

## ABSTRACT

WEEKS, KENDRICK COLLINS. The foraging and nesting ecology of Black-throated Blue Warbler (*Dendroica caerulescens*) and Hooded Warbler (*Wilsonia citrina*) in the southern Appalachians. (Under the direction of Dr. Theodore Simons.)

Some species of Neotropical-Nearctic migrant birds have been showing declines in populations for the past thirty years. Black-throated Blue Warbler (*Dendroica caerulescens*) is one such forest interior species that breeds in the southern Appalachians. The southern Appalachians are approximately 70% forested and these forests may provide important habitat for source populations of this species. Hooded Warbler (*Wilsonia citrina*) is an ecologically similar species and overlaps in range with *D. caerulescens* in the southern Appalachians. This research documents the foraging and nesting habitat use and nest fate of these two species primarily in cove forests at elevations of 2800-3200 ft. Two cove forests were delineated: acidic cove hardwood and rich cove hardwood. I conducted foraging observations randomly while searching for nests. I also collected structural and floristic vegetation data to relate foraging, nest-site selection, and nest fate to habitat.

*D. caerulescens* was three times more abundant ( $2.5 \pm 1.0$  SD mean detections per count) in these forests than *W. citrina* ( $0.8 \pm 0.5$  SD). *D. caerulescens* and *W. citrina* show no interspecific territoriality and forage at similar heights throughout the vegetation strata. Females of *D. caerulescens* and *W. citrina* forage at lower heights ( $6.5 \pm 5.4$  SD and  $3.7 \pm 3.8$  SD, respectively) than males ( $8.4 \pm 5.6$  SD and  $7.1 \pm 5.5$  SD, respectively). The females of both species prefer to forage in eastern hemlock (*Tsuga canadensis*). Female *D. caerulescens* also prefer to forage in red maple (*Acer rubrum*). Male *W.*

*citrina* prefer white pine (*Pinus strobus*) but male *D. caerulescens* have no tree species preferences. Both species' primary foraging substrate was leaves and there were no intra- or interspecific differences in foraging substrate preference. Both species primarily hovered at leaves in order to obtain prey; however, *W. citrina* gleaned less than *D. caerulescens*. Both species gleaned less in acidic cove hardwood than when foraging in rich cove hardwood. Foraging maneuver was significantly correlated with substrate for both species but less so for *W. citrina*.

There was no difference in nest success for either species between forest types. Both species readily utilized rhododendron as a nesting substrate but *W. citrina* avoided herbs. *D. caerulescens* experienced the highest Mayfield daily nest survival rate when nesting in herbs ( $0.9707 \pm 0.007$ ) and the lowest success in blackberry (*Rubus* spp;  $0.9405 \pm 0.018$ ). *W. citrina* experienced significantly higher nesting success in blackberry ( $0.9886 \pm 0.007$ ) than in any other nesting substrate ( $\chi^2 = 9.1$ ,  $df = 2$ ,  $p < 0.05$ ). Nesting success of *D. caerulescens* and *W. citrina* was lowest for nests initiated mid-season ( $0.9472 \pm 0.009$  and  $0.9519 \pm 0.012$ , respectively) as opposed to early ( $0.9664 \pm 0.008$  and  $0.9652 \pm 0.009$ , respectively) or late ( $0.9708 \pm 0.006$  and  $0.9862 \pm 0.006$ , respectively) in the season.

Both species selected nest sites with high cover of low shrubs and small disturbances. However, *D. caerulescens* avoided taller shrubs. For habitat specific models, the effect of disturbance was eliminated in acidic cove hardwood forests for both species. *W. citrina* nests and nest substrates were significantly taller than *D. caerulescens* nests in rhododendron ( $t = 3.58$ ,  $df = 56$ ,  $p < 0.05$ ) and over all ( $t = 6.89$ ,  $df = 122$ ,  $p < 0.001$ ). Nest fate was dependent on cover 1 m above the nest for both species.

These results highlight the subtle differences in the ecology of similar species that may allow for species coexistence. Additionally, small changes in management can potentially affect similar species differently. High nest success of *D. caerulescens* and *W. cetrina* in the southern Appalachians indicates that these forests may indeed be source populations. Future research should be directed towards mortality during other times in these species' annual cycle.

**THE FORAGING AND NESTING ECOLOGY OF BLACK-THROATED BLUE  
WARBLER (*DENDROICA CAERULESCENS*) AND HOODED WARBLER  
(*WILSONIA CITRINA*) IN THE SOUTHERN APPALACHIANS**

by

**KENDRICK COLLINS WEEKS**

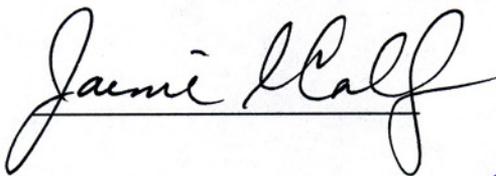
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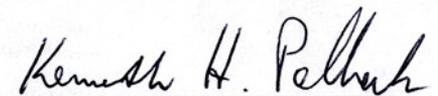
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**APPROVED BY:**







Chair of Advisory Committee

## **DEDICATION**

This thesis is dedicated to my mother, whose unending support of my life surely saved me from a fate far worse than I ever want to imagine.

## **PERSONAL BIOGRAPHY**

Kendrick C. Weeks was born in Greensboro, North Carolina. He graduated from Cary High School in 1988. Previously an outcast and outlaw, Kendrick went on to pursue his truest love: the study of nature. He graduated from Appalachian State University with a Bachelor of Science degree in biology. Not sure whether to go small scale, molecular biology, or large scale, ecology, he traveled around the Great North State working as a wildlife technician and in other sundrious capacities. On a final lurch to work with southern Appalachian flora and fauna, Kendrick was accepted in the Department of Zoology's Masters Program at North Carolina State University.

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## **Introduction**

The topography of the southern Appalachian Mountains creates diverse microclimatic and edaphic conditions which supports high biological diversity. The region supports many species of plants and animals found in the northeastern and southeastern United States. Unlike the northeastern United States flora and fauna, a few species in the southern Appalachians have differentiated from their northern conspecifics to become sub-species or varieties and even distinct species (endemics) (Martin et al. 1993). This has resulted in a unique community of organisms assembled from both southeastern and northeastern species pools and allows interspecific interactions among ecologically similar species that are allopatric in distribution elsewhere. Black-throated Blue Warbler (*Dendroica caerulescens*) and Hooded Warbler (*Wilsonia citrina*) are two such songbird species in the family Parulidae. The core range of *D. caerulescens* is the northeastern United States while that of *W. citrina* is in the southeast but, both are sympatric at mid-elevations in the southern Appalachians (Dunn and Garrett 1997). Forest management and global climate change are two phenomena that have the potential to change or shift the zone of sympatry for these two species (Rodenhouse 1992). *D. caerulescens* has been declining in the Blue Ridge Province for the past two decades (Hunter et al. 1999). Determining the factors that influence survival are crucial to developing effective conservation strategies.

### *Coexistence*

Ecologists have attempted to explain resource partitioning by invoking competition, predation, developmental or physiological constraints, and/or diverse environments. Resource partitioning can be apparent with or without differences in diet. For example,

many insectivorous bird species consume similar prey but obtain these prey in different locations or at different times such that the partitioning is spatial or temporal. Space may be considered a resource for sessile or territorial organisms, such as tunicates or warblers, respectively (Wiens 1989). Nest sites are spatial resources and nest predation may explain patterns of spatial partitioning in the nest placement of different species which are not interspecifically territorial (Martin 1988a, 1988b, 1996; Martin and Martin 2001). It has been shown that a higher density of nests in any one strata of nest placement leads to higher nest predation (Martin 1988b; Schmidt and Whelan 1998). This has also been termed “apparent competition” due to the competition for suitable nest sites in the face of nest predation (Holt and Kotler 1987). Competition was once invoked as the major factor responsible for resource partitioning but has been thoroughly challenged since the 1970s (Wiens 1977). Most likely, a combination of factors explain patterns of resource partitioning and the relative influence of each factor species-specific and/or regionally specific.

Ecological theory predicts that no two species may occupy the exact same niche (Hutchinson 1959). Corrolaries include the principles of ecological exclusion, character release, and character displacement (Brown and Wilson 1956). Partitioning of food resources in sympatric birds has been shown to occur by substrate type (Holmes et al. 1979; Morse 1980; Robinson and Holmes 1982), substrate species (Franzreb 1978; Holmes and Robinson 1981; Airola and Barrett 1985), height or other spatial differences (MacArthur 1958; Morse 1980), prey species or type (Robinson and Holmes 1982), and prey size (Holmes et al. 1979; Morse 1980). Behavioral differences (Holmes et al. 1979; Morse 1980), and the timing of breeding or foraging have also been shown to be

important (Anderson and Shugart 1974; Hutto 1981; Hejl and Verner 1990; Vilá 1992). These differences are used to differentiate guilds such as ground foraging or bark probing (Holmes et al. 1979). Within guilds however, very little is known about resource partitioning by similar species in zones of sympatry.

Interference competition is well documented in some warblers due to behavior (Pearson 2000; Pearson and Manuwal 2000; Pearson and Rohwer 2000) but exploitative competition and the “ghost of competition past” (Connell 1980) are much more difficult to document due to temporal variation in intensity and the difficulty of finding evidence of past competition, respectively (Wiens 1989). Careful characterization of the ecology of coexisting species must be undertaken before attempting to test hypotheses of interspecific interaction. *D. caerulescens* and *W. citrina* are ecologically very similar in foraging and nesting behavior, belonging to foliage-gleaning insectivore and shrub-nesting guilds (Evans Odgen and Stutchbury 1994; Holmes 1994). They show no interspecific territoriality or agnostic behaviors towards one another in the sympatric zone (pers. obs.). I characterized the foraging and nesting ecology of *D. caerulescens* and *W. citrina* in mesic habitats in an effort to understand their ecology in the southern Appalachians and how these two species coexist. Differences in foraging behavior and differences in nest success between habitats and nesting substrates can identify patterns of habitat quality for these two species at mid-elevations in the southern Appalachians.

### *Study Sites*

Three main study sites, Cold Springs, Lemon Gap, and White Oak Flats, were located in the French Broad District of the Pisgah National Forest near Hot Springs, NC at elevations between 805 and 1119 m (Figures 1 and 2). Nest and foraging observations

were mainly collected in mesic habitats of two types: acidic cove hardwood and rich cove hardwood (Schafale and Weakley 1990). Species were treated as in Radford et al. (1968). Acidic cove hardwood (Figure 3) is characterized by a canopy of cherry birch (*Betula lenta*), yellow birch (*B. alleghaniensis*), tulip poplar (*Liriodendron tulipifera*), and eastern hemlock (*Tsuga canadensis*) with scatterings of basswood (*Tilia americana*), northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), and yellow buckeye (*Aesculus octandra*). The midstory consisted of various species found in the canopy (especially dominants and maples) in addition to sourwood (*Oxydendron arboreum*) and witch hazel (*Hamamelis virginiana*). The understory consisted mainly of rosebay (*Rhododendron maximum*) with patchy dog-hobble (*Leucothoe axillaris*). Acidic cove hardwood is referred to as just “cove hardwood” in this study.

Rich cove hardwood (Figure 4) canopy consisted of tulip poplar, sugar maple, black cherry (*Prunus serotina*) northern red oak, basswood, white ash (*Fraxinus americana*), and yellow buckeye with scatterings of cherry birch. The midstory contained various canopy species (mainly buckeye and maple). The understory was made up of deciduous shrubs such as blackberry (*rubus* sp.) and hydrangea (*Hydrangea arborea*) and/or herbaceous species such as blue cohosh (*Caulophyllum thalictroides*), black cohosh (*Cimicifuga racemosa*), false goatsbeard (*Astilbe biternata*) and wood nettle (*Laportea canadensis*). This classification is a conglomerate of several classifications (Schafale and Weakley 1990) lumped into “mixed mesic hardwood” in this study due to similar physiognomy. Both vegetation associations were present on each site and therefore

represent paired sites. Other plant associations were classified qualitatively as xeric oak, pine-oak, pine, etc. (Simons and Shriner 1998).

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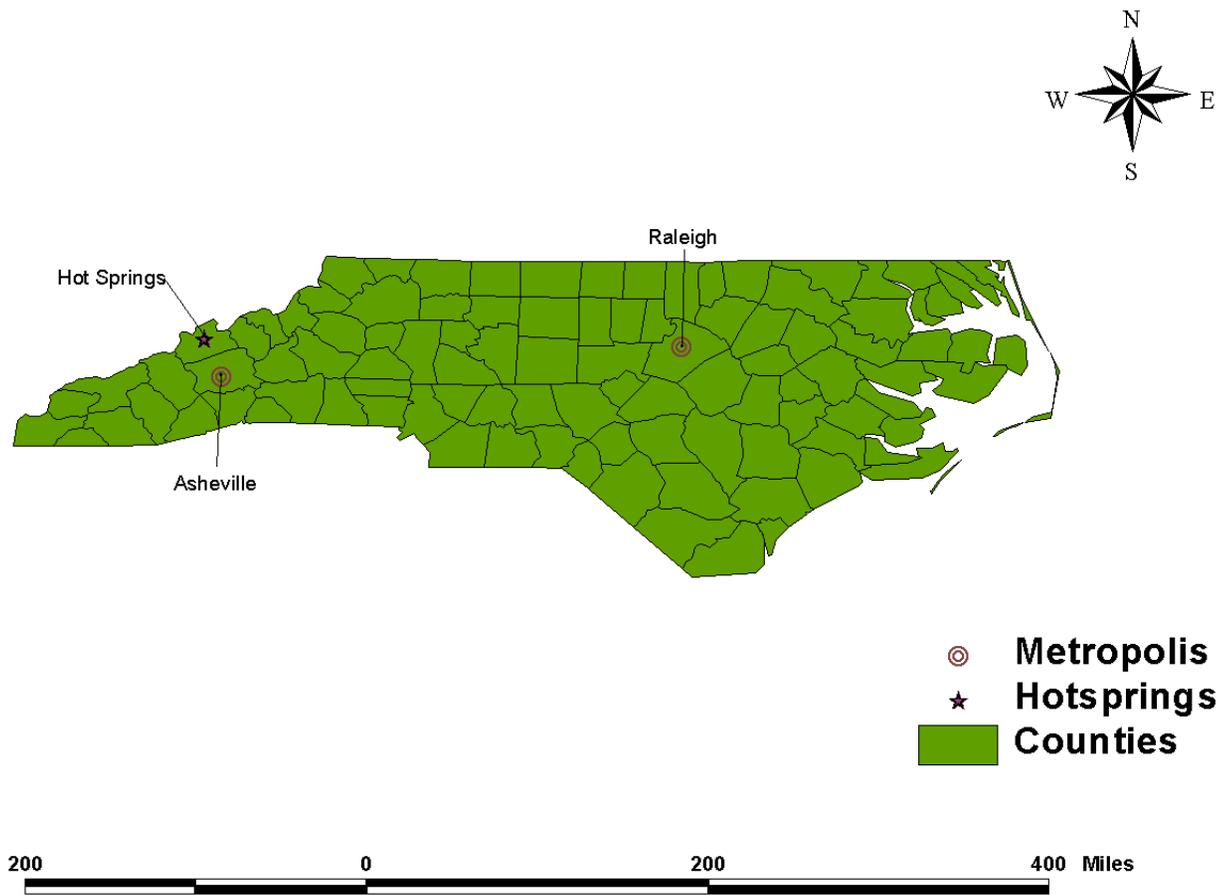


Figure 1. Study areas were located near Hot Springs, NC.

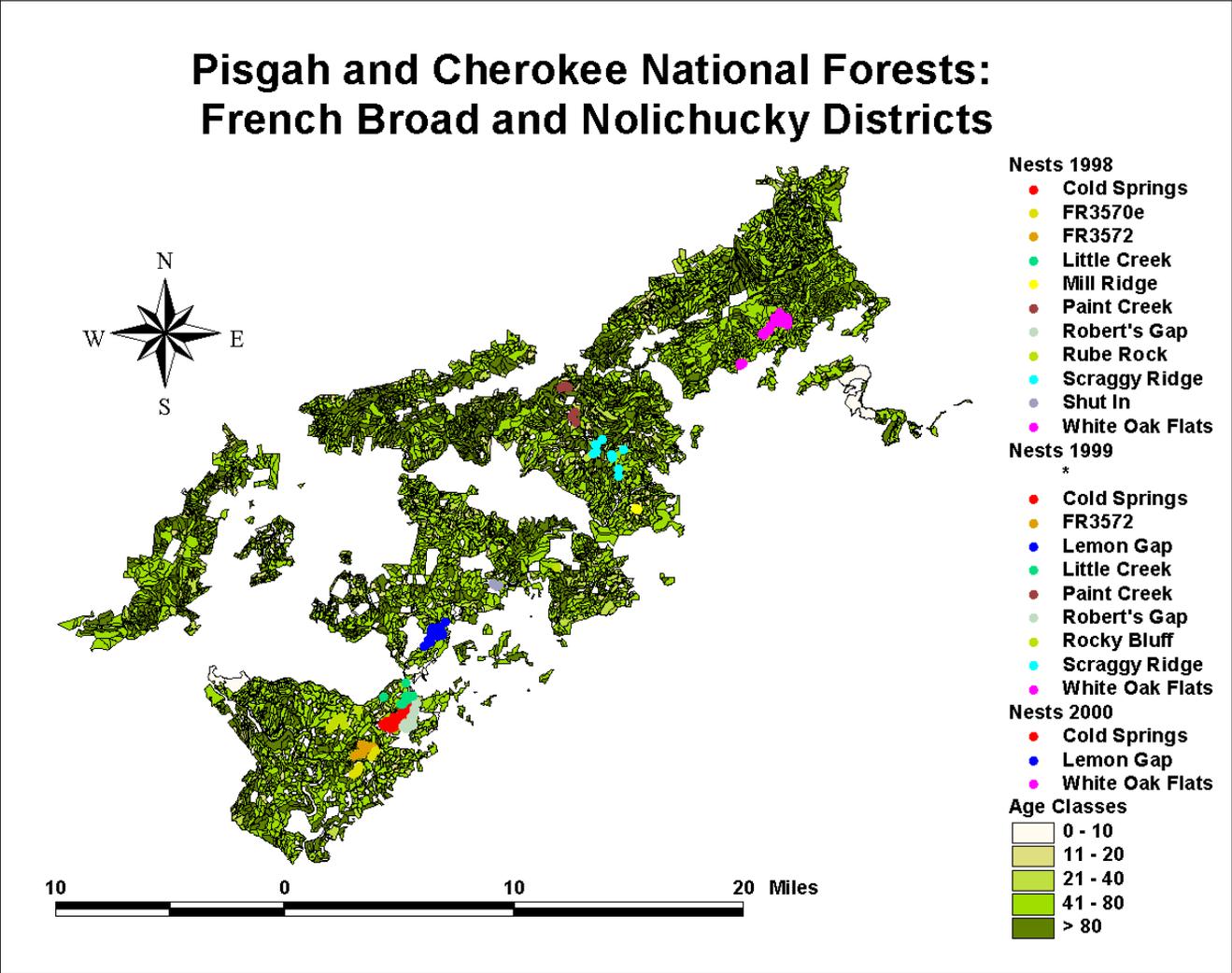


Figure 2. Nest searching areas (1998-2000) in Pisgah and Cherokee National Forests.



Figure 3. Rhododendron thicket in acidic cove hardwood (CH) habitat.



Figure 4. Diverse herb layer of rich cove hardwood forests. These were classified with similar habitats as mixed mesic hardwood habitat (MM).

## **Chapter 1: Foraging Behavior of Black-throated Blue Warbler and Hooded Warbler in the southern Appalachian Cove Forests**

### **Introduction**

Food is one of the most important resources of all living organisms. Food availability, cover, as well as other biotic interactions and the abiotic environment, influence the distribution of species (Ricklefs and Miller 1999). Studies of avian foraging range from characterizing the microhabitats in which birds forage to determining diet and food availability. Most studies have documented when, where, and how birds forage due to the difficulty of obtaining unbiased diet and resource abundance data. Most research assumes that these data reflect how birds encounter and use food resources. This assumption is reasonable but may be affected by other factors and has rarely been tested (Wiens 1989; Moremond 1990). Since MacArthur's (1958) famous study of northeastern U.S. warblers, the niche concept has been especially useful to ornithologists asking questions about avian foraging. Avian foraging niches have been shown to differ in space (e.g. habitat or foraging height) (MacArthur 1958; Morse 1980), time (i.e. seasonal and diel) (Anderson and Shugart 1974; Hutto 1981; Hejl and Verner 1990; Vilá 1992), tree species use (Franzreb 1978; Holmes and Robinson 1981; Airola and Barrett 1985), foraging maneuvers (Holmes et al. 1979), foraging substrates (e.g. leaves, branches, and twigs) (Holmes et al. 1979; Morse 1980; Robinson and Holmes 1982), prey size (Holmes et al. 1979; Morse 1980), and prey type (Cooper et al. 1990). Variation within species for any of these foraging variables can also be considered an element of niche and, in particular, the degree of specialization (Recher 1990). Variation of foraging behavior across space and time may reflect differences in resource

distributions (Majer et al. 1990; Recher 1990). Birds may be able to track these resources and this is a problem with data collected over the short-term (Hejl and Verner 1990; Miles 1990).

Interspecific habitat differences in foraging and nesting are the most obvious and largest scale of spatial partitioning of resources. However, many species inhabit more than one habitat or plant association and intraspecific foraging behavior has been shown to vary geographically, regionally and between habitats (Brooks 1947; Rabenold 1978; Morse 1980; Morse 1989; Petit et al. 1990). Determining these differences is important to understanding avian ecology and the constraints that species face so that management and conservation strategies can be applied effectively at many scales.

Within habitats, species have been shown to partition vegetation spatially (MacArthur 1958). The foraging height of birds can reflect preferences in microhabitat, food, other resources (e.g. cover), intra- and interspecific interactions, or the availability of resources. Even intraspecifically, it is rather well documented that male wood warblers forage higher in the vegetation than females (Morse 1968; Franzreb 1983; Holmes 1986; Kelly and Wood 1996). Because numerous factors affect the height at which a bird forages, it is difficult to assess causality without measuring each potential variable (e.g. competitive interactions, food resource distributions, and food preferences). Interspecific interactions are especially difficult to measure and the “ghost of competition past” is always an elusive concept (Connell 1980). However, when all else is equal, foraging height can indicate partitioning of resources.

Tree species foraging preferences among species of insectivorous birds can be due to several factors. Differences in abundance or types of arthropods can be due to host-

specificity or secondary compounds in the foliage (Holmes and Robinson 1981). Limited accessibility to prey because of foliage architecture can also have the potential to affect foraging preferences (Holmes and Robinson 1981; Airola and Barrett 1985; Whelan 1989a). Foraging preferences may also be apparent for more general groups of tree species such as conifers and deciduous trees (Franzreb 1978).

Foraging maneuvers can vary among insectivorous birds in many ways. This element of foraging behavior has the potential to be influenced by many factors including foliage architecture (Whelan 1989a; Parrish 1995; Whelan 2001), morphological limitations such as wing loading and aspect ratio (Pulliam 1985), and prey type or size (Robinson and Holmes 1982). A few species, such as Yellow-rumped Warbler (*Dendroica coronata*) and Blackburnian Warbler (*D. fusca*), show intersexual differences in foraging maneuvers (Morse 1968). However, most wood warblers and many other forest songbird species are regularly placed into guilds based upon distinct foraging behaviors (Holmes et al. 1979; Rusterholz 1981; Mac Nally 1994). Gleaners, birds that capture prey while perched, and flycatchers, birds that capture prey from the air, are two such insectivorous guilds. It is obvious that classifications such as these are warranted and useful because they can be strongly dependent on prey preferences (i.e. crawling vs. flying arthropods).

Substrate, the actual surface from which prey is taken, is another widely used guild partitioning criterion that is often correlated with maneuvers (e.g. foliage gleaner). For example, bark-foraging insectivores might be expected to probe the bark in order to forage effectively due to the structure of bark and the innate response of prey such as moving away from light (negative phototaxis) or away from sudden changes in light.

### *Ecomorphology*

Differences in foraging behavior, prey size, prey type, and substrate can sometimes be explained by morphological analysis, the study of which is called ecomorphology (Brown and Wilson 1956; Schoener 1965; Smith et al. 1997). Differences in culmen length of Black-throated Blue Warbler (*Dendroica caerulescens*; BB) and Hooded Warbler (*Wilsonia citrina*; HW) are small (Table 1). Size and shape should be considered together in morphological analyses (Wiens 1989). Bill width or depth may be a better indication of foraging habit in insectivorous birds (Root 1967). There is some evidence that *W. citrina* have a depressed mandible, a trait of the flycatching guild (Harrison 1984). However, some researchers have noticed that bill size differences are less common in sympatric insectivorous birds and have suggested that body or other character size ratios may be a better indication of resource partitioning (Schoener 1965; Hespenheide 1971; Cody 1974). A character size ratio threshold has been suggested as indicative of non-competitive coexistence (1.2) (Hutchinson 1959). Species with ratios below this value are hypothesized to not be able to coexist without competition. *D. caerulescens* and *W. citrina* show only a small difference in mass, wing chord and tail length (Table 1). However, a fairly large difference in tarsus length may or may not translate into a functional response in their foraging locations and/or behaviors. Although morphology can sometimes predict foraging behavior, considerable morphological variation is unrelated to the foraging variables that characterize the species' ecological relationships (Miles and Ricklefs 1984).

### *Foraging Behavior*

*D. caerulescens* foraging behavior has been quantified in northeastern forests and in parts of its non-breeding range. On breeding grounds in the northeastern U. S., males forage slightly higher (3-9m) than females (1-6m) (Sabo and Holmes 1983; Holmes 1986; Steele 1993). The foraging maneuver repertoire of birds there consists mainly of aerial maneuvers (65%; 55% of which were hovers) and gleaning (35%) mainly from leaves. Winter studies in the Caribbean suggest similar foraging heights with possibly more gleaning (75%) (Holmes 1994).

Published accounts of *W. citrina* foraging behavior on the breeding grounds are more anecdotal, except in eastern Tennessee lowland forests (Bennett 1980). Bennett classified the *W. citrina* as belonging to the flycatching/foilage-gleaning guild and found them foraging at heights of 5-35m with most activity constrained between 5-18m (76%). She further showed that the *W. citrina* foraging maneuver repertoire consists mainly of hovering and taking prey from foliage. The foraging ecology of *W. citrina* has been studied in great detail on the wintering grounds and, the species was found to direct aerial foraging maneuvers (hovering, hawking and sallying) towards airborne prey over 70% of the time (Rappole and Warner 1980). It has been hypothesized that the nervous tail-spreading behavior of *W. citrina* aids in foraging by flushing insects from foliage (Evans Odgen and Stutchbury 1994; Schorre 1998).

### *Resources*

Food resources are the ultimate variable of interest in almost every investigation of foraging ecology. The spatial and temporal availability of these resources has the potential to influence all aspects of foraging behavior (Holmes and Schultz 1988).

Optimal foraging theory predicts many foraging behaviors and food preferences using economic models of costs and benefits to individuals (Martin 1996). Resources are difficult to measure and the availability of resources to one species may be different than for another species. The behavioral or morphological constraints of the birds and the escape behavior, cryptic coloration, and size of prey can determine availability (Holmes and Schultz 1988). Thus, availability cannot be measured just by determining relative or absolute abundance of arthropods (Hutto 1990). Determining how birds perceive their environment is necessary to fully understand diet preferences.

Diet is also difficult to quantify because digestibility is not the same for different prey items (Rosenberg and Cooper 1990) but extensive work has shown that *D. caerulescens* heavily utilize lepidopteran larvae during nesting (Goodbred and Holmes 1996). Coleopterans, dipterans, and spiders are used as well during the breeding season and proportions probably vary with seasonal and spatial availability. Yellow birch (*Betula alleghaniensis*) has been shown to be a preferred tree species and to contain more lepidopteran prey than other tree species (Holmes and Robinson 1981). Winter diet consists of arthropods (75%) but is supplemented with berries and nectar (Holmes 1994). These proportions, however, may be habitat-specific (Wunderle 1995).

There are no available studies on the diet of *W. citrina* on the breeding grounds (Evans Odgen and Stutchbury 1994). Diet analysis in winter identified many coleopterans and hymenoptera (Evans Odgen and Stutchbury 1994). It is not known whether *W. citrina* utilize fruit during the life cycle.

Attempting to understand all of the factors involved in avian foraging is a daunting task to say the least. However, understanding how insectivorous birds forage in relation to the

physiognomy and composition of the vegetation gives insight into their resource use and ecology and thus, conservation. Neotropical-nearctic migrants are an exceptional example of the evolutionary adaptation of migratory behavior to seasonal resources. Their conservation will ultimately rely on a deep understanding of their survival and ecology at all stages of their seasonal cycle and multi-national cooperation.

### **Objectives**

In order to better understand the ecology of *D. caerulescens* and *W. citrina* in different habitats of the southern Appalachians, I determined whether or not the foraging heights, foraging maneuvers, and foraging substrates of *D. caerulescens* and *W. citrina* are similar in the southern Appalachians where they coexist. Documenting the foraging ecology will help us to understand coexistence and develop conservation strategies of these species in the southern Appalachians. I tested the following null hypotheses:

- 1) *W. citrina* and *D. caerulescens* do not differ in foraging heights, substrates, or maneuvers in all habitats and within each habitat and
- 2) *D. caerulescens* and *W. citrina* do not differ in tree species preference for foraging within all habitats and within each habitat.

I expected that differences in foraging ecology would be minor due to similar morphology.

### **Methods**

#### *Relative Abundance*

Fixed 75m radius point counts were conducted in 2000 at White Oak Flats, Lemon Gap, and Cold Springs in order to determine relative abundances. Counts were

conducted four times throughout the season, two in May and two in June. The maximum counts for each point were used to determine mean detections per point.

### *Foraging Observations*

Foraging observations were collected opportunistically during point counts and nest-searching in 1999 (May and June). Observations in 2000 were only collected on birds whose nests were found and effort was reduced, which limited the sample size.

Observations were collected in mature forests (> 60 yrs) before noon. The first foraging attack seen after the foraging bird was located was recorded on data sheets (Appendix A). Field assistants recorded observer initials, date, site, location, tag number (point count or nest), weather, time, bird species, bird sex, height of bird (to nearest meter), height of plant, height of lowest branch, plant species, foraging substrate (leaf, twig < 1 cm diameter, branch > 1 cm diameter, trunk, air, flower, and ground), foraging maneuver (glean, hover, hawk, and sally), position of the bird (proximal, medial, or distal), approximate age of forest, direction bird moved (lateral, up, or down) after foraging attack, and estimated plant association (e.g. cove hardwood, mixed mesic hardwood, etc.). All height measurements were estimated using range finders. Vegetation plots for each species were combined with the assumption that vegetation is similarly available to both sexes. Low sample sizes in other plant associations in 1999, observations in plant associations other than cove hardwood and mixed mesic hardwood were excluded from analyses.

### *Vegetation Sampling*

In 1999, a 10m radius vegetation sampling plot was centered on the location of the foraging bird. Percent cover was estimated for each plant species ( $\geq 5\%$ ) in five height

ranges, 0-2 m, 2-5 m, 5-10 m, 10-15m, and >15m (Appendix B). All woody plants were identified to species except for blackberry (*Rubus* spp.), hickory (*Carya* spp.), huckleberry (*Gaylussacia* spp.) and evergreen rhododendron (*Rhododendron* spp.). However, the great majority of rhododendron were *Rhododendron maximum*. Percent cover was defined as the percent of the ground shaded by the plants. The finer divisions in the lower strata were made due to vegetation physiognomy (high cover at low heights), the difficulty of determining qualitative strata (e.g. shrub and subcanopy), and the foraging habits of the bird species (see *Foraging* in Introduction).

### *Analysis*

Nonparametric tests of foraging height differences were conducted using Komolgorov-Smirnov (K-S) method (Sokal and Rohlf 1995). Parametric estimates of average foraging heights were calculated and Student's t-tests were conducted for comparison to previous research in other regions. The floristic structural and compositional data were combined into a large matrix by using species-height range cover estimates as pseudospecies. For example, one pseudospecies would be zRhodo and another would be tRhodo. zRhodo and tRhodo indicate rhododendron cover at 0-2 m and 2-5 m, respectively. Since *D. caerulescens* and *W. citrina* are mainly thought to take prey from plant substrates, particularly foliage, these data are appropriate to characterize foraging habitat. These data were submitted to cluster analysis using PC-ORD (McCune and Mefford 1999) to verify qualitative habitat (plant association) categories and for further analyses of foraging preferences. Cluster analysis employed euclidean distances and Ward's group linkage, a hierarchical method also known as "error sum of squares" (McCune and Mefford 1999). Student's t-tests were also used to test differences of total

average cover between habitat type using PROC TTEST in SAS, Version 8.0 (SAS 1999).

Plant species use was the number of foraging events observed for each species. Foraging Veg cover estimates for each species were averaged to obtain proportion of total cover (availability) for each species in each height range. Expected observations for each plant species were summed across height ranges to determine expected observations for each species. Plant species use vs. availability was determined using goodness-of-fit G-tests ( $G_{adj}$ ) using only those species with  $\geq 5$  expected observations (Sokal and Rohlf 1995). The remaining species were lumped into an “other” category.

Foraging substrate and foraging maneuver differences were determined using R X C G-tests of independence ( $G_{adj}$ ) (Sokal and Rohlf 1995). Trunk, ground, and flower were foraged from  $< 5\%$  and were removed from substrate comparisons. Air was highly correlated with hawk and sally maneuvers and, therefore, was also removed from substrate analysis. Hawk and sally were combined into the single category ‘hawk’ due to presumably similar energetic costs and heavy correlation of both maneuvers with flying insect prey. All data were entered into Microsoft Access and manipulated using Microsoft Excel. I performed categorical analyses to investigate correlations of substrate and maneuver using PROC CATMOD and PROC FREQ in SAS, Version 8.0 (SAS 1999).

## **Results**

*D. caerulescens* was three times more abundant ( $2.5 \pm 1.0$  SD mean detections per count) in these forests than *W. citrina* ( $0.8 \pm 0.5$  SD). Mean detections per count were

$2.3 \pm 1.0$  SD and  $2.7 \pm 1.0$  SD *D. caerulescens* and  $0.9 \pm 0.4$  SD and  $0.7 \pm 0.6$  SD *W. citrina* in cove hardwood and mixed mesic hardwood, respectively.

Both female *W. citrina* and *D. caerulescens* foraged significantly lower than males in all habitats ( $3.7 \pm 3.8$  SD,  $6.5 \pm 5.4$  SD,  $7.1 \pm 5.5$  SD, and  $8.4 \pm 5.6$  SD, respectively;  $p < 0.05$ ). This agrees with published values for *D. caerulescens* (Holmes 1986) and anecdotal information for *W. citrina* (Evans Odgen and Stutchbury 1994). Female *W. citrina* foraged significantly lower than female *D. caerulescens* ( $p < 0.05$ ) for all years combined (Figure 1). K-S tests showed similar results (Table 2 and 3) with males not differing in foraging height (Figure 2). Cluster analysis generally verified qualitative plant association categories (Figure 3). Therefore, estimated plant associations were used as discriminating variables for comparisons. Females of both species may be changing their foraging height distribution depending upon habitat but this is not entirely clear (Tables 2c and 3c). There was more average cover from 2-15 m in cove hardwood than in mixed mesic hardwood (Figure 4;  $p < 0.001$ ). However, mixed mesic hardwood had more average cover from 0-2 m ( $p < 0.05$ ).

Females of both species showed strong non-random preferences for plant species (HW:  $G_{adj} = 24.7$ ,  $df = 6$ ,  $p < 0.001$  and BB:  $G_{adj} = 40.1$ ,  $df = 14$ ,  $p < 0.001$ ) whereas male *W. citrina* did exhibit preferences ( $G_{adj} = 30.5$ ,  $df = 13$ ,  $p < 0.01$ ) and male *D. caerulescens* did not ( $G_{adj} = 21.1$ ,  $df = 13$ ,  $p > 0.10$ ). The females of both species prefer eastern hemlock and avoid forbs (Figures 5 and 6). Female *D. caerulescens* also preferred red maple and, to some extent, yellow buckeye. *W. citrina* males appear to prefer 'other' species and in particular white pine (*Pinus strobus*). Deviation from expectation for white pine was greater than seven observations.

Leaves were by far the preferred foraging substrate across species and sexes for all habitats (Figures 7-9). There were no foraging substrate preference differences between species (Male-Males:  $G_{\text{adj}} = 0.25$ ,  $df = 2$ ,  $p > 0.80$ ; Female-Female:  $G_{\text{adj}} = 1.1$ ,  $df = 2$ ,  $p > 0.50$ ) or sexes (HW:  $G_{\text{adj}} = 2.0$ ,  $df = 2$ ,  $p > 0.20$ ; BB:  $G_{\text{adj}} = 5.3$ ,  $df = 2$ ,  $p > 0.10$ ). Across both habitats, *D. caerulescens* gleaned and hovered in equal proportions and rarely hawked. Both male and female *W. citrina* gleaned in  $\leq 30\%$  of the observations and hawked more than *D. caerulescens* (Figure 10). Male *D. caerulescens* ( $G_{\text{adj}} = 7.9$ ,  $df = 2$ ,  $p < 0.05$ ) and female *W. citrina* ( $G_{\text{adj}} = 11.3$ ,  $df = 2$ ,  $p < 0.005$ ) used significantly more aerial maneuvers (i.e. hovers and hawks) in cove hardwood (Figure 11) relative to their foraging behavior in mixed mesic hardwood (Figure 12). Female *D. caerulescens* and male *W. citrina* exhibited the same trend but the difference was not significant ( $G_{\text{adj}} = 2.9$  and  $G_{\text{adj}} = 2.4$ ,  $df = 2$ ,  $p > 0.2$ ). There were no differences between male and female foraging maneuvers within habitats (HW:  $G_{\text{adj}} = 5.69$ ,  $df = 2$ ,  $p > 0.05$  and BB:  $G_{\text{adj}} = 5.39$ ,  $df = 2$ ,  $p > 0.05$ ). Both sexes of *W. citrina* gleaned less than *D. caerulescens* in both habitats combined (Male-Male:  $G_{\text{adj}} = 21.2$ ,  $df = 2$ ,  $p < 0.001$  and Female-Female:  $G_{\text{adj}} = 14.9$ ,  $df = 2$ ,  $p < 0.001$ ; Figures 10-12). This result was fairly consistent within habitats but Female-Female differences were not significant in mixed mesic hardwood ( $G_{\text{adj}} = 5.09$ ,  $df = 2$ ,  $p > 0.15$ ).

Foraging substrate had a significant effect on foraging maneuvers for all species and genders (Fisher's Exact Test;  $p < 0.05$ ). The proportion of aerial maneuvers increased as foraging birds moved from branches to twigs to leaves for all species. However, this effect was not as pronounced for *W. citrina* as for *D. caerulescens* (Figures 13-16).

## Discussion

The foraging behavior of *D. caerulescens* and *W. citrina* in the southern Appalachians is very similar but there are noticeable differences as well. Both *W. citrina* and *D. caerulescens* forage at similar heights and use similar species of plants, substrates, and maneuvers. In addition, they showed no interspecific territoriality. The lower average foraging height in cove hardwood, though significant only for *D. caerulescens* females, appears to reflect differences in plant physiognomy and forest structure (Figure 4). Rhododendron forms thick cover up to 5m and eastern hemlock can have extensive foliage below the canopy. This may be providing additional foraging sites for these birds at lower heights in cove hardwood.

*W. citrina* foraging behavior seems to be more stereotyped than the foraging behavior of *D. caerulescens* in this zone of sympatry. *W. citrina* use more energetically expensive aerial foraging maneuvers, such as hovering and hawking, even when prey can presumably be captured easily with a less energetically expensive maneuver (i.e. gleaning). Greater mass could explain some of this behavior but, *W. citrina* are only 1 gram heavier than *D. caerulescens* (Table 1). It might also be suggested that *W. citrina* are actually choosing different prey than *D. caerulescens* (i.e. flying insects). Flying insects resting on branches and twigs may explain the aerial maneuvers. Aerial maneuvers may make it less likely that the insect would detect the warbler and try to escape before capture. Determining diet from field observations is extremely difficult but when we could see the prey item, it was usually soft-bodied lepidopteran larvae for both species.

### *Relation of Foraging Behavior to Resources*

Studies of canopy arthropods in the southern Appalachians are usually general and geared more towards defoliation studies with no integration of higher trophic level phenomenon with explanations of observed distributions. However, canopy arthropods tend to be most abundant and cause high levels of defoliation in the subcanopy (Reynolds and Crossley 1997). This may indicate an unusually large food source that both species are able to exploit without interspecific aggression being necessary. Also, arthropod size has been shown to decrease with increasing elevation and that this correlates with body size of bird species along that gradient (Janes 1994). Although there is not much size difference between *D. caerulescens* and *W. citrina* in general, the documented foraging habits of *W. citrina* in winter may be indicative of optimal prey types (e.g. optimally sized flying insects), which may decline with elevation in the southern Appalachians. However, no differences in dominant foraging substrate (leaves) or dominant foraging maneuver (hovering) between species suggests that *D. caerulescens* and *W. citrina* may be exploiting similar types of prey. The large supply of lepidopteran larvae may play a role in coexistence but this remains to be determined experimentally. Arthropod sampling, diet analyses, and comparisons with quantitative foraging data from other parts of the range of *W. citrina* may shed light on this dilemma.

The relative abundance of *W. citrina* on these sites was approximately one third that of *D. caerulescens* in both habitats on my study sites. Mean detections per count were  $2.3 \pm 1.0$  SD and  $2.7 \pm 1.0$  SD *D. caerulescens* and  $0.9 \pm 0.4$  SD and  $0.7 \pm 0.6$  SD *W. citrina* in cove hardwood and mixed mesic hardwood, respectively. *W. citrina* territories seem to be larger than most *D. caerulescens* but this was not measured. This may

indicate that *W. citrina* is occupying habitat at the edge of its functional tolerance. Physiologically, low ambient temperatures may have a greater cost to *W. citrina* than to *D. caerulescens*. However, low abundances of large flying arthropods or preferred foraging substrates (i.e. conifers) may be limiting this species' elevational distribution in the southern Appalachians. This could be creating a conflict between hard-wired (stereotypic) foraging adaptation and the local environment.

#### *Use vs. Availability*

Determining use vs. availability is problematic for ecologists and depends greatly on what the researcher perceives and not on the perception of animals (Hutto 1990). Determining plant use vs. availability may have been biased since multiple observations on individual birds were taken and vegetation samples were pooled for each species to determine availability. This ignores the fact that individual territories may have different available plant species. Multiple observations on individual birds and random vegetation sampling within territories would not only detect individual variation but also individual as well as more general preferences for various plant species within the territory (Steele 1992). However, I believe these biases to be negligible due to the restriction of analyses to two main physiognomic plant associations, the relative homogeneity of vegetation throughout these sites, and the large sample sizes.

Of course, resources (e.g. prey) are presumably the ultimate determinant of plant species preferences and their distribution among plant species may vary from territory to territory. This type of variation could indicate that the birds indeed track resources regardless of plant species. However, if some plant species regularly have higher relative abundances of prey (Holmes and Schultz 1988), this should be detected by my method.

The fact that females of both species showed a significant preference for eastern hemlock suggests that this species may be rich in prey or harbor preferred prey. A soft-bodied lepidopteran larvae, hemlock looper (*Lambdina fiscellaria*) is a common outbreak pest of conifers in the northeastern U.S. and may be of some significance in this documented plant species foraging preference of *D. caerulescens* and *W. citrina* females.

#### *Habitat Structure*

Conifer preference may provide insight into the large difference in tarsus length between these two species (Table 1). Although eastern hemlock have short leaves, male *W. citrina* exhibited a foraging preference for white pine, which has longer leaves. Longer tarsi could function to prevent feathers from becoming soiled with sap or make it less difficult to perch on branches with long, needle-like leaves. Additionally, the tail spreading behavior of *W. citrina* is apparent on the breeding grounds (pers. observation) even though the majority of its prey are taken from stationary substrates (i.e. leaves). However, it is obvious that both species are able, in varying degrees, to modify behavior to local plant physiognomy (Figures 10-12).

Foliage architecture may constrain foraging behavior to particular maneuvers (Whelan 1989a, 1989b, 2001). Although, foliage architecture was not measured in this study, the general architectural differences of different foraging substrates of the plant (branch, twig, leaf) have been shown to affect foraging maneuvers. However, birds that take flying insects may not be effected due to behavioral constraints. Neophobia has been suggested as a possible explanation for a lack of foraging plasticity (Greenberg 1983). Data presented here suggest that *W. citrina* are stereotyped due to their continual

use of aerial maneuvers regardless of substrate (Figures 13-16). However, I cannot fully rule out diet differences due to the lack of specific diet data.

Future studies should collect information on morphology, foraging behavior, prey availability and especially diet in conjunction with nest survival along elevational gradients containing similar habitat, such as hemlock forest and acidic cove hardwood forest, to evaluate the coexistence of these very similar species. However, plant associations change with elevation and separating confounding factors may prove much more difficult than imagined.

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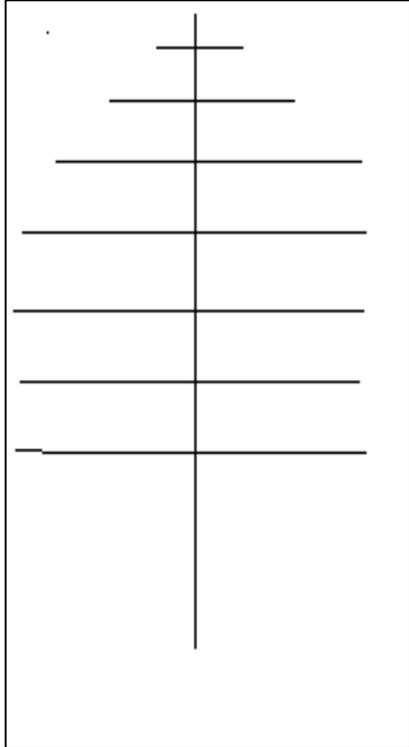
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Appendix A

Observer: \_\_\_\_\_ Date: \_\_\_\_\_ Observa#: \_\_\_\_\_ Site: \_\_\_\_\_

Location: \_\_\_\_\_ Nest/tag#: \_\_\_\_\_ Clouds: \_\_\_\_\_ temp: \_\_\_\_\_



BB HW \_\_\_\_\_ Time: \_\_\_\_\_

leaf \_\_\_\_\_ Mixed Mesic \_\_\_\_\_ Age: \_\_\_\_\_

twig \_\_\_\_\_ Cove Hardwood

branch \_\_\_\_\_ Other \_\_\_\_\_

trunk \_\_\_\_\_

ground \_\_\_\_\_ Lepidopteran L A

Glean \_\_\_\_\_ Coleopteran L A

Hawk \_\_\_\_\_ Dipteran

Hover \_\_\_\_\_ Other \_\_\_\_\_

Sally \_\_\_\_\_ Unk \_\_\_\_\_

PSpecies: \_\_\_\_\_ **Pheight:** \_\_\_\_\_ Where'd it go? \_\_\_\_\_

**Notes:**

## Appendix B. Foraging Veg Data Sheet

Obs:	Date:	Observa#:				
		0-2m	2-5m	5-10m	10-15m	>15m
Species						
Ash, White						
Basswood						
Beech, American						
Birch, Cherry						
Birch, Yellow						
Black Gum						
Buckeye						
<i>Carpinus</i>						
Cherry, Black						
Chestnut, American						
Crotched Herb						
Dead Wood						
Dogwood, Flowering						
Ferns						
Forbs						
<i>Gaylussacia</i> sp						
Grass						
Hemlock						
Hickory sp						
Hickory, Mockernut						
Holly, American						
Holly, Mountain						
Locust, Black						
Magnolia, Fraser						
Maple, Red						
Maple, Striped						
Maple, Sugar						
Moss						
MOUNTAIN LAUREL						
Oak, Black						
Oak, Chestnut						
Oak, Northern Red						
Oak, Scarlet						
Oak, White						
Pine, Pitch						
Pine, Short-leaf						
Pine, Table Mountain						
Pine, Virginia						
Pine, White						
RHODODENDRON						
<i>Rubus</i> sp.						
Sassafras						
Serviceberry						
Silverbell						
Sourwood						
Spruce, Red						
Tulip Poplar						
Vaccinium						
Walnut, Black						
Witch Hazel						
Yellowwood						

Canopy
h:
%
Subcanopy
h:
%
Tall Shrub
h:
%
Low Shrub
h:
%
Herb
h:
%
Dead Wood
h:
%

### Cover Class Categories

1 < 0.1%	6 > 10 - 25%
2 > 0.1 - 1%	7 > 25 - 50%
3 > 1 - 2%	8 > 50 - 75%
4 > 2 - 5%	9 > 75 - 95%
5 > 5 - 10%	10 > 95%

Black-throated Blue Warblers <sup>1</sup>			Hooded Warblers <sup>2</sup>
Character	Male (17) Mean (mm or g)	Range	Male AHY (Mean ± SE)
Wing Length	65.2	62.0-67.0	68.0 ± 0.19 (75)*
Tail Length	51.1	49.0-54.0	56.2 ± 0.62 (16)
Tarsus Length	18.7	17.5-19.5	22.6 ± 0.07 (78)
Exposed Culmen	9.4	8.5-10.0	10.0 ± 0.11 (31)
Breeding Mass	9.8	(± 0.5 SD, n =70)	11.2 ± .0.07 (67)
Wintering Mass	9	(± 0.6 SD, n =30)	10.3 ± 0.08 (35)*

Black-throated Blue Warblers <sup>1</sup>			Hooded Warblers <sup>2</sup>
Character	Female (10) Mean (mm or g)	Range	Female AHY (Mean ± SE)
Wing Length	61.1	60.0-63.0	64.5 ± 0.17 (99)
Tail Length	48.5	47.5-51.0	54.9 ± 0.48 (11)
Tarsus Length	18.6	18.0-19.0	22.2 ± 0.06 (99)
Exposed Culmen	9.2	9.0-9.5	10.0 ± 0.18 (13)
Breeding Mass	10.1	(± 0.9 SD, n =55)	11.2 ± 0.11 (71)
Wintering Mass	8.7	(± 0.6 SD, n =21)	9.7 ± 0.09 (24)

Table 1. General morphological comparison of *D. caerulescens* and *W. citrina*. Adapted from Ogden and Stutchbury (1994)<sup>2</sup> and Holmes (1994)<sup>1</sup>. Sample sizes in parentheses. \* Significant male-female differences (t-test, p<0.05).

Table 2. Kolmogorov-Smirnov p-values comparing foraging height differences in a) mixed mesic hardwood (MM), b) cove hardwood (CH), c) between MM and CH and d) combined MM and CH. Data includes both 1999 and 2000. Sample sizes are in parentheses.

A.

Sex-Species	♀bb (145)	♂bb (124)	♀hw (53)
♂bb (124)	< <b>0.05</b>	*****	*****
♀hw (53)	< <b>0.05</b>	*****	*****
♂hw (49)	*****	> 0.90	< <b>0.05</b>

B.

Sex-Species	♀bb (104)	♂bb (102)	♀hw (56)
♂bb (102)	> 0.20	*****	*****
♀hw (56)	> 0.15	*****	*****
♂hw (55)	*****	> 0.90	< <b>0.05</b>

C.

Sex-Species	♀bb (104)	♂bb (102)	♀hw (56)	♂hw (55)
♀bb (145)	> 0.90			
♂bb (124)		> 0.90		
♀hw (53)			> 0.075	
♂hw (49)				> 0.90

D.

Sex-Species	♀bb (249)	♂bb (226)	♀hw (109)
♂bb (226)	< <b>0.05</b>	*****	*****
♀hw (109)	< <b>0.05</b>	*****	*****
♂hw (104)	*****	> 0.50	< <b>0.05</b>

Table 3. Kolmogorov-Smirnov p-values comparing foraging height differences in a) mixed mesic hardwood (MM), b) cove hardwood (CH), c) between MM and CH and d) combined MM and CH. Data includes only 1999. Sample sizes are in parentheses.

A.

Sex-Species	♀bb (90)	♂bb (94)	♀hw (42)
♂bb (94)	< <b>0.05</b>	*****	*****
♀hw (42)	< <b>0.0001</b>	*****	*****
♂hw (46)	*****	> 0.90	< <b>0.05</b>

B.

Sex-Species	♀bb (58)	♂bb (76)	♀hw (38)
♂bb (76)	< <b>0.05</b>	*****	*****
♀hw (38)	> 0.30	*****	*****
♂hw (44)	*****	> 0.50	< <b>0.05</b>

C.

Sex-Species	♀bb (58)	♂bb (76)	♀hw (38)	♂hw (44)
♀bb (90)	< <b>0.05</b>			
♂bb (94)		> 0.90		
♀hw (42)			> <b>0.075</b>	
♂hw (46)				> 0.90

D.

Sex-Species	♀bb (148)	♂bb (170)	♀hw (80)
♂bb (170)	< <b>0.05</b>	*****	*****
♀hw (80)	< <b>0.05</b>	*****	*****
♂hw (90)	*****	> 0.50	< <b>0.05</b>

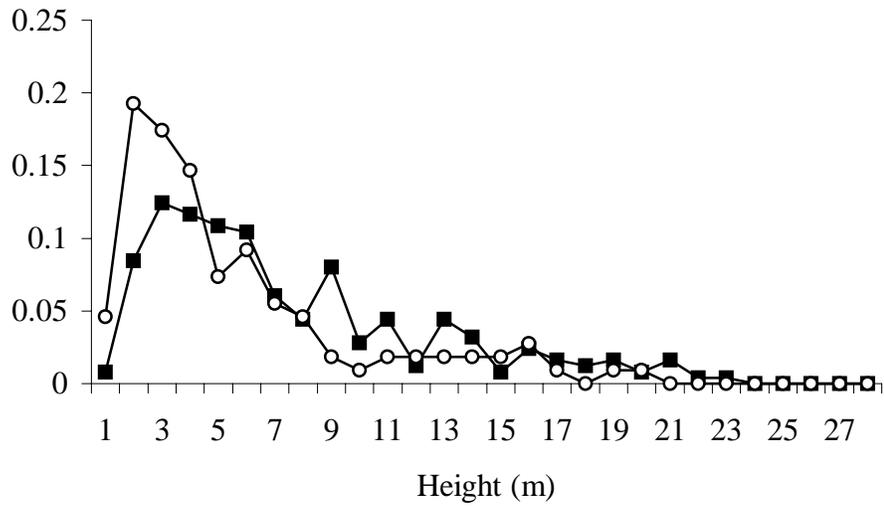


Figure 1. Foraging height distribution (proportion of observations) in both habitats combined for *D. caerulea* (squares) and *W. citrina* (open circles) females.

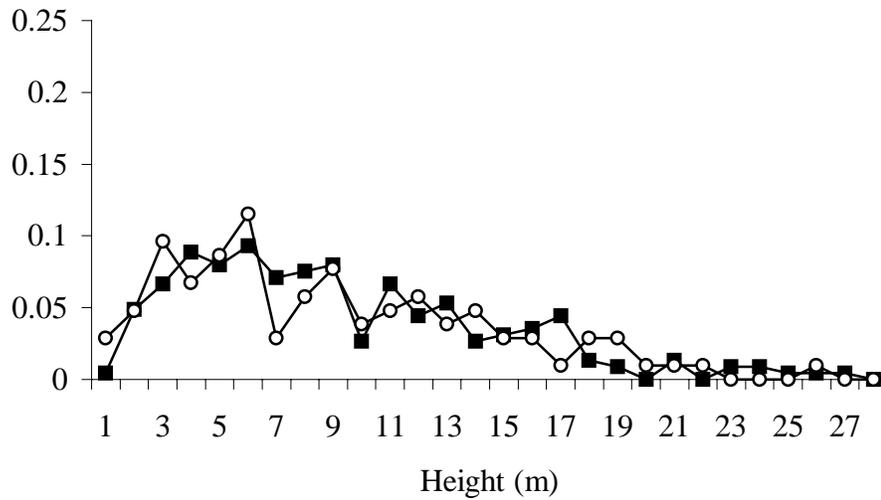


Figure 2. Foraging height distribution (proportion of observations) in both habitats combined for *D. caerulea* (squares) and *W. citrina* (open circles) males.

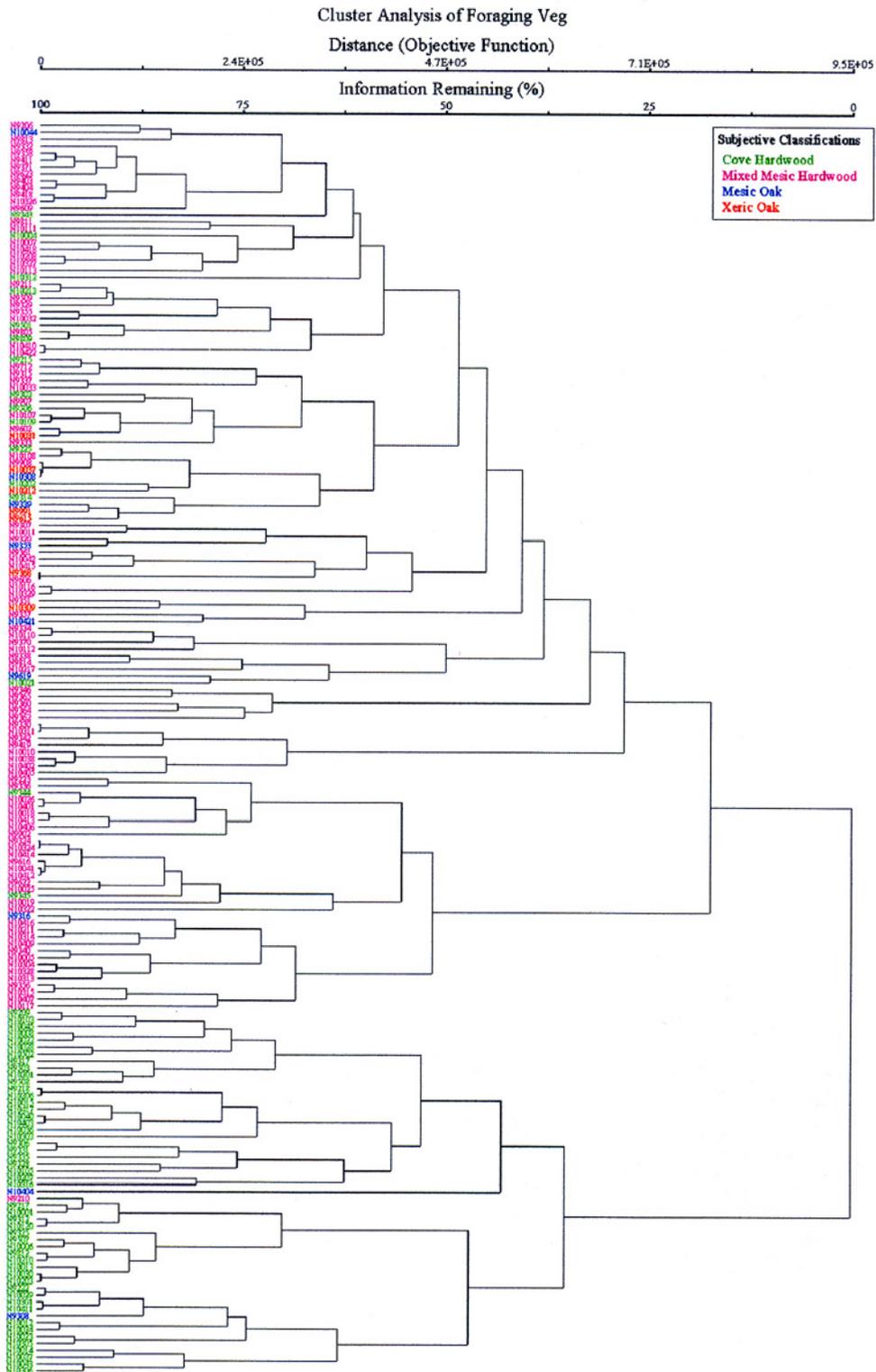


Figure 3. Cluster analysis dendrogram of floristic and structural vegetation data (Foraging Veg) collected for each nest. Qualitative classifications are color-coded and agree with cluster analysis. See text for details of hierarchical classification method.

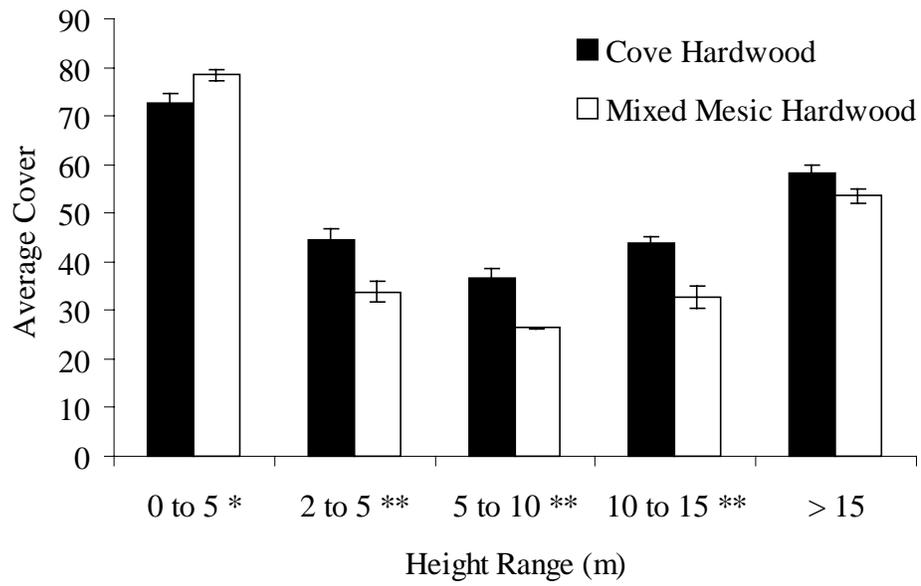


Figure 4. Foliage height distribution of cove hardwood and mixed mesic hardwood forest habitat. \*-  $p < 0.05$ , \*\* -  $p < 0.001$

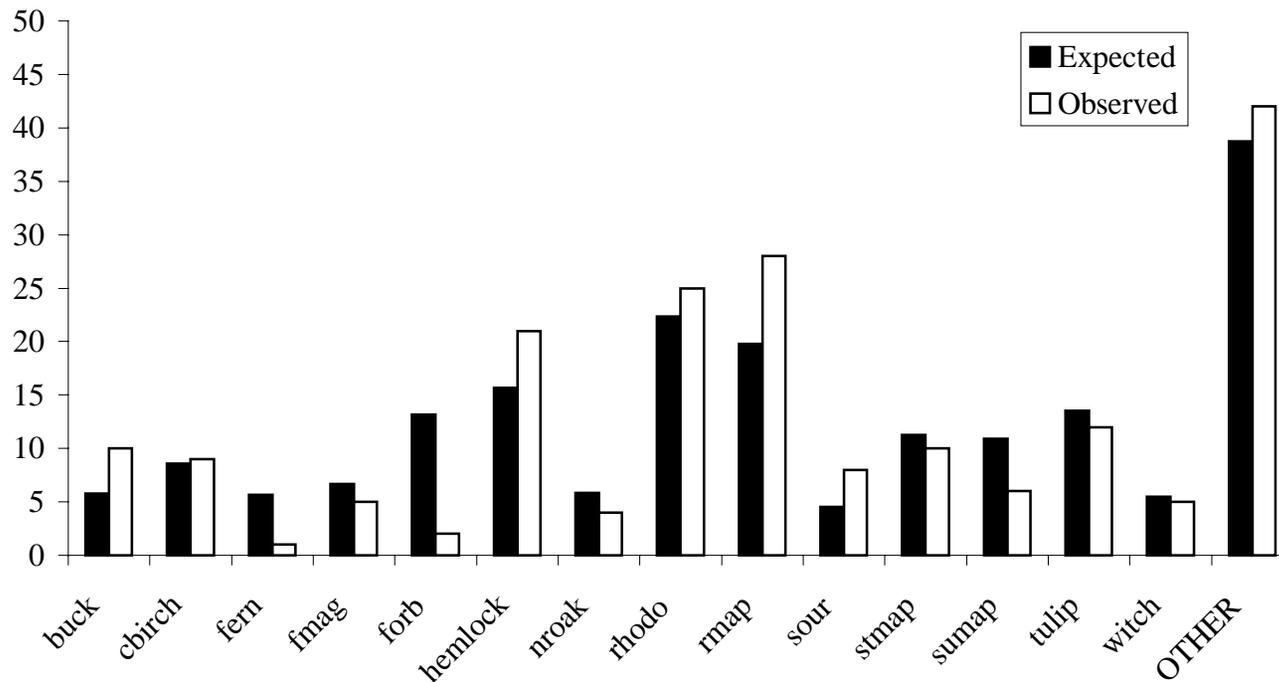


Figure 5. Observed and expected foraging frequencies (number of observations) for female *D. caerulea* on plant species or groups. buck = yellow buckeye, cbirch = cherry birch, fern = ferns, fmag = fraser magnolia, forb = other herbaceous plants, hemlock = eastern hemlock, nroak = northern red oak, rhodo = rhododendron spp., sour = sourwood, stmap = striped maple, sumap = sugar maple, tulip = tulip poplar, witch = witch hazel, and OTHER = all other species < 5 expected observations ( $G_{adj} = 40.1$ ,  $df = 14$ ,  $p < 0.001$ ).

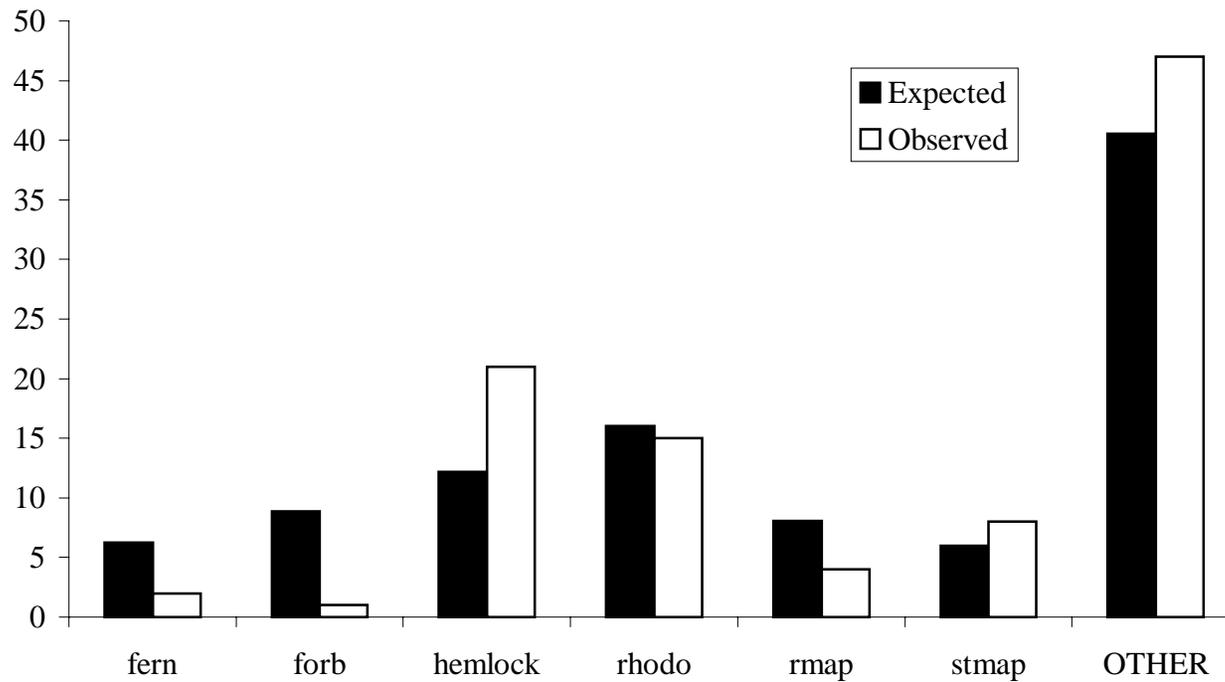


Figure 6. Observed and expected foraging frequencies (number of observations) for female *D. caerulescens* on plant species or groups. fern = ferns, forb = other herbaceous plants, hemlock = eastern hemlock, rhodo = rhododendron spp., rmap = red maple, stmap = striped maple, and OTHER = all other species < 5 expected observations ( $G_{adj} = 24.7$ ,  $df = 6$ ,  $p < 0.001$ ).

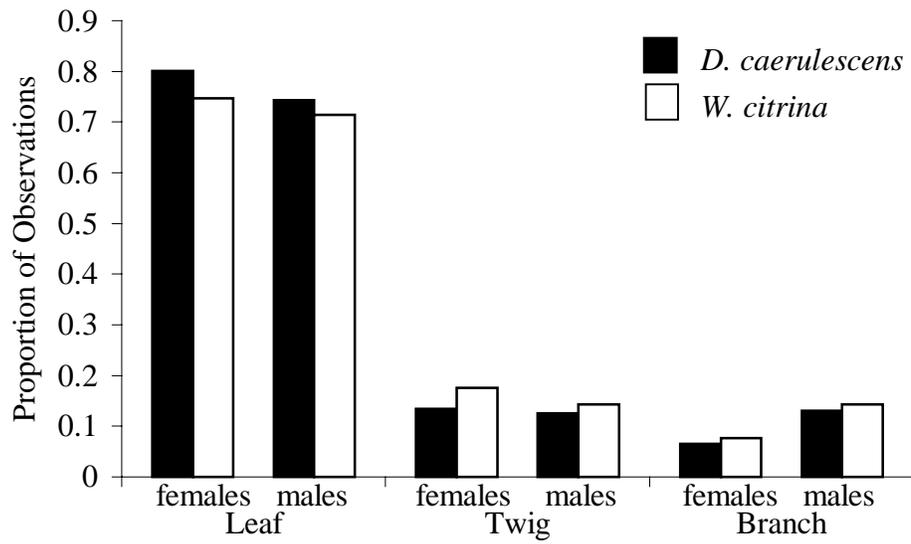


Figure 7. Proportion of foraging substrates used in both habitats by *D. caerulescens* (dark bars) females (n = 231) and males (n = 199) and *W. citrina* (light bars) females (n = 91) and males (n = 77).

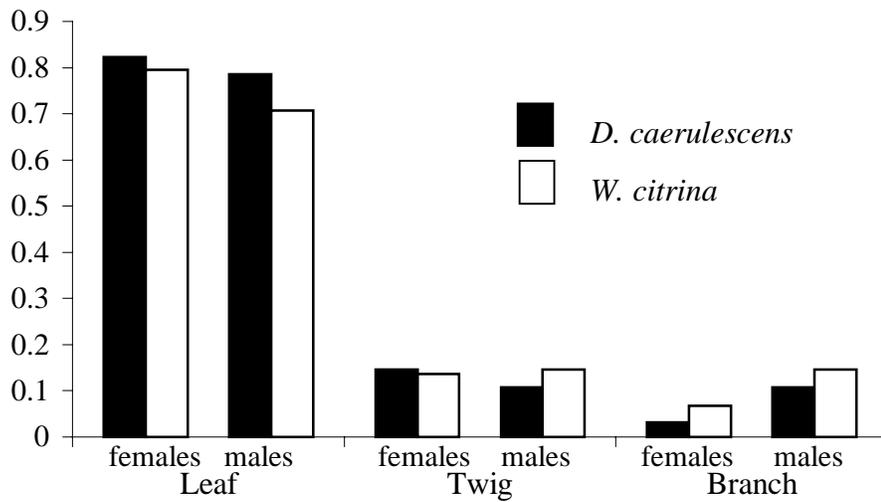


Figure 8. Proportion of foraging substrates used in acidic cove hardwood by *D. caerulescens* (dark bars) females (n = 96) and males (n = 84) and *W. citrina* (light bars) females (n = 44) and males (n = 41).

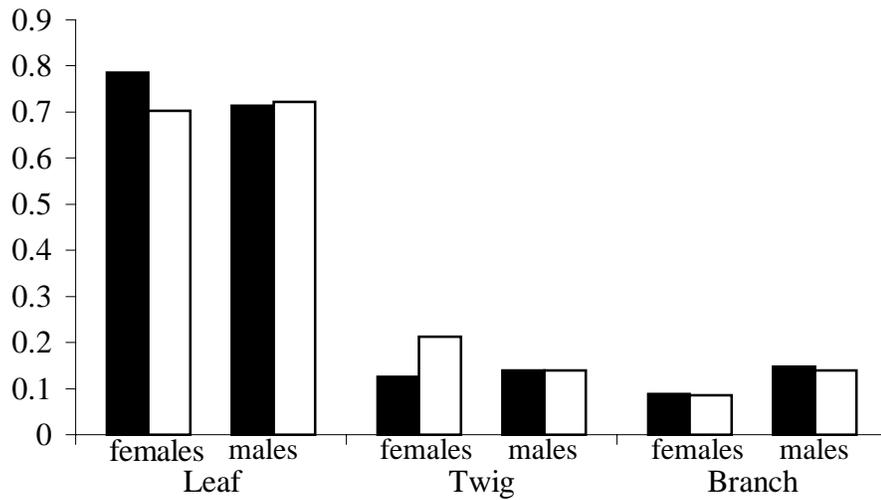


Figure 9. Proportion of foraging substrates used in rich cove hardwood by *D. caerulescens* (dark bars) females (n = 135) and males (n = 115) and *W. citrina* (light bars) females (n = 47) and males (n = 36).

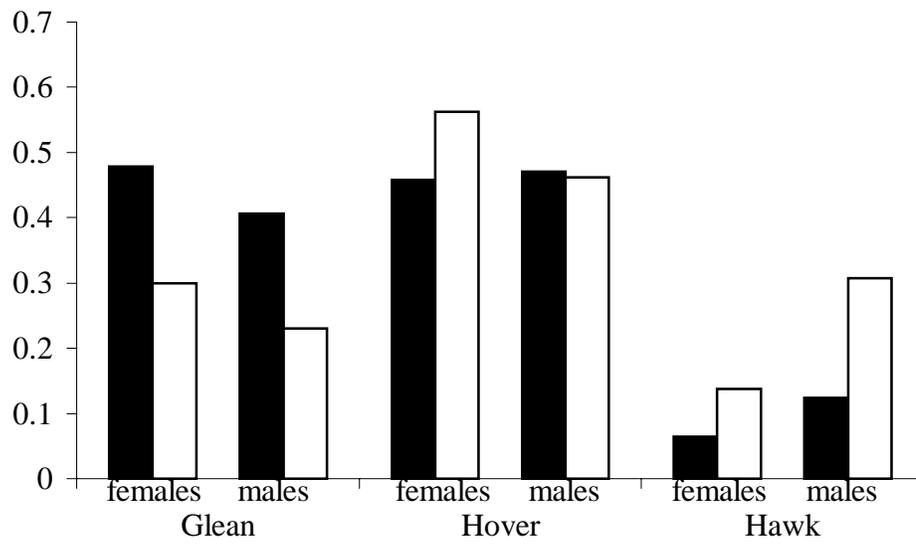


Figure 10. Proportion of total foraging maneuvers observed in both habitats combined by black-throated blue warbler (dark bars) females (n = 249) and males (n = 226) and hooded warbler (light bars) females (n = 109) and males (n = 104).

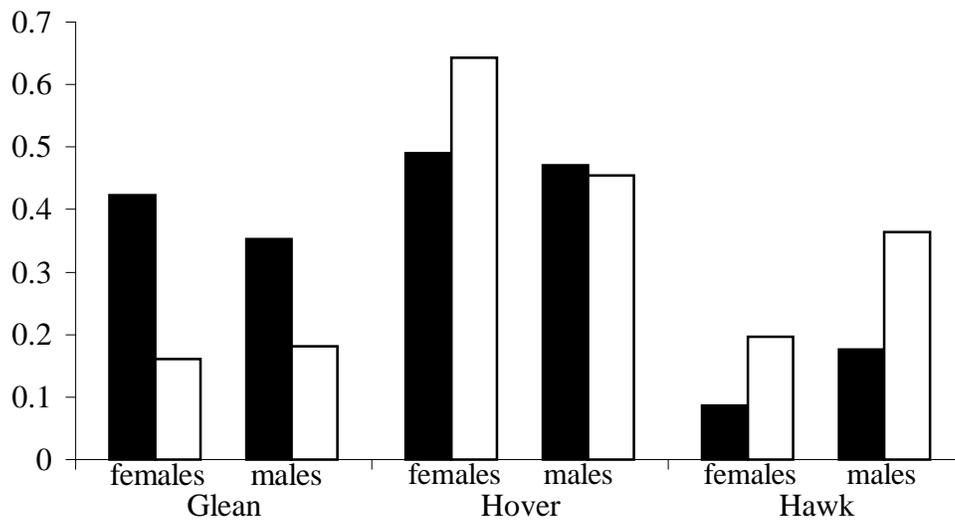


Figure 11. Proportion of total foraging maneuvers observed in acidic cove hardwood by black-throated blue warbler (dark bars) females (n = 104) and males (n = 102) and hooded warbler (light bars) females (n = 56) and males (n = 55).

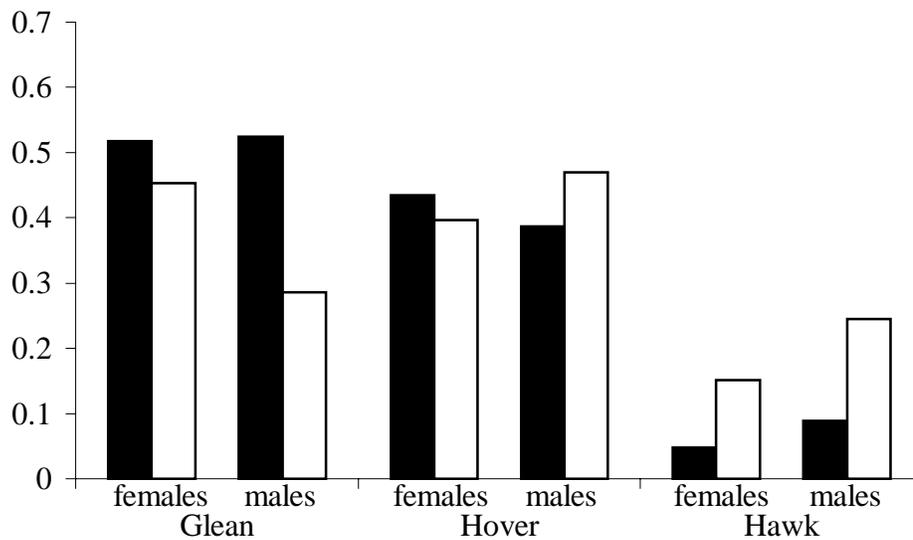


Figure 12. Proportion of foraging maneuvers observed in mixed mesic hardwood by black-throated blue warbler (dark bars) females (n = 145) and males (n = 124) and hooded warbler (light bars) females (n = 53) and males (n = 49).

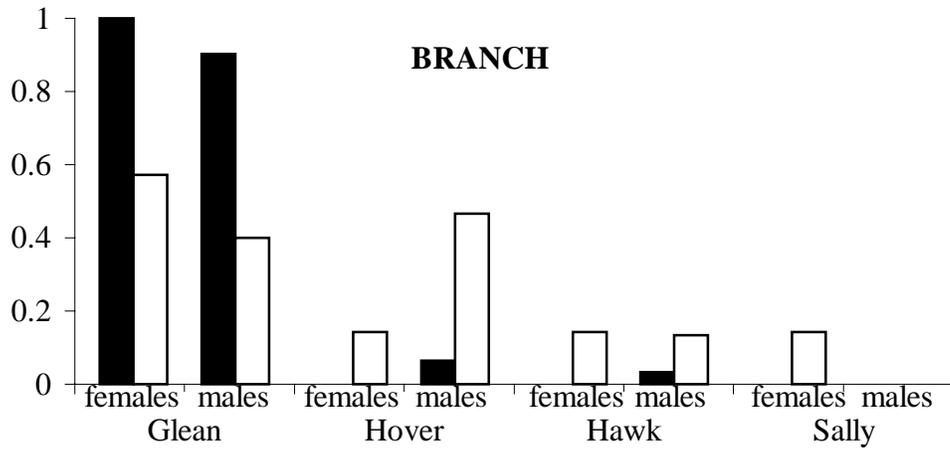


Figure 13. Proportion of maneuvers directed toward branches across all habitats for black-throated blue warbler (dark bars) females (n = 18) and males (n = 31) and hooded warbler (light bars) females (n = 7) and males (n = 15).

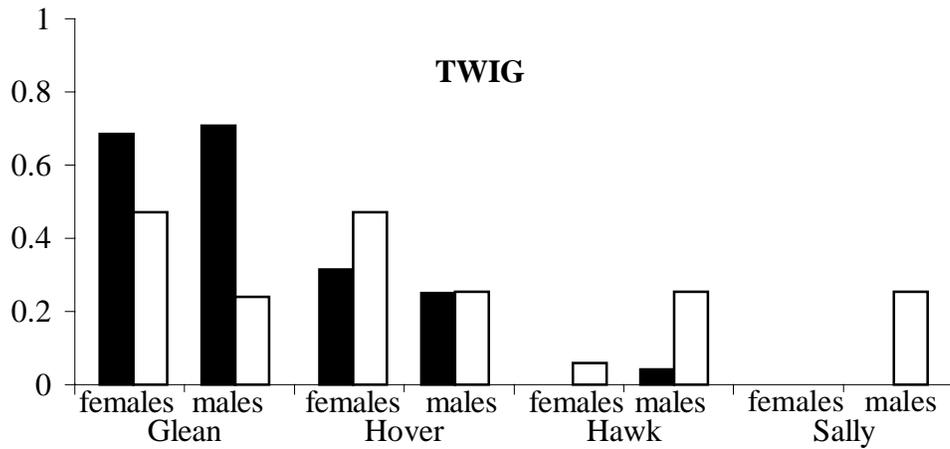


Figure 14. Proportion of maneuvers directed toward twigs across all habitats for black-throated blue warbler (dark bars) females (n = 35) and males (n = 24) and hooded warbler (light bars) females (n = 17) and males (n = 71).

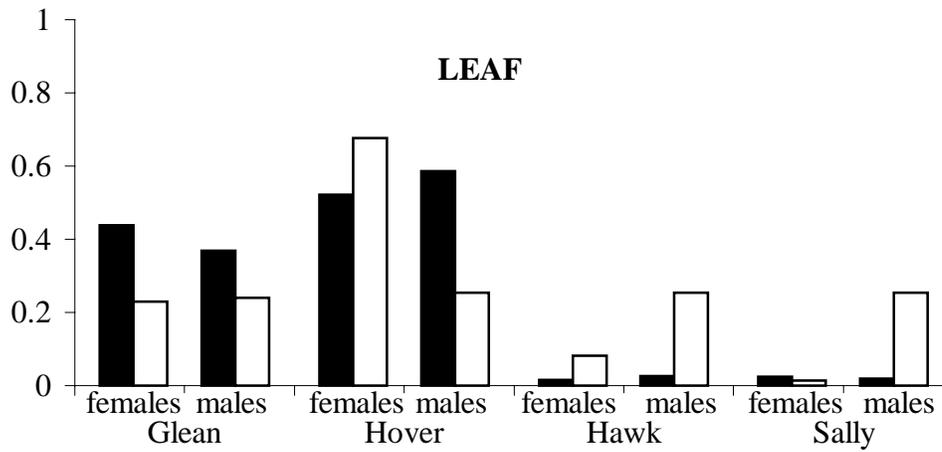


Figure 15. Proportion of maneuvers directed toward leaves across all habitats for black-throated blue warbler (dark bars) females (n = 201) and males (n = 157) and hooded warbler (light bars) females (n = 74) and males (n = 71).

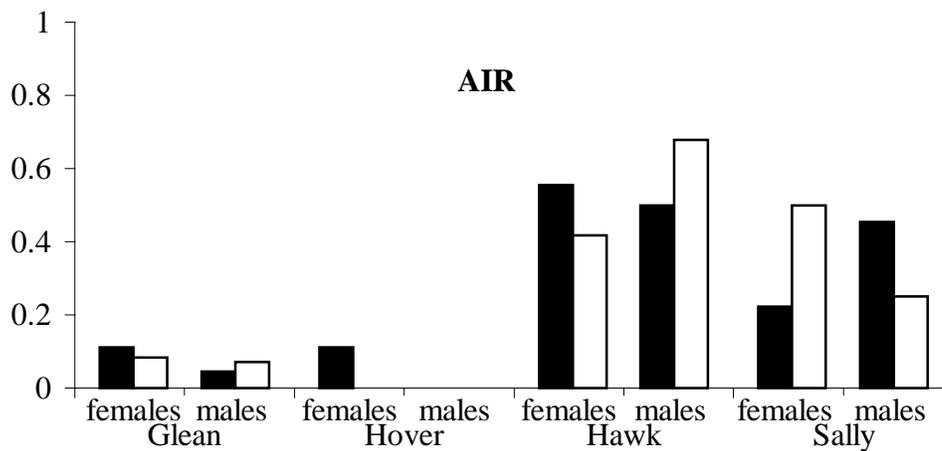


Figure 16. Proportion of maneuvers directed toward leaves across all habitats for black-throated blue warbler (dark bars) females (n = 9) and males (n = 22) and hooded warbler (light bars) females (n = 12) and males (n = 28).

## **Chapter 2: Nesting Ecology of Black-throated Blue Warbler (*Dendroica caerulescens*) and Hooded Warbler (*Wilsonia citrina*) in the southern Appalachians**

### **Introduction**

Much concern has been given to Neotropical-Nearctic migrants over the past thirty years due to regional and local declines in populations of many species (Keast and Morton 1980; Hagan III and Johnston 1989; Askins et al. 1990). Debates continue over the causes of declines and the relative contribution of recruitment and survival on the breeding grounds, survival during migration, and survival on the “wintering” grounds. Population dynamics of neotropical-nearctic migrants can be complicated by source-sink dynamics that vary over space and time (Brawn and Robinson 1996). Source *and* sink populations can be valuable to a species conservation but source populations are needed for persistence (Pulliam 1988). Data on nest survival can support or refute hypotheses about the relative contribution of nest survival to declines in populations. Understanding the factors associated with nesting success are important to determining habitat quality. Nevertheless, accurate survival estimates for the entire life cycle are still necessary to identify causes of population change (Sherry and Holmes 1995, 1996).

Although causality is not certain, analyses of Breeding Bird Survey (BBS) data suggest Black-throated Blue Warblers (*Dendroica caerulescens*) have experienced declines on their breeding grounds in the southern Appalachians (Hunter et al. 1999). The southern Appalachians are experiencing economic development and the roads where BBS routes are located may be biasing estimates of decline (Hunter et al. 1999). Development is highly correlated with roads and there are few BBS routes in this region.

In addition, wintering grounds are restricted to the Caribbean, particularly the Greater Antilles (Holmes 1994). This region is also undergoing extensive economic development (Lugo 1994). For these reasons, *D. caerulescens* is an Audubon Watchlist species and a conservation priority of Partners in Flight for the Blue Ridge Province, which contains 10% of the continental breeding population (Hunter et al. 1999). The southern Appalachians have been hypothesized as the center of highest quality habitat and, consequently, a source population of *D. caerulescens* (Graves 1997). High nest survival in this region will likely point to causes of regional declines other than breeding habitat destruction.

Predation is the number one cause of nest failure in many species that build cup nests (Martin 1988a, 1988b, 1992). Vegetation features around the nest can influence the probability of predation and are important in habitat selection (Martin 1992). Nest site selection seems to be less plastic than foraging in many birds. Thus, management for nesting sites may be more critical than foraging substrates for management (Steele 1993; Matsuoka et al. 1997). However, although the relative importance of one factor may be greater in one locale, both foraging and nesting resources are important to productivity and their relative importance over space and time may vary. Understanding how these factors relate to survival and productivity are essential for effective management and conservation planning.

Competition for nest sites may increase predation due to spatial autocorrelation of depredation events (Martin 1996; Schmidt and Whelan 1998). Two hypotheses associated with this idea are generally noted: 1) predators respond to the increase in resource (nests with eggs) numerically and 2) predators respond to the increase

behaviorally by ‘shifting’ their search image (Martin and Martin 2001). Before testing these hypotheses for any species, it is important to document the characteristic nest sites and nesting success of coexisting species so that research efforts can be focused and efficient.

*D. caerulescens* has been studied intensively for over 30 years in the Hubbard Brook Experimental Forest, New Hampshire (Holway 1991; Holmes et al. 1992, 1996; Steele 1992; Goodbred and Holmes 1996) and to a lesser extent in various locales of the winter range (Holmes et al. 1989; Wunderle 1995; Sherry and Holmes 1996). Empirical evidence suggests that these populations are limited by multiple factors such as nest survival, juvenile survival, and adult survival but non-breeding survival may be most important (Sherry and Holmes 1996). However, relatively few nest survival studies have been conducted in other parts of its range (Guzy 1995; Williams 1996). The unique situation of high densities of *D. caerulescens* and coexistence with *W. citrina* in the southern Appalachians can shed light on habitat specific nest survival.

Studies of *W. citrina* have also been studied in breeding areas (Howlett and Stutchbury 1996, 1997; Nagy and Smith 1997; Bisson and Stutchbury 2000) and wintering areas (Lynch et al. 1985; Morton et al. 1987). Demographics of this species have been less well studied but nesting success is high in managed forests (Howlett and Stutchbury 1996; Nagy and Smith 1997; Bisson and Stutchbury 2000). *W. citrina* is considered a species of management concern in some areas but is not an Audubon Watchlist species (Muehler 1998) and is of low priority for conservation in the southern Appalachians (Hunter et al. 1999).

*D. caerulescens* and *W. citrina* breed in mature or secondary forests that contain a moderate to dense low shrub and/or herb component in which they place their nests (Holway 1991; Simpson Jr. 1992; Steele 1992; Evans Odgen and Stutchbury 1994; Holmes 1994; Guzy 1995; Dunn and Garrett 1997). Recent evidence suggests that *W. citrina* abundance is positively correlated with disturbance (edges, roads, and trails) and the amount of mature forests in the landscape (Lichstein 2000). Similar correlations with nest-site selection have been found elsewhere (Bisson and Stutchbury 2000). This implies that disturbance within a forest matrix is the preferred habitat of *W. citrina*. Abundance of *D. caerulescens* seems to be more associated with contiguous forest (Lichstein 2000). Two of the mesic habitats utilized by *D. caerulescens* and *W. citrina* in the southern Appalachians are acidic cove hardwood and mixed mesic hardwood forests.

## **Objectives**

The objectives of this study are to determine what, if any, microhabitat differences there are between nest success and nest site selection of *D. caerulescens* and *W. citrina*.

My null hypotheses are

- 1) There is no difference in nest success between mixed mesic hardwood and cove hardwood forests for each species
- 2) There is no difference in nest success between the two species within each plant association
- 3) There is no difference in nest success between *D. caerulescens* and *W. citrina* in different nest substrates

- 4) The nest site characteristics of each species do not differ within each vegetation association.

## **Methods**

### *Study Area*

Nest searching was primarily conducted in mesic habitats for 1998-2000. The final year, 2000, nest-searching was limited to three main watersheds and 1<sup>st</sup> to 3<sup>rd</sup> order streams: Little Prong Creek (White Oak Flats), Roaring Fork (Lemon Gap), and Cold Springs Creek (Cold Springs) in the Pisgah National Forest, French Broad District (Thesis Introduction: Figure 1). Plant associations of interest were mature (> 60 yr.) cove forests of two types, acidic cove hardwood and rich cove hardwood, and both were present in each site. Cove forests without the characteristic predominance of a diverse herb layer typically found in rich cove hardwood were included in this group and, hereafter, considered collectively as mixed mesic hardwood. A detailed description of habitats can be found in the Thesis Introduction. Acidic cove hardwood will be referred to as simply cove hardwood. In 1998, nests were sampled from ten different locations: Little Creek, Roberts Gap, Cold Springs Creek, FR3750, Hurricane Ridge, Rube Rock, Hurricane Gap, Scraggy Ridge, Paint Creek, and White Oak Flats. In 1999, an additional site, Lemon Gap, was added (Thesis Introduction: Figure 1).

### *Nest Searching*

Nest searching began in early May and included visually searching the shrubs and herbs and observing adult birds for nesting behaviors (Martin and Geupel 1993). Nests were flagged to within 10m and flagged to the nearest trail or road. Nests were monitored every 3-4 days, number of eggs or nestlings recorded, and disturbance was

minimized. Location of nests were recorded with a Global Positioning System (GPS) and incorporated into a geographic information system (GIS). Relative abundance of each bird species in each habitat was indexed using established point counts (Lichstein 2000). Point counts were conducted four times during the field season on all three sites (22 cove hardwood and 19 mixed mesic hardwood). Maximum detection was used to determine relative abundance. In 2000, searching effort was equalized among plant associations (2 person-days/plant association/visit). This helped to determine if nest encounter rates were different between habitat types.

### *Habitat Sampling*

Nest height, plant (substrate) height, and plant species were measured to the nearest centimeter. Concealment from above, below, and in each cardinal direction 2m, 5m, and 10m from the nest was estimated using an ordinal scale (1-4, complete visibility to no visibility). Disturbance caused by observers was also estimated using an ordinal scale (1-4, no disturbance to completely disturbed). Completely disturbed nests were those in which there was a visible trail to the nest or visible damage to the vegetation. Percent cover of nest substrate species and similar substrates was also estimated within 10m and 50m of the nest. Percent cover was defined as the amount of ground shaded by the foliage of the plants of interest. Vegetation was sampled at the nests using a protocol developed in the Great Smoky Mountains National Park and Pisgah National Forest (Point Count Veg) (Simons and Shriner 1998; Simons et al. 1999). When a nest was no longer active or within 50m of a currently active nest, five 10 m radius vegetation plots were sampled. One was centered upon the nest and the remaining four were 35 m from the center plot in the four cardinal directions. Within the plots, three data sets were

recorded for Point Count Veg: i) a tree sample by species using a 10 factor prism ii) coverage and height estimates for five vertical layers of foliage (canopy, subcanopy, tall shrub, low shrub, and herbaceous) and iii) primary species composition of each layer. Small-scale disturbances within the forests such as streams, treefalls, and roads were considered disturbances and recorded as such if within the 10m-radius vegetation sampling plot. Plant associations were classified qualitatively as cove hardwood, mixed mesic hardwood, tulip poplar, xeric oak, pine-oak, pine, etc. (Simons and Shriner 1998). In addition, the vegetation sampling protocol for floristic composition used for a foraging study (Foraging Veg; Chapter 1) was conducted at each plot.

### *Analysis*

Nest survival was calculated using the Mayfield method (Mayfield 1961; Mayfield 1975) and comparisons were made using z-tests (Mayfield 1975; Johnson 1979) and  $\chi^2$  tests with the program CONTRAST (Sauer and Williams 1989). Three *W. citrina* and four *D. caerulescens* nests were parasitized by brown-headed cowbird (*Molothrus ater*) parasitized at Lemon Gap. Therefore, the only nest that failed due to parasitism was excluded from analysis along with three abandoned nests of *D. caerulescens*. Thus estimated nest survival represents predation effects only. With such a large sample size, this method has little effect on the results. Comparisons of nest success were made between plant associations, nest substrates, sample sites, and across years. In addition, I tested within season differences in nest success by designating nests initiated (clutch completed) in May and after May 30. Nests that were not found during laying were back calculated to determine initiation date. Nests that failed during laying were forward calculated to initiation date based on average clutch size. Most of the nests initiated after

May 30 are nesting attempts after a failed first attempt or possibly a successful first attempt (double brooding).

I performed a cluster analysis using PC-ORD (McCune and Mefford 1999) on a matrix of pseudospecies (cover of each species in each height range) from Foraging Veg to verify qualitative vegetation classifications in order to justify the habitat comparisons. The method is a hierarchical and divisive using Euclidean distances and Ward's group linkage method (McCune and Mefford 1999). In addition, detrended correspondence analysis (DCA) was used to detect gradients in vegetation composition and structure that could affect nest site selection or nesting success and to further validate vegetation classifications. I employed the CATMOD and LOGISTIC procedures in SAS/STAT software to investigate nest site selection (Point Count Veg) and concealment effects on nest success (SAS 1999). Nest site selection was determined by creating models by stepwise selection with 16 structural variables (percent cover, upper and lower height limits of vegetation layers, and disturbance) from Point Count Veg (Appendix A). Composition as related to nest site selection was thought to be irrelevant because both bird species nested in both habitats. Entry into the model was limited to  $p < 0.3$  and retention was limited to  $p < 0.10$ . Fit of the model was assessed with Hosmer and Lemeshow Goodness-of-Fit Test. Nest fate and concealment estimates were modeled using categorical logistic regression. T-tests were used to test for differences in nest and substrate height and mean detections per point count. An alpha level  $< 0.10$  was considered biologically significant for all statistical tests.

## Results

Daily survival rates (DSR) and cumulative nest survival rates (NSR) of *W. citrina* and *D. caerulescens* are summarized by year in Tables 1 and 2. Nest survival across years was not significantly different (Figures 1 and 2) so nests were pooled across years. Cluster analysis of vegetation physiognomy and composition at the nest verified qualitative plant association classifications (Figure 3). DCA produced an ordination of the structure and composition of the entire vegetation profile that agreed with the cluster analysis (Figure 4). The axes are based on vegetation structure and composition and show two groupings of points. Each grouping represents major understory composition: herbaceous and rhododendron (Figures 4 and 5). Mesic oak was included in the mixed mesic hardwood category based on this analysis.

### *Habitats*

*D. caerulescens* and *W. citrina* showed no pattern of differential nest survival across plant associations ( $p > 0.10$ ; Figure 6). Analysis of nests found in 2000, when search effort and habitats were more controlled, showed a contrasting trend but differences were non-significant ( $p > 0.10$ ; Figure 7). Fewer *D. caerulescens* nests were found in cove hardwoods although relative abundances were similar between habitats (Chapter 1).

### *Nest Substrates*

Nest substrate use is summarized in Table 3. Both species readily utilized rhododendron whereas *W. citrina* tended to avoid herbs (one nest in 3 years). Comparing nest success between nests in rhododendron, herbs, and deciduous shrubs/saplings, *D. caerulescens* had significantly greater success when nesting in herbs than in deciduous shrubs and saplings ( $z = 1.89$ ,  $df = 1$ ,  $p < 0.05$ ; Figure 8). *W. citrina* nest success was not

significantly different between nesting substrates but was significantly higher in deciduous shrubs and saplings than *D. caerulescens* ( $z = 1.67$ ,  $df = 1$ ,  $p < 0.05$ ). These trends are evident in 2000 data as well (Figure 9). For all years combined, an additional comparison of the substrate *Rubus* spp. was conducted. Even with low sample size and thus low power, *D. caerulescens* experienced significantly lower nest survival in blackberry than *W. citrina* ( $z = 2.48$ ,  $df = 1$ ,  $p < 0.01$ ; Figure 10). *W. citrina* experienced significantly higher nesting success in rubus than any other nesting substrate ( $\chi^2 = 9.1$ ,  $df = 2$ ,  $p < 0.05$ ).

#### *Stage-specific Survival*

Egg and nestling period survival did not differ among substrates or habitats in any year. However, significantly different nest survival was detected between egg and nestling survival periods at White Oak Flats ( $z = 1.5$ ,  $df = 1$ ,  $p < 0.10$ ; Figure 11). Lemon Gap had an opposite trend but differences were not significant ( $z = 1.23$ ,  $df = 1$ ,  $p > 0.10$ ; Figure 12).

The peak of *D. caerulescens* nest initiation, regardless of when nests were found, was May 18-24 for all years combined (Figures 13). *W. citrina* may initiate nests earlier but sample size is too low for comparison (Figure 14). Nests initiated in May had lower survival than nests initiated after May (Figure 15) for *D. caerulescens* ( $z = 1.95$ ,  $df = 1$ ,  $p < 0.05$ ) and *W. citrina* ( $z = 2.68$ ,  $df = 1$ ,  $p < 0.005$ ). Figure 16 shows that nests initiated on May 20 or before had significantly higher survival than the remaining May nests for *D. caerulescens* ( $z = 1.66$ ,  $df = 1$ ,  $p < 0.05$ ). A similar trend was apparent for *W. citrina* although not significant ( $z = 0.88$ ,  $df = 1$ ,  $p > 0.15$ ).

### *Nest Site Selection and Fate*

Nest site selection was positively correlated with low shrub cover and disturbance (i.e. roads, trails, streams and canopy gaps) for *D. caerulescens* ( $\chi^2 = 11.95$ ,  $df = 1$ ,  $p < 0.001$  and  $\chi^2 = 7.15$ ,  $df = 1$ ,  $p < 0.01$ ) and *W. citrina* ( $\chi^2 = 16.6$ ,  $df = 1$ ,  $p < 0.001$  and  $\chi^2 = 6.34$ ,  $df = 1$ ,  $p < 0.05$ ). In addition to these significant variables, *D. caerulescens* nest sites were positively correlated with herb layer height and negatively correlated with low shrub layer height ( $\chi^2 = 6.13$ ,  $df = 1$ ,  $p < 0.01$  and  $\chi^2 = 3.92$ ,  $df = 1$ ,  $p < 0.05$ ). In contrast, *W. citrina* nests were additionally negatively correlated with subcanopy cover and herb cover ( $\chi^2 = 5.61$ ,  $df = 1$ ,  $p < 0.05$  and  $\chi^2 = 6.18$ ,  $df = 1$ ,  $p < 0.05$ ) and positively correlated with height of the lowest level of the canopy ( $\chi^2 = 3.35$ ,  $df = 1$ ,  $p < 0.10$ ; Tables 4 and 5). Hosmer and Lemeshow Goodness-of-Fit Tests suggest models were appropriate for *D. caerulescens* ( $\chi^2 = 6.52$ ,  $df = 8$ ,  $p > 0.59$ ) and *W. citrina* ( $\chi^2 = 6.32$ ,  $df = 8$ ,  $p > 0.89$ ). Habitat specific models distinguished several structural parameters as being important only in one habitat. Disturbance was not important for nest site selection in cove hardwood for either species.

Out of three concealment estimates, only concealment 1 m above the nest was positively correlated with nesting success for *W. citrina* ( $\chi^2 = 9.36$ ,  $p < 0.01$ ) and *D. caerulescens* ( $\chi^2 = 11.06$ ,  $p < 0.001$ ). Nest fate was not correlated with vegetation gradients of detrended correspondence analysis (Cumulative  $R^2 < 0.01$ ). Nest height and nest substrate height (Table 6) were significantly different between both species ( $t = 6.89$ ,  $df = 122$ ,  $p < 0.001$  and  $t = 3.86$ ,  $df = 203$ ,  $p < 0.01$ , respectively). Even within Rhododendron, average nest heights were significantly different between *D. caerulescens* and *W. citrina* ( $t = -3.4$ ,  $df = 67.4$ ,  $p < 0.005$  and  $t = -2.3$ ,  $df = 95$ ,  $p < 0.05$ ).

## Discussion

### *Nest Habitat and Substrate*

Coves in the southern Appalachians greatly affect the spatial distribution of nesting substrates important for shrub-nesting passerines such as *W. citrina* and *D. caerulescens* (Ford et al. 2000). Habitat alone does not explain differences in nest survival between *D. caerulescens* and *W. citrina* in the southern Appalachians as there were no differences in nest success between habitats or along vegetation gradients. However, nest survival was affected by the species of plant chosen for nest placement, which may indicate microhabitat separation of these two species. Blackberry (*Rubus* spp.) occurs in areas within the forest where small disturbances such as treefalls and roads occur (pers. observation). This could benefit *W. citrina* but possibly act as an “ecological trap” for *D. caerulescens* (Gates and Gysel 1978; Rudnický and Hunter 1993). These small forest openings may be high quality habitat for *W. citrina* (Bisson and Stutchbury 2000). This makes sense in conjunction with the nest site selection models, which differ in parameter direction and significance. Subcanopy cover and low canopies block sunlight that facilitates dense shrub layers and would also be low and high in small disturbances, respectively.

*D. caerulescens* nest sites are also regularly in areas of small disturbances presumably for the same reasons as *W. citrina*. However, the statistically significant difference in nest height between these species may represent stereotypic nest building behavior and reduce the amount of spatial overlap of nest site selection. The avoidance of nesting in taller low shrubs by *D. caerulescens* supports this and agrees with nest site cover vs.

random site cover at 2-3m in this species northern range (Steele 1993). Small differences in the size of or time since disturbance can have large effects on the height and density of shrubs taking advantage of the greater solar irradiation.

Rich herb layers in mixed mesic hardwood habitats (Figure 17) containing species such as blue cohosh (*Caulophyllum thalictroides*), black cohosh (*Cimicifuga racemosa*), and false goatsbeard (*Astilbe biternata*) may provide a nesting refuge from possible predator mediated competition. Herbaceous communities are less limited by light than by soil fertility (Gilliam and Turrill 1993).

Cove hardwood understories are dominated by rosebay (*Rhododendron maximum*) and this species is the dominant nest substrate used by both *D. caerulescens* and *W. citrina* in this habitat. These understories sometimes form continuous thickets that are difficult to search for nests (Figure 18). Habitat specific nest site selection suggests that disturbance may be necessary in some habitats more than others. Blackberry is shade intolerant and quality of this substrate for nesting may depend on small disturbances in mixed mesic hardwood forests (Boring and Swank 1984). Rosebay is a shade tolerant species that is only light limited when competing with dense stands of regenerating or mature hemlock and thus does not depend on gaps for proficient growth. Disturbance may be important in these situations, especially old growth acidic cove forests with many hemlocks in the canopy.

#### *Stage Specific Survival*

Differential nest stage survivorship was not prevalent in this system although a site difference and a within season temporal difference were detected. It is interesting that both White Oak Flats and Lemon Gap had similar cumulative survivorship but different

egg and nestling survivorships of opposite trends (Figures 11 and 12). This could possibly be due to differing predator communities or possibly natural variation in predator pressure (Martin 1988b). Predators that specifically cue in on behavior may be more likely to find a nest with nestlings due to increased parental activity at the nest (Holway 1991). However, the lack of DSR heterogeneity for any other comparison suggests that this result could be spurious.

The difference in survival between early and late nests may indicate density dependent effects. Conflicting results have been presented for seasonal differences in *D. caerulescens* nest success in different regions (Holmes et al. 1992; Guzy 1995), which is probably due to methods of comparison. However, peak density of nests may result in higher overall predation rates due to autocorrelation or opportunistic predator switching (Martin 1988b; Martin and Martin 2001). My results suggest that this may be the case due to high survival rates of nests initiated outside of the peak in nest initiation date and low survivorship of nests initiated from May 21 to May 30. Although separating nests by initiation date causes overlap in the time active, it is still a reasonable comparison due to the trend apparent after further partitioning (Figure 16). It is generally thought that males arriving earlier have better territories and hence, better nesting success (Holmes et al. 1996). However, the high density of initiated shrub nests in late May relative to June might increase the probability of nest predation due to predator switching or spatial autocorrelation (Martin 1988b; Martin and Martin 2001).

#### *Selection and Fate*

*W. citrina* and *D. caerulescens* are similar in nest site selection in that both require a significant cover of understory plants in which to place their nests (Anderson and Shugart

1974; Holway 1991; Evans Odgen and Stutchbury 1994; Holmes 1994; Howlett and Stutchbury 1996). However, the height of the understory (i.e. shrub layer) can significantly affect whether or not they place their nests in a particular patch, furthering the potential ecological separation that is evident in herbaceous understories. This line of reasoning is supported by the significant difference in nest and nest substrate height (Table 4). Although a *W. citrina* nest was found in an herb, the vegetation was atypical at the nest site (pers. observation). There were taller saplings interspersed where a disturbance had created a canopy gap. Whether or not just a difference in nest height preference could ameliorate apparent competition or higher predation rates is uncertain. However, in several instances nests of both species were found less than 50m apart. In one cove hardwood case, two nests were found less than 5m apart and both fledged young. These birds were observed on many occasions foraging without aggressive interactions. Out of two years of foraging observations and nest searching, no aggressive interactions between *W. citrina* and *D. caerulescens* were observed and both species foraged together in many instances. Thus, exploitative competition is the only possible competition between these two species, if any, and can only be investigated by carefully designed experiments (Wiens 1989; Martin and Martin 2001).

Many field studies of shrub nesting passerines have found no significant effects of cover on nest success (Holway 1991; Howlett and Stutchbury 1996; Hoover and Brittingham 1998). However, large differences in cover above nests compared to non-use sites have been shown (Holway 1991; Howlett and Stutchbury 1996) although experimental removal of cover has shown conflicting results (Steele 1993; Howlett and Stutchbury 1996). Predation pressure from a diverse predator assemblage and stochastic

depredation events are usually invoked as the cause of the lack of cover effects. However, I was able to detect an effect of cover above the nest on the fate of the nest. I was not able to document cause of depredation events but avian nest predators such as American crows (*Corvus americanus*) and blue jays (*Cyanocitta cristata*) may be the dominant predator on these two species' nests in this region. However, the predator assemblage is diverse and, in addition to corvids, consists of black rat snakes (*Elaphe guttata*), red squirrels (*Tamiasciurus hudsonicus*), raccoon (*Procyon lotor*), black bear, (*Ursus americanus*), eastern chipmunks (*Tamias striatus*), bobcat (*Lynx rufus*), weasels (Mustelidae), and mice (Rodentia). Documentation of nest predators is needed to fully evaluate the relative contribution of predator species on depredation events in each habitat. Further, experiments relating this to experimental defoliation are also needed. Even if most nest predators are opportunistic and predation events stochastic, cover should influence this dynamic. It is also possible that the incubating female is weighing the tradeoffs associated with risk of predation to herself with that of her nest (Trivers 1974). If cover does not influence predation, nest site selection would not be evolutionarily advantageous.

### *Implications*

The relative importance of nesting and foraging resources is a focus of current research and nesting habitat is considered more limiting to tree and shrub nesting warblers (Steele 1993; Matsuoka et al. 1997). However, territory sizes have been shown to fluctuate with food availability (Cooper et al. 1990) and both of these important resources are necessary for successful reproduction. The relative importance of each resource may vary over space and time due to their abundances and factors that influence

their value (e.g. predator abundance or diversity, competition, etc.). The high nest success and similar foraging behavior of *D. caerulescens* and *W. citrina* in sympatric zones of the southern Appalachians suggests that these areas are rich in both nest substrates and arthropod prey. In particular, the diverse herb layer of rich cove hardwood forests are important for high *D. caerulescens* nest survival.

Due to the diversity of Neotropical-Nearctic migrants and the habitats they utilize, management must keep habitat at the forefront of planning. Supplementing specific habitat-based life history needs with artificial “band-aids” such as nest boxes, predator removal, and mass extermination of nest parasites ignores the ecological causes of population declines. Nesting substrate availability, abundance of predators and nest parasites can be influenced by low intensity management techniques (Marzluff et al. 2000).

Survival of Neotropical-Nearctic adults on breeding grounds is generally thought to be high (Donovan et al. 1995b) and low nest abandonment rates support this idea. Nest survival in the southern Appalachians seems to be within the range required for source populations if survival at other times are consistent with reported values (Donovan et al. 1995a; Guzy 1995). Nevertheless, survival of nestlings and adults once nestlings fledge and at other times throughout the annual cycle needs to be determined to better understand population trends (Sherry and Holmes 1996). High nest success may be indicative of high quality habitats. Populations below carrying capacity or in decline because of low survivorship during other stages in the life cycle may also experience high nest success. Future studies would benefit from long term studies with banded birds on permanent gridded plots in breeding and wintering habitats. These studies are generally

few and far between and funding agencies are reluctant to fund long term projects. Studies such as these would give invaluable insights into the spatial and temporal variation of the many factors affecting bird populations.

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Appendix A. Structural variable codes used in logistic models

1. C ..... % canopy cover
2. CLL ..... Lower level of canopy (m)
3. CUL ..... Upper level of canopy (m)
4. S ..... % subcanopy cover
5. SLL ..... Lower level of subcanopy
6. SUL ..... Upper level of subcanopy
7. T ..... % tall shrub layer cover (> 2m tall)
8. TLL ..... Lower level of tall shrub layer
9. TUL ..... Upper level of tall shrub layer
10. L ..... % low shrub layer cover
11. LLL ..... Lower level of low shrub layer (<2m)
12. LUL ..... Upper level of low shrub layer
13. H ..... % herb cover
14. HLL ..... Lower level of herb layer
15. HUL ..... Upper level of herb layer
16. Disturb\_ ..... Disturbance (roads, trails, treefalls, etc.)

Year	Active Nests	Nest Days	Failed	Successful	DSR	NSR	Eggs	Chicks	Fledglings	Fledglings/successful nest
1998	28	330.5	8	20	0.976	0.596	79	75	63	3.15
1999	37	410	16	21	0.961	0.433	81	69	63	3.00
2000	22	294	11	11	0.966	0.483	77	46	39	3.55
All Years	87	1034.5	35	52	0.966	0.485	237	190	165	3.17

Table 1. Yearly summary of nest data for Hooded Warbler (*Wilsonia citrina*). DSR is Mayfield daily survival rate. NSR is Mayfield cumulative (nest) survival rate.

Year	Active Nests	Nest Days	Failed	Successful	DSR	NSR	Eggs	Chicks	Fledglings	Fledglings/successful nest
1998	31	344	13	18	0.962	0.445	93	82	65	3.61
1999	57	678	34	23	0.954	0.374	155	93	80	3.48
2000	76	952.5	35	41	0.964	0.467	218	174	144	3.51
All Years	164	1974.5	82	82	0.96	0.429	466	349	289	3.52

Table 2. Yearly summary of nest data for Black-throated Blue Warbler (*Dendroica caerulescens*). DSR is Mayfield daily survival rate. NSR is Mayfield cumulative (nest) survival rate.

Substrate (n)	Mayfield DSR $\pm$ SE			Mayfield Cumulative Survival 95% CI
	Egg	Nestling	Total	
<i>D. caerulescens</i>				
Rhododendron (60)	0.9558 $\pm$ 0.0099	0.9658 $\pm$ 0.0112	0.9596 $\pm$ 0.0075	0.3027-0.5823
Deciduous Woody (46)*	0.9552 $\pm$ 0.0117	0.9412 $\pm$ 0.0172	0.9479 $\pm$ 0.0099	0.2085-0.5032
Rubus (15)*	0.9450 $\pm$ 0.0218	0.9322 $\pm$ 0.0327	0.9405 $\pm$ 0.0183	0.1200-0.6133
Herbs (48)	0.9686 $\pm$ 0.0093	0.9735 $\pm$ 0.0099	0.9707 $\pm$ 0.0068	0.3985-0.7177
<i>W. citrina</i>				
Rhododendron (40)	0.9705 $\pm$ 0.011	0.9516 $\pm$ 0.0157	0.9599 $\pm$ 0.0095	0.2775-0.6395
Deciduous Woody (35)*	0.9679 $\pm$ 0.0109	0.9729 $\pm$ 0.012	0.9693 $\pm$ 0.0081	0.3650-0.7351
Rubus (16)*	0.9936 $\pm$ 0.006	0.99813 $\pm$ 0.0131	0.9886 $\pm$ 0.0065	0.5939-1.0361

Table 3. Mayfield daily survival rate (DSR) and 95% CSR for *D. caerulescens* and *W. citrina* nests in different substrates for pooled years. \* indicates significant differences ( $p < 0.10$ ) in nest survival between species.

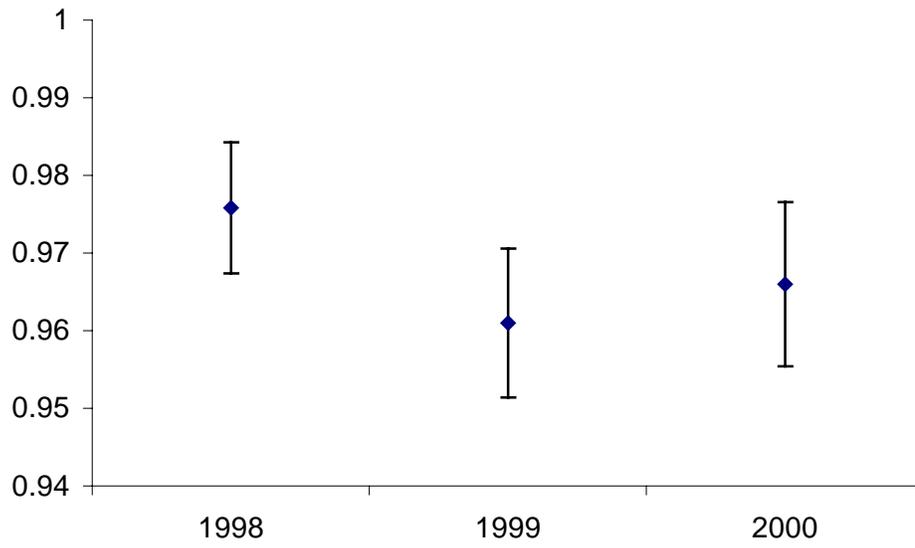


Figure 1. Mayfield daily survival rate of *W. citrina* across years for all nests.

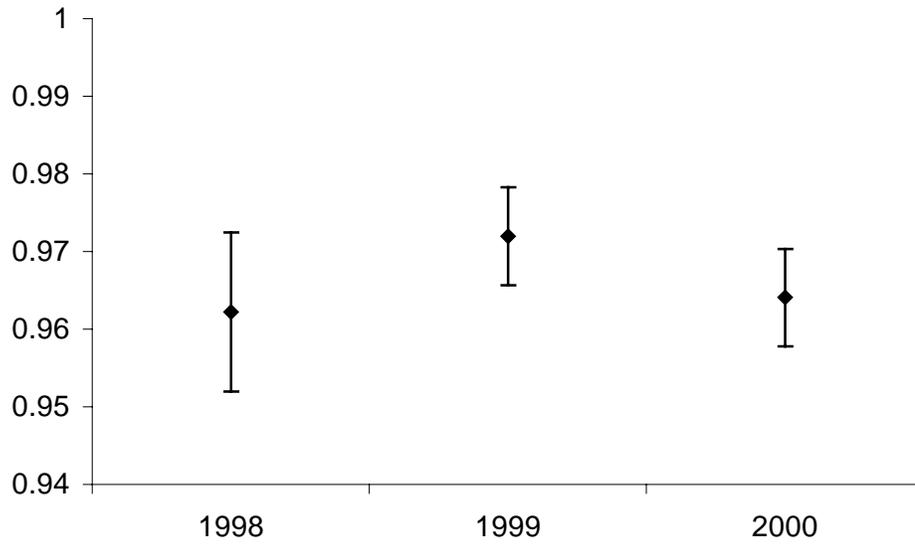


Figure 2. Mayfield daily survival rate of *D. caerulea* across years for all nests.

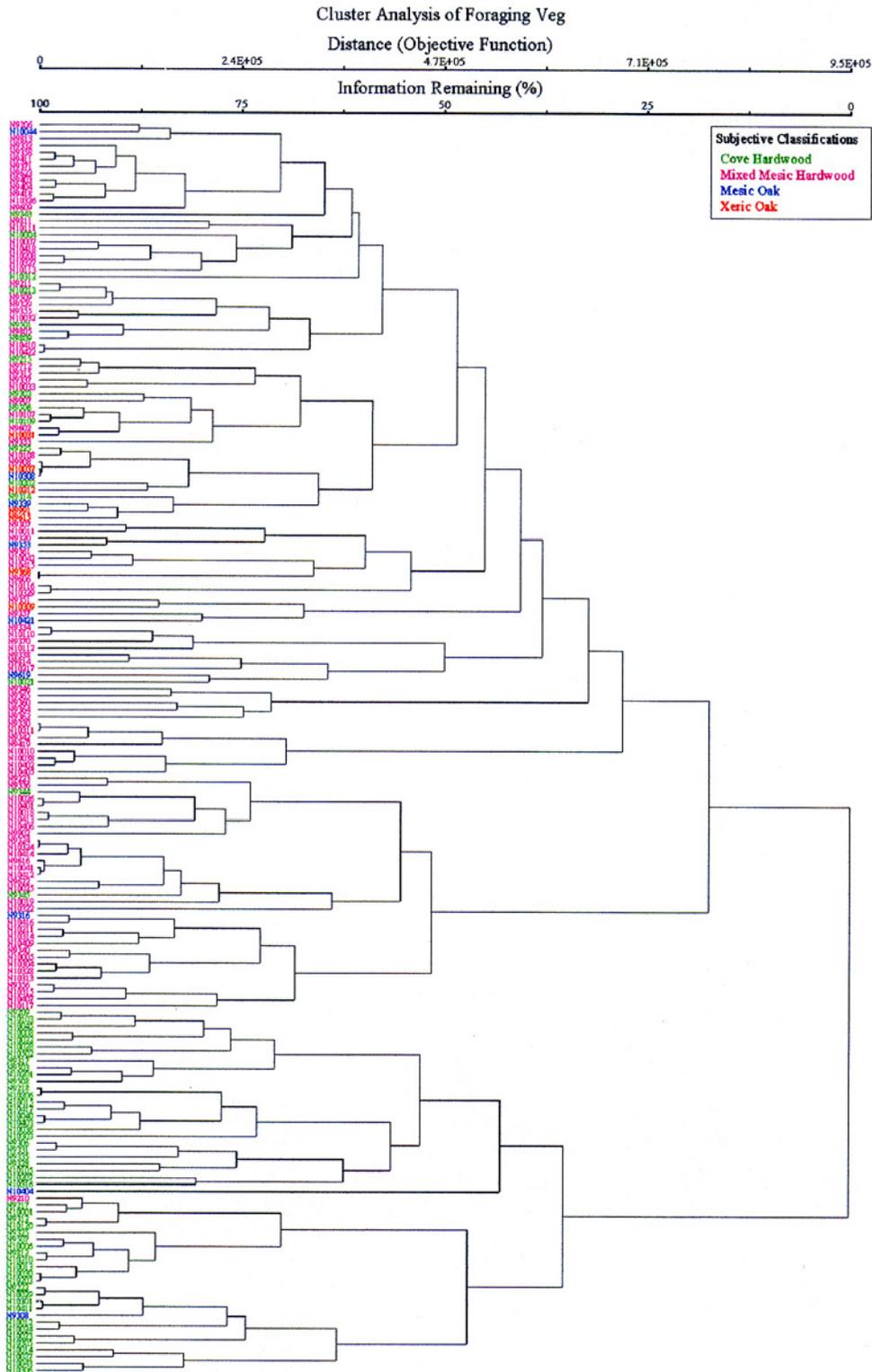


Figure 3. Cluster analysis dendrogram of floristic and structural vegetation data (Foraging Veg) collected for each nest. Qualitative classifications are color-coded and agree with cluster analysis. See text for details of hierarchical classification method.

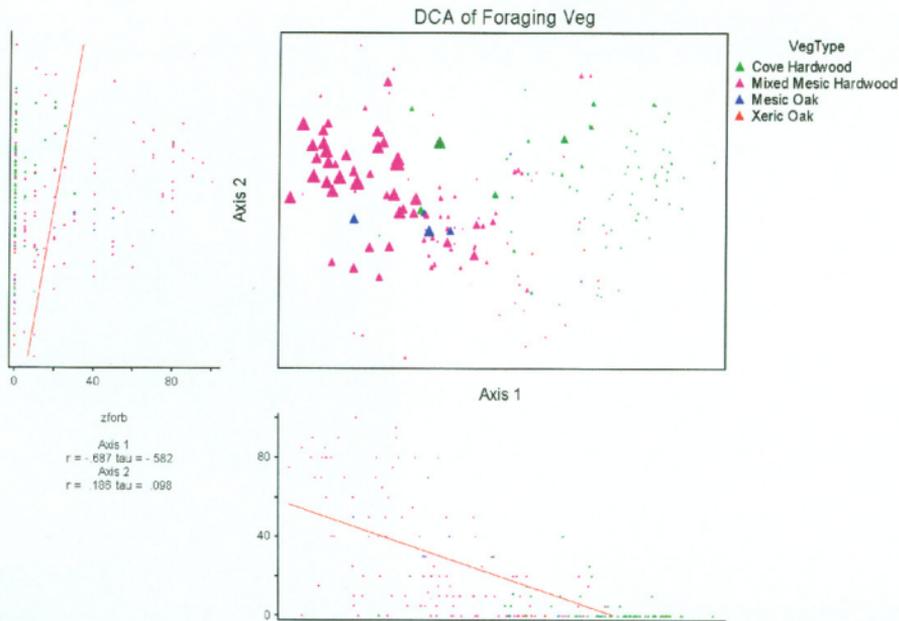


Figure 4. Detrended correspondence analysis (DCA) of Foraging Veg sampled at *D. caeruleus* and *W. citrina* nests. The size of triangles represents amount of cover of herbaceous species at a height range of zero to two meters (zforb). VegTypes are the qualitative plant association classifications. Pearson correlation coefficient ( $r = -0.687$ ) shows strong negative correlation of first axis and percent cover zforb.

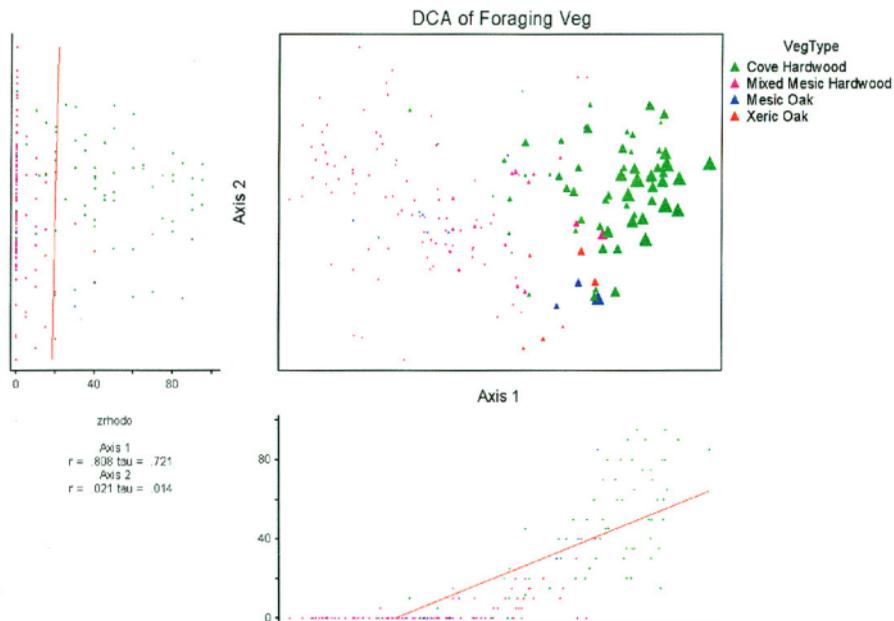


Figure 5. Detrended correspondence analysis (DCA) of Foraging Veg (see Methods) sampled at *D. caerulescens* and *W. citrina* nests. The size of triangles represents amount of cover of *Rhododendron* sp. at a height range of zero to two meters (zrhodo). VegTypes are the qualitative plant association classifications. Pearson correlation coefficient ( $r = 0.808$ ) shows strong positive correlation of first axis and percent cover zrhodo.

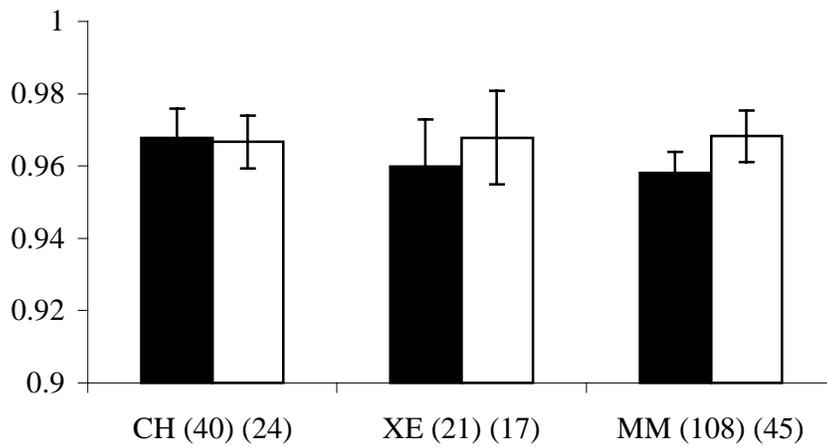


Figure 6. Mayfield daily survival rate (DSR) of *D. caerulea* (dark bars) and *W. citrina* (light bars) 1998, 1999, and 2000 in acidic cove hardwood (CH), mixed-mesic hardwood (MM), and xeric oak (XE). Sample sizes are in parentheses.

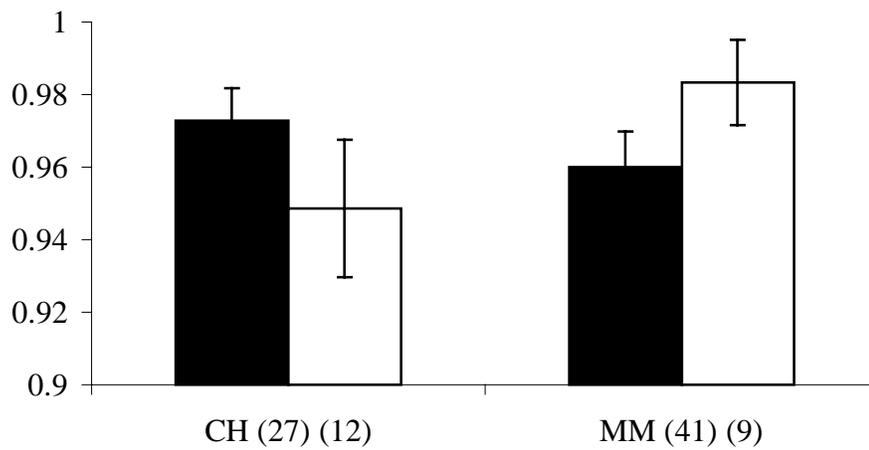


Figure 7. Mayfield daily survival rate (DSR) of *D. caerulea* (dark bars) and *W. citrina* (light bars) in 2000 in acidic cove hardwood (CH) and mixed-mesic hardwood (MM). Sample sizes are in parentheses.

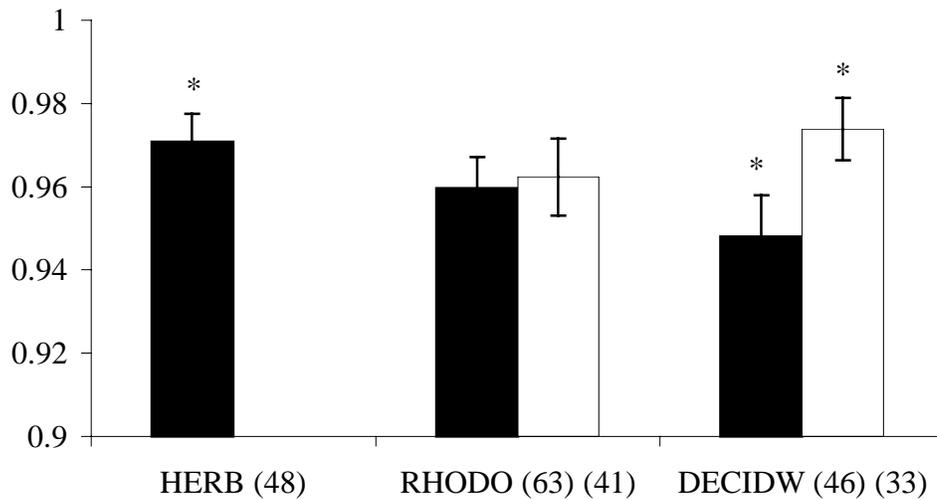


Figure 8. Mayfield daily survival rate (DSR) of *D. caerulescens* (dark bars) and *W. citrina* (light bars) for all years (1998, 1999, and 2000) by nest substrate: herbaceous (HERB), rhododendron (RHODO), and deciduous woody shrubs/saplings. Sample sizes are in parentheses.

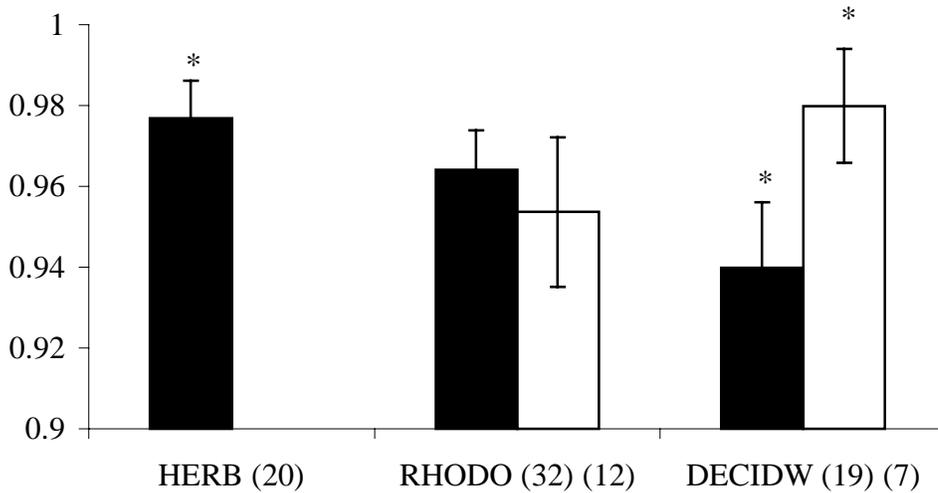


Figure 9. Mayfield daily survival rate (DSR) of *D. caerulescens* (dark bars) and *W. citrina* (light bars) in 2000 in three substrates: herbaceous (HERB), rhododendron (RHODO), and deciduous woody shrubs/saplings (DECIDW). Sample sizes are in parentheses. \*-  $p < 0.05$

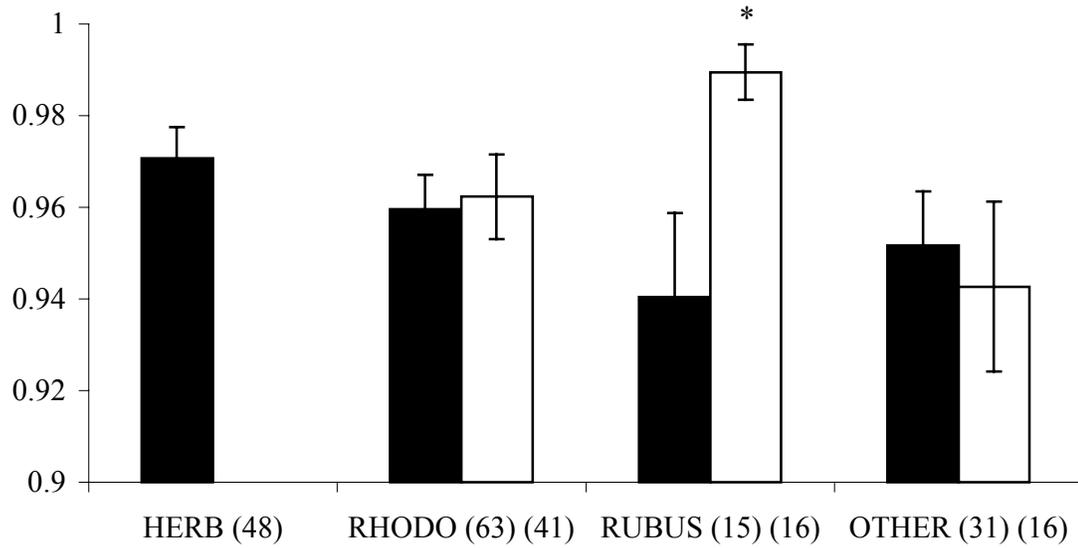


Figure 10. Mayfield daily survival rate of *D. caerulescens* (dark bars) and *W. citrina* (light bars) for all years (1998, 1999, and 2000) by nest substrate: herbaceous (HERB), rhododendron (RHODO), blackberry (RUBUS) and other deciduous woody shrubs/saplings (OTHER). Sample sizes are in parentheses. \*  $\chi^2 = 9.1$ ,  $df = 2$ ,  $p < 0.05$

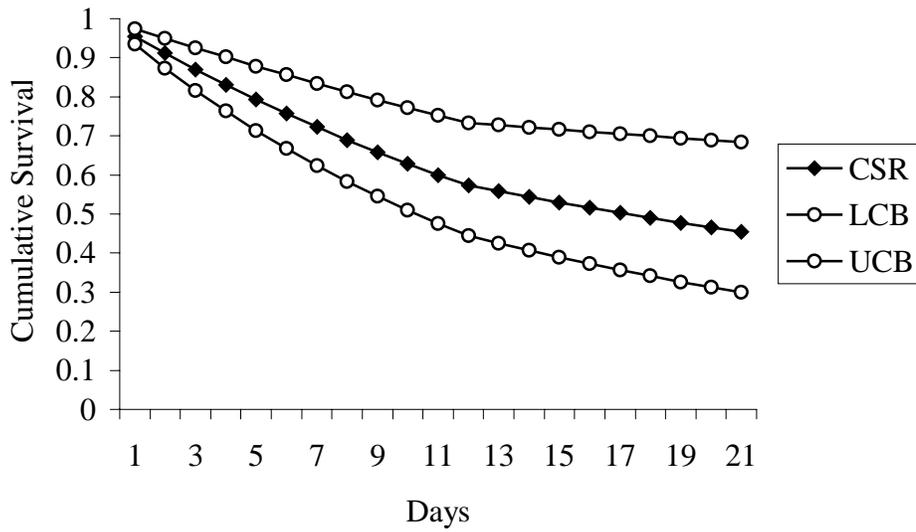


Figure 11. Cumulative nest survival (CSR) of *D. caerulscens* at White Oak Flats with upper 95% (UCB) and lower 95% confidence bounds (LCB). Nestling period daily survival was higher than egg stage (laying + incubation) survival ( $z = 1.5$ ,  $df = 1$ ,  $p < 0.10$ ).

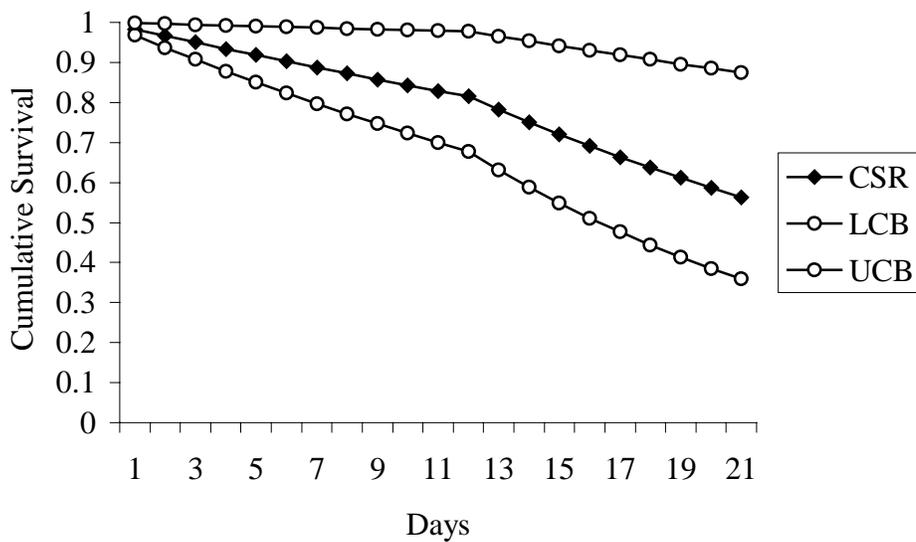


Figure 12. Cumulative nest survival (CSR) of *D. caerulscens* at Lemon Gap with upper 95% (UCB) and lower 95% confidence bounds (LCB). Nestling period daily survival was lower than egg stage (laying + incubation) survival ( $z = 1.47$ ,  $df = 1$ ,  $p < 0.10$ ).

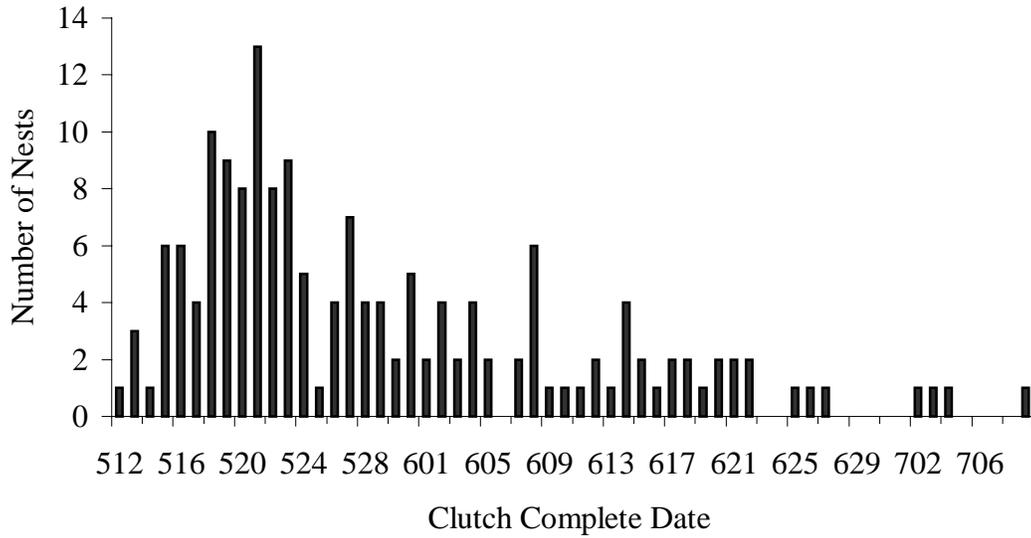


Figure 13. Number of *D. caerulescens* nests found that were initiated on a given date. Dates include nests of known initiation and approximate (calculated) initiation. Nests that could not be back-calculated to within several days of clutch complete date were excluded. 512 = May 12.

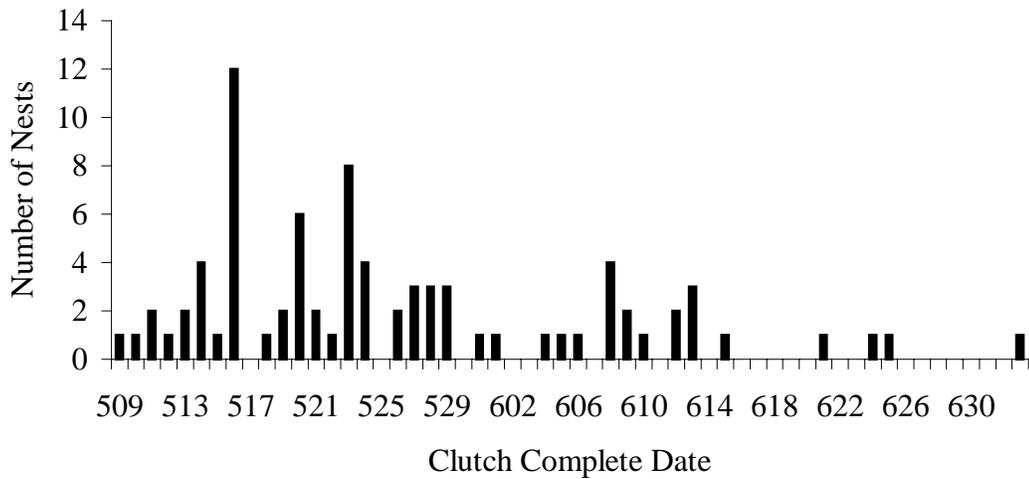


Figure 14. Number of *W. citrina* nests found that were initiated on a given date. Dates include nests of known initiation and approximate (calculated) initiation. Nests that could not be back-calculated to within several days of clutch complete date were excluded. 509 = May 9.

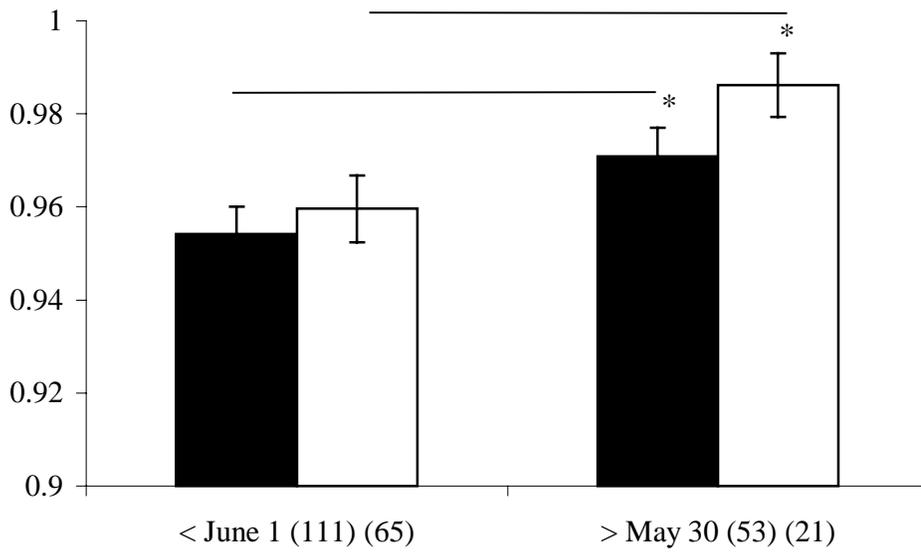


Figure 15. Daily survival rate (DSR) of *D. caerulescens* (Black) and *W. citrina* (White) nests initiated in May and after May. Sample sizes are in parentheses. \*  $p < 0.05$

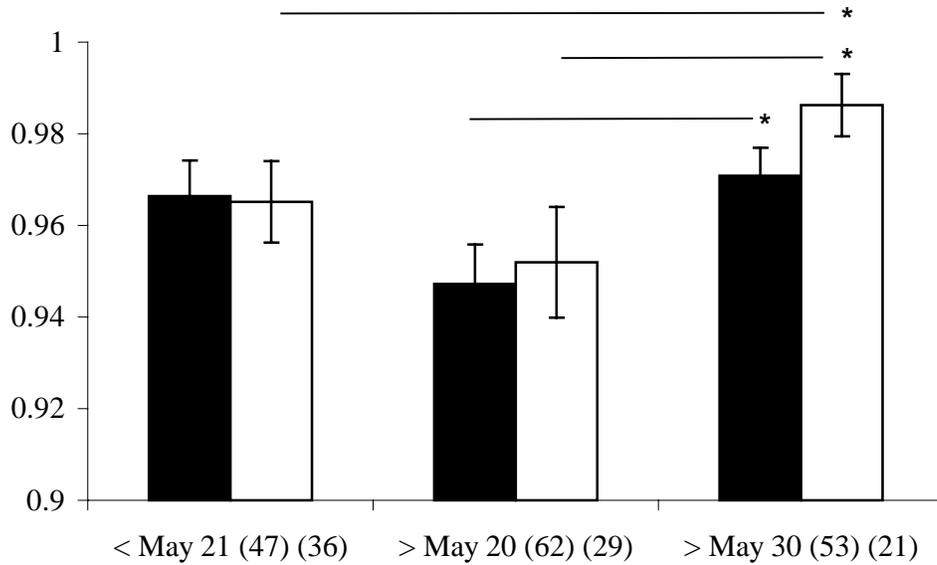


Figure 16. Daily survival rate (DSR) of *D. caerulescens* (Black) and *W. citrina* (White) nests initiated in May and after May. Sample sizes are in parentheses. \*  $p < 0.05$

A.

Parameter	DF	Estimate	SE	Chi-square	p-value
Intercept	1	-2.8709	0.7266	15.6122	< 0.0001
CLL	1	0.0582	0.0318	3.3516	0.0671
S	1	-0.0172	0.0069	6.1754	0.013
L	1	0.0206	0.00505	16.6401	< 0.0001
H	1	-0.013	0.00551	5.6055	0.0179
Disturb_	1	0.7215	0.2864	6.3449	0.0118

B.

Cove Hardwood Specific Model					
Intercept	1	-11.3027	3.0852	13.421	0.0002
SLL	1	0.1342	0.0725	3.4262	0.0642
T	1	0.5975	0.2359	6.4122	0.0113
L	1	0.5289	0.1886	7.8658	0.005

C.

Mixed Mesic Hardwood Specific Model					
Intercept	1	-4.4116	0.9401	22.0191	< 0.0001
L	1	0.3797	0.1294	8.6132	0.0033
Disturb_	1	1.0788	0.3573	9.1168	0.0025

Table 4. Stepwise logistic regression models of *W. citrina* nest sites vs. random sites 35 m from nests for (A) all nests (n = 83, random = 336), (B) nests in cove hardwood forests (n = 28, random = 99), and (C) nests in mixed mesic hardwood forests (n = 48, random = 192). See Appendix A for variables subjected to analysis.

A.

Parameter	DF	Estimate	SE	Chi-square	p-value
Intercept	1	-1.4275	0.4484	10.137	0.0015
L	1	0.0118	0.00353	11.1432	0.0008
LUL	1	-0.387	0.1955	3.9196	0.0477
HUL	1	0.5367	0.2168	6.1301	0.0133
Disturb_	1	0.466	0.1958	5.6645	0.0173

B.

Cove Hardwood Specific Model					
Intercept	1	-2.6416	0.8504	9.6485	0.0545
L	1	0.2245	0.1192	3.5472	0.0596

C.

Mixed Mesic Hardwood Specific Model					
Intercept	1	0.1336	0.9416	0.0201	0.8871
T	1	-0.1953	0.0995	3.8516	0.0497
LUL	1	-0.5052	0.2603	3.7674	0.0523
HUL	1	0.7441	0.2791	7.1085	0.0077
Disturb_	1	0.6726	0.2498	7.2506	0.0071

Table 5. Stepwise logistic regression models of *D. caeruleascens* nest sites vs. random sites 35 m from nests for (A) all nests (n = 161, random = 639), (B) nests in cove hardwood forests (n = 47, random = 148), and (C) nests in mixed mesic hardwood forests (n = 99, random = 409). See Appendix A for variables subjected to analysis.

	Height (Mean $\pm$ SD)					
	All Nests (m)***	All Substrates (m)**	Rhodo Nests**	Rhodo Substrates*	Rubus Nests**	Rubus Substrates
<i>D. caerulescens</i>	0.52 $\pm$ 0.26	1.11 $\pm$ 1.31	0.63 $\pm$ 0.33	1.38 $\pm$ 0.93	0.45 $\pm$ 0.22	1.09 $\pm$ 0.87
<i>W. citrina</i>	0.84 $\pm$ 0.38	1.71 $\pm$ 0.11	0.92 $\pm$ 0.44	1.83 $\pm$ 0.94	0.76 $\pm$ 0.23	1.37 $\pm$ 0.25

Table 6. Mean nest and nest substrate heights for all *D. caerulescens* and *W. citrina* nests, nests in *Rhododendron* spp., and nests in *Rubus* spp. \*- p < 0.05, \*\*-p < 0.005, \*\*\*-p < 0.0001.