4286	
								<0.0001	<0.0001	
								<b>1.0000</b>	-0.5594	
									<0.0001	
									<b>1.0000</b>	

Pearson correlation coefficients (*r*) and associated p-values for covariates in the Yellow Warbler model suite. N = 1231.

	<b>Elevation</b>	<b>Home Density (6 km)</b>	<i>Nest Height<sup>-1</sup></i>	<b>Patch Area</b>	<b>Date</b>	<b>Parasitism</b>	<i>Nest Substrate Height<sup>-1</sup></i>	<b>1997</b>	<b>1998</b>	<b>1999</b>
<b>Elevation</b>	<b>1.0000</b>	-0.9109	-0.2639	0.2733	0.1310	-0.2414	-0.2650	0.0419	-0.0120	-0.0243
		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.1419	0.6752	0.3939
<b>Home Density (6 km)</b>		<b>1.0000</b>	0.2770	-0.2409	-0.1289	0.2223	0.2568	0.0140	-0.0072	-0.0049
			<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.6235	0.8020	0.8628
<i>Nest Height<sup>-1</sup></i>			<b>1.0000</b>	-0.0354	-0.0093	0.1999	0.8436	-0.1864	0.0444	0.1172
				0.2144	0.7443	<0.0001	<0.0001	<0.0001	0.1198	<0.0001
<b>Patch Area</b>				<b>1.0000</b>	-0.0766	0.0101	0.0088	0.0687	-0.0002	-0.0596
					0.0072	0.7244	0.7585	0.0160	0.9942	0.0367
<b>Date</b>					<b>1.0000</b>	-0.0836	-0.0226	-0.1474	-0.0394	0.1683
						0.0033	0.4278	<0.0001	0.1672	<0.0001
<b>Parasitism</b>						<b>1.0000</b>	0.2638	0.0362	-0.0817	0.0514
							<0.0001	0.2046	0.0041	0.0716
<i>Nest Substrate Height<sup>-1</sup></i>							<b>1.0000</b>	-0.1928	0.0744	0.0923
								<0.0001	0.0090	0.0012
<b>1997</b>								<b>1.0000</b>	-0.4455	-0.4181
									<0.0001	<0.0001
<b>1998</b>									<b>1.0000</b>	-0.6269
										<0.0001
<b>1999</b>										<b>1.0000</b>

APPENDIX C

DUSKY FLYCATCHER MODEL SUITE

Complete list of all candidate models of daily survival rate considered for Dusky Flycatchers. Names of spatial and temporal scales represent additive combinations of all variables within that spatial scale: Nest (nest height + nest substrate height), Patch (patch area), Landscape (home density + elevation), and Time (date + year). Two  $\Delta AIC_c$  values are shown, one from the model suite ( $\Delta AIC_{c\text{ suite}}$  the distance in  $AIC_c$  units of a model from the best model in the suite) and one for the smaller set of models ( $\Delta AIC_{c\text{ set}}$  the distance in  $AIC_c$  units of a model from the best model in the set), where the sets are Nest, Patch, Landscape, Temporal, Parasitism, Scale-level, Interactions, and Exploratory below.

	Model	$k$	$AIC_c$	$\Delta AIC_{c\text{ suite}}$	$\Delta AIC_{c\text{ set}}$
<b>Nest</b>	Nest Height	2	770.437	19.883	5.997
	$NestHt^{-1}$	2	769.902	19.348	5.462
	$expNestHt$	2	770.71	20.156	6.270
	Nest Substrate Height	2	768.631	18.077	4.191
	$NestSubstHt^{-1}$	<b>2</b>	<b>764.44</b>	<b>13.886</b>	<b>0.000</b>
	$expNestSubstHt$	2	771.018	20.464	6.578
	$B_0$	1	769.397	18.843	4.957
<b>Patch</b>	Stand Area	2	770.552	19.998	1.155
	<b><math>B_0</math></b>	<b>1</b>	<b>769.397</b>	<b>18.843</b>	<b>0.000</b>
<b>Landscape</b>	Home Density (1 km)	2	768.539	17.985	5.247
	Home Density (3 km)	2	764.377	13.823	1.085
	<b>Home Density (6 km)</b>	<b>2</b>	<b>763.292</b>	<b>12.738</b>	<b>0.000</b>
	Elevation	2	769.736	19.182	6.444
	$B_0$	1	769.397	18.843	6.105
<b>Temporal</b>	Date	2	770.584	20.030	1.187
	Date <sup>2</sup>	3	772.169	21.615	2.772
	Year	3	771.904	21.350	2.507
	<b><math>B_0</math></b>	<b>1</b>	<b>769.397</b>	<b>18.843</b>	<b>0.000</b>
<b>Parasitism</b>	<b>Parasitism</b>	<b>2</b>	<b>762.286</b>	<b>11.731</b>	<b>0.000</b>
	$B_0$	1	769.397	18.843	7.112

## Appendix B cont'd.

	Model	$k$	$AIC_c$	$\Delta AIC_{c \text{ suite}}$	$\Delta AIC_{c \text{ set}}$
<b>Scale-Level</b>					
<i>without</i>	Nest + Time	6	767.051	16.497	13.173
<i>Parasitism</i>	Patch + Time	5	774.122	23.568	20.244
	Landscape + Time	6	766.296	15.741	12.417
	Nest + Patch + Time	7	768.906	18.352	15.028
	Nest + Landscape + Time	8	763.584	13.030	9.706
	Patch + Landscape + Time	7	762.364	11.810	8.486
	Nest + Patch + Landscape + Time	9	759.923	9.368	6.044
<i>with</i>	Nest + Parasitism + Time	7	761.355	10.801	7.477
<i>Parasitism</i>	Patch + Parasitism + Time	6	765.07	14.516	11.192
	Landscape + Parasitism + Time	7	756.051	5.496	2.172
	Nest + Patch + Parasitism + Time	8	762.451	11.897	8.573
	Nest + Landscape + Parasitism + Time	9	755.483	4.929	1.605
	Patch + Landscape + Parasitism + Time	8	754.304	3.750	0.426
	<b>Nest + Patch + Landscape + Parasitism + Time</b>	<b>10</b>	<b>753.879</b>	<b>3.324</b>	<b>0.000</b>
	$B_0$	1	769.397	18.843	15.519
<b>Interactions</b>	Parasitism + Date	3	761.883	11.329	0.940
	Parasitism*Date	4	763.143	12.589	2.200
	Home Density + Date	3	763.854	13.300	2.911
	Home Density * Date	4	765.681	15.127	4.738
	<b><math>NestSubstHr^{-1}</math> + Home Density</b>	<b>3</b>	<b>760.943</b>	<b>10.389</b>	<b>0.000</b>
	$NestSubstHr^{-1}$ *Home Density	4	762.336	11.782	1.393
	$NestSubstHr^{-1}$ + Date	3	765.171	14.617	4.228
	$NestSubstHr^{-1}$ *Date	4	766.927	16.373	5.984
	$B_0$	1	769.397	18.843	8.454
<b>Exploratory</b>	<b>Nest + Patch + Landscape + Parasitism + Date</b>	<b>8</b>	<b>750.554</b>	<b>0.000</b>	<b>0.000</b>
	$B_0$	1	769.397	18.843	8.454

APPENDIX D

WARBLING VIREO MODEL SUITE

Complete list of all candidate models of daily survival rate considered for Warbling Vireos. Names of spatial and temporal scales represent additive combinations of all variables within that spatial scale: Nest (nest height + nest substrate height), Patch (patch area), Landscape (home density + elevation), and Time (date + year). Two  $\Delta AIC_c$  values are shown, one from the model suite ( $\Delta AIC_{c\text{ suite}}$  the distance in  $AIC_c$  units of a model from the best model in the suite) and one for the smaller set of models ( $\Delta AIC_{c\text{ set}}$  the distance in  $AIC_c$  units of a model from the best model in the set), where the sets are Nest, Patch, Landscape, Temporal, Parasitism, Scale-level, Interactions, and Exploratory below.

	Model	$k$	$AIC_c$	$\Delta AIC_{c\text{ suite}}$	$\Delta AIC_{c\text{ set}}$
<b>Nest</b>	Nest Height	2	417.639	20.818	5.111
	$NestHt^{-1}$	2	416.355	19.534	3.827
	$expNestHt$	2	418.043	21.222	5.515
	Nest Substrate Height	2	412.776	15.955	0.248
	$NestSubstHt^{-1}$	2	416.609	19.788	4.081
	<b><math>expNestSubstHt</math></b>	<b>2</b>	<b>412.528</b>	<b>15.707</b>	<b>0.000</b>
	$B_0$	1	417.505	20.684	4.977
<b>Patch</b>	Patch Area	2	419.253	22.432	1.748
	<b><math>B_0</math></b>	<b>1</b>	<b>417.505</b>	<b>20.684</b>	<b>0.000</b>
<b>Landscape</b>	Home Density (1 km)	2	419.380	22.559	1.875
	Home Density (3 km)	2	419.491	22.670	1.986
	Home Density (6 km)	2	419.498	22.677	1.993
	Elevation	2	419.466	22.645	1.961
	<b><math>B_0</math></b>	<b>1</b>	<b>417.505</b>	<b>20.684</b>	<b>0.000</b>
<b>Temporal</b>	<b>Date</b>	<b>2</b>	<b>400.497</b>	<b>3.676</b>	<b>0.000</b>
	Date <sup>2</sup>	3	402.410	5.589	1.913
	Year	3	418.695	21.874	18.198
	$B_0$	1	417.505	20.684	17.008
<b>Parasitism</b>	Parasitism	2	417.897	21.076	0.392
	<b><math>B_0</math></b>	<b>1</b>	<b>417.505</b>	<b>20.684</b>	<b>0.000</b>

## Appendix C cont'd.

	Model	$k$	AIC <sub>c</sub>	$\Delta$ AIC <sub>c suite</sub>	$\Delta$ AIC <sub>c set</sub>
<b>Scale-Level</b>					
<i>without</i>	Nest + Time	6	399.612	2.791	1.725
<i>Parasitism</i>	Patch + Time	5	402.413	5.592	4.526
	Landscape + Time	6	404.562	7.741	6.675
	Nest + Patch + Time	7	399.647	2.826	1.760
	Nest + Landscape + Time	8	401.419	4.598	3.532
	Patch + Landscape + Time	7	405.561	8.740	7.674
	Nest + Patch + Landscape + Time	9	401.769	4.948	3.882
<i>with</i>	Nest + Parasitism + Time	7	399.475	2.654	1.588
<i>Parasitism</i>	Patch + Parasitism + Time	6	398.032	1.211	0.145
	Landscape + Parasitism + Time	7	402.704	5.883	4.817
	<b>Nest + Patch + Parasitism + Time</b>	<b>8</b>	<b>397.887</b>	<b>1.066</b>	<b>0.000</b>
	Nest + Landscape + Parasitism + Time	9	401.821	5.000	3.934
	Patch + Landscape + Parasitism + Time	8	401.828	5.007	3.941
	Nest + Patch + Landscape + Parasitism + Time	10	400.742	3.921	2.855
	B <sub>0</sub>	1	417.505	20.684	19.618
<b>Interactions</b>	expNestSubstHt + Date	3	397.856	1.035	0.033
	<b>expNestSubstHt*Date</b>	<b>4</b>	<b>397.823</b>	<b>1.002</b>	<b>0.000</b>
	Elevation + Date	3	401.543	4.722	3.720
	Elevation*Date	4	403.422	6.601	5.599
	expNestSubstHt + Elevation	3	414.528	17.707	16.705
	expNestSubstHt*Elevation	4	416.332	19.511	18.509
	expNestSubstHt + Area	3	414.014	17.193	16.191
	expNestSubstHt*Area	4	414.859	18.038	17.036
	B <sub>0</sub>	1	417.505	20.684	19.682
<b>Exploratory</b>	<b>expNestSubstHt + Patch + Parasitism + Date</b>	<b>5</b>	<b>396.821</b>	<b>0.000</b>	<b>0.000</b>
	expNestSubstHt + Patch + Parasitism + Date + expNestSubstHt*Date	6	397.113	0.292	0.292
	expNestSubstHt + Patch + Elevation + Parasitism + Time + expNestSubstHt*Date	9	397.164	0.343	0.343
	expNestSubstHt + Patch + Elevation + Parasitism + Date + expNestSubstHt*Date	7	398.612	1.791	1.791
	expNestSubstHt + Elevation + Parasitism + Date + expNestSubstHt*Date	6	399.157	2.336	2.336
	Nest + Patch + Elevation + Parasitism + Time + expNestSubstHt*Date	10	399.180	2.359	2.359

APPENDIX E

YELLOW WARBLER MODEL SUITE

Complete list of all candidate models of daily survival rate considered for Yellow Warblers. Names of spatial and temporal scales represent additive combinations of all variables within that spatial scale: Nest (nest height + nest substrate height), Patch (patch area), Landscape (home density + elevation), and Time (date + year). Two  $\Delta AIC_c$  values are shown, one from the model suite ( $\Delta AIC_{c \text{ suite}}$  the distance in  $AIC_c$  units of a model from the best model in the suite) and one for the smaller set of models ( $\Delta AIC_{c \text{ set}}$  the distance in  $AIC_c$  units of a model from the best model in the set), where the sets are Nest, Patch, Landscape, Temporal, Parasitism, Scale-level, Interactions, and Exploratory below.

	Model	$k$	$AIC_c$	$\Delta AIC_{c \text{ suite}}$	$\Delta AIC_{c \text{ set}}$
<b>Nest</b>	Nest Height	2	929.715	5.279	14.636
	$NestHt^1$	2	925.908	1.472	10.829
	$expNestHt$	2	929.375	4.939	14.296
	Nest Substrate Height	2	928.340	3.904	13.261
	$NestSubstHt^1$	<b>2</b>	<b>924.435</b>	<b>0.000</b>	<b>9.357</b>
	$expNestSubstHt$	2	929.782	5.346	14.703
	$B_0$	1	927.780	3.344	12.701
<b>Patch</b>	Patch Area	2	929.780	2.001	14.702
	$B_0$	<b>1</b>	<b>927.780</b>	<b>0.000</b>	<b>12.701</b>
<b>Landscape</b>	Home Density (1 km)	2	927.837	7.683	12.758
	Home Density (3 km)	2	923.820	3.667	8.742
	<b>Home Density (6 km)</b>	<b>2</b>	<b>920.154</b>	<b>0.000</b>	<b>5.075</b>
	Elevation	2	922.497	2.343	7.418
	$B_0$	1	927.780	7.626	12.701
<b>Temporal</b>	Date	2	925.602	0.322	10.523
	<b>Date<sup>2</sup></b>	<b>3</b>	<b>925.280</b>	<b>0.000</b>	<b>10.201</b>
	Year	3	929.697	4.417	14.618
	$B_0$	1	927.780	2.500	12.701
<b>Parasitism</b>	<b>Parasitism</b>	<b>2</b>	<b>921.516</b>	<b>0.000</b>	<b>6.437</b>
	$B_0$	1	927.780	6.264	12.701

## Appendix D cont'd.

	Model	$k$	$AIC_c$	$\Delta AIC_{c \text{ suite}}$	$\Delta AIC_{c \text{ set}}$
<b>Scale-Level</b>					
<i>without</i>	Nest + Time	7	925.744	7.042	10.666
<i>Parasitism</i>	Patch + Time	6	928.377	9.675	13.299
	Landscape + Time	7	921.047	2.345	5.969
	Nest + Patch + Time	8	927.680	8.978	12.602
	Nest + Landscape + Time	9	922.855	4.153	7.777
	Patch + Landscape + Time	8	922.748	4.045	7.669
	Nest + Patch + Landscape + Time	10	924.760	6.057	9.681
	<i>with</i>	Nest + Parasitism + Time	8	923.235	4.532
<i>Parasitism</i>	Patch + Parasitism + Time	7	923.405	4.703	8.327
	<b>Landscape + Parasitism + Time</b>	<b>8</b>	<b>918.702</b>	<b>0.000</b>	<b>3.624</b>
	Nest + Patch + Parasitism + Time	9	925.204	6.502	10.126
	Nest + Landscape + Parasitism + Time	10	921.752	3.050	6.674
	Patch + Landscape + Parasitism + Time	9	920.592	1.889	5.513
	Nest + Patch + Landscape + Parasitism + Time	11	923.716	5.013	8.637
	$B_0$	1	927.780	9.077	12.701
	<b>Interactions</b>				
	Parasitism + Date	4	919.640	1.814	4.561
	Parasitism*Date	5	920.450	2.625	5.372
	Home Density + Date	<b>4</b>	<b>917.826</b>	<b>0.000</b>	<b>2.747</b>
	Home Density * Date	5	918.359	0.534	3.281
	$NestSubstHr^{-1}$ + Home Density	3	919.443	1.617	4.364
	$NestSubstHr^{-1}$ *Home Density	4	920.915	3.089	5.836
	$NestSubstHr^{-1}$ + Date	4	922.332	4.506	7.253
	$NestSubstHr^{-1}$ *Date	5	921.699	3.873	6.620
	$B_0$	1	927.780	9.954	12.701
<b>Exploratory</b>					
	Home Density + Parasitism + Date + Date <sup>2</sup>	5	915.275	0.197	0.197
	$NestSubstHr^{-1}$ + Home Density + Date + Date <sup>2</sup> + Parasitism + $NestSubstHr^{-1}$ *Date <sup>2</sup>	<b>7</b>	<b>915.079</b>	<b>0.000</b>	<b>0.000</b>
	$NestSubstHr^{-1}$ + Home Density + Date + Date <sup>2</sup> + Year + Parasitism + $NestSubstHr^{-1}$ *Date <sup>2</sup>	9	917.368	2.289	2.289
	$NestSubstHr^{-1}$ + Home Density + Elevation + Date + Date <sup>2</sup> + Year + Parasitism + $NestSubstHr^{-1}$ *Date <sup>2</sup>	10	919.084	4.005	4.005
	$B_0$	1	927.780	12.701	12.701