ASSESSING CONSERVATION UTILITY

A case study of the Cerulean Warbler in eastern Ontario.

by

JASON JONES

A thesis submitted to the Department of Biology

in conformity with the requirements for

the degree of Doctor of Philosophy.

Queen's University

Kingston, Ontario, Canada

December 2000

Canada

ABSTRACT

The use of surrogate species, in which a focal species is used to represent other species of. interest, is a common practice in conservation. However, the validity of this concept has been rarely tested. This 1996-1999 study assessed the utility of the Cerulean Warbler (*Dendroica cerulea*) as a surrogate species in eastern Ontario and was undertaken at the Queen's University Biological Station (44°34'N, 76°20'W).

A documentation of Cerulean Warbler habitat requirements, achieved while avoiding inconsistencies uncovered in a review of the avian habitat literature, indicated that Cerulean Warblers have potential as indicators of the deciduous forest health as Cerulean Warbler reproductive success appears to be dependent on complex forest canopies (based on analyses of 115 territories and 95 nests). A January 1998 ice storm drastically altered canopy structure and subsequent nesting success dropped to 8.9% ($n =$ 45 nests) from a pre-storm average of 75.7% ($n = 37$, 1994-7). The decrease may be related to damage-induced reductions in foliage arthropod populations, indicating potential utility of the Cerulean Warblers as indicators of insect populations. Interestingly, 1999 nesting success increased (36.4%, $n = 30$) as did average territory size (pre-storm mean - 0.69ha, 1998 - 0.74ha, 1999 - 1.17ha). This increase was accompanied by a significant shift in 1999 nest-site selection patterns towards locations higher in larger trees with more foliage cover. The utility of Cerulean Warblers as a population or health indicator was compromised by the plasticity in their habitat affinities that may render this species resilient to certain habitat disturbances.

The results of extensive survey indicated that, while Cerulean Warblers were the fourth most common warbler in the study area, they have no potential as indicators of

high avian biodiversity. However, their broad distribution did confer the Cerulean

Warbler potential as an umbrella species. The spatial distribution of this species matched

those of other mature forest species implying that Cerulean Warbler habitat management

would provide for other species. Finally, Cerulean Warblers could be used as a flagship

species by focusing efforts aimed at the preservation of mature, deciduous forest and the

conservation of other species that require similar habitats.

ACKNOWLEDGMENTS

The collection of the data for this dissertation took the sweat of many individuals to whom I owe a debt of gratitude. In particular, I would like to acknowledge Bill McLeish. Bill was with me for the first three years of this project and his quiet enthusiasm and competence provided the foundation upon which this thesis is built. I would also like to single out the efforts of Ryan Debruyn. Ryan joined our lab in 1998 and, over the last three years, has developed into a fine field biologist and has contributed greatly to this thesis and our knowledge of Cerulean Warblers. Many other people also provided very important assistance in the field: Catherine Oliarnyk, Ruth Woodward, Lisa Veit, Javier Salgado Ortiz, Tim Demmons, Jesus Vargas, Sergio Harding, Ben Risk, Susanne Millard, Nicole Vreeswyk, Robyn O'Hare (nee Varey), and numerous volunteers from the Kingston Field Naturalists and the Rideau Valley Naturalists.

I would also like to thank several landowners and agencies who graciously allowed me on their properties to look for and study birds and who assisted me greatly, both logistically and in the collection of data: Turid Forsyth, Rhonda Elliott, David Hahn, Gary Nielsen, Alfred and Patty Pick, Murphy's Point Provincial Park, and the Kingston Field Naturalists.

I am indebted to my supervisor, Raleigh Robertson, for letting me run with my ideas, for letting me make mistakes and learn from them, and for teaching me to play the game. My supervisory committee of Drs. Laurene Ratcliffe, Chris Eckert and Dennis Jelinski has also assisted greatly in the development and fine-tuning of this dissertation. Dr. Richard T. Holmes, my external examiner, also provided invaluable advice and suggestions. The staff at the Queen's University Biological Station, notably Frank and

Finally, I need to express heartfelt gratitude to several special individuals without whom this dissertation could never have been conceived, let alone completed. To my dogs, Mode, Katahdin, and Parker, for their constant reminders to keep life simple – food, water, play, belly rubs. To Erin Carruthers, whose support and understanding

enabled me to make the move from my comfortable life on the west coast to begin this endeavour here in Ontario. To my parents, Kathie and Barry Jones, and my sister, Caitlin, who may not have always understood why I do what I do or why I chose the path I did, but never once doubted my abilities and ambitions and never once wavered in their unconditional support.

And to Jennifer Barg, soon to be Jennifer Barg-Jones, for so many things. For reading every word of this dissertation, for your insight and field savvy, for helping me curb my rampant speculations, for your brownies, for getting IT, for joining our dreams, for teaching me the true meaning of patience, for never giving up. Thank-you.

TABLE OF CONTENTS

CO-AUTHORSHIP

Ryan DeBruyn is included as an author of Chapter 4 as much of the work on the

relationships between forest damage and territory characteristics grew out of his honours

thesis at Queen's University. Mr. DeBruyn played a large role in data collection and data

analysis, and provided editorial assistance. Jennifer Barg is included as an author of the

same chapter as she was involved both in data collection and editing the manuscript.

Raleigh Robertson is a co-author on Chapters 3-5 as his support and guidance were an

integral part of the entire research process.

LIST OF TABLES

LIST OF FIGURES

Chapter 1

General Introduction

Jason Jones

TRENDS IN CONSERVATION BIOLOGY

The history of conservation biology is rooted in natural history and habitat studies (Simberloff 1988). In the last 30 years this focus has shifted from island biogeography theory and refuge design to population genetics and metapopulation biology (Soulé 1986, 1987). Like the growth of any new discipline, the evolution of conservation biology has been filled with disagreement and controversy. Topics of debate have ranged from what is the most appropriate taxonomic unit upon which to focus conservation efforts (Lawton 1991; Lesica and Allendorf 1995) to how best organize a system of protected areas (Diamond 1976; Simberloff and Abele 1976; Gilpin and Diamond 1980). Currently, I perceive a major dichotomy dominating the theory and practice of conservation biology and wildlife management - the division between single-species and community based approaches (Maurer 1993). I believe that the unification of this dichotomy is an important step in the evolution of conservation biology.

Historically, single-species have been the focus of wildlife management practices. These efforts generally focused on game species (American Game Policy 1930) although the majority of endangered species management is likewise carried out on a species-by species basis (Caughley 1994). Single-species approaches tend to provide valuable information that is pertinent for a particular place and time but do not provide much opportunity for the development of rules or general theory (Block et al. 1995). In contrast, management at the scale of communities or ecosystems is a relatively new development (Hunter 1991; Block et al. 1995). One of the advantages of the community approach is that more species will be accounted for with an effort and cost that approximates that incurred by single-species approaches (Verner 1983). The primary

disadvantage of this approach is that very little species-specific information is available with which to inform management decisions. Consequently, management efforts focusing on habitats, ecosystems, or communities run the risk of missing population fluctuations of individual species (Mannan et al. 1984; Verner 1984).

The integration of single-species and community-based approaches to wildlife management and conservation remains a serious issue. This integration becomes increasingly critical when dealing with species of conservation concern, where an accurate understanding of the specific requirements of a focal species and its surrounding ecological context is of paramount importance (Simberloff 1988; Caughley 1994). However, the unraveling of such detail is often intractable from empirical and logistical perspectives. Delaying action until all facets of a species' life history are understood is both impractical and potentially dangerous (Gilpin 1987; Simberloff 1988). On the other hand, initiating conservation schemes without an understanding of ecosystem or community context can have similarly serious consequences (Mooney and Drake 1986; Spencer et al. 1991).

DISSERTATION OBJECTIVES

A common thread running through the history of conservation is that there are few tools available to managers effective on a large-scale, both empirically and theoretically. Certain existing tools, such as captive breeding, are effective only in controlled situations (Caughley 1994; Cade and Jones 1993) while others tend to be site-specific, such as removal of Brown-headed Cowbirds (*Molothrus ater*) to enhance breeding success of the Kirtland's Warbler (*Dendroica kirtlandii*, Kelly and DeCapita 1982).

One idea that is becoming increasingly common is the surrogate species concept (Thomas 1972). Surrogates have been employed in situations ranging from monitoring changes in environmental conditions to identifying areas of high biodiversity (Phillips 1980; Humphries et al. 1995). However, despite this widespread use, there remains considerable disagreement about the ecological and empirical validity of surrogate species (Inhaber 1976; Landres et al. 1988). Foremost among the criticisms is the lack of standardized, rigourous methodology for assessing the suitability of a chosen species as a surrogate (Landres et al. 1988; Caro and O'Doherty 1999). Often, species are chosen because they are a species of conservation concern themselves or as a result of public perception of their value (Caro and O'Doherty 1999).

A broad goal of my dissertation is to outline the steps necessary to make an informed decision as to the appropriateness of a given species as a conservation or management surrogate. As an example, I chose to assess the conservation utility of the Cerulean Warbler in eastern Ontario. Due to precipitous breeding population declines, up to 3.4% per year since 1966 (Robbins et al. 1992, Peterjohn et al. 1995, James et al. 1996), this species has been variously designated as threatened, rare, or of special concern in the United States and of special concern in Canada (Robbins et al.1992, COSEWIC 2000, Hamel 2000b). While the conservation of Cerulean Warbler populations and habitats is an worthwhile endeavour, I feel that it is important to assess whether the benefits of these efforts exceed the single-species objectives. That is, there needs to be an integration of the needs of a single species and the community context in which it is embedded.

The first step in the assessment process is to accurately describe the habitat requirements of the candidate species; in this case, I needed to document habitat requirements for successful Cerulean Warbler reproduction. The second step is to examine how the Cerulean Warbler fits into the larger avian assemblage context so I can explore the potential impacts of managing for Cerulean Warblers on other species in the management area. The final step is to determine, in light of conservation and management goals, what conservation role the Cerulean Warbler is best suited for in eastern Ontario.

Study Species. – The Cerulean Warbler is a small (~9g), canopy-foraging, insectivorous bird that breeds in mature deciduous forests (Hamel 2000a). Relative to its congeners, this species tends to forage and nest higher in the canopy (Bent 1953, Hamel 2000a). This species also tends to migrate both earlier and farther than other congeners (Hamel 2000a) and spends the winter season in the Andes Mountains of South America (Robbins et al. 1992, Jones et al. 2000b).

The eastern Ontario population of this species is relatively recently established with the first published nest record for the region dating from 1963 (Quilliam 1973) and is on the leading edge of a northward range expansion for this species (Robbins et al. 1992). The eastern Ontario population size is approximately 3,000 breeding pairs (Jones et al. unpublished data) and exhibits very high densities in some regions (Jones et al. 2000a). Annual adult male survivorship is estimated to be 51% (Jones et al. unpublished manuscript). The operational sex ratio of the study population on the property of the Queen's University Biological Station (44°34'N, 76°20'W) is close to 1:1 with some yearly variation (Jones et al. unpublished data). Cerulean Warblers are socially

monogamous (Hamel 2000a) although there are observations of bigamy in our study

population (Jones and Barg personal observations). Males and female do participate in

extra-pair copulations and these copulations have resulted in extra-pair young (Jones et

al. unpublished data). Cerulean Warblers are predominantly single-brooded (Hamel

2000a) although they will re-nest following nest failure (Jones et al. in press).

Synopsis of chapters. —Chapters 2 through 4 focus on habitat selection and habitat

requirements of Cerulean Warblers in eastern Ontario. In Chapter 2, I present a critical

review of the last 14 years of avian habitat related research published in the four premier

North American avian journals (*The Auk, The Condor, The Journal of Field Ornithology,*

The Wilson Bulletin). Chapter 3 addresses many of the methodological and empirical

concerns raised by the critical review in an analysis of territory and nest-site selection by

Cerulean Warblers on the property of the Queen's University Biological Station (QUBS).

Chapter 4 documents the response of Cerulean Warblers to a severe natural disturbance,

the ice storm of January 1998. This response assessment is used to examine habitat

requirements for successful reproduction. The unpredictable loss of habitat resulting

from the storm afforded the opportunity to examine the relationship between population

age structure, site fidelity, disturbance response and habitat selection in Cerulean

Warblers and provided insight into the relative importance of the physical and social

features that contribute to resilience to habitat disturbance. The documentation of this

resilience is an important component of the surrogate species assessment process. In

Chapter 5, I attempt to place the habitat affinities of the Cerulean Warbler in a

community context. I then use the results of Chapters 3 and 4 and data presented in

Chapter 5 to assess the suitability of Cerulean Warblers as a surrogate species for forest

management and wildlife conservation in eastern Ontario. Chapter 6 presents a general summary of the dissertation.

LITERATURE CITED

American Game Policy. 1930. 17th American Game Conference, American Game Association, NY.

Bent, A. C. 1953. Life histories of North American wood warblers. Pt. 1. U. S. National Museum Bulletin 203.

Block, W. M., D. M. Finch, and L. A. Brennan. 1995. Single-species versus multiple-species approaches for management. Pages 461-476 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, Oxford, UK.

Cade, T. J., and C. G. Jones. 1993. Progress in restoration of the Mauritius Kestrel. Conservation Biology 7: 169-175.

Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. Conservation Biology 13: 805-814.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63: 215-244.

COSEWIC. 2000. Canadian species at risk, May 2000. Committee of the Status of Endangered Wildlife in Canada, Ottawa, ON.

Diamond, J. M. 1976. Island biogeography and conservation: strategy and limitations. Science 193: 1027-1029.

Gilpin, M. E. 1987. Theory vs. practice. Trends in Ecology and Evolution 2: 169.

Gilpin, M. E., and Diamond, J. M. 1980. Subdivision of nature reserves and the maintenance of species diversity. Nature 285: 567-569.

Hamel, P. B. 2000a. Cerulean Warbler (*Dendroica cerulea*). No. 511 *in* A. Poole and F. Gill, editors. The Birds of North America. The Birds of North America, Inc., Philadelphia, PA.

Hamel, P. B. 2000b. Cerulean Warbler status assessment. United States Fish and Wildlife Service, Fort Snelling, MN.

Humphries, C. J., P. H. Williams, and R. I. Vane-Wright. 1995. Measuring biodiversity value for conservation. Annual Review of Ecology and Systematics 26: 93-111.

Hunter, M. L., Jr. 1991. Coping with ignorance: the coarse filter strategy for maintaining biodiversity. Pages 266-281 in K. A. Kohm, editor. Balancing on the brink of extinction. Island Press, Washington, DC.

Inhaber, H. 1976. Environmental indices. John Wiley and Sons, New York, NY.

James, F. C., C. E. McCulloch, and D. A. Wiedenfeld. 1996. New approaches to the analysis of population trends in land birds. Ecology 77: 13-27.

Jones, J., R. D. DeBruyn, J. J. Barg, and R. J. Robertson. in press. Assessing the effects of natural disturbance on a Neotropical migrant songbird. Ecology.

Jones, J., W. J. McLeish, and R. J. Robertson. 2000a. Density influences census technique accuracy for Cerulean Warblers in eastern Ontario. Journal of Field Ornithology 71: 46-56.

Jones, J., P. R. Perazzi, E. H. Carruthers, and R. J. Robertson. 2000b. Sociality and foraging behavior of the Cerulean Warbler in Venezuelan shade-coffee plantations. Condor 102: 958-962.

Kelly, S. T., and M. E. DeCapita. 1982. Cowbird control and its effect on Kirtland's

    Warbler reproductive success. Wilson Bulletin 94: 363-365.

Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator

    species: a critique. Conservation Biology 2: 316-327.

Lawton, J. L. 1991. Are species useful? Oikos 62: 3-4.

Lesica, P., and F. W. Allendorf. 1995. When are peripheral populations valuable for

    conservation? Conservation Biology 9: 753-760.

Mannan, R. W., M. L. Morrison, and E. C. Meslow. 1984. The use of guilds in forest bird

    management. Wildlife Society Bulletin 12: 426-430.

Maurer, B. A. 1993. Biological diversity, ecological integrity, and Neotropical migrants:

    new perspectives for wildlife management. Pages 24-31 in D. M. Finch and P. W.

    Stangel, editors. Status and management of Neotropical migratory birds. Gen.

    Tech. Rep. RM-229, USDA Forest Service, Fort Collins, CO.

Mooney, H. A., and J. A. Drake, editors. 1986. Ecology of biological invasions of North

    America and Hawaii. Ecological Studies 58. Springer-Verlag, New York, NY.

Quilliam, H. R. 1973. History of the birds of Kingston, Ontario. Kingston Field

    Naturalists, Kingston, Ontario.

Peterjohn, B.C., J.R. Sauer, and C.S. Robbins. 1995. Population trends from the North

    American Breeding Bird Survey. Pages 3-39 in Ecology and management of

    neotropical migratory birds: A synthesis and review of critical issues (T. E.

    Martin and D. M. Finch, Eds.). Oxford University Press, New York.

Phillips, D. J. H. 1980. Quantitative aquatic biological indicators. Applied Science

    Publishers, London, UK.

Robbins, C. S., J. W. Fitzpatrick, and P. B. Hamel. 1992. A warbler in trouble: *Dendroica cerulea*. Pages 549-562 in J.M. Hagan III and D.W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. Annual Review of Ecology and Systematics 19: 473-511.

Simberloff, D., and L. G. Abele. 1976. Island biogeography and conservation: strategy and limitations. Science 193: 1032.

Soulé, M. E., editor. 1986. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, MA.

Soulé, M. E., editor. 1987. Viable populations for conservation. Cambridge University Press, Cambridge, UK.

Spencer, C. N., B. R. McLelland, and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagle displacement. BioScience 41: 14-21.

Thomas, W. A., editor. 1972. Indicators of environmental quality. Plenum Press, New York, NY.

Verner, J. 1983. An integrated system for monitoring wildlife on the Sierra National Forest. Transactions of the North American Wildlife and Natural Resources Conference 48: 355-366.

Verner, J. 1984. The guild concept applied to management of bird populations. Environmental Management 8: 1-14.

Chapter 2

Habitat selection studies in avian ecology: a critical review.

Jason Jones

The study of habitat use and selection in birds has a long tradition (Grinnell 1917, Kendeigh 1945, Svärdson 1949, Hildén 1965; Block and Brennan 1993). Early habitat-selection theory was characterized by correlative models of habitat characteristics and species abundance (MacArthur and Pianka 1966, Verner et al. 1986, Rosenzweig 1991), which subsequently evolved into models that involved density-dependence: the "ideal-free distribution" and "ideal-despotic distribution" models (Fretwell and Lucas 1970, Fretwell 1972). More recently, habitat-selection studies have shown that many factors, such as landscape structure, can influence exactly how 'ideal' and 'free' animals are while moving through a landscape and selecting habitats (Karr and Freemark 1983, Pulliam and Danielson 1991, Petit and Petit 1996).

Habitat-selection studies have recently assumed a new urgency, partially as a result of the importance of incorporating both habitat and demographic information into conservation planning (Caughley 1994). Nevertheless, ornithologists tend to be inconsistent in their conceptual framework and terminology with regard to: (1) what constitutes habitat use versus selection, (2) the behavioral and evolutionary context of their findings, and (3) the order or scale of their study, from microhabitat to geographic range (Johnson 1980, Orians and Wittenberger 1991). The purpose of this review is to address these concerns through a survey of recent literature and highlight areas where improvements or advances can be made in avian habitat ecology.

THREE AREAS OF CONCERN

Definitions.- The semantic and empirical distinctions between the terms "habitat use" and "habitat selection" are often unclear (Hall et al. 1997). "Habitat" refers to a distinctive set of physical environmental factors that a species uses for its survival and reproduction (Block and Brennan 1993). "Habitat use" refers to the way in which an individual or species uses habitats to meet its life history needs (Block and Brennan 1993). The study of habitat-use patterns describes the actual

distribution of individuals across habitat types (Hutto 1985). "Habitat selection" refers to a hierarchical process of behavioral responses that may result in the disproportional use of habitats to influence survival and fitness of individuals (Hutto 1985, Block and Brennan 1993). "Habitat selection" carries a connotation of understanding complex behavioral and environmental processes that "habitat use" does not; habitat-use patterns are the end result of habitat-selection processes. "Nest-site selection" is a subset of habitat selection focusing solely on nest-sites.

Context.- The ability of researchers to place their findings in an appropriate behavioral or evolutionary context varies widely. Much of this variation lies in researchers' ability to generate specific questions and to place the answers to these questions into broader theoretical frameworks. There are two aspects of habitat selection that are crucial to understanding the adaptive significance of disproportionate use of habitats; demonstration of choice and an assessment of the fitness consequences associated with the choice.

First, habitat selection is a decision-making process and researchers need to make an attempt to describe how the observed patterns reflect individual choice. This attempt can be improved by the recognition that individuals are faced with choices that differ not only in terms of habitat quality but also in terms of the costs and benefits of acquiring space (Fretwell and Lucas 1972, Kennedy and Gray 1994).

Second, habitat preferences are assumed to be adaptive without demonstration of increased fitness in preferred habitats (Robertson 1972, Pulliam and Danielson 1991, Martin 1998). There is no guarantee that the presence of individuals in a given habitat is positively related to habitat quality (Van Horne 1983, Pulliam 1988, Caughley 1994). In the absence of behavioral or life-history information, there is no way to know if detected differences have any bearing on choices of individuals (Martin 1992, 1998).

In addition, many non-habitat related phenomena influence habitat selection in birds (Cody 1981, 1985), including nest predation (Sonerud 1985, Martin 1993), competition (Svärdson 1949, Martin 1993, Petit and Petit 1996), intraspecific attraction (Danchin et al. 1998, Forsman et al. 1998, Pöysä et al. 1998), and food limitation (Martin 1993, McCollin 1998). There needs to be explicit recognition of how these phenomena affect both the choices made by individuals and the fitness consequences of those choices.

Methodology.- The empirical and statistical methods by which habitat selection is inferred differ greatly in their precision and applicability (Alldredge and Ratti 1986, 1992). There are two main ways in which habitat selection is tested for breeding birds with territorial systems: comparing used habitats with unused habitat and comparing used habitats with available habitats. "Used" habitat is habitat currently occupied by the focal individual or species; "unused" habitat is not currently occupied. "Available" habitat refers to all habitat types in a prescribed area and includes habitats currently in use.

The used vs. unused comparison is considered the less informative of the two methods (Johnson 1980). Information on the quality of used vs. unused space is only informative about habitat selection if the unused habitat is actually available to the birds of interest. Further, absence from a particular habitat does not mean that the habitat is being avoided (Wiens 1989, Haila et al. 1996). Population density and demographics may have a major impact on which habitats are used or unused (Rotenberry and Wiens 1980, Wiens 1986, Wiens et al. 1987, Haila et al. 1996).

In addition, there are statistical issues concerning the comparison of used and unused areas. Of particular importance is the concern raised over statistical methods that fail to consider that an individual's use of a particular habitat affects its use of other habitats (Thomas and Taylor 1990, Aebischer et al. 1993). The lack of independence negatively affects the power of many of the

statistical techniques used to analyze such proportional use (Alldredge and Ratti 1986, 1992, James and McCulloch 1990, Aebischer et al. 1993). Analytical techniques should test for departures from random use. If non-random use is detected, techniques should then assess which habitats are used more or less than expected by chance (Aebischer et al. 1993). Johnson's (1980) unit-sum constraint is an example of such a technique.

Used versus available tests involve comparisons of habitats currently used by individuals to habitats available to be used. These comparisons are preferable to used versus unused comparisons because they allow researchers to make inferences about choice. However, the used versus available comparisons are also problematic in that the measurement of habitat availability is very difficult. First, availability refers to both the accessibility and procurability of resources, not just their abundance (Wiens 1984, Hall et al. 1997, Martin 1998). The definition of availability based solely on the basis of the proportional area of habitat types makes a rarely tested assumption that all parts of the study area are equally available (Kennedy and Gray 1994, Arthur et al. 1996, Spencer et al. 1996). In addition, many researchers assume that a random sampling of habitats estimates habitat availability, although this assumption is seldom tested in the field.

Second, both the spatial and temporal scales of the study influence the perception of habitat availability (Wiens 1973, Kotliar and Wiens 1990, Orians and Wittenberger 1991) and, hence, our sense of habitat selection (Clark and Shutler 1999). Johnson (1980) defined four orders of habitat selection that acknowledge its hierarchical nature and provide a useful empirical framework for habitat studies. Johnson's framework ranges from the macroscale descriptions of the geographical or physical range of a species (first-order selection) to microscale descriptions of the actual attainment of food items or selection of nest sites from those available (fourth-order selection). If the scale of study and analysis is not tailored to the species and question of interest, key influences

on habitat selection may be missed by the research (Orians and Wittenberger 1991). For example, when examining habitat use within territories, the individual has likely already made a crucial selection by choosing a territory. Researchers should be explicit about the constraints that prior decisions made by the animal place on its current options (Johnson 1980).

Third, habitat availability often is not assessed in a manner relevant to the individual or species in question (Aebischer et al. 1993, Gates and Evans 1998). Available habitat is usually assessed within a study area, the boundaries of which are often arbitrarily drawn. A more accurate assessment of habitat availability is one that is informed by the natural- and life-history characteristics of the focal species. For example, when considering selection of habitat components from within territories or home ranges (third-order selection; *sensu* Johnson 1980), the measurement of habitat availability should be constrained by the boundaries of the territory or home range (Evans and Gates 1997, Gates and Evans 1998).

METHODS

I surveyed the last 14 years (1986 to 1999) of four North American ornithological journals – *The Auk*, *The Condor*, *Journal of Field Ornithology*, and *The Wilson Bulletin*. I considered the content of these four journals to be representative of the state of the avian research to date. I chose 1986 as the starting point as it was the first full publication year following the publication of *Habitat Selection in Birds*, edited by Cody (1985). I searched titles, abstracts, and key words for the terms habitat use, habitat characteristics, habitat associations, habitat selection, and nest-site selection. Papers were grouped into three exclusive categories: habitat use papers, habitat selection papers and nest-site selection papers. Within each category, papers were classified according to the characteristics of both the research within each manuscript and how the research was presented. I asked several questions of each paper: 1) Were the authors consistent and accurate in their usage

of habitat terminology throughout the paper? 2) If the paper examined habitat or nest-site selection, did the authors contrast used habitats with unused habitats or did they address habitat availability? 3) If the authors addressed habitat availability, did they define availability arbitrarily (e.g. within preset study area boundaries) or did they consider the ecology of the study system when designing their habitat sampling method (e.g. within territory boundaries when assessing nest-site selection)? 4) If the authors addressed habitat or nest-site selection, did they attempt to place their findings in a behavioral or fitness context?

I assessed whether or not the frequency of "errors" changed over time by grouping papers into the following time intervals: 1986 to 1989, 1990 to 1994, and 1995 to 1999. I compared the percentage of total papers committing semantic, methodological, and contextual, errors across each of the three time intervals using Chi-square tests. In the *Results and Discussion*, I deal with semantic concerns first as the papers that suffered from such concerns were not included in the assessment of methodological and contextual issues.

RESULTS AND DISCUSSION

In total, 185 papers were included in this review: 73 habitat use, 51 habitat selection, 61 nest-site selection. Forty-two were published in the period 1986-1989, 56 during 1990-1994, and 87 during 1995-1999.

Semantics. - Overall, 24% (44/185) of the surveyed papers suffered from semantic inconsistencies. Problems ranged from using "habitat use" and "habitat selection" as synonyms (e.g. Darveau et al. 1992) to solely describing nest-site characteristics without reference as evidence of nest-site selection (e.g. Schaffner 1991). This study is not the first to raise concern over the lack of semantic standardization in the habitat field (Romesburg 1981, Morrison et al. 1992, Hall et al. 1997). That nearly one-quarter of the papers surveyed in this review misinterpreted and/or misused the terms

habitat use, habitat selection and nest-site selection indicates that the problem remains pervasive in avian ecology. Further, the situation does not appear to be improving; there was no difference in the propensity for error across the three time periods ($\chi^2 = 3.05$, df $= 184$, $P = 0.22$). Why the problem remains is perhaps related to the commonness of the terminology; authors may assume that everybody "knows" what habitat selection is and, therefore, pay less attention to providing operational definitions when presenting their research. While the avian habitat literature appears to have fewer semantic inconsistencies than other fields (Hall et al. 1997), researchers need to strive to insure that essential concepts are clearly defined if habitat ecology is to continue to develop and maintain its position as one of the central fields in avian research. The lack of semantic clarity carries over into the ability of researchers to develop a meaningful context surrounding their results.

Metholodogy.- Of the 141 papers without semantic concerns, 46% ($n = 65$) made empirical decisions that rendered many of the results difficult to interpret and, possibly, inaccurate. There was no difference in the propensity for error across the three time periods ($\chi^2 = 2.13$, df $= 140$, $P = 0.34$). Most of the reviewed papers that examined habitat selection described a used vs. available comparison (76%) rather than a used vs. unused comparison (24%), although the latter is widely used in wildlife management (White and Garrott 1990). Very few of the reviewed papers that employed used vs. unused comparisons addressed issues of accessibility and availability. For example, Frederick and Gutiérrez (1992) tested habitat selection in White-tailed Ptarmigan (*Lagopus leucurus*) by restricting the location of "unused" sites to sites within regions of concentrated use, thereby guaranteeing habitat accesibility. Unless accessibility can be addressed, a better approach is to examine areas where birds are found and look at probability or frequency of usage across used areas (e.g. Anderson and Tacha 1999). Finally, few papers utilized statistical

methodology designed to account for the non-independence of proportional use of habitats (e.g. Ryan and Renkin 1987).

The majority of the papers that actually examined habitat selection employed a form of the used vs. available habitat comparison. While this is encouraging, many researchers failed to explicitly recognize that not all habitats are equally available for use and did not structure their habitat sampling methodology accordingly. Less than half of the papers that employed a used vs. available comparison to test habitat selection defined availability in a manner relevant to the species or individual in question. For example, when examining nest-site selection, many authors compared nest-site characteristics with habitat characteristics at random sites that were selected without reference to territory boundaries (e.g. Pampush and Anthony 1993, Linder and Anderson 1998). The assessment of habitat availability likely included habitat not available to the focal individual and, consequently, erroneous differences between nest-sites and available habitat could have been described. Constraining the assessment of habitat availability to within territory boundaries will provide a more accurate picture of nest-site or foraging site selection (e.g. Ramsay et al. 1999).

The issue of availability can be compounded when dealing with species having unique habitat requirements. Smith et al. (1999) documented nest-site selection by Great Horned Owls (*Bubo virginianus*), a species that requires nest structure built by other species. However, in their selection of random sites to document "availability", they did not record the presence or absence of potential nest-sites, such as old corvid nests. If there are no potential nest-sites, the habitat is technically not available. On the other hand, Sieg and Becker (1990) provided a truer assessment of availability for Merlins (*Falco columbarius*), which also require nests built by heterospecifics, by centering their non-nest habitat plots on unused Black-billed Magpie (*Pica pica*) nests.

Context. – Thirty-eight percent (46/121) of the papers that examined habitat or nest-site selection did not provide a behavioral or fitness context for their findings. There was no difference in the propensity for "error" across the three time periods ($\chi^2 = 0.32$, df $= 120$, $P = 0.85$). Given so many known non-environmental influences on habitat selection, it is perhaps troubling that over one-third of habitat selection papers neglected to acknowledge the potential effects of non-environmental factors on patterns they describe. Obviously, no single research project can cover all potential influences but the existence of multiple constraints on individual behavior needs to be explicitly noted. For example, Hooge et al. (1999) focused their efforts in documenting nest-site selection by Acorn Woodpeckers (*Melanerpes formicavorus*) on the potential influence of microclimate on habitat selection but expanded their discussion to include the role of nest predation. In contrast, Wilson et al. (1998) offer only a cursory explanation of observed patterns of habitat selection by peatland birds which limits the ability of the reader to appreciate the historical dynamics of the system.

The results of this review indicate that few habitat and nest-site selection papers have addressed why the selection of certain habitats was adaptive for the species in question. One notable exception was Badyaev et al.'s (1996) examination of habitat selection in female Wild Turkeys (*Meleagris gallopavo*); not only did the authors examine the reproductive consequences of habitat selection by individuals, they documented the process by which females behaviorally sampled habitat availability.

Summary. – The results of my time period analysis, coupled with the frequency of "error" detected in this review, indicate that my concerns regarding the general state of avian habitat selection research were valid. One concern was that ornithologists tend not to consistently evaluate the behavioral and fitness context of their findings. This can be ameliorated by recognizing that (1)

habitat selection refers to a process and not a pattern, (2) that there are many extrinsic factors that influence habitat selection, and (3) that a complete test of habitat selection involves an assessment of whether or not the documented habitat preferences are adaptive. A second concern was that ornithologists do not consistently use and perceive habitat-related terminology. This lack of consistency can be remedied by providing operational definitions to limit misunderstanding. A third concern was that methodologies commonly employed to document habitat selection do not account for the hierarchical nature of habitat selection and do not generate accurate representations of habitat availability. Comparisons of used habitat with available habitat are more appropriate than comparisons of used and unused habitat. Definitions of habitat availability ought to be informed by the natural- and life-history characteristics of the focal species.

ACKNOWLEDGMENTS

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.

Alldredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 50:157-165.

Alldredge, J. R. and J. T. Ratti. 1992. Further comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 56:1-9.

Anderson, J. T., and T. C. Tacha. 1999. Habitat use by Masked Ducks along the Gulf Coast of Texas. Wilson Bulletin 111:119-121.

Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. Ecology 77:215-227.

Badyaev, A. V., T. E. Martin, and W. J. Etges. 1996. Habitat sampling and habitat selection by female wild turkeys: Ecological correlates and reproductive consequences. Auk 113: 636-646.

Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology: Theory and applications. Pages 35-91 *in* Current Ornithology, Vol. 11 (D.M. Power, Ed.). Plenium Press, New York.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215-244.

Clark, R. G., and D. Shutler. 1999. Avian habitat selection: Pattern from process in nest-site use by ducks? Ecology 80:272-287.

Cody, M. L. 1981. Habitat selection in birds: The roles of vegetation structure, competitors and productivity. BioScience 31:107-113.

Cody, M. L. (Ed.). 1985. Habitat selection in birds. Academic Press, Orlando, FL.

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. Ecology 79:2415-2428.

Darveau, M., J. L. Desgranges, and G. Gauthier. 1992. Habitat use by three insectivorous birds in declining maple forests. Condor 94: 72-82.

Evans, D. R., and J. E. Gates. 1997. Cowbird selection of breeding areas: The role of habitat and bird species abundance. Wilson Bulletin 109:470-480.

Forsman, J. T., M. Mönkkönen, P. Helle, and J. Inkeröinen. 1998. Heterospecific attraction and

food resources in migrants' breeding patch selection in northern boreal forest. Oecologia

115:278-286.

Frederick, G. P., and R. J. Gutiérrez. 1992. Habitat use and population characteristics of the

White-tailed Ptarmigan in the Sierra Nevada, California. Condor 94:889-902.

Fretwell, S. D. 1972. Populations in seasonal environments. Princeton University Press, Princeton,

NJ.

Fretwell, S. D., and H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing

habitat distributions of birds. Acta Biotheoretica 19:16-36.

Gates, J. E., and D. R. Evans. 1998. Cowbirds breeding in the central Appalachians: Spatial and

temporal patterns and habitat selection. Ecological Applications 8:27-40.

Grinnell, J. 1917. Field tests of theories concerning distributional control. American Naturalist

51:115-128.

Haila, Y., A. O. Nicholls, I. K. Hanski, and S. Raivio. 1996. Stochasticity in bird habitat selection:

Year-to-year changes in territory in a boreal forest birds assemblage. Oikos 76:536-552.

Hall, L. S., P. R. Krausman and M. L. Morrison. 1997. The habitat concept and a plea for standard

terminology. Wildlife Society Bulletin 25:173-182.

Hildén, O. 1965. Habitat selection in birds: a review. Annals Zoologica Fennici 2:53-75.

Hooge, P. N., M. T. Stanback, and W. D. Koenig. 1999. Nest-site selection in the Acorn

Woodpecker. Auk 116: 45-54.

Hutto, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. Pages 455-476 *in*

Habitat selection in birds (M.L. Cody, Ed.). Academic Press, New York.

James, F. C., and C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: Panacea or Pandora's Box. Annual Review of Ecology and Systematics 21:129-166.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Karr, J. R., and K. E. Freemark. 1983. Habitat selection and environmental gradients: Dynamics in the "stable" tropics. Ecology 64:1481-1494.

Kendeigh, S. C. 1945. Community selection in birds on the Heldenberg Plateau of New York. Auk 62:418-436.

Kennedy, M., and R. D. Gray. 1994. Agonistic interactions and the distributions of foraging organisms: Individual costs and social information. Ethology 96:155-165.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. Oikos 59:253-260.

Linder, K. A., and S. H. Anderson. 1998. Nesting habitat of Lewis' Woodpeckers in southeastern Wyoming. Journal of Field Ornithology 69: 109-116.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist 100:603-609.

Martin, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455-473 *in* Ecology and conservation of neotropical migrants (J. M. Hagan, and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, DC.

Martin, T. E. 1993. Nest predation and nest sites: New perspectives on old patterns. BioScience 43:523-532.

Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79:656-6670.

McCollin, D. 1998. Forest edges and habitat selection in birds: A functional approach. Ecography 21:247-260.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: Concepts and applications. University of Wisconsin Press, Madison, WI.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:S29-S49.

Pampush, G. J., and R. G. Anthony. 1993. Nest success, habitat utilization and nest-site selection of Long-billed Curlews in the Columbia Basin, Oregon.. Condor 95: 957-967.

Petit, L. J., and D. R. Petit. 1996. Factors governing habitat selection by Prothonotary Warblers: Field tests of the Fretwell-Lucas models. Ecological Monographs 66:367-387.

Pöysä, H., J. Elmberg, K. Sjöberg, and P. Nummi. 1998. Habitat selection rules in breeding Mallards (*Anas platyrhynchos*): A test of two competing hypotheses. Oecologia 114:283-287.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652-661.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: A landscape perspective on population dynamics. American Naturalist 137:S50-S66.

Ramsay, S. M., K. Otter, and L. M. Ratcliffe. 1999. Nest-site selection by female Black-capped Chickadees: Settlement based on conspecific attraction. Auk 116:604-617.

Robertson, R. J. 1972. Optimal niche space of the Red-winged Blackbird (*Agelaius phoenicus*). I. Nesting success in marsh and upland habitat. Canadian Journal of Zoology 50:247-263.

Romesburg, H. C. 1981. Wildlife science: Gaining reliable knowledge. Journal of Wildlife Management 45:293-313.

Rosenzweig, M. L. 1991. Habitat selection and population interactions: The search for

mechanism. American Naturalist 137:S5-S28.

Rotenberry, J. T., and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in

North American steppe vegetation: A multivariate analysis. Ecology 61:1228-1250.

Ryan, M.R., and R.B. Renkin. 1987. Habitat use by breeding Willets in the northern Great Plains.

Wilson Bulletin 99: 175-189.

Schaffner, F.C. 1991. Nest-site selection and nesting success of White-tailed Tropicbirds (*Phaethon

lepturus*) at Cayo Luís Peña, Puerto Rico. Auk 108: 911-922.

Sieg, C.H., and D.M. Becker. 1990. Nest-site habitat selected by Merlins in southeastern Montana.

Condor 92: 688-694.

Smith, D.G., T. Bosakowski, and A. Devine. 1999. Nest site selection by urban and rural Great

Horned Owls in the northeast. Journal of Field Ornithology 70: 535-542.

Sonerud, G. A. 1985. Nest hole shift in Tengmalm's Owl *Aegolius funereus* as defence against

nest predation involving long-term memory in the predator. Journal of Animal Ecology

54:179-192.

Spencer, H. G., M. Kennedy, and R. D. Gray. 1996. Perceptual constraints on optimal foraging:

The effects of variation among foragers. Evolutionary Ecology 10:331-39.

Svärdson, G. 1949. Competition and habitat selection in birds. Oikos 1:157-174. .

Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and

availability. Journal of Wildlife Management 54:322-330.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife

Management 47:893-901.

Verner, J., M. L. Morrison, and C. J. Ralph (Eds.). 1986. Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, WI.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radiotracking data. Academic Press, San Diego, CA.

Wiens, J. A. 1973. Pattern and process in grassland bird communities. Ecological Monographs 43:237-270.

Wiens, J. A. 1984. Resource systems, populations, and communities. Pages 397-436 *in* A new ecology: novel approaches to interactive systems (P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, Eds.). John Wiley and Sons, New York, NY.

Wiens, J. A. 1986. Spatial scale and temporal variation in studies of shrubsteppe birds. Pages 154-172 *in* Community ecology (J. Diamond and T. J. Case, Eds.). Harper and Row, New York, NY.

Wiens, J. A. 1989. The ecology of bird communities. Vol. 1. Foundations and patterns. Cambridge University Press, New York.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: The effects of spatial scale. Oikos 48:132-147.

Wilson, W.H., Jr., R.E. Zierzow, and A.R. Savage. 1998. Habitat selection by peatland birds in a central Maine bog: the effects of scale and year. Journal of Field Ornithology 69: 540-548.

Chapter 3

Territory and nest-site selection of the Cerulean Warbler in eastern Ontario.

Jason Jones and Raleigh J. Robertson

ABSTRACT

We examined habitat selection by breeding Cerulean Warblers at three spatial scales in eastern Ontario over 3 years (1997-1999). Territories were characterized by well-spaced large trees and dense foliage cover at heights between 12 – 18m. The results of our nest-patch (0.04ha circle around nest) and nest-site (0.01ha circle) analyses indicate that male Cerulean Warblers may take active roles in nest-site selection when selecting territories. We conclude from our nest-patch and nest-site selection analyses that territories likely contain multiple nest patches and sites and that male Cerulean Warblers may defend areas with multiple nest patches or sites which may attract females to settle with them. Whether or not Cerulean Warbler females use nest-site availability as a mate- or territory choice cue is unknown. We also tested the validity of the assumption that a random sampling of habitat by researchers is representative of the habitat actually available to the birds and found that, in our study area at least, the assumption was invalid. In addition, discriminant function analyses indicated that the differences between successful and unsuccessful nest-sites were greater than the differences between nest-sites and available habitat. One interpretation is that the habitat in eastern Ontario is unsaturated with Ceruleans and that unoccupied "good" habitat confounds comparisons between used and available habitats. A second possibility is that nest-site selection processes in our study area have been altered by a recent large habitat disturbance in the form of an ice storm in 1998. Both interpretations indicate that we need to be conservative with forest management plans, and protect large tracts of mature forest.

INTRODUCTION

Preferences for certain habitats are presumed to be adaptive (i.e., fitness is higher in selected habitats), yet few studies of avian habitat selection address fitness (Martin 1998, Clark and Shutler 1999). Those that do rarely focus on individual fitness despite the fact that detailing the potential fitness consequences of individual microhabitat choices (e.g. nest-sites) within habitat types may provide the best appreciation of the adaptive foundation of habitat selection patterns (Martin 1986, 1998). It is equally important to recognize that habitat selection (including selection of microhabitats) is a hierarchical process, both in space and time (Johnson 1980, Wiens et al. 1987, Kotliar and Wiens 1990, Orians and Wittenberger 1991). For birds, habitat likely affects nest placement and success at two spatial scales: the nest-patch (characteristics of the habitat surrounding the nest-site) and the nest-site (characteristics in the immediate vicinity of the nest) (Martin and Roper 1988). For species that maintain all-purpose territories, these influences are felt after the selection of general breeding habitat (i.e., territory selection). Understanding the hierarchical processes leading to observed habitat use patterns becomes can help prevent critical management errors when dealing with species of conservation concern (Caughley 1994).

The focus of this study is the Cerulean Warbler (*Dendroica cerulea*). Data from the North American Breeding Bird Surveys indicate that this species is exhibiting severe local population declines (Robbins et al. 1992, Peterjohn et al. 1995, James et al. 1996). this species has been variously designated as threatened, rare, or of special concern in the United States and of special concern in Canada (Robbins et al.1992, COSEWIC 2000, Hamel 2000). In general, Cerulean Warblers are thought to require large tracts of mature,

deciduous forest (Robbins et al. 1992); however, its small-scale habitat affinities are poorly understood beyond a general conclusion that large trees with dense canopies are preferred as nest habitat (Robbins et al.1992, Oliarnyk 1996).

In this paper we examine habitat selection by Cerulean Warblers at several spatial scales. First, we describe territory selection by males. Second, we test the assumption that habitat sampling randomly provides an accurate assessment of habitat availability. We hypothesize that this assumption is not valid for birds that defend all-purpose territories. Using the results of these tests, we then test for evidence of habitat selection at two nest scales (nest-patch and nest-site) by examining differences between nests and random locations within territories as evidence of long-term natural selection and between successful and unsuccessful nest locations as evidence of current natural selection (*sensu* Clark and Shutler 1999).

STUDY AREA

This investigation was conducted at the Queen's University Biological Station (QUBS), Ontario, Canada (44°34'N, 76°20'W), within the Great Lakes- St. Lawrence mixed forest region. Our study area was restricted to approximately 2600 ha of research tracts managed by QUBS (Jones et al. 2000). All nest-searching activities were carried out in two study grids (11.4 and 6.4 ha) that were characterized as mature, secondary-growth, lowland mixed deciduous forest with a canopy layer dominated by sugar maple (*Acer saccharum*), and to a lesser extent oak (*Quercus* spp.), and elm (*Ulmus* spp.). The population studied in this research is located at the extreme northern edge of the breeding range of this species (Dunn and Garrett 1997).

METHODS

Nest searching and territory mapping. - From May to June of 1997-99, the two sites were searched for Cerulean Warbler nests. Nests were located by following females with nesting material or, for nests found at later stages, by following males delivering food to incubating females or by witnessing a feeding trip by either parent. Nests were checked every 2-3 days. Nests that fledged at least one young were considered successful. All failed nests, whether succumbing to predation, exposure or abandonment, were lumped as unsuccessful as we were unable to ascertain the cause of nest failure in all cases.

Territories of males were mapped using playback (Falls 1981) and by noting location of counter-singing bouts and aggressive interaction between neighboring males. Over two-thirds of the adult males in our study population were color-marked which simplified identification of territory boundaries.

Territory habitat sampling. – In 1998 and 1999, we sampled habitat in 115 territories throughout the study area (including the two study grids). For each territory, habitat was sampled in a single 5 m radius circle plot located within the territory boundaries. This location was selected by moving a random distance (restricted to ≤ 40 m) and direction (both generated by a random number generator) from the first detected location of the target male on the day of sampling. Within each of the plots, nine habitat variables were measured and calculated: number of saplings (SAPS; diameter at breast height < 3.0 cm), number of trees (TREE; diameter at breast height ≥ 3.0 cm), basal area of all trees (AREA), the ratio of AREA to TREE (ARAT), foliage cover in four height categories (< 6 m, FC1; ≥ 6-12 m, FC2; ≥ 12-18 m, FC3; ≥ 18 m, FC4), and maximum tree height (MAX). Foliage cover was measured in a 1 m radius cylinder, centered within the 5 m

radius plot, which was projected from the forest floor to the top of the canopy. Total

cover and percent cover of each species was estimated by eye in each height interval on a

scale of 0 to 10 (0 = 0% cover, 10 = 100% cover). Foliage cover was estimated by the

same observer in all years.

Identical habitat measurements were made at 111 non-territory locations within

the study area. These locations were selected by moving a random distance and direction

from the territory habitat sampling location and were restricted in two ways. Each 5 m

radius circle could not contain water (e.g. not on a pond edge) and each point had to be at

least 200 m away from the nearest singing male to limit the likelihood that the sampling

point fell within a male's territory.

Nest-patch and nest-site habitat sampling. – The same habitat variables were measured

for nest patch and nest-site analyses. Five 5m radius plots were used; one plot was

centered on the nest and the other 4 were centered on points 11.4 m away from the nest in

each of the cardinal directions (cf. James and Shugart 1970). Measurements from all 5

plots were averaged for the nest-patch analyses and only the central plot was used for the

nest-site analyses (Fig. 1). In 1997 and 1998, all foliage cover estimates were made by

the same two observers who standardized their estimates at the start of each season; one

of these observers performed all foliage cover estimates in 1999.

All habitat variables were also measured at a random location (5 - 5 m plots) for

each nest-site or patch, the randomly selected center representing a nest location.

Random locations were selected by moving a randomly generated distance and direction

from the focal nest. To test the assumption that a random sampling of habitat was

representative of the habitat actually available to a bird when making nest-site decisions,

random locations were chosen in two ways. In the first set of analyses, only those random locations that fell within the territory boundaries of the focal male were accepted and measured. These locations and analyses are referred to throughout the manuscript as "available" locations (Fig. 1); in this sense, habitat availability is defined by the behavior of the bird. In the second set of analyses, all random locations were accepted and measured, irrespective of territory boundaries; some random location fell within territory boundaries. These locations and analyses are referred to throughout the manuscript as "random" locations (Fig. 1).

Analyses - Statistical analyses were performed with JMP 3.2.1 (SAS Institute 1997) and SPSS 9.0.1. (SPSS Inc. 1999). All habitat variables that were not normally distributed (as determined by Shapiro-Wilk tests) were optimally transformed before using them in analyses (square-root transformations for SAPS in all analyses, square root transformation for TREE in territory analyses, square root transformation for AREA in territory analyses, log transformation for ARAT in the territory analyses, square root transformation for ARAT in the nest-site analyses). Bartlett's tests for homogeneity of variances were performed on both the transformed and remaining untransformed variables and no significant heteroscedasticity was detected. Means ± SE of untransformed data are presented in the tables for ease of interpretation.

To test the assumption that "random" equals "available", t-tests were performed on each of the habitat variables comparing between nest locations and random locations and between nest locations and available locations. Univariate analyses (t-tests) were also used to compare successful nest-patches and nest-sites with unsuccessful ones. We lumped all nests from 1997-99 for the nest-patch analyses and 1998-99 for the nest-site

analyses due to within-year sample size constraints and due to subtle differences in

habitat sampling regimes in 1997 and 1998-9.

We also examined the differences in habitat variables between first nest-sites and

re-nest sites in 1999. First nest-sites are defined as the first nest found for a given pair in

a given territory; re-nests are any other nests found subsequently in the same territory,

following failure of the first nest. Sequential Bonferroni corrections were applied where

appropriate to control the group-wide type-I error rates (Rice 1989).

We then tested for multicollinearity among the nine habitat variables using

principal components analysis. For each nest and available location, the first principal

component explained less variation than could occur by chance (Legendre and Legendre

1983, Jackson 1993) from which we inferred that the variables were orthogonal. Hence,

the original transformed variables were used in a discriminant function analysis (DFA).

Covariance matrices were tested for homogeneity and no significant heteroscedasticity

was detected. The DFA collapsed the nine habitat variables into one composite function

that maximized differences between sites. The first DFA tested whether nest locations

differed from available locations, at either nest scale. The second DFA tested whether

successful nests differed from unsuccessful nests, at either scale. We compensated for

unequal sample sizes among groups by setting prior classification probabilities

proportional to initial sample sizes for each group. For both DFAs, habitat variables with

loadings of $< |0.40|$ were deemed uninformative (Cooley and Lohnes 1971). In addition to

examining the original classification derived by the DFAs, we also performed cross-

validated classifications whereby each observation (i.e. 30min watch) is classified by the

derived functions of all the other observations. Further, as DFA can correctly classify

observations by chance alone, we calculated chance-corrected classification values to determine the percent improvement over chance generated by both the original and cross-validated DFAs (Titus et al. 1984). We calculated Kappa statistics and Z-tests to test whether the improvement over chance was statistically significant (Titus et al. 1984).

RESULTS

Territory selection. – Differences in mean habitat variables between territories and non-territory sites were consistent across the years 1998 and 1999 (Table 1). Territories had significantly higher mean basal areas (AREA), basal area:stem ratios (ARAT), and foliage cover between 12-18 m (FC3) in both years. In 1998, the maximum tree (TREE) was significantly higher in territories.

Univariate tests of nest-patch and nest-site selection. - In total, 79 nests found in 1997-9 were included in the nest patch analyses and 71 nests from 1998-9 were included in the nest-site analyses. At the level of the nest-patch, results using available patches were different than results using random patches (Table 2). Following Bonferroni corrections, however, only comparisons of nest-patches and random patches yielded significant differences in the means of habitat variables, and only in 1997 and 1999. In both years, random patches had higher mean TREE than did nest-patches (1997 nests 9.7 ± 0.9, random 18.2 ± 1.3, $t = -4.05$, df $= 32$, $P = 0.0003$; 1999 nests 12.9 ± 0.8, random 17.1 ± 0.8, $t = -3.82$, df $= 64$, $P = 0.0003$). In 1999, random patches were additionally characterized by lower mean ARAT (nests 0.02 ± 0.002 m^2/stem, random 0.01 ± 0.001 m^2/stem, $t = 4.63$, df $= 64$, $P < 0.0001$).

At the level of the nest-site, differences were also detected between analyses using random and available locations (Table 3) although these differences were not the

same ones detected at the level of the nest patch. In 1998, there were significant

differences in mean habitat variables between nest-sites and random sites (nests with

higher mean AREA and ARAT) while there were no significant differences between

nest-sites and available sites. In 1999, both available and random sites had lower mean

FC3 and lower mean MAX. For foliage cover above 18 m (FC4), however, available

sites had lower mean cover than did nest-sites while random sites had higher cover than

did nest-sites.

Very few habitat characteristics were linked to nest success. At the scale of the

nest-patch, no significant habitat differences were detected in the univariate analyses of

successful and unsuccessful patches (Table 4). The only significant difference detected

between successful and unsuccessful nest-sites was higher mean cover between 6-12m

for successful nest-sites (Table 5). There were no significant differences in mean habitat

values in 1999 between 1999 first nests and re-nests, regardless of how they were

grouped (Table 6).

Multivariate tests of nest-patch and nest-site selection. - The first DFA revealed that nest-

patches did not exhibit significant separation from available patches (Table 7, top part of

Fig. 2). However, nest-sites did show significant separation from available sites on the

first discriminant function and had higher loading on FC3, FC4 and ARAT than did

available sites (Table 7, bottom part of Fig. 2). The first discriminant function correctly

classified nest-sites more often than it did nest-patches for both the original and cross-

validated classifications although only the original nest-site classification represented a

significant improvement ($Z = 2.69$, $P = 0.004$; all other $Z < 1.40$, all other $P > 0.05$).

Likewise, the second DFA revealed significant differences between successful and unsuccessful nest locations but not at both scales. Successful nest-patches exhibited no significant separation from unsuccessful nest-patches on the first discriminant function (Table 7, top part of Fig. 3). Successful nest-sites showed significant separation from unsuccessful nest-sites on the first discriminant function and had higher loading on AREA, ARAT, and FC3 and lower loading TREE than unsuccessful nest-sites (Table 7, bottom part of Fig. 3). The first discriminant function correctly classified successful nests at the scale of nest-site more so than it did at the scale of the nest-patch and only at the scale of the nest-site did the function represent a significant improvement over chance ($Z = 2.84$, $P = 0.002$; all other $Z < 1.63$, all other $P > 0.05$).

DISCUSSION

Territory selection by male Cerulean Warblers at QUBS was influenced by the number and size (i.e. girth) of trees in an area and the foliage cover in the midstory. Male Ceruleans generally selected territories characterized by large, well-spaced trees with dense canopies. Territory selection by males was consistent between 1998 and 1999 with the exception of foliage cover below 6 m. As this height stratum is infrequently utilized by Cerulean Warblers (Jones personal observation), this discrepancy is likely not ecologically significant to this species.

Different nest-patch selection patterns emerged when nest-patches were compared with available patches and with random patches. More differences were detected between nest-patches and random patches; in fact, no significant differences between nest-patches and available patches were detected in any year. At the scale of the nest-site, differences between comparisons with available sites and random sites were also

evident. The most striking differences were detected in foliage cover over 18 m; not only did the two analyses generate different results, they generated opposite results. In 1999, nest-sites had higher foliage cover in this stratum than available sites but lower foliage cover than random sites.

These inconsistencies highlight the need to test, in the field, the assumption that a random sampling of habitats generates an accurate picture of available habitat (Aebischer et al. 1993, Jones in press). Wherever possible, the selection of habitat sampling methodology ought to be informed by the natural history of the focal species (e.g., Ramsay et al. 1999). Given the evidence for territory selection by Cerulean Warblers in this region, it comes as no surprise that using sampling points outside of territory boundaries might provide an inaccurate representation of nest-site selection. In terms of determining which habitat variables are important in nest-patch and nest-site selection in this species, we believe that comparisons with random locations located within the males' territory boundaries (i.e. available locations) are more meaningful than comparisons with random locations not so constrained. The magnitude of the differences between available and random analyses also likely depends on the number of random locations that actually fall within territory boundaries; the greater the overlap, the fewer the differences. This degree of overlap will be influenced by the sociality of the study species. For species that tend to have densely packed territories, such as the Cerulean Warbler (Hamel 2000, Jones and Robertson unpublished data), the likelihood that a random location will fall within a territory boundary is higher than for more solitary species (e.g., Scarlet Tanager, *Piranga olivacea*).

The low number of detected differences between nest locations and available locations, at both nest scales, may indicate that important nest-patch and nest-site selection decisions were made when males chose their territories. As females likely make the final nest-patch and site selection decisions in our study area, male Cerulean Warblers may try to defend areas with multiple nest-patches or sites in order to maximize the probability that females settle with them. The importance of nest-site availability as a mate- or territory choice cue for females has been hypothesized for other species (Leonard and Picman 1987, Martin 1988, Sedgwick and Knopf 1990, Steele 1993). Whether or not this is the case for Cerulean Warblers remains untested. Multiple nest-patches or sites within a territory may be attractive for several reasons. One reason is that multiple nest-patches or sites may provide insurance sites in case of nest failure. A second reason is that nesting in an area with many potential nest-patches or sites may act to lower nest predation pressures by increasing the number of potential locations a predator must examine (Martin and Roper 1988). The lack of detected differences between first nests and re-nests, at the scale of the nest-site, when coupled with the fact that most pairs in our study area will re-nest within the male's original territory boundaries after nest failure (Jones et al. unpublished data), lends support to the notion that males are choosing territories with multiple nesting opportunities. The presence of multiple nest-patches or sites within a single territory would affect our ability to detect differences between nest-sites or patches and available habitat if the "available" sampling point fell near a suitable but unused nest-site or patch. The results of this portion of the study highlight the need to be aware that habitat selection is a hierarchical process and

that, if the scale of study and analysis is inappropriate, key influences on habitat selection may be missed by the research (Orians and Wittenberger 1991, Aebischer et al. 1993).

The results of the first DFA indicated no significant differences between nest and available locations at the scale of the nest-patch, although significant differences were detected at the scale of nest-site, which can be taken as evidence of long-term (phenotypic) selection pressures; that is, long-term natural selection may lead to habitat preferences that are learned or genetic (Hildén 1965, Sonerud 1985, Clark and Shutler 1999). The most important distinguishing variables at the level of nest-site were foliage cover above 12m and basal area ratio, both of which were higher at nest-sites. These results are in concordance with previous findings for this species, both in this region (Oliarnyk 1996) and elsewhere within its breeding range (Hamel 2000). Cerulean Warblers generally nest on the bottom edge of the forest canopy (12-15m high, Oliarnyk 1996, Jones et al. in press) and likely cue on sites that offer, among other things, sufficient foliage coverage to conceal parental movements to and from the nest site. Nest cover is known to have a powerful influence on nest-site selection patterns of many species (Martin 1998) and forest stands characterized by widely-spaced large trees (i.e. high basal area ratios) tend to have suitable canopy structure for Cerulean Warblers in our study area.

Examination of the differences between nest and random sites highlights patterns of habitat use rather than habitat selection processes (Wiens 1986, Clark and Shutler 1999). To examine habitat selection *processes*, we contrasted the characteristics of successful and unsuccessful nests to assess the fitness consequences of nest-site selection decisions (Martin 1998, Clark and Shutler 1999). The results from the second DFA

indicated no significant differences between successful and unsuccessful nests at the scale of the nest-patch but did so at the level of the nest-site. The most important distinguishing variables at the nest-site were number of trees (higher at unsuccessful nests), basal area and basal area ratio (both higher at successful nests), and foliage cover between 6-12m (also higher at successful nests). Within forest stands with large trees and well-developed canopy layers, successful breeders made microhabitat choices at the high extreme of availability spectrum (e.g., the largest trees). Most of these patterns are similar to those observed in previous work on this species in the region (Oliarnyk 1996). The patterns we observed at the level of the territory were thus amplified at the level of the nest-site. Unlike Oliarnyk (1996), however, we found a connection between nest success and high foliage cover between 6-12m, which is the foliage layer just below most nest locations. The difference between Oliarnyk's work (1996) and ours may reflect the short-term variability in, and stochastic nature of, factors contributing to nest success (Wiens 1985, Burger 1987, Filliater et al. 1994, Hogstad 1995).

The DFA performed better at the scale of the nest-site than at the scale of nest-patch for both nest vs. available (64% and 68%, respectively) and successful vs. unsuccessful nests (80% and 92%, respectively). This is largely a scale issue in that important nest-site selection decisions that have not already occurred in the selection of the territory by the male, occur at the microhabitat (i.e. nest-site) level.

At the nest-site scale, the DFA performed better in distinguishing successful vs. unsuccessful nests than it did in distinguishing nest-sites vs. available sites (92% and 68%, respectively). This is contrary to existing theory which contends that differences between successful and unsuccessful nests are usually more subtle than differences

between nest and non-nest habitat (Clark and Shutler 1999). The lack of distinction between nest-sites and available sites relative to that between successful and unsuccessful nests has several possible explanations. The first one parallels our univariate results; that is, there are multiple suitable nest-sites within each territory.

The second explanation revolves around the recent establishment of the study population. The first Cerulean Warbler nest record in eastern Ontario is from 1963 (Quilliam 1973) and our study population is on the leading edge of a northward range expansion for this species (Robbins et al. 1992). The young "age" of the study population may contribute to the apparent lack of habitat saturation resulting in suitable Cerulean Warbler habitat going unused. This would confound efforts to consistently distinguish differences between used and available habitats (Wiens 1986, Wiens et al. 1987).

A third explanation follows from the second in that nest-site selection in this region is driven by current selection pressures which may have been recently altered by the ice storm in the winter of 1998. In fact, Cerulean Warblers in our study area appear to have altered certain aspects of their nest location preferences, such as the distance to nearest canopy gap, following the ice storm (Jones et al. in press). Large scale disturbances such as the ice storm can play major roles in altering selection pressures and can have major impacts on habitat selection patterns exhibited by bird populations (Brokaw and Grear 1991, Thurber et al. 1994, Paine et al. 1998).

ACKNOWLEDGEMENTS

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74: 1313-1325.

Brokaw, N. V. L., and J. S. Grear. 1991. Forest structure before and after Hurricane Hugo at three elevation in the Luquillo Mountains, Puerto Rico. Biotropica 23: 386-392.

Burger, J. 1987. Physical and social determinants of nest-site selection in Piping Plovers in New Jersey. Condor 89: 811-818.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63: 215-244.

Clark, R. G., and D. Shutler. 1999. Avian habitat selection: pattern from process in nest-site use by ducks? Ecology 80: 272-287.

Cooley, W. W., and P. R. Lohnes. 1971. Multivariate data analysis. John Wiley & Sons, Ltd., New York, USA.

COSEWIC. 2000. Canadian species at risk, May 2000. Committee of the Status of Endangered Wildlife in Canada, Ottawa, ON.

Dunn, J. L., and K. L. Garrett. 1997. Warblers. Houghton Mifflin Co., New York, NY.

Falls, J. B. 1981. Mapping territories with playback: an accurate census method for songbirds. Studies in Avian Biology 6: 86-91.

Filliater, T. S., R. Breitwisch, and P. M. Nealen. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? Condor 96: 761-768.

Hamel, P. B. 2000. Cerulean Warbler (*Dendroica cerulea*). *In* The birds of North America, no. 511 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D. C.

Hildén, O. 1965. Habitat selection in birds: a review. Annals Zoologica Fennici 2:53-75.

Hogstad, O. 1995. Do avian and mammalian nest predators select for different nest dispersion patterns of fieldfares *Turdus pilaris*? A 15-year study. Ibis 137: 484-489.

Jackson, D. A. 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology 74: 2204-2214.

James, F. C., C. E. McCulloch, and D. A. Wiedenfeld. 1996. New approaches to the analysis of population trends in land birds. Ecology 77: 13-27.

James, F. C., and H. H. Shugart. 1970. A quantitative method of habitat description. Audubon Field Notes 24: 727-737.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65-71.

Jones, J. in press. Habitat selection studies in avian ecology: a critical review. Auk.

Jones, J., R. D. DeBruyn, J. J. Barg, and R. J. Robertson. in press. Assessing the effects of natural disturbance on a Neotropical migrant songbird. Ecology.

Jones, J., W. L. McLeish, and R. J. Robertson. 2000. Density influences census technique accuracy for Cerulean Warblers in eastern Ontario. Journal of Field Ornithology 71: 46-56.

Kotliar, N. B. and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59: 253-260.

Legendre, L., and P. Legendre. 1983. Numerical ecology. Elsevier, Amsterdam, The Netherlands.

Leonard, M. L., and J. Picman. 1987. The adaptive significance of multiple nest building by male marsh wrens. Animal Behavior 35: 271-277.

Martin, T. E. 1986. Competition in breeding birds: on the importance of considering processes at the level of the individual. Current Ornithology 4: 181-210.

Martin, T. E. 1988. Process organizing open-nesting bird assemblages: competition or nest predation? Evolutionary Ecology 2: 37-50.

Martin, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79: 656-670.

Martin, T. E. and J. J. Roper. 1988. Nest predation and nest site selection in a western population of Hermit Thrush. Condor 90: 51-57.

Oliarnyk, C. J. 1996. Habitat selection and reproductive success in a population of Cerulean Warblers in southeastern Ontario. M.Sc. thesis, Queen's University, Kingston, ON.

Orians, G. and J. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137: 829-849.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1: 535-545.

Peterjohn, B.C., J.R. Sauer, and C.S. Robbins. 1995. Population trends from the North American Breeding Bird Survey. Pages 3-39 *in* Ecology and management of neotropical migratory birds: A synthesis and review of critical issues (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.

Quilliam, H. R. 1973. History of the birds of Kingston, Ontario. Kingston Field Naturalists, Kingston, Ontario.

Ramsay, S. M., K. Otter, and L. M. Ratcliffe. 1999. Nest-site selection by female Black-capped Chickadees: settlement based on conspecific attraction. Auk 116: 604-617.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 223-225.

Robbins, C. S., J. W. Fitzpatrick, and P. B. Hamel. 1992. A warbler in trouble: *Dendroica cerulea*. Pages 549-562 *in* Ecology and conservation of Neotropical migrant

landbirds (J.M. Hagan III, and D.W. Johnston, Eds.). Smithsonian Institution
Press, Washington, D.C.

SAS Institute Inc. 1997. JMP 3.1.7. SAS Institute Inc., Cary, NC, USA.

Sedgwick, J. A., and F. L. Knopf. 1990. Habitat relationships and nest site characteristics
of cavity-nesting birds in cottonwood floodplains. Journal of Wildlife
Management 54: 112-124.

Sonerud, G. A. 1985. Nest hole shift in Tengmalm's owl *Aegolius funereus* as defense
against nest predation involving long term memory of the predator. Journal of
Animal Ecology 54: 179-192.

SPSS Inc. 1999. SPSS 9.0.1. SPSS Inc., Chicago, IL.

Steele, B. B. 1993. Selection of foraging and nesting sites by Black-throated Blue
Warblers: their relative influence on habitat choice. Condor 95: 568-579.

Thurber, D. K., W. T. McClain, and R. C. Whitmore. 1994. Indirect effects of gypsy
moth defoliation on nest predation. Journal of Wildlife Management 58: 493-500.

Titus, K., J. A. Mosher, and B. K. Williams. 1984. Chance-corrected classification of use
in discriminant analysis: ecological applications. American Midland Naturalist
111: 1-7.

Wiens, J. A. 1985. Habitat selection in variable environments: shrub-steppe birds. Pages
227-251 *in*. Habitat selection in birds (M.L. Cody, Ed.). Academic Press, Toronto,
Ontario, Canada.

Wiens, J. A. 1986. Spatial scale and temporal variation in studies of shrubsteppe birds.
Pages 154-172 *in* Community ecology (J. Diamond and T. Case, Eds.). Harper
and Row, New York.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of

North American shrubsteppe birds: the effects of spatial scale. Oikos 48: 132-147.

Table 1. Comparison of habitat variables within and outside of occupied territories. Values shown are mean ± SE of untransformed variables. *P*-values for the territory vs. non-territory *t*-tests are given in parentheses. Bold face values are significant after sequential Bonferroni corrections with a group-wide α of 0.05 (Rice 1989).

	Within territories		
	1998	1999	Non-territories
	($n = 67$)	($n = 48$)	($n = 111$)
# of saplings (SAPS)	38.9 ± 2.51	42.5 ± 2.77	50.2 ± 2.79
	(0.016)	(0.221)	
# of trees (TREE)	15.9 ± 0.80	15.2 ± 0.93	16.6 ± 0.83
	(0.584)	(0.311)	
tree basal area (m^2) (AREA)	0.23 ± 0.017	0.23 ± 0.024	0.17 ± 0.014
	(0.0004)	**(0.004)**	
AREA:TREE (m^2/stem) (ARAT)	0.02 ± 0.002	0.02 ± 0.003	0.010 ± 0.001
	(<0.0001)	**(<0.0001)**	
Foliage cover below 6m (FC1)	4.8 ± 0.27	5.0 ± 0.21	5.2 ± 0.18
	(0.231)	(0.532)	
Foliage cover 6-12m (FC2)	4.4 ± 0.32	4.8 ± 0.34	4.9 ± 0.23
	(0.137)	(0.745)	
Foliage cover 12-18m (FC3)	4.5 ± 0.32	4.4 ± 0.38	3.0 ± 0.28
	(0.0006)	**(0.005)**	

Foliage cover over 18m (FC4)	1.8 ± 0.33	1.2 ± 0.29	1.1 ± 0.22
	(0.053)	(0.733)	
maximum tree height (m) (MAX)	17.3 ± 0.48	15.7± 0.60	13.3 ± 0.59
	(<0.0001)	(0.015)	

Table 2. Comparison of nest-patches with available and random patches. Shown are means ± SE of untransformed variables. P-values for nest vs. random t-tests in brackets. Bold values significant after sequential Bonferroni corrections (group-wide $\alpha = 0.05$).

Variable	1997			1998			1999		
	Nest (n = 8)	Available (n = 8)	Random (n = 23)	Nest (n = 43)	Available (n = 24)	Random (n = 42)	Nest (n = 28)	Available (n = 20)	Random (n = 35)
SAPS	60.9 ± 7.5	55.6 ± 11.0 (0.61)	54.0 ± 4.5 (0.42)	36.3 ± 1.9	38.2 ± 3.9 (0.79)	44.6 ± 3.1 (0.034)	41.9 ± 2.7	38.2 ± 2.4 (0.37)	45.3 ± 2.6 (0.39)
TREE	9.7 ± 0.9	16.5 ± 2.7 (0.03)	18.2 ± 1.3 **(0.0003)**	15.3 ± 0.8	14.2 ± 1.0 (0.35)	16.2 ± 0.9 (0.034)	12.9 ± 0.8	15.6 ± 0.9 (0.02)	17.1 ± 0.8 **(0.0003)**
AREA (m²)	0.20 ± 0.05	0.21 ± 0.03 (0.82)	0.19 ± 0.01 (0.70)	0.20 ± 0.01	0.22 ± 0.02 (0.52)	0.19 ± 0.01 (0.071)	0.21 ± 0.01	0.22 ± 0.02 (0.29)	0.18 ± 0.01 (0.03)
ARAT (m²/stem)	0.02 ± 0.001	0.02 ± 0.003 (0.43)	0.01 ± 0.001 (0.023)	0.02 ± 0.001	0.02 ± 0.002 (0.90)	0.01 ± 0.001 (0.074)	0.02 ± 0.002	0.02 ± 0.001 (0.012)	0.01 ± 0.001 **(<0.0001)**
FC1	4.4 ± 0.5	4.8 ± 0.4 (0.46)	5.2 ± 0.2 (0.04)	4.9 ± 0.2	4.6 ± 0.2 (0.23)	4.9 ± 0.1 (0.86)	5.3 ± 0.2	5.0 ± 0.2 (0.25)	5.1 ± 0.1 (0.57)
FC2	3.9 ± 0.6	4.9 ± 0.5 (0.25)	5.3 ± 0.2 (0.02)	4.1 ± 0.2	3.9 ± 0.3 (0.53)	4.6 ± 0.2 (0.11)	4.3 ± 0.2	4.5 ± 0.3 (0.69)	5.0 ± 0.2 (0.03)
FC3	4.4 ± 0.9	4.4 ± 0.6 (0.95)	3.6 ± 0.3 (0.25)	3.5 ± 0.2	3.5 ± 0.3 (0.83)	3.4 ± 0.2 (0.86)	3.4 ± 0.3	2.6 ± 0.4 (0.09)	2.9 ± 0.3 (0.21)
FC4	3.7 ± 0.6	3.2 ± 0.6 (0.58)	1.7 ± 0.3 (0.01)	1.6 ± 0.3	1.1 ± 0.3 (0.13)	1.1 ± 0.2 (0.083)	0.9 ± 0.2	0.3 ± 0.1 (0.01)	0.7 ± 0.2 (0.54)
MAX (m)	18.8 ± 1.4	18.8 ± 1.4 (0.80)	15.5 ± 0.8 (0.21)	16.0 ± 0.6	15.5 ± 0.7 (0.62)	14.9 ± 0.6 (0.17)	14.8 ± 0.4	12.8 ± 0.7 (0.01)	13.4 ± 0.5 (0.06)

Table 3. Comparison of nest-sites with available sites and random sites. Available sites were located within known territorial boundaries, while random sites were placed without reference to territory boundaries. Values shown are means ± SE of untransformed variables. *P*-values for nest vs. random *t*-tests are in parentheses. Bold face values are significant after sequential Bonferroni corrections with a group-wide α of 0.05 (Rice 1989).

| | 1998 | | | 1999 | | |
	Nest ($n = 43$)	Available ($n = 24$)	Random ($n = 42$)	Nest ($n = 28$)	Available ($n = 20$)	Random ($n = 35$)
SAPS	36.2 ± 1.9	38.2 ± 3.9 (0.794)	43.0 ± 3.3 (0.137)	43.2 ± 3.9	41.5 ± 3.9 (0.84)	45.2 ± 3.3 (0.67)
TREE	15.3 ± 0.8	14.2 ± 1.0 (0.35)	14.3 ± 1.0 (0.29)	13.3 ± 1.2	17.8 ± 1.3 (0.01)	16.2 ± 1.1 (0.09)
AREA (m^2)	0.22 ± 0.01	0.21 ± 0.02 (0.37)	0.17 ± 0.02 **(0.004)**	0.22 ± 0.03	0.25 ± 0.04 (0.60)	0.19 ± 0.03 (0.25)
ARAT (m^2/stem)	0.02 ± 0.001	0.02 ± 0.002 (0.87)	0.01 ± 0.002 **(0.003)**	0.02 ± 0.004	0.01 ± 0.002 (0.33)	0.01 ± 0.002 (0.02)
FC1	4.8 ± 0.2	4.6 ± 0.2 (0.23)	4.9 ± 0.3 (0.97)	5.1 ± 2.8	4.9 ± 0.3 (0.70)	5.1 ± 0.3 (0.97)

FC2	4.1 ± 0.2	3.9 ± 0.3	3.8 ± 0.4	4.8 ± 4.6	4.9 ± 0.5	4.3 ± 0.5
		(0.53)	(0.47)		(0.93)	(0.48)
FC3	3.5 ± 0.2	3.5 ± 0.3	2.9 ± 0.4	5.7 ± 0.3	2.6 ± 0.6	2.3 ± 0.4
		(0.83)	(0.17)		(<0.0001)	(<0.0001)
FC4	1.7 ± 0.3	1.1 ± 0.3	0.93 ± 0.2	0.2 ± 0.4	0.1 ± 0.1	0.4 ± 0.2
		(0.13)	(0.03)		(0.001)	(0.001)
MAX (m)	16.0 ± 0.6	15.5 ± 0.7	13.0 ± 0.9	17.8 ± 0.4	12.7 ± 1.0	11.3 ± 0.8
		(0.62)	(0.01)		(<0.0001)	(<0.0001)

Table 4. Comparison of successful and unsuccessful nest-patches (successful = 17, unsuccessful = 62, df = 77). Values shown are means ± SE of untransformed variables. Results of t-tests are shown.

	Successful	Unsuccessful	t (P)
SAPS	43.8 ± 4.3	39.8 ± 1.9	0.890 (0.376)
TREE	13.0 ± 1.1	14.2 ± 0.6	-0.881 (0.381)
AREA (m^2)	0.23 ± 0.02	0.22 ± 0.01	0.906 (0.368)
ARAT (m^2/stem)	0.02 ± 0.003	0.02 ± 0.001	1.289 (0.201)
FC1	5.1 ± 0.3	4.9 ± 0.1	0.807 (0.422)
FC2	4.4 ± 0.3	4.1 ± 0.2	0.696 (0.488)
FC3	4.0 ± 0.5	3.4 ± 0.2	1.498 (0.138)
FC4	2.1 ± 0.4	1.4 ± 0.2	1.571 (0.120)
MAX (m)	16.7 ± 1.2	15.5 ± 0.4	1.195 (0.236)

Table 5. Comparison of successful and unsuccessful nest-sites in 1998 and 1999 (successful = 12, unsuccessful = 59, df = 69). Values shown are means ± SE of untransformed variables. Results of t-tests are shown. Bold face values are significant after sequential Bonferroni corrections with a group-wide α of 0.05 (Rice 1989).

	Successful	Unsuccessful	t (P)
SAPS	38.3 ± 4.1	39.1 ± 2.20	-0.085 (0.932)
TREE	14.7 ± 2.0	14.5 ± 0.71	-0.080 (0.936)
AREA (m^2)	0.28 ± 0.045	0.21 ± 0.096	1.928 (0.058)
ARAT (m^2/stem)	0.02 ± 0.004	0.02 ± 0.002	1.599 (0.115)
FC1	5.2 ± 0.36	4.9 ± 0.16	1.069 (0.298)
FC2	5.9 ± 0.49	4.1 ± 0.22	**3.383 (0.001)**
FC3	5.1 ± 0.60	4.2 ± 0.23	1.555 (0.125)
FC4	2.9 ± 0.57	1.6 ± 0.24	2.121 (0.038)
MAX (m)	18.1 ± 0.84	16.4 ± 0.43	1.604 (0.113)

Table 6. Comparisons among first nests and re-nests for 1999. There are no significant differences between any of the columns. Values shown are mean ± SE values of untransformed variables.

	all 1st nests ($n = 15$)	failed 1st nests ($n = 13$)	all re-nests ($n = 13$)	successful re-nests ($n = 6$)
SAPS	40.2 ± 4.1	40.2 ± 4.7	46.6 ± 7.0	33.0 ± 7.5
TREE	12.8 ± 1.9	11.7 ± 1.9	13.9 ± 1.4	12.8 ± 2.5
AREA (m^2)	0.22 ± 0.04	0.20 ± 0.04	0.24 ± 0.05	0.33 ± 0.09
AREA (m^2/stem)	0.02 ± 0.01	0.02 ± 0.01	0.02 ± 0.01	0.03 ± 0.01
FC1	4.7 ± 0.3	4.6 ± 0.3	5.5 ± 0.5	5.0 ± 0.6
FC2	4.5 ± 0.6	4.1 ± 0.6	5.2 ± 0.7	6.7 ± 0.6
FC3	5.7 ± 0.3	6.0 ± 0.4	5.6 ± 0.6	6.2 ± 0.9
FC4	1.6 ± 0.6	1.5 ± 0.7	2.5 ± 0.6	3.7 ± 0.8
MAX (m)	17.6 ± 0.5	17.6 ± 0.6	18.2 ± 0.7	19.2 ± 0.8

Table 7. Results of discriminant function analyses distinguishing between nest locations and available locations and sites and between successful and unsuccessful nests based on listed habitat variables. Loadings > |0.40| on DF1 are in bold.

	Nest vs. Available		Successful vs. Unsuccessful	
	nest-patch (79/52) [a]	nest-site (71/44)	nest-patch (17/62)	nest-site (12/59)
SAPS	-0.15	-0.03	0.04	-0.13
TREE	-0.16	0.28	-0.27	**-0.87**
AREA (m²)	-0.07	-0.37	-0.03	**1.29**
ARAT (m²/stem)	**0.55**	**0.49**	0.37	**0.90**
FC1	**0.55**	0.06	0.33	0.22
FC2	-0.10	-0.15	0.38	**0.80**
FC3	-0.03	**0.58**	0.31	-0.04
FC4	**0.82**	**0.64**	**0.75**	0.35
MAX (m)	-0.33	0.01	-0.31	0.17
Wilks' Lambda (P)	0.946	0.850	0.924	0.734
	(0.647)	(0.039)	(0.767)	(0.018)
correct classification (%)	64.1	67.8	79.7	91.5
% better than chance [b]	3.7	28.0	8.6	62.5
cross-validation classification (%)	58.0	61.7	74.7	84.5
% better than chance	2.1	14.3	6.8	34.0

[a] numbers in brackets are sample sizes of each category (e.g. 79 nests and 52 available

sites); [b] Percent improvement on chance discrimination. See Titus et al. (1984).

FIGURE CAPTIONS.

Figure 1. Schematic diagram of nest patch and nest-site habitat sampling regime. Large circles represent hypothetical territory boundaries and asterisks denote nest locations. A) Only the central 5 m radius plot at each location was included in the nest-site vs. available site or random site analyses. All five 5 m radius plots were averaged for the nest patch vs. available patch or random patch analyses. The following habitat variables were measured in each 5 m radius plot: number of saplings, number of trees, basal area of all trees, a basal area : stem ratio, foliage cover under 6m, foliage cover between 6-12 m, foliage cover between 12-18 m, foliage cover above 18 m, and maximum tree height. B) Both available and random locations are situated at a random distance and direction from the nest location. Available locations for nest patch and nest-site selection analyses fell within known territorial boundaries, while random locations were selected without reference to territorial boundaries although they were accepted if they fell wholly or partially within territory boundaries.

Figure 2. Distribution of discriminant function scores for nest patch analysis (top) and nest- site analysis (bottom) for comparisons of nest locations with available habitat. Arrows indicate direction of increasing values of habitat variables strongly influencing the first discriminant function (loadings > |0.40|).

Figure 3. Distribution of discriminant function scores for nest patch analyses (top) and nest-site analyses (bottom) for comparisons of successful and unsuccessful nests. Arrows

indicate direction of increasing values of habitat variables strongly influencing the first

discriminant function (loadings > |0.40|).

A)
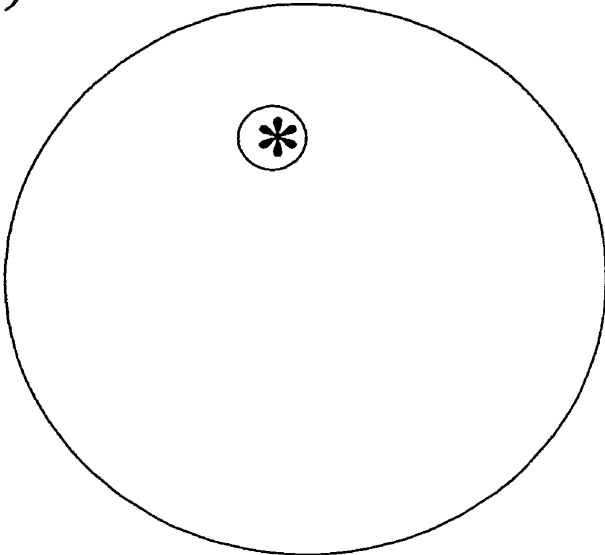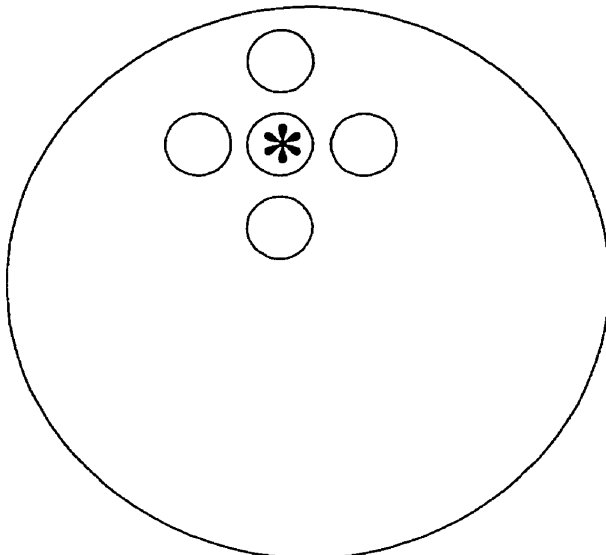
nest-site analyses   nest-patch analyses

B)
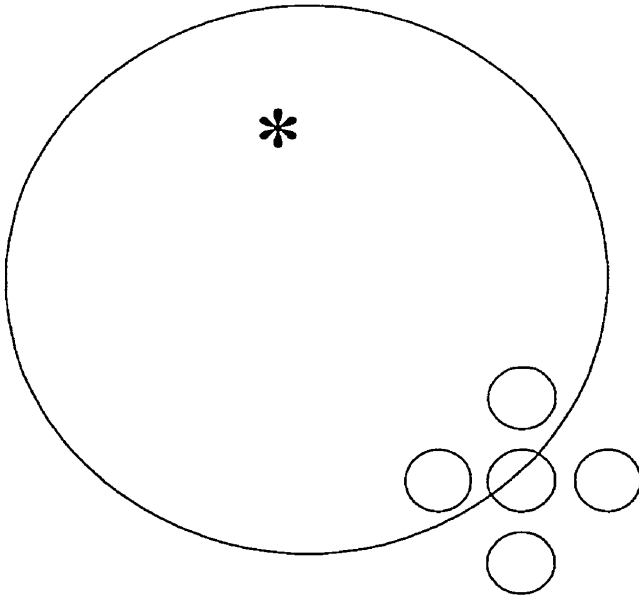
available location   random location
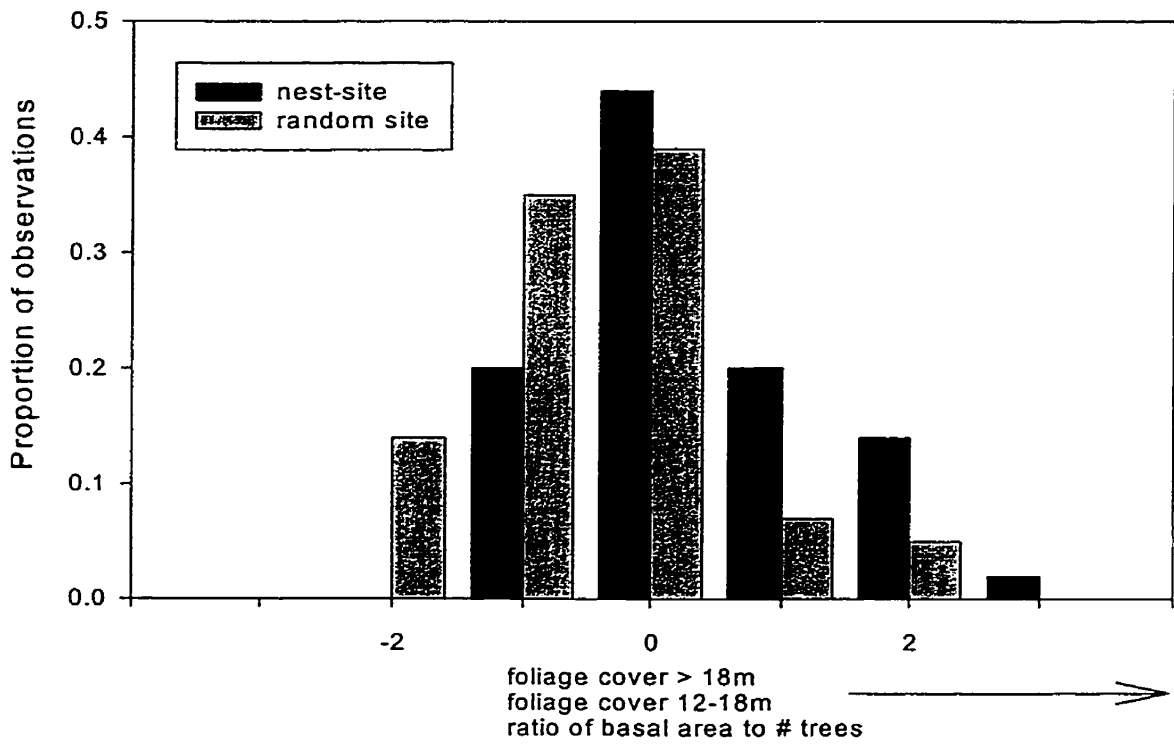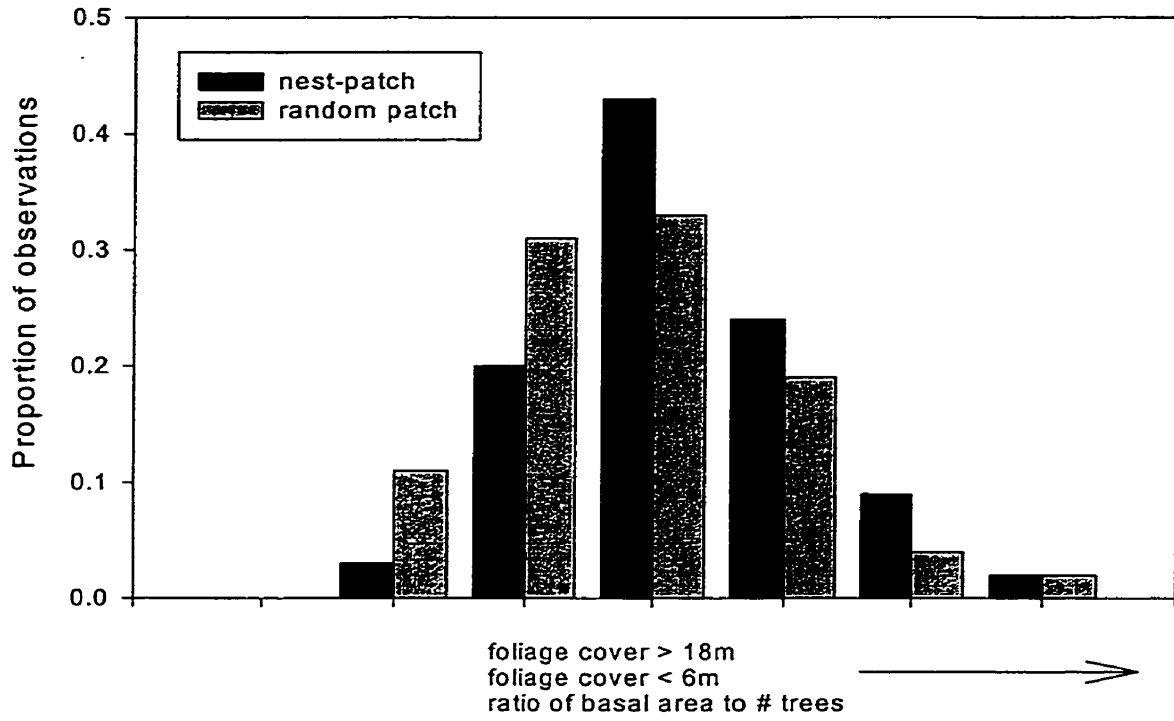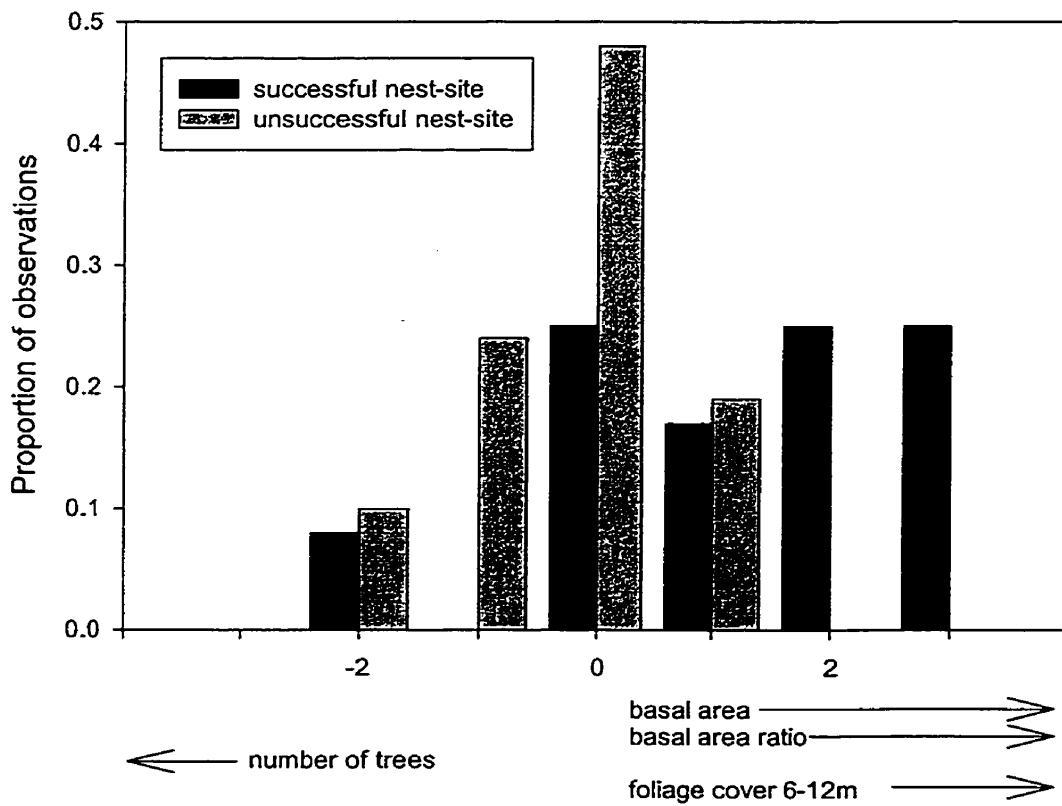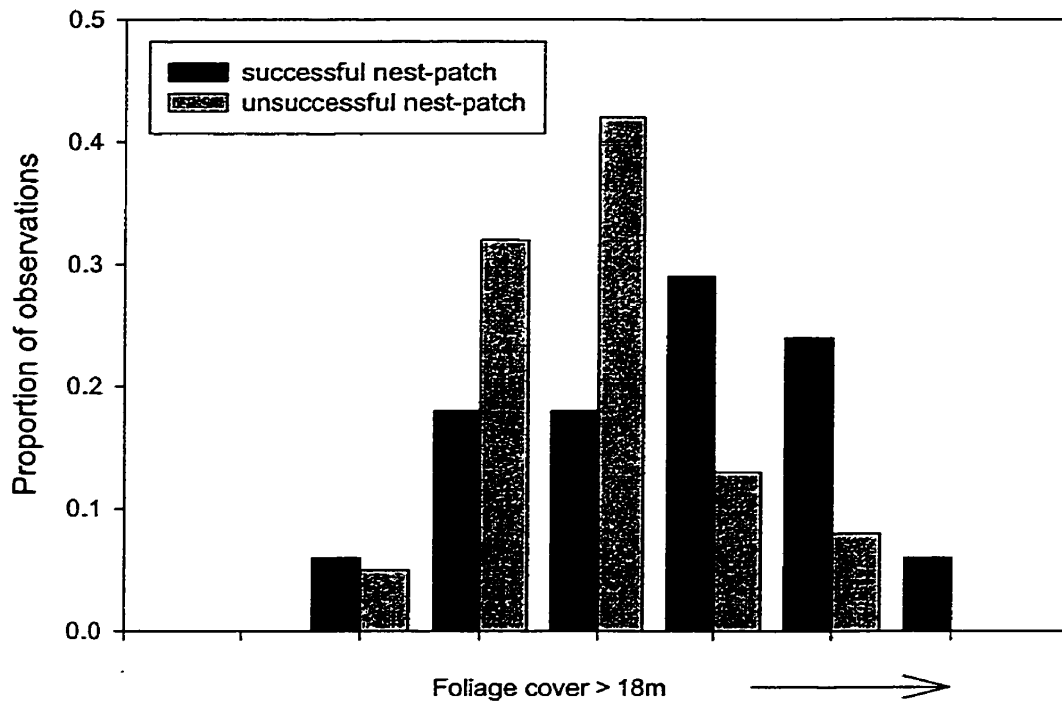
Chapter 3 – Figure 3

Chapter 4

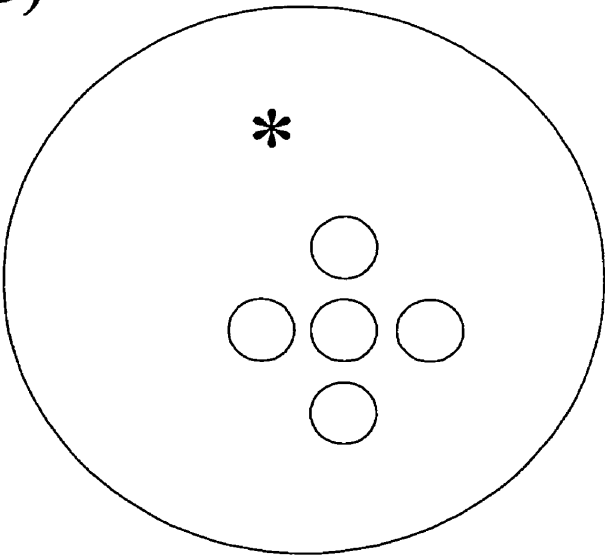Assessing the effects of natural disturbance on a Neotropical migrant songbird.

Jason Jones, Ryan D. DeBruyn, Jennifer J. Barg, and Raleigh J. Robertson

Abstract. Large-scale natural habitat disturbances can play major roles in structuring the distribution of individuals and ecosystems and can exert substantial selective pressures. The magnitude of these effects depends on the spatial and temporal scale of the disturbance, as well its frequency, intensity and predictability. In January 1998, the worst ice storm in documented Canadian history struck southern Ontario and Quebec. This storm affected over 10 million hectares of forest causing widespread damage. One of the regions negatively affected by the storm is home to a large breeding population of Cerulean Warblers, *Dendroica cerulea*. This population has been studied since 1994 thereby allowing a unique opportunity to examine the effects of a large-scale natural habitat disturbance on the reproductive ecology and behavior of this Neotropical migrant songbird. We addressed two main questions: (1) Did Cerulean Warbler reproductive success change after this habitat disturbance?, and (2) Did the breeding population exhibit a shift in habitat selection patterns in response to this habitat disturbance? The January 1998 ice storm resulted in a significant reduction in the amount of foliage in the forest canopy of our study area in the following spring. This was followed by a significant decline in Cerulean Warbler reproductive output in the 1998 breeding season. In 1999, Cerulean Warblers demonstrated a significant increase in territory size and a significant shift in nest-site location patterns; these shifts were accompanied by a significant increase in reproductive success. The 1999 shifts in territory and nest-site location patterns were affected by the same individuals who were failed breeders in 1998. This suggests that Cerulean Warblers possess a degree of plasticity in their habitat affinities and that this plasticity rendered the population somewhat resilient to this particular disturbance.

INTRODUCTION

A disturbance can be defined as "a relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985: 7). Natural disturbances vary greatly in their scale, frequency, predictability, intensity, severity, and duration (Paine et al. 1998, Turner and Dale 1998, Turner et al. 1998). They have profound influence on the abundance and distribution of individuals and exert substantial selective pressures on organisms and ecosystems (Levin and Paine 1974, Wootton 1998).

The majority of research into the effects of natural disturbances on animal populations has focussed on short-term population trends and changes in community patterns (Askins and Ewert 1991, Willig and Camilo 1991, Woolbright 1991), while few have examined long-term effects (Hughes 1994, Singer and Harter 1996, Canterbury and Blockstein 1997). Despite the importance of accurately describing the effects of natural disturbances and the ability of organisms to recover from them, these factors are often overlooked (Cade and Jones 1993, Caughley 1994, McCarthy 1996). This oversight can have serious implications when dealing with species of conservation concern (Dale et al. 1998).

In the week of January 4-10, 1998, the worst ice storm in documented Canadian history hit regions of eastern Ontario, southern Quebec and New Brunswick, as well as the northeastern United States (Irland 1998, Kerry et al. 1999). Over 10 million hectares of forest were affected by the storm and the accumulation of ice was extraordinary, as much as 80mm in some regions (Kerry et al. 1999). While freezing rain and ice storms

are not uncommon occurrences in Canada, storms as severe as the 1998 event are very

rare; this was the only storm of this magnitude to hit Canada in 100 years (Irland 1998).

Eastern Ontario, one of the areas hardest hit by the storm (Kerry et al. 1999), is

home to a large population of Cerulean Warblers (*Dendroica cerulea*) that we have been

monitoring since 1994 (Martin 1994, Oliarnyk 1996, Oliarnyk and Robertson 1996). The

Cerulean Warbler is a Neotropical migrant passerine that is thought to require large tracts

(~200ha) of mature deciduous forest to maintain successful breeding populations

(Robbins et al. 1992; Hamel 2000a). However, its small-scale habitat affinities are

poorly understood beyond a general conclusion that large trees with high, dense canopies

are preferred as nesting habitat (Robbins et al.1992, Oliarnyk 1996; Hamel 2000a). Due

to precipitous breeding population declines, up to 3.4% per year since 1966 (Robbins et

al. 1992, Peterjohn et al. 1995, James et al. 1996), this species has been variously

designated as threatened, rare, or of special concern in the United States and of special

concern in Canada (Robbins et al.1992, COSEWIC 2000, Hamel 2000b).

Given our four years of pre-storm data on Cerulean Warbler reproductive

behavior and habitat selection, we were in a unique position to monitor the response of a

species of conservation concern to a large-scale natural disturbance. In a preliminary

assessment of ice storm effects, we determined that the canopy foliage structure was

drastically altered by the 1998 ice storm, with reductions in average cover as high as 60%

(DeBruyn 1999). The dramatic reduction of foliage volume is likely to have strong

negative impacts on species like the Cerulean Warbler that are dependent on forest

canopy resources. In this study we addressed two main questions: (1) Did Cerulean

Warbler reproductive success change after this habitat disturbance?, and (2) Did the

breeding population exhibit a shift in habitat selection patterns in response to this habitat

disturbance? Following we describe hypotheses, predictions and tests for these two

questions.

Did Cerulean Warbler reproductive success change after this habitat disturbance?

We addressed this question by comparing reproductive success in the two years

following the ice storm with those before the storm. We hypothesized that canopy

foliage is important for successful Cerulean Warbler reproduction, both in terms of nest-

site cover and provision of foraging opportunities (Oliarnyk 1996; Jones and Robertson

in review). Based on this possibility and the level of canopy foliage damage, we

predicted that reproductive success would decrease following the ice storm disturbance.

Did the breeding population exhibit a shift in habitat selection patterns in response to

this habitat disturbance?

We addressed potential responses of breeding birds to the ice storm disturbance at

two spatial scales: breeding territory and nest-site. At the territory scale, we measured

the amount of canopy and midstory damage contained within Cerulean Warbler

territories. We hypothesized that male Cerulean Warbler territory size is inversely

related to the amount of nesting and foraging habitat contained within the territory

(Conner et al. 1986, Smith and Shugart 1987, Steele 1993). Given the level of canopy

foliage damage, we made the following two predictions: (1) post-storm territories will be

larger than pre-storm territories, and (2) territories containing areas of high damage will

be larger than those containing areas of low damage. An additional possibility is that

male Cerulean Warblers may entirely avoid areas of high canopy damage when selecting their territories.

At the scale of the nest-site, we compared nest-site characteristics (e.g. nest height) in the two years following the ice storm with those from the four years before the storm. If the population demonstrated reduced reproductive success following the disturbance, we would expect Cerulean Warblers to shift their nest-site location patterns to accommodate new habitat realities and selective pressures. Conversely, if the habitat damage caused by the ice storm did not result in a decrease in reproductive success, we would predict no changes in nest-site selection patterns in the two years following the storm. We analyzed 1998 and 1999 nest-site characteristics separately to assess the potential of a lag response in our study population.

METHODS

Study area

This investigation was conducted at the Queen's University Biological Station (QUBS), Ontario, Canada (44°34'N, 76°20'W), within the Great Lakes- St. Lawrence mixed forest region. Our study area was restricted to within approximately 2600ha of research tracts managed by QUBS (Jones et al. 2000). All nest-searching activities and ice storm damage assessments were carried out in two study grids (11.4 and 6.4ha, 25m x 25m grid resolution) that were characterized as mature, secondary-growth, lowland mixed deciduous forest with a canopy layer predominated by sugar maple (*Acer saccharum*), and to a lesser extent oak (*Quercus* spp.) and elm (*Ulmus* spp.). The average canopy height in our study area is approximately 24m.

Reproductive output and nesting success

From May to June of 1996-99, the two study grids were searched for Cerulean Warbler nests. Once found, nests were checked every 2-3 days and parental activity was used to assess nest status. As the high location of our nests rendered it difficult to determine their precise fates, all unsuccessful nests, whether succumbing to predation, exposure, abandonment, or unknown failure, were lumped together. Nests that fledged at least one young were considered successful. During the first one or two weeks post-fledging, both parents and fledglings remain within the territory and are conspicuously vocal. This enabled us to obtain a direct count of surviving fledglings.

Reproductive output (fledglings per breeding pair) was compared among pre-storm years,1998, and 1999 using Mann-Whitney U tests. Nest success and mortality were calculated using the Mayfield method (Mayfield 1961, 1975) with the modifications suggested by Johnson (1979) and Hensler and Nichols (1981). We used the z-test of Hensler and Nichols (1981) to test for differences in nest success and mortality for the entire nesting cycle. Due to difficulties in examining canopy nest contents, some nests were not included in the Mayfield calculations.

Territory size and damage

In 1996-1999, we mapped the breeding territories for all males on our two study grids. The mapping method used was similar to the spot mapping method described by Kendeigh (1944). Territories were mapped between 0530 and 1300 hrs from between 13 May and 28 June 1998, and between 6 May and 12 July 1999. Attempts were made to spend the same amount of time with each male. Identification of individuals was facilitated by the fact that over 75% of the territorial males on our study grids have been

fitted with unique combinations of color bands and Canadian Wildlife Service aluminum bands. Given the relatively low height of the forest canopy in our study site, color-band combinations were easily readable with binoculars from the forest floor. Any individuals that remained unbanded were distinguished by unique song characteristics (Woodward 1997). The high degree of Cerulean Warbler experience possessed by our field crew allowed us to make these vocal identifications with confidence.

Locations of males were recorded on maps in reference to grid points (25m x 25m grid) of known coordinates and digitized using AutoCAD Map®. Territory sizes were then estimated by the minimum convex polygon method (Mohr 1947). We used a one-way ANOVA to compare pre-storm territory sizes (1996 and 1997) to post-storm territory sizes (1998 and 1999). We could not include territory size estimates from 1994 and 1995 as a different sampling methodology was used (Oliarnyk 1996). We then used a post-hoc Tukey-Kramer test to test for significant differences among years.

In July and August 1998, we established 285 damage plots on the study site, the center of each corresponding to a point on our study grids. Each plot was a circle of 5m radius (0.01ha). For all trees $\geq$ 3cm diameter at breast height (dbh), we recorded species, status (alive or dead), and dbh. In addition, each of the trees was assigned a crown class (canopy or midstory) and a damage class (Rebertus et al. 1997). The damage classes ranged from 0 to 3, with 0 representing no damage and 3 representing severe damage. In total, 4285 trees were measured and assessed. For each plot, a total damage index was created by adding together the average damage class of canopy trees and the average damage class of midstory trees.

The location of each of the damage plots was mapped using a Global Positioning System and recorded using the Universal Transverse Mercator Projection NAD 1927 scale. These data were used to generate a spatially explicit map of tree damage for the study site (DeBruyn 1999). To generate this map, circular buffer zones of 13m were created around the 0.01ha plots represented by the damage index. We made the assumption that the damage in the area immediately outside the 0.01ha damage plot could be predicted by the nearest damage index. Best-fit polygons were drawn for each damage index in order to enclose all areas of similar damage. We examined the relationship between territory size and canopy and midstory tree damage by overlaying the territory maps onto this spatially explicit map of damage. Within each territory boundary, the area of each damage class was calculated. Pearson correlation coefficients were calculated to examine relationships between damage and territory size.

In order to compare 1999 territory data to the ice storm damage documented in 1998, we needed to test whether the canopy foliage structure of the study area had changed significantly between 1998 and 1999. In 1998, we generated foliage height profiles at 39 locations (DeBruyn 1999) and re-visited these locations in 1999. Foliage cover was measured in a 1m radius cylinder which was projected from the forest floor to the top of the canopy. We estimated cover within 3m height intervals from the ground to the top of the canopy. Total cover and percent cover of each species was estimated by eye in each height interval on a scale of 0 to 10 (0 = 0% cover, 10 = 100% cover). For these comparisons, foliage cover was estimated by the same observer in both years (JJ). We compared 1998 and 1999 foliage height profiles using t-tests.

Patterns of nest-site location

From 1994 to 1999, the following location variables were measured at each nest:
nest height above ground, nest tree species, nest tree height, tree diameter at breast height
(dbh), distance between the nest and the trunk, distance between the nest and the distal
end of nest branch, and distance of the nest to the nearest canopy gap. In order to
examine the nest location relative to tree height, nest height and tree height were
combined to create a height ratio; similarly, distance from trunk and distance to distal end
of nest branch were combined to create a horizontal ratio. For this study, a canopy gap is
defined as an area $\geq 25\text{m}^2$ in which the highest foliage layer is $\geq 50\%$ lower than the
surrounding vegetation. In 1996-9, we also estimated cover surrounding the nest by
estimating foliage cover within 1m in each of the four cardinal directions and within 1m
directly above the nest; these five estimates were averaged to provide a single cover
estimate for each nest. All cover estimates were made by the same individual (JJ) during
these years.

We also generated foliage height profiles for each nest. Foliage profiles were
generated in the previously described manner (see *Methods: Territory size and damage*) ,
with the exception in this case that each profile was centered on the nest location. These
cover estimates were only performed from 1996 to 1999, and were performed by two
individuals whose estimates were standardized prior to data collection.

Nest location data for 1994 and 1995 were taken from Oliarnyk (1996) and
included in our analyses of patterns of nest location. Tree dbh and distance from trunk
were transformed using $\log_{10}$ transformations while distance from branch end was
transformed using a square-root transformation. Nest location variables were compared

between pre-storm years (1994-1997) and 1998, and between 1998 and 1999, using t - tests. Due to operational differences in defining canopy gaps, we excluded the 1994 and 1995 distance to gap data (from Oliarnyk 1996) from our analyses.

We also used t-tests to examine differences in foliage cover within each of our height intervals at our nest locations between pre-storm years (1996 - 7) and 1998, and between 1998 and 1999. One nest from 1999 had to be excluded from the analyses as we were unable to accurately project the nest location onto the ground. We also averaged cover within 3m above and below each nest location, subtracted cover below from cover above, and then tested for differences in the result using a Mann-Whitney U test.

To examine if birds responded to ice storm damage by avoiding areas of high damage for their nest-sites, we described the damage to the canopy and midstory trees within a 5m radius circle centered on the nest location. Within this circle, we performed tree damage estimates identical to those used in the territory comparisons. Damage to canopy and midstory trees was compared between 1998 and 1999 nest locations using Mann-Whitney U tests.

General analyses

All variables were tested for departures from normality using Shapiro-Wilks' tests; variables were also tested for heteroscedasticity using Bartlett's test (Sokal and Rohlf 1995). Non-parametric tests were performed on any variables that could not be satisfactorily transformed. All univariate analyses were performed using JMP 3.2.1 (SAS Institute 1997). Multivariate analyses were performed using SPSS 9.0.1. (SPSS Inc. 1999). Sequential Bonferroni corrections were applied where appropriate to control the

group-wide type-I error rates (Rice 1989). Values presented in the manuscript are means

± 1 standard error for untransformed variables.

RESULTS

Reproductive output and nesting success

During the 1998 breeding season, the reproductive output of the study population,

measured as average number of fledglings per breeding pair, was significantly lower than

the output before the storm ($U = 10.46$, $P = 0.001$; Table 1). There was a significant

increase in daily mortality following the ice storm in 1998 ($z = 6.81$, $P < 0.0001$),

accompanied by a drastic drop in nesting success (Table 1). Daily mortality decreased

significantly in 1999 relative to 1998 ($z = 2.44$, $P = 0.005$) although the 1999 daily

mortality was still significantly higher than pre-storm levels ($z = 2.51$, $P = 0.006$; Table

1). Fledglings produced per breeding pair also increased in 1999 relative to 1998 ($U =$

4.24, $P = 0.04$; Table 1). There was no statistically significant difference between 1999

and pre-storm fledgling outputs ($U = 1.34$, $P = 0.25$; Table 1).

Territory size and damage

Territories defended by Cerulean Warbler males in 1999 (1.17 ± 0.12 ha, $n = 10$)

were significantly larger than territories in 1996 (0.74 ± 0.05 ha, $n =11$), 1997 (0.63 ±

0.05 ha, $n = 9$), and 1998 (0.57 ± 0.05 ha, $n = 13$) (one-way ANOVA, df = 39, F = 13.99,

$P < 0.0001$; Tukey-Kramer post-hoc). There were no significant differences in the

general foliage height profiles between 1998 and 1999 (df = 74, all $|t| < 0.90$, all $P >$

0.35), which allowed us to use the 1998 damage classifications (DeBruyn 1999) when

analyzing the 1999 territory data. In neither post-storm year did we detect significant

correlations between territory size and the percentage of a given damage class within a

territory (1998, $n = 13$, all $r < |0.51|$, all $P > 0.08$; 1999, $n = 10$, all $r < |0.65|$, all $P > 0.04$).

Patterns of nest-site location

The distances from nest-site to the nearest canopy gap were much shorter in 1998 than before the storm (Table 2). Relative to 1998 nests, nests in 1999 were significantly higher above the ground and in significantly bigger trees (both height and girth) but were in the same position relative to the height of the tree (Table 2).

The foliage structure surrounding the nest locations was drastically different after the ice storm, with a significant reduction in the amount of foliage present in the upper layers of the canopy (Figure 1; Table 3). The ratio of foliage cover within 3m above the nest to that within 3m below the nest was significantly higher in pre-storm years than in post-storm years (pre-storm = 4.54 ± 0.50, post-storm = 1.35 ± 0.40, $U = 11.5$, P = 0.0007). Furthermore, 1999 nests were located in areas of higher canopy and midstory damage than were 1998 nests (canopy $U = 2.05$, $P = 0.04$, midstory $U = 3.34$, $P = 0.0008$).

DISCUSSION

Did Cerulean Warbler reproductive success change after this habitat disturbance?

The ice storm of January 1998 severely altered the forest structure in our study area by causing a significant and widespread reduction in the amount of foliage in the canopy layer of the forest. However, despite the fact that the habitat in our study area is not saturated with breeding individuals (Jones and Robertson in review), birds did not move away from our study sites in an effort to avoid areas of heavy canopy foliage

damage. Although, given the extensive damage in the region, it is possible that there was nowhere else to move.

Our results revealed this disturbance had a negative impact on the breeding success of Cerulean Warblers in our study area. As we predicted, there was a significant decrease in nesting success and reproductive output in the years following this large natural habitat disturbance. Given the extensive nest-searching effort expended in each year of this study (Oliarnyk 1996; Jones unpublished data), we believe that the drop in nesting success observed in 1998 was not an artifact of the increase in the number of nests found that year, but was a realistic reflection of the pressures facing the birds during the 1998 breeding season.

There are several potential explanations for the drop in reproductive success during the first post-storm breeding season. First, there may have been a coincidental increase in regional nest predator populations (e.g. Blue Jay, *Cyanocitta cristata*; Black Rat Snake, *Elaphe obsoleta*). This possibility seems unlikely since populations of the dominant nest predators in our study area have remained constant over the duration of our study (Jones unpublished data, Gabriel Blouin-Demers personal communication). However, the reduction in the absolute amount of foliage available for nesting may have, by itself, rendered Cerulean Warbler nests more susceptible to predation (the potential-prey-site hypothesis; *sensu* Martin 1993).

Second, the damage suffered by canopy trees may have negatively affected insect populations in 1998 and, consequently, foraging opportunities for Cerulean Warblers (Crawford et al. 1981, Schowalter 1985, Bell and Whitmore 1997). A decrease in overall insect abundance may also have had an indirect effect by triggering prey switching

behavior in nest predators that also depend on canopy arthropod populations, such as

Blue Jays (Cornell 1976, Patterson et al. 1998).

Did the breeding population exhibit a shift in habitat selection patterns in response to

this habitat disturbance?

Reproductive success in our study population increased in the second breeding

season following the storm (1999). This increase was associated with a significant

increase in territory size and a significant shift in nest-site selection patterns. Contrary to

our prediction, average territory size in 1998 was the same as before the ice storm (1996-

7), although average territory size in 1999 was almost double that of previous years. This

suggests that in 1999, the birds may have responded to the 1998 decrease in nesting

success by expanding the area defended in order to increase the amount of resources

available, such as potential nest-sites or foraging locations (Smith and Shugart 1987,

Steele 1993, Conner et al. 1986). However, this interpretation is weakened by the fact

that we detected no significant relationships between area of canopy damage and territory

size in either post-storm breeding season.

Our results indicate that, despite the habitat damage, individuals in 1998

attempted to nest in locations similar to ones used before the storm. In fact, only two

nest-site characteristics differed between pre-storm and 1998 nests: distance to nearest

canopy gap (much shorter in 1998) and the amount of foliage cover above average nest

height (lower in 1998). Given the extent of the ice storm damage at our study site, there

were few potential nest-site locations that were not closer to a canopy gap or in an area

that did not suffer damage to canopy foliage.

In 1999, we observed a marked shift in nest-site location patterns. This shift was accompanied by an increase in nesting success and reproductive output. Birds tended to nest higher up in bigger trees (in height and girth) in 1999 than in 1998. The 1999 nest tree species distribution matched that of the pre-storm years, while the 1998 distribution differed from all other years. Unfortunately, nesting success was so low in 1998 that we were unable to discern if the selection of certain tree species influenced nest success. The shift in nest-site locations did not involve avoidance of areas of high canopy foliage damage. The increase in reproductive output in 1999 without significant foliage re-growth (Figure 1; Table 3) lowers the likelihood of a link between foliage loss and predation risk.

We know that at least six of the color-marked males that bred successfully in 1999 were breeding successfully on our study site in the years before the storm (either 1996 or 1997). Although we have not been as successful in banding females, it is possible that a similar pattern exists for females given that, within-species and within-habitats, return rates of adult wood-warblers tend to be similar for males and females (Holmes and Sherry 1992). This creates the possibility that the observed shift in nest-site selection patterns in 1999 has been generated at the scale of the individual. It appears that Cerulean Warblers possesses a degree of plasticity with respect to their habitat affinities at certain scales and that this plasticity confers a certain degree of resilience to habitat disturbance.

ACKNOWLEDGEMENTS

LITERATURE CITED

Askins, R. A., and D. N. Ewert. 1991. Impact of Hurricane Hugo on bird populations on St. John, U.S. Virgin Islands. Biotropica **23**: 481-487.

Bell, J. L., and R. C. Whitmore. 1997. Bird populations and habitat in *Bacillus thuringiensis* and Dimilin-treated and untreated areas of hardwood forest. The American Midland Naturalist **137**: 239-250.

Cade, T. J, and C. G. Jones. 1993. Progress in restoration of the Mauritius Kestrel. Conservation Biology **7**: 169-175.

Canterbury, G. E., and D. E. Blockstein. 1997. Local changes in a breeding bird community following forest disturbance. Journal of Field Ornithology **68**: 537-546.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology **63**: 215-244.

Conner, R. N., M. E. Anderson, and J. G. Dickson. 1986. Relationships among territory size, habitat, song, and nesting success of northern cardinals. The Auk **103**: 23-31.

Cornell, H. 1976. Search strategies and the adaptive significance of switching in some general predators. The American Naturalist **110**: 317-320.

COSEWIC. 2000. Canadian species at risk, May 2000. Committee of the Status of Endangered Wildlife in Canada, Ottawa, ON.

Crawford, H. S., R. G. Hooper, and R. W. Titterington. 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. Journal of Wildlife Management **45**: 680-692.

Dale, V. H., A. E. Lugo, J. A. MacMahon, and S. T. A. Pickett. 1998. Ecosystem management in the context of large, infrequent disturbances. Ecosystems **1**: 546-557.

DeBruyn, R. D. 1999. The effects of a large scale disturbance on a mature mixed species deciduous forest and territory characteristics of the Cerulean Warbler (*Dendroica cerulea*). B. Sc. thesis, Queen's University, Kingston, Ontario.

Hamel, P. B. 2000a. Cerulean Warbler (*Dendroica cerulea*). No. 511 *in* A. Poole and F.

Gill, editors. The Birds of North America. The Birds of North America, Inc.,

Philadelphia, PA.

Hamel, P. B. 2000b. Cerulean Warbler status assessment. United States Fish and Wildlife

Service, Fort Snelling, MN.

Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting

success: a model, estimators and simulation results. The Wilson Bulletin 93: 42-

53.

Holmes, R. T., and T. W. Sherry. 1992. Site fidelity of migratory warblers in temperate

breeding and Neotropical wintering areas: Implications for population dynamics.

habitat selection, and conservation. Pages 563 – 575 *in* J.M. Hagan III and D.W.

Johnston, editors. Ecology and conservation of Neotropical migrant landbirds.

Smithsonian Institution Press, Washington, D.C., USA.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a

Caribbean coral reef. Science 265: 1547-1551.

Irland, L. C. 1998. Ice storm 1998 and the forests of the northeast. Journal of Forestry 96:

32-40.

James, F. C., C. E. McCulloch, and D. A. Wiedenfeld. 1996. New approaches to the

analysis of population trends in land birds. Ecology 77: 13-27.

Johnson, D. H. 1979. Estimating nesting success: the Mayfield method and an alternative.

The Auk 96: 651-661.

Jones, J., W. J. McLeish, and R. J. Robertson. 2000. Density influences census technique accuracy for Cerulean Warblers in eastern Ontario. Journal of Field Ornithology 71: 46-56.

Kendeigh, J. R. 1944. Measurements of bird populations. Ecological Monographs 14: 67-106.

Kerry, M., G. Kelk, D. Etkin, I. Burton, and S. Kalhok. 1999. Glazed over: Canada copes with the ice storm of 1998. Environment 41: 6-11, 28-33.

Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. Proceedings of the National Academy of Science, USA 71: 2744-2747.

Martin, P.R. 1994. Effects of forest management practices and forest-cutting history on the songbird communities of mature hardwood forest stands, Lake Opinicon, Leeds/Frontenac Cos., Ontario. Prepared for the Eastern Ontario Model Forest Program.

Martin, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. BioScience 43: 523-532.

Mayfield, H. 1961. Nesting success calculated from exposure. The Wilson Bulletin 73: 255-261.

Mayfield, H. 1975. Suggestions for calculating nest success. The Wilson Bulletin 87: 456-466.

McCarthy, M. A. 1996. Extinction dynamics of the helmeted honeyeater: effects of demography, stochasticity, inbreeding and spatial structure. Ecological Modelling 85: 151-163.

Mohr, C. O. 1947. Table of equivalent populations of north American small mammals. The American Midland Naturalist 37: 223-249.

Oliarnyk, C. J. 1996. Habitat selection and reproductive success in a population of Cerulean Warblers in southeastern Ontario. M.Sc. thesis, Queen's University, Kingston, ON.

Oliarnyk, C. J., and R. J. Robertson. 1996. Breeding behavior and reproductive success of Cerulean Warblers in southeastern Ontario. Wilson Bulletin 108: 673-684.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1: 535-545.

Patterson, B. R., L. K. Benjamin, and F. Messier. 1998. Prey switching and feeding habits of eastern coyotes in relation to snowshoe hare and white-tailed deer densities. Canadian Journal of Zoology 76: 1885-1897.

Peterjohn, B.C., J.R. Sauer, and C.S. Robbins. 1995. Population trends from the North American Breeding Bird Survey. Pages 3-39 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of neotropical migratory birds: A synthesis and review of critical issues. Oxford University Press, New York, New York, USA.

Rebertus, A. J., S. R. Shifley, R. H. Richards, and L. M. Roovers. 1997. Ice storm damage to an old-growth oak-hickory forest in Missouri. The American Midland Naturalist 137: 48-61.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 223-225.

Robbins, C. S., J. W. Fitzpatrick, and P. B. Hamel. 1992. A warbler in trouble: *Dendroica cerulea*. Pages 549-562 in J.M. Hagan III and D.W. Johnston, editors. Ecology

and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

SAS Institute Inc. 1997. JMP 3.1.7. SAS Institute Inc., Cary, NC, USA.

Schowalter, T. D. 1985. Adaptations of insects to disturbance. Pages 235-252 *in* S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbances and patch dynamics. Academic Press, New York, New York, USA.

Singer, F. J., and M. K. Harter. 1996. Comparative effects of elk herbivory and 1988 fires on northern Yellowstone National Park grasslands. Ecological Applications 6: 185-199.

Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the Ovenbird: the role of habitat structure. Ecology **68**: 695-704.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. 3rd edition. W.H. Freeman and Co., New York, New York, USA.

SPSS Inc. 1999. SPSS 9.0.1. SPSS Inc., Chicago, IL.

Steele, B. B. 1993. Selection of foraging and nesting sites by Black-throated Blue Warblers: their relative influence on habitat choice. The Condor **95**: 568-579.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1: 511-523.

Turner, M. G. and V. H. Dale. 1998. Comparing large, infrequent disturbances: what have we learned? Ecosystems 1: 493-496.

White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3-13 *in* S. T. A. Pickett and P. S. White, editors. The ecology

of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Willig, M. R., and G. R. Camilo. 1991. The effect of Hurricane Hugo on six invertebrate species in the Luquillo Experimental Forest, Puerto Rico. Biotropica **23**: 455-461.

Woodward, R. C. 1997. Characterization and significance of song variation in the Cerulean Warbler (*Dendroica cerulea*). M. Sc. Thesis, Department of Biology, Queen's University, Kingston, Ontario.

Woolbright, L. L. 1991. The impact of Hurricane Hugo on forest frogs in Puerto Rico. Biotropica **23**: 462-467.

Wootton, J. T. 1998. Effects of disturbance on species diversity: a multitrophic perspective. The American Naturalist **152**: 803-925.

Table 1. Cerulean Warbler reproductive success and nest mortality before (1994-7) and

after (1998 and 1999) the ice storm of January 1998 in eastern Ontario.

Year	# Nests	Nest success (%)	Days exposed	Daily nest mortality (variance)	Predicted nest success (%)	# fledglings per breeding pair
Pre-storm	37	75.7	640	0.014 (0.00002)	73.2	2.0 (36)[a]
1998	36	8.9	363.5	0.089 (0.00010)	13.2	0.4 (25)
1999	22	36.4	299.5	0.047 (0.00015)	34.9	1.2 (21)

Notes: A modified Mayfield method (Johnson 1979; Hensler and Nichols 1981) was used

to estimate daily mortality, daily mortality variance and predicted nest success.

[a] number of breeding pairs in parentheses

Table 2. Cerulean Warbler nest location characteristics compared between (1) pre-storm years (1994-7) and 1998, and (2) 1998 and 1999.

				Pre-storm vs. 1998		1998 vs. 1999	
Characteristic	Pre-storm ($n = 30$)	1998 ($n = 45$)	1999 ($n = 28$)	t	P	t	P
nest height (m)	11.6 ± 0.5	10.6 ± 0.5	15.4 ± 0.6	-1.35	0.18	-6.44	**<0.001**
tree height (m)	19.9 ± 1.1	16.8 ± 0.7	22.0 ± 0.6	-2.44	0.02	-5.26	**<0.001**
height ratio	0.61 ± 0.03	0.64 ± 0.02	0.71 ± 0.03	0.75	0.45	-2.00	0.05
tree dbh (cm)	43.2 ± 3.5	35.0 ± 2.2	45.1 ± 2.7	-1.92	0.04	-3.00	**0.004**
from trunk (m)	3.5 ± 0.2	3.6 ± 0.2	4.7 ± 0.4	0.35	0.77	-2.03	0.05
from end (m)	2.3 ± 0.2	2.2 ± 0.1	2.7 ± 0.2	-0.68	0.60	-1.89	0.06
horizontal ratio	0.59 ± 0.02	0.62 ± 0.02	0.62 ± 0.03	0.89	0.39	-0.01	0.99
from gap [a] (m)	14.9 ± 2.9	3.0 ± 0.4	3.3 ± 0.4	-7.05	**<0.001**	-0.49	0.63
avg. cover [a] (%)	53.5 ± 6.4	52.9 ± 2.9	63.3 ± 3.2	-0.09	0.93	-2.34	0.02

Notes: Values presented are means ±1 SE. Bold-faced *P*-values are significant following sequential Bonferroni corrections (Rice 1989).

[a] only 1996 and 1997 nests are included in the pre-storm category (df = 55)

Table 3. Comparisons of foliage cover in each height interval between nest foliage height profiles between (1) pre-storm years (1996 - 7) and 1998 and (2) 1998 and 1999.

Height interval (m)	Pre-storm ($n = 13$)	1998 ($n = 45$)	1999 ($n = 28$)	Pre-storm vs. 1998		1998 vs. 1999	
				t	P	t	P
0 – 3	4.2 ± 0.3	4.2 ± 0.3	4.8 ± 0.2	0.003	0.99	-1.21	0.23
3 – 6	3.5 ± 0.5	3.2 ● 0.4	3.0 ± 0.5	-0.38	0.71	0.32	0.75
6 – 9	3.5 ± 0.6	3.0 ± 0.4	3.5 ± 0.5	-0.64	0.52	-0.78	0.44
9 – 12	4.3 ± 0.7	3.2 ± 0.4	3.6 ± 0.5	-1.42	0.16	-0.76	0.45
12 – 15	4.6 ● 0.7	3.5 ± 0.4	4.7 ● 0.5	-1.27	0.21	-1.87	0.07
15 – 18	5.4 ± 0.7	2.8 ± 0.4	3.6 ± 0.4	-2.93	**0.005**	-1.17	0.25
18 – 21	5.2 ± 0.6	1.7 ± 0.4	2.0 ± 0.4	-4.52	**<0.0001**	-0.54	0.60
21 – 24	3.5 ● 0.5	0.6 ± 0.3	0.3 ± 0.3	-4.76	**<0.0001**	1.05	0.30
24 – 27	3.0 ± 0.8	0.3 ± 0.2	0	-5.17	**<0.0001**	1.24	0.22
27 – 30	1.7 ± 0.3	0.2 ± 0.2	0	-3.29	**0.0002**	0.91	0.36
over 30	0.2 ± 0.1	0.1 ± 0.1	0	-1.49	0.14	0.81	0.42

Notes: Values presented are means ± 1 SE. Bold-faced *P*-values are significant following sequential Bonferroni corrections (Rice 1989).

Figure Captions

Figure 1. Foliage height profiles for pre-storm (1996-7, $n = 13$), 1998 ($n = 45$) and 1999

($n = 28$) nest sites. The dashed line represents the average nest height for each year or

years.
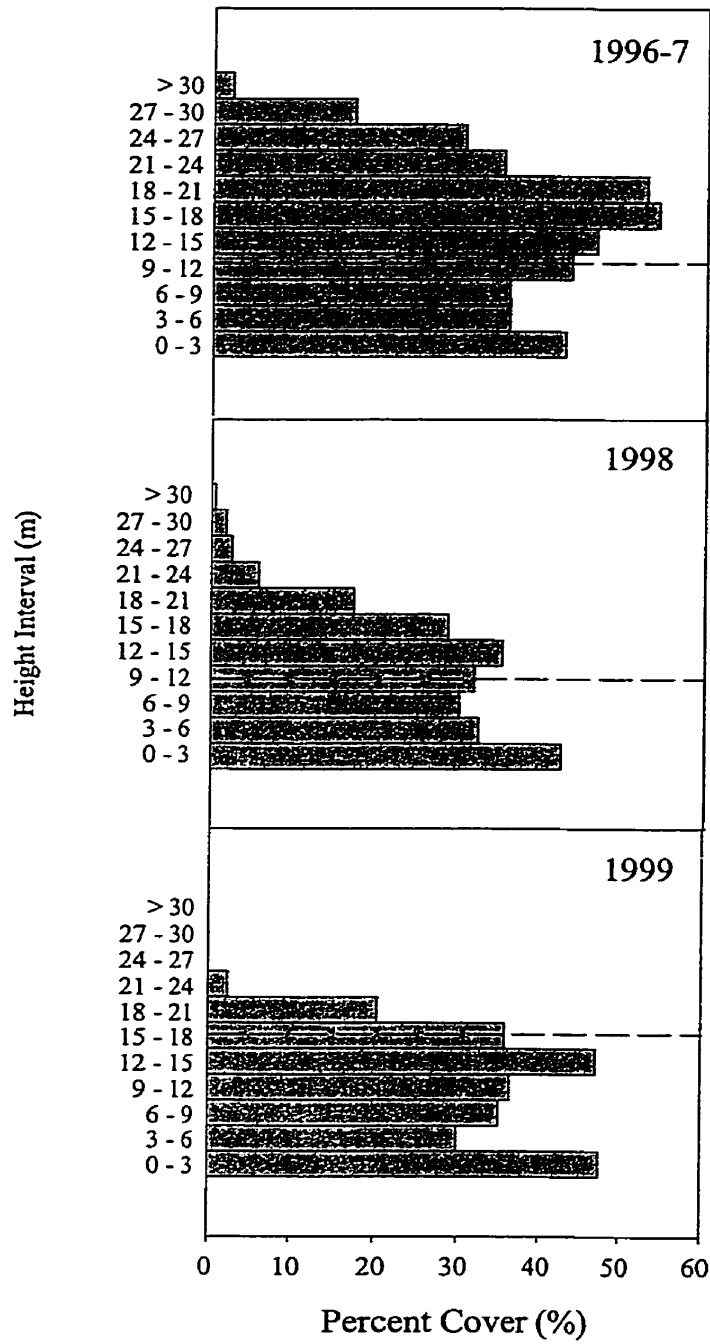
Chapter 5

Assessing the conservation utility of the Cerulean Warbler.

Jason Jones and Raleigh J. Robertson

ABSTRACT

The surrogate species concept is a tool often used by wildlife managers and conservation biologists. Using a single species or group of species as a management proxy can be an efficient use of available time and resources. Indicator species are used to index attributes difficult to assess in other species of interest and have been used to assess changes in environmental conditions, to track population fluctuations, and to identify areas of high biodiversity. Umbrella species have been used to determine the type and extent of habitat to be protected, given a set of management or conservation goals. Flagship species have been used to generate public interest and improve public education of conservation issues. However, there is little agreement on the criteria by which the surrogate value of a species of interest can be assessed. The selection of a species as a surrogate is often motivated by expediency and species often are chosen because they are of conservation concern themselves. We attempt to provide a critical evaluation of the conservation utility of a species, the Cerulean Warbler (*Dendroica cerulea*), that has received considerable conservation and research attention by critically examining its potential as a surrogate species. Previous research has indicated that the Cerulean Warbler has limited potential as an indicator species, either in monitoring the health and succession of eastern deciduous forest or in tracking populations of forest canopy arthropods. The results of this study indicate that the Cerulean Warbler would not be an effective biodiversity indicator. This study also showed that Cerulean Warblers could be an effective umbrella and flagship species by focusing conservation efforts aimed at the preservation of mature, deciduous forest and the maintenance of populations of other species that require similar habitats.

INTRODUCTION

The use of surrogate species is a common conservation and wildlife management practice (Thomas 1972). Surrogate species have been used in a variety of capacities and can be classified into three subgroups: indicator species, umbrella species, and flagship species (Caro and O'Doherty 1999). An indicator species is a species whose traits are used to index attributes difficult to measure for other species (Landres et al. 1988). Health indicator species serve to assess changes in environmental conditions (Phillips 1980). Population indicators are used to track changes in populations of other species (Montevecchi 1993). Biodiversity indicators are used to identify areas of high biodiversity by using the presence and diversity of a well-known suite of species as an index of diversity for other groups (Humphries et al. 1995; Caro and O'Doherty 1999).

Umbrella species are employed when the conservation or management goal is to preserve a community or habitat (Berger 1997). The protection of the habitat of the umbrella species ideally results in the protection of the habitat of those species whose requirements are subsumed by those of the umbrella (Launer and Murphy 1994). A flagship species is a species that is used to generate public interest and concern for a conservation issue and can be valuable public relations tools for education and the preservation of habitats (Kleiman et al. 1986, Caro and O'Doherty 1999).

Although the use of surrogate species represents an efficient deployment of resources, there is considerable disagreement about their usefulness (Inhaber 1976; Landres et al. 1988; Andelman and Fagan 2000). One of the major criticisms is that the identification and selection of surrogate species is not always performed in a rigorous or standardized manner (Landres et al. 1988). For example, the selection of species as a

surrogate is often motivated by expediency and species often are chosen because they are of conservation concern themselves or as a result of public perception of their value (Caro and O'Doherty 1999). One such example is the focus that has been placed on Neotropical migrant songbirds as a result of documented declines in the breeding populations of certain species (Robbins et al. 1989). Despite the lack of evidence in support of birds as effective surrogate species, Neotropical migrant species are commonly used as indices of environmental disturbance (Temple and Wiens 1989).

In particular, the Cerulean Warbler (*Dendroica cerulea*) has received considerable attention (Robbins et al. 1992, Oliarnyk and Robertson 1996, Jones et al. 2000a, Jones et al. 2000b). The rapid population declines of this species are thought to be representative of the widespread destruction of mature, bottomland hardwood forests in eastern North America (Robbins et al. 1992). These declines have led to the designation of the Cerulean Warbler as threatened, rare, or of special concern in the United States and of special concern in Canada (Robbins et al.1992, COSEWIC 2000, Hamel 2000). Previous research in eastern Ontario indicates that the habitat affinities and population characteristics of the Cerulean Warbler may confer limited utility as a health or population indicator on this species (Jones et al. 2000a, Jones et al. in press). The goal of this study was to complement previous efforts and assess the utility of the Cerulean Warbler as a biodiversity indicator species, umbrella species, or flagship species. This utility assessment allowed us to determine, in light of conservation and management goals, what conservation role best suits the Cerulean Warbler.

STUDY AREA AND METHODS

This investigation was conducted at the Queen's University Biological Station (QUBS), Ontario, Canada (44°34'N, 76°20'W), within the Great Lakes- St. Lawrence mixed forest region. Our study area was restricted to approximately 2600 ha of research tracts managed by QUBS (Jones et al. 2000a). The landscape in the area is dominated by mature, secondary-growth, lowland mixed deciduous forest. Interspersed in this forest matrix are numerous rocky outcrops, beaver marshes, permanent water bodies and abandoned agricultural fields.

Bird surveys. - In 1997 and 1998, we surveyed birds on QUBS property using variable-circular-plot point counts (Reynolds et al. 1980). We surveyed 80 stations in 1997 (17 May – 20 June) and 67 stations in 1998 (21 May – 21 June); the 1998 stations were a subset of those sampled in 1997. Each point count was 10 min long and each station was separated by at least 200 m to minimize the potential for double counting individuals (Reynolds et al. 1980; Hutto et al 1986). Point counts were conducted between 0.5 hr before sunrise and 3 hr after sunrise EST in order to sample during peak song activity, and were only conducted under calm weather conditions. For this analysis we included only birds detected within 50 m of the plot center. Probability of detection was equivalent for all species included in the analyses, since the detection thresholds for all species included was beyond 50m (Jones unpublished data). Data from two visits per station each year was used in the analyses.

Vegetation Surveys. - We collected vegetation data at 59 point count stations in 1997 at five circular subplots (5m radius). The first subplot was centered on the point count station center and the other 4 were located 50 m away in each of the cardinal directions.

Within each of the subplots we counted the number of saplings [stems < 3.0 cm diameter

at breast height (dbh)] and measured the dbh of all stems ≥ 3.0 cm and grouped them into

5 size classes (3.0–8.0 cm dbh, 8.1-15.0 cm, 15.1-23.0 cm, 23.1-30.0 cm, >30.0 cm).

Basal areas of all stems ≥ 3.0 cm were combined to give an estimate of the total basal

area (m^2/ha). We also estimated foliage cover at several height intervals. Foliage cover

was estimated in a 1m radius cylinder which was projected from the forest floor to the top

of the canopy. We estimated cover within 3 m height intervals from the ground to the top

of the canopy. Total cover and percent cover of each woody plant species was estimated

by eye in each height interval on a scale of 0 to 10 (0 = 0% cover, 10 = 100% cover). All

cover estimates were made by two trained observers. For the purposes of this study, we

reduced these cover estimates to two variables: maximum cover below 6 m (understory

cover) and maximum cover above 12 m (canopy cover). Each vegetation variable was

averaged across subplots to describe the habitat of the point count station.

Data Analysis. - In our analyses, we included only those species known to breed in our

study area. We excluded species that are not adequately sampled by diurnal point counts,

such as colonial nesters (e.g. Barn Swallow, *Hirundo rustica*), nocturnal species (e.g.

Whip-poor-will, *Caprimulgus vociferus*), waterfowl (e.g. Wood Duck, *Aix sponsa*), and

waders (e.g. Great Blue Heron, *Ardea herodias*).

To evaluate the potential of the Cerulean Warbler as a biodiversity indicator, we

tested whether the presence of Cerulean Warblers was an indicator of overall bird species

richness. For the purposes of these analyses, we defined species richness as the number

of species detected in two visits to a point count station, excluding the Cerulean Warbler

if present. We used randomization tests to compare the mean species richness at stations

where Cerulean Warblers were present to the expected species richness at a randomly

generated sample of points (Chase et al. 2000). In these tests, the mean species richness

was calculated for a random sample of point count stations, with the number of random

stations equaling the number of stations where Cerulean Warblers were detected in a

given year. We iterated this procedure 1000 times to generate an expected distribution of

mean species richness values. We then compared the observed species richness

associated with Cerulean Warblers and determined its statistical significance. These

randomization tests were preformed using S-PLUS 4.0 (Mathsoft 1997). Values reported

in the results are means ± SE.

The initial step in evaluating the potential of the Cerulean Warbler as an umbrella

species was to establish an ecological context. We categorized the bird species detected

during our surveys into functional groups based on habitat preferences, diet and foraging

substrate, and nesting substrate. These classifications were based on observations

reported in the literature (Ehrlich et al. 1988, Robbins et al. 1989, Freemark and Collins

1992, Canterbury et al. 2000). We did not include our survey data in these

classifications. We created a conservation concern grouping that included species which

were experiencing population declines as indexed by North American Breeding Bird

Survey data (Sauer and Droege 1992). For the purposes of these analyses we focused on

the groups to which Cerulean Warblers belonged: mature forest habitat, insect-foliage

foragers, canopy nesters, and species of concern.

We used two methods to test if the distribution of Cerulean Warblers was

representative of the distributions of other species in the same functional group. First, we

calculated C-scores (observed C-score) for each functional group to which Cerulean

Warblers belonged in order to examine if species within each functional group were distributed randomly across the landscape with respect to one another. We used the checkerboard score (*C*-score) developed by Stone and Roberts (1990) to test for non-randomness in presence-absence matrices. For each survey year, we used re-sampling techniques to calculate 10,000 *C*-scores based on the original presence-absence matrix. The observed *C*-score was then compared with the generated distribution of expected *C*-scores and its significance determined. A *C*-score significantly greater than expected by chance indicates that the assemblage is competitively structured; that is, that individual species have distinct, and often exclusive, distributions (Stone and Roberts 1990). Conversely, a *C*-score significantly smaller that expected by chance indicates that there is a degree of cohesion in the distribution patterns of the species included in the matrix. All *C*-score calculations were carried out using EcoSim 5.0 (Gotelli and Entsminger 2000). For each iteration, the number of species detected at each point count station was kept consistent with the original matrix and each station was equally likely to be inhabited by a given species. Survey results from 1997 and 1998 were analyzed separately.

In our second test, we used logistic regression analyses to predict the probability of occurrence along a habitat gradient for all species within each functional group to which Cerulean Warblers belonged. The Red-eyed Vireo (*Vireo olivaceus*) was not included in these analyses due to its near ubiquitous distribution. For these analyses we included only the 1997 surveys of the 59 point count stations for which we collected vegetation data. The habitat gradient was generated by entering all 9 vegetation variables into a principal components analysis. The first principal component axis (PC1) was then used in the regression analyses. All these analyses were performed with JMP 3.2.1 (SAS

Institute 1997). We calculated 95 % confidence intervals around the logistic regression coefficient to facilitate comparison of occurrence probabilities across species.

RESULTS

Biodiversity indicator. - The presence of Cerulean Warblers was not a significant predictor of avian species richness in either 1997 (observed richness 12.69 ± 0.75, expected richness 13.95 ± 0.03, $P = 0.12$) or 1998 (observed richness 9.75 ± 0.63, expected richness 9.82 ± 0.03, $P = 0.83$).

Umbrella species. — All three of the functional groups to which Cerulean Warblers belong exhibited cohesive distributions in both 1997 and 1998, as indexed by their *C*-scores (Table 1). Species of conservation concern also exhibited cohesive distributions in both 1997 and 1998 (Table 1).

In the description of the habitat gradients, the first PC axis (PC1) explained 27% of the variance of the vegetation data and the first four principal component axes cumulatively described 73% (Table 2). Examination of the eigenvalues for each variable indicated that positive values of PC1 represented sites of mature deciduous forest and negative values represented early successional forest. The second axis (PC2) also represented a successional gradient but one that ended at an earlier stage of succession than the one represented by PC1; closer examination of the raw data sheets indicated that much of the foliage density that contributed to high values of canopy cover was between 12 and 14 m, characteristic of a mid-successional forest dominated by young, low stature trees.

The results of the logistic regression analyses using PC1 indicate that species within each of the functional groups to which Cerulean Warblers belonged were

distributed differentially along the generated habitat gradient (Table 3). Within the

mature forest group, 14 % of member species (2 of 14) did not overlap with the Cerulean

Warbler confidence intervals. Values for the insect-foliage, canopy nesting and

conservation concern groups were 40 % (6 of 15), 17 % (2 of 12), and 29 % (4 of 14),

respectively.

DISCUSSION

On the basis of life history traits and practical considerations, it appears that the Cerulean

Warbler fits reasonably well into all three indicator subgroups. Most importantly, the

habitat affinities and breeding biology of Cerulean Warblers are well-known in eastern

Ontario and this species is easy to sample and observe (Oliarnyk 1996; Oliarnyk and

Robertson 1996; Jones et al. 2000a). Its small body size (~9g) and relatively short

generation time indicate a potential as an effective health or population indicator as both

these characteristics tend to render species sensitive to environmental fluctuations (Blus

et al. 1974; Siemann et al. 1996).

A large population size and a wide geographic range are useful attributes for all

three indicator subgroups. Effective health indicators also tend to be relatively

specialized in their habitat use patterns. Cerulean Warblers are habitat specialists

(Robbins et al. 1992) and our research indicates that the population in eastern Ontario

may be as a large as 3,000 breeding pairs (Jones and Robertson unpublished data). Most

effective health and population indicators tend to be sedentary (Caro and O'Doherty

1999). However, migratory species that exhibit high site fidelity on either the breeding or

wintering grounds have been used effectively in this capacity (Anderson et al. 1975).

The Cerulean Warbler is highly site faithful on the breeding grounds, both within and between years (Jones et al. unpublished manuscript).

The results of our previous research supports the potential of the Cerulean Warbler as a health and population indicator in eastern Ontario. First of all, Cerulean Warbler reproductive success is closely tied to the existence of a complex canopy foliage structure (Oliarnyk 1996; Jones and Robertson, Chapter 3). This characteristic may enable managers to monitor Cerulean Warbler reproductive success as an index of forest succession or of forest health in eastern Ontario. Furthermore, Cerulean Warblers are thought to be reliant on healthy populations of forest canopy insect populations (Jones et al. in press) and, consequently, may have utility as a population indicator in tracking food resources for other species reliant on the same resources. Our research also indicates that Cerulean Warblers are sensitive to disturbance and exhibit low variability in their response to disturbance (Jones et al. in press). The low variability of response is critical in order to extrapolate the response of the individuals measured to the whole population.

Effective biodiversity indicators tend to be habitat specialists with wide geographic ranges; they also tend to have well-known natural histories (Caro and O'Doherty 1999). Despite fitting this profile, our analyses indicate that the Cerulean Warbler would not be effective as a biodiversity indicator in our study area as its distribution across the landscape does not coincide with areas of high avian species richness.

Cerulean Warblers are better suited to a role as an umbrella species in eastern Ontario. Like indicator species, effective umbrella species should have relatively well-known life histories and should be easy to survey and observe. While small body size

may appear to render the Cerulean Warbler unsuitable as an umbrella species (Caro and O'Doherty 1999), any limitation imposed by small size is likely offset by its large regional population and its widespread distribution. A wide distribution may also offset the need for an umbrella species to have a large home range size (Caro and O'Doherty 1999).

Traditional functional groups based on diet or nest location also tended to be more variable in their distributions relative to vegetation changes along a succession gradient than were the habitat groupings. The distribution of the Cerulean Warbler paralleled those of other mature forest species, such as the Ovenbird (*Seiurus aurocapillus*) and Scarlet Tanager (*Piranga olivacea*), implying that management for habitat needs of the Cerulean Warbler would provide for other species. The Cerulean Warbler's potential as an umbrella species is enhanced by its migratory nature which tends to maximize minimum area requirements (Berger 1997; Caro and O'Doherty 1999).

Given the hierarchical nature of habitat selection, broad habitat requirements are likely more important in determining species distributions than are species' food and nesting requirements (Hutto 1985; Block and Brennan 1993). Within the conservation concern group, there was a division between mature forest and shrubland species (Table 3). This separation sets up a potential conservation conflict in which decisions regarding the relative importance of species at risk may need to be made; for example, management for shrubland species, such as the Golden-winged Warbler (*Vermivora chrysoptera*), will necessarily conflict with management aimed at maximizing Cerulean Warbler populations.

Unlike the other surrogate types, flagship species do not need to have well-researched life histories nor do they have to be particularly easy to study or observe. One of the distinguishing characteristics of a flagship species is that it has few selection criteria. These species tend to be large, although this likely has more to do with the perception of charisma than any biological necessity (Caro and O'Doherty 1999). Indeed, many small animals have been used successfully as flagship species, such as the golden lion tamarin (*Leontopithecus rosalia*; Kleiman et al. 1986).

Cerulean Warblers fit well into the category of flagship species. They belong to a group of birds, the Neotropical migrant songbirds, that have entered the conservation spotlight in the last 30 years due to documented declines in the breeding populations of certain species (Robbins et al. 1989). The species is a beautiful bird with an elusive nature that has a high profile in the region due to extensive public education and activism (Jones, personal observations) and is highly valued by birders and ornithologists alike.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Upon review of the evidence, it appears that the Cerulean Warbler may be able to fulfill a role in most of the surrogate categories. However, we believe that it is more suited to a role as an umbrella or flagship species in eastern Ontario. Primarily, the Cerulean Warbler can be used as the focus of conservation efforts aimed at the preservation of mature, deciduous forest and the maintenance of populations of other species that require similar habitats. Ideally, the identification and use of surrogate species will not preclude effective, directed action and research on other species or habitats of conservation concern. However, if carefully selected and employed, surrogate species can provide valuable tools for the rapid implementation and monitoring of conservation efforts.

ACKNOWLEDGMENTS

LITERATURE CITED

Andelman, S. J., and W. F. Fagan. 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes. Proceedings of the National Academy of Sciences, USA 97: 5954-5959.

Anderson, D. W., J. R. Jehl, R. W. Risebrough, L. A. Woods Jr., L. R. DeWeese, and W. G. Edgecomb. 1975. Brown Pelicans: improved reproduction off the southern California coast. Science 190: 806-808.

Berger, J. 1997. Population constraints associated with the use of black rhinos as and

umbrella species for desert herbivores. Conservation Biology 11: 69-78.

Block, W. M. and L. A. Brennan. 1993. The habitat concept in ornithology: theory and

applications. Current Ornithology 11: 35-91.

Blus, L. J., B. S. Neely Jr., A. A. Belisle, and R. M. Prouty. 1974. Organochloride

residues in Brown Pelican eggs: relation to reproductive success. Environmental

Pollution 7: 81-91.

Canterbury, G. E., T. E. Martin, D. R. Petit, L. J. Petit, and D. F. Bradford. 2000. Bird

communities and habitat as ecological indicators of forest condition in regional

monitoring. Conservation Biology 14: 544-558.

Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation

biology. Conservation Biology 13: 805-814.

Chase, M. K., W. B. Kristan III, A. J. Lynam, M. V. Price, and J. T. Rotenberry. 2000.

Single species as indicators of species richness and composition in California

coastal sage scrub birds and small mammals. Conservation Biology 14: 474-487.

COSEWIC. 2000. Canadian species at risk, May 2000. Committee of the Status of

Endangered Wildlife in Canada, Ottawa, ON.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook. Simon &

Schuster, New York.

Freemark, K., and B. Collins. 1992. Landscape ecology of birds breeding in temperate

forest fragments. Pages 443- 454 in J. M. Hagan III and D. W. Johnston, editors.

Ecology and conservation on Neotropical migrant landbirds. Smithsonian

Institution Press, Washington, DC.

Gotelli, N. J., and G. L. Entsminger. 2000. EcoSim: null models software for ecology. Version 5.0. Acquired Intelligence Inc. & Kesey-Bear. http://homepage.together.net/~gentsim/ecosim.htm.

Hamel, P. B. 2000. Cerulean Warbler status assessment. United States Fish and Wildlife Service, Fort Snelling, MN.

Humphries, C. J., P. H. Williams, and R. I. Vane-Wright. 1995. Measuring biodiversity value for conservation. Annual Review of Ecology and Systematics 26: 93-111.

Hutto, R. L. 1985 Habitat selection by nonbreeding, migratory land birds. Pages 455-476 in M.L. Cody, editor. Habitat selection in birds. Academic Press, NY.

Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk 103:593-602.

Inhaber, H. 1976. Environmental indices. John Wiley and Sons, New York, New York.

Jones, J., W. J. McLeish, and R. J. Robertson. 2000a. Density influence census technique accuracy for Cerulean Warblers in eastern Ontario. Journal of Field Ornithology 71: 46-56

Jones, J., P. R. Perazzi, E. H. Carruthers, and R. J. Robertson. 2000b. Sociality and foraging behavior of the Cerulean Warbler in Venezuelan shade coffee plantations. Condor 102: 958-962.

Jones, J., R. D. DeBruyn, J. J. Barg, and R. J. Robertson. in press. Assessing the effects of natural disturbance on a Neotropical migrant songbird. Ecology.

Kleiman, D. G., B. B. Beck, J. M. Dietz, L. A. Dietz, J. D. Ballou, and A. D. Coimbra-Filho. 1986. Conservation program for the golden lion tamarin: captive research and management, ecological studies, educational strategies and reintroduction.

Pages 959-979 in E. Benirschke, editor. Primates: the road the self-sustaining populations. Springer-Verlag, New York.

Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology 2: 316-327.

Launer, A. E., and D. D. Murphy. 1994. Umbrella species and the conservation of habitat fragments: a case of a threatened butterfly and a vanishing grassland ecosystem. Biological Conservation 69: 145-153.

Mathsoft, Inc. 1997. S-Plus 4.0. Data Analysis Products Division, Mathsoft, Inc. Seattle, WA.

Montevecchi, W. A. 1993. Birds as indicators of change in marine bird prey stocks. Pages 217-266 in R. W. Furness and J. J. D. Greenwood, editors. Birds as monitors of environmental change. Chapman and Hall, New York, New York.

Oliarnyk, C. J. 1996. Habitat selection and reproductive success in a population of Cerulean Warblers in southeastern Ontario. M.Sc. thesis, Queen's University, Kingston, ON.

Oliarnyk, C. J., and R. J. Robertson. 1996. Breeding behavior and reproductive success of Cerulean Warblers in southeastern Ontario. The Wilson Bulletin 108: 673-684.

Phillips, D. J. H. 1980. Quantitative aquatic biological indicators. Applied Science Publishers, London, England.

Reynolds, R. T., J. M. Scott, and R. A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. Condor. 82:309-313.

Robbins, C. S., D. S. Dawson, and B. A. Dowell. 1989. Habitat area requirements of

breeding forest birds of the middle Atlantic states. Wildlife Monographs 103: 1-

34.

Robbins, C. S., J. W. Fitzpatrick, and P. B. Hamel. 1992. A warbler in trouble: *Dendroica*

cerulea. Pages 549-562 in J.M. Hagan III, and D.W. Johnston, editors. Ecology

and conservation of Neotropical migrant landbirds. Smithsonian Institution Press,

Washington, D.C.

SAS Institute Inc. 1997. JMP 3.1.7. SAS Institute Inc., Cary, NC, USA.

Sauer, J. R., and S. Droege. 1992. Geographic patterns in populations trends of

Neotropical migrants in North America. Pages 26-42 in J. M. Hagan III and D. W.

Johnston, editors. Ecology and conservation on Neotropical migrant landbirds.

Smithsonian Institution Press, Washington, DC.

Siemann, E., D. Tilman, and J. Haarstad. 1996. Insect species diversity, abundance and

body size relationships. Nature 380: 704-706.

Stone, L., and A. Roberts. 1990. The checkerboard score and species distributions.

Oecologia 85: 74-79.

Temple, S. A., and J. A. Wiens. 1989. Bird populations and environmental changes: can

birds be bio-indicators. American Birds 43: 260-270.

Thomas, W. A., editor. 1972. Indicators of environmental quality. Plenum Press, New

York, New York.

Table 1. Tests for cohesive distributions of functional groups, as indexed by the C-score of Stone and Roberts (1990). Estimated values are mean ± SE for a generated random distribution based on the actual presence-absence matrix for each group for each year.

Functional Group	1997			1998		
	Observed	Estimated	P	Observed	Estimated	P
Mature forest	80.76	91.94 ± 0.03	0.0003	41.42	48.13 ± 0.02	0.0017
Insect-foliage	86.02	92.29 ± 0.02	0.0050	52.96	65.15 ● 0.02	<0.0001
Canopy nesters	67.03	71.92 ± 0.02	0.0078	36.63	40.90 ± 0.02	0.0068
Species of Concern	136.11	147.68 ± 0.12	0.0049	73.32	85.04 ± 0.03	0.0001

Table 2. Successional interpretation of the principal components axes from analysis of 9

vegetation variables [a] for 59 point count stations.

Axis	Cumulative percent variance explained	Interpretation of positive axis values
PC1	26.9	mature deciduous forest: high density of large trees (>30cm dbh)
PC2	45.1	mid-successional forest: high density of saplings and poles (8.1-15.0cm dbh)
PC3	61.0	early successional forest: high density of small stems (3.0-8.0cm), very few trees >15cm dbh
PC4	73.3	rocky outcrop, forest gaps: high understory cover, very few trees <23.0cm dbh, low density of large remnant trees (>30.0cm dbh)

[a] Canopy cover (% cover > 12.0m); understory cover (% cover < 6.0m); sapling density

(stems/m^2); stem densities (stems/m^2) for 5 size classes (3.0-8.0cm dbh, 8.1-15.0cm,

15.1-23.0cm, 23.1-30.0cm, and >30.0cm); total tree basal area (m^2/ha). Axis

interpretation includes all variable loadings > |0.40| from principal components analysis.

Table 3. Logistic regression coefficients and upper and lower 95 % confidence intervals (C. I.) predicting occurrence across a habitat gradient for member species of the mature forest (MF), insect-foliage (IF), canopy nesting (CN) and conservation concern (CC) functional groups. The confidence intervals of the species in bold face do not overlap with the confidence interval of the Cerulean Warbler.

Species	Functional group	Regression coefficient	Lower 95 % C. I.	Upper 95 % C. I.
Cerulean Warbler (*Dendroica cerulea*)	all	0.519	0.121	0.917
American Redstart (*Setophaga ruticilla*)	MF, IF, CN, CC	0.144	-0.299	0.587
Ovenbird (*Seiurus aurocapillus*)	MF, CC	0.475	0.024	0.926
Black-and-white Warbler (*Mniotilta varia*)	MF	-0.290	-0.645	0.065
Scarlet Tanager (*Piranga olivacea*)	MF, IF, CN, CC	0.106	-0.239	0.451
Least Flycatcher (*Empidonax minimus*)	MF, CN, CC	0.116	-0.290	0.522
Yellow-throated Vireo (*Vireo flavifrons*)	MF, IF, CN	0.066	-0.381	0.513
Wood Thrush (*Hylocichla flavipes*)	MF, CC	-0.287	-0.791	0.217

Black-throated Green Warbler (*Dendroica virens*)	MF, CN, CC	0.134	-0.272	0.540
Northern Waterthrush (*Seiurus noveboracensis*)	MF	-0.195	-0.777	0.387
Hairy Woodpecker (*Picoides villosus*)	MF	0.087	-0.466	0.640
Warbling Vireo (*Vireo gilvus*)	MF, IF	-0.995	-1.936	-0.054
Ruffed Grouse (*Bonasa umbellus*)	MF	-0.140	-0.620	0.340
Veery (*Catharus fuscescens*)	MF, CC	-0.622	-1.786	0.542
Yellow-rumped Warbler (*Dendroica coronata*)	MF, IF, CN	0.009	-0.483	0.501
Common Yellowthroat (*Geothlypis trichas*)	IF, CC	-0.192	-0.555	0.171
Golden-winged Warbler (*Vermivora chrysoptera*)	IF, CC	-0.534	-0.955	-0.113
Indigo Bunting (*Passerina cyanea*)	IF, CC	-0.535	-0.974	-0.096
Chestnut-sided Warbler (*Dendroica pensylvanica*)	IF, CC	-0.705	-1.438	0.028

Yellow Warbler (*Dendroica petechia*)	IF	-0.232	-0.585	0.121
Black-capped Chickadee (*Poecile atricapilla*)	IF	0.058	-0.279	0.395
Rose-breasted Grosbeak (*Pheuticus ludovicianus*)	IF, CC	-0.725	-1.270	-0.180
Baltimore Oriole (*Icterus galbula*)	IF, CN, CC	0.281	-0.217	0.779
Blue-grey Gnatcatcher (*Polioptila caerulea*)	IF, CN	-0.279	-0.781	0.223
Cedar Waxwing (*Bombycilla cedrorum*)	CN	-0.066	-0.440	0.308
Blue Jay (*Cyanocitta cristata*)	CN	-0.873	-1.528	-0.218
Eastern Wood-Pewee (*Contopus virens*)	CN, CC	-0.202	-0.670	0.266
Ruby-throated Hummingbird (*Archilochus colubris*)	CN	-0.592	-1.202	0.018
American Crow (*Corvus brachyrhynchos*)	CN	-0.304	-0.835	0.227

Chapter 6

General Summary

Jason Jones

The use of surrogate species has become a relatively common conservation and wildlife management practice and surrogates have been employed in situations ranging from monitoring changes in environmental conditions to identifying areas of high biodiversity. However, there is a lack of standardized methodology for assessing the suitability of a candidate species as a surrogate. Often, species are chosen because they are species of conservation concern themselves or as a result of public perception of their value. This dissertation follows the steps necessary to (a) assess the suitability of the Cerulean Warbler as a surrogate species in eastern Ontario and (b) determine what the most suitable role for this species may be. This was accomplished by first describing the habitat requirements for successful Cerulean Warbler reproduction. I then attempted to place the Cerulean Warbler in a community context to better predict the potential effects of management for Cerulean Warblers on other bird species in the area.

Habitat requirements. - The elucidation of habitat requirements involves an accurate assessment of habitat use and selection. The critical review in Chapter 2 highlighted that the current state of affair in avian habitat selection research is not all positive. Inconsistencies in the avian habitat literature are common in the use and application of terminology, in the development and implementation of standard methodologies, and in the ability of researchers to develop an appropriate behavioural or evolutionary context for their findings. I endeavoured to avoid these inconsistencies in my assessment of habitat selection in breeding Cerulean Warblers in eastern Ontario. The results of this assessment indicate that Cerulean Warblers appear to require a complex canopy structure to breed successfully. It is still unclear whether the canopy structure is more important in providing necessary nest-site characteristics or in influencing prey abundance.

Perhaps the most important finding of the research presented in this dissertation is that Cerulean Warblers appear to possess a degree of plasticity in their habitat affinities and this plasticity renders them somewhat resilient to habitat disturbances. Following a drastic decline in reproductive success following an ice storm that drastically altered canopy foliage, Cerulean Warblers affected a significant shift in nest-site selection patterns and territorial behaviour. These shifts were accompanied by a significant resurgence in reproductive success.

Community context. - Cerulean Warblers are the fourth most common warbler species in the study area. This species is a mature forest specialist, its diet is entirely insectivorous on the breeding grounds, and it is a canopy nester. Mature forest species tended to be less variable in their distributions along a succession gradient than were the species within the more traditional functional groups based on diet or nest location. The distribution of the Cerulean Warbler paralleled those of other mature forest species, such as the Ovenbird and Scarlet Tanager, implying that management for habitat needs of the Cerulean Warbler would provide for other species.

A role for the Cerulean Warbler? - This dissertation has found that the Cerulean Warbler has limited potential as an indicator species, either in monitoring the health and succession of eastern deciduous forest or in tracking populations of forest canopy arthropods. This species is not, however, a suitable candidate for a biodiversity indicator, at least not for predicting avian species richness. I feel that the Cerulean Warbler is best suited to a role as an umbrella or flagship species in eastern Ontario. Primarily, the

Cerulean Warbler can be used as the focus of conservation efforts aimed at the preservation of mature, deciduous forest and the maintenance of populations of other species that require similar habitats.

FUTURE RESEARCH CONSIDERATIONS

There are several avenues of research that I feel will not only enhance our understanding of Cerulean Warbler ecology but also will lead to an improvement in our ability to effectively manage species of interest in a landscape context.

- The relative behavioural roles of male and female Cerulean Warblers in nest-site selection and brood rearing.

- General habitat requirements and habitat use patterns of female Cerulean Warblers (i.e. off-nest habitat use patterns).

- Mating system of Cerulean Warblers and its influence on large-scale habitat patterns.

- The influence of interspecific interactions on habitat use patterns and habitat suitability.

- The suitability of managed forests (e.g. maple syrup plantations) as Cerulean Warbler habitat.

- A Geographical Information Systems approach to estimating Cerulean Warbler population size.

- Continued collaboration with other Cerulean Warbler researchers to determine the potential importance of a large, successful population situated at the northern periphery of the breeding range.

Appendix A – Papers included in "Chapter 2 - Habitat selection studies in avian ecology: a critical review".

Taxonomic Grouping	Category	Reference
Apterygidae	habitat use	Taborsky and Taborsky 1995
Spheniscidae	nest-site selection	Seddon and Davis 1989
Gaviidae	habitat selection	Haney 1990
Podicipedidae	nest-site selection	Boe 1994; Burger and Gochfeld 1995
seabirds	habitat use	Day et al. 1997
	habitat selection	Ainley et al. 1993
	nest-site selection	Burger and Gochfeld 1991; Hagelin and Miller 1997
Ardeidae	habitat use	Powell 1987; Mora 1992; Erwin et al. 1996
	habitat selection	Boulinier 1996
Phoenicopteridae	habitat use	Espino-Barros and Baldassarre 1989
Dendrocygnidae	habitat use	Zwank et al. 1988
Anatidae	habitat use	Maxson and Pace 1992; Merendino and Ankney 1994; Losito and Baldassarre 1995; Bustnes 1996; Carriére et al. 1999; Anderson and Tacha 1999
	habitat selection	Laing and Raveling 1993
	nest-site selection	Petersen 1990; Gloutney and Clark 1997
Accipitridae	habitat use	Plumpton and Andersen 1997
	habitat selection	Schmutz 1989; Bosakowski et al. 1992; Marzluff et al. 1997b; Berkelman et al. 1999
	nest-site selection	Speiser and Bosakowski 1987; Titus and Mosher 1987; Berkelman 1995; Moorman and Chapman 1996
Falconidae	habitat use	Hustler and Howells 1988; Sodhi and Oliphant 1992; Squires et al. 1993; Varland et al. 1993

	habitat selection	Bohall-Wood and Collopy 1986; Marzluff et al. 1997a
	nest-site selection	Warkentin and James 1988; Sieg and Becker 1990
Phasianidae	habitat use	Frederick and Gutiérrez 1992; Giesen and Braun 1992; Gonzalez et al. 1998; Scott et al. 1998
	habitat selection	Badyaev et al. 1996; Martínez-Morales 1999
	nest-site selection	Badyaev 1995; Thogmartin 1999
Odontophoridae	habitat use	Brennan et al. 1987
Rallidae	habitat use	Ritter and Savage 1999
	nest-site selection	Sutherland and Maher 1987; Sánchez-Lafuente et al. 1998
Scolopacidae	habitat use	Ryan and Renkin 1987; Bolster and Robinson 1990; Hayes and Fox 1991; Withers and Chapman 1993; Krementz et al. 1995; Colwell and Dodd 1997
	habitat selection	Warnock and Takekawa 1995
	nest-site selection	Pampush and Anthony 1993
Charadriinae	habitat use	Nicholls and Baldassarre 1990; Evans and Harris 1994; Thibault and McNeil 1994; Boettcher et al. 1995; Knopf and Rupert 1995; Lauro and Nol 1995; Andres 1998; Goldin and Regosin 1998
	nest-site selection	Burger 1987; Lauro and Burger 1989
Laridae	habitat use	Shealer 1996
	habitat selection	Burger and Gochfeld 1988a; Rodway and Regehr 1999
	nest-site selection	Burger and Gochfeld 1987; Burger and Gochfeld 1988b, 1988c; Saliva and Burger 1989; Spear and Anderson 1989; Ramos and del Nevo 1995
Phaethontidae	nest-site selection	Schaffner 1991
Columbidae	habitat use	Jones and Mirarchi 1990
	habitat selection	Ostrand et al. 1996
Psittacidae	habitat use	Gilardi and Munn 1998

	habitat selection	Sol et al. 1997
Strigidae	habitat use	Ganey and Balda 1989; Solis and Gutiérrez 1990; Sparks et al. 1994; Hunter et al. 1995; Linkhart et al. 1998
	habitat selection	Call et al. 1992; Ganey and Balda 1994; Seamans and Gutiérrez 1995; Mazur et al. 1998; Ward et al. 1998
	nest-site selection	Goad and Mannan 1987; McCallum and Gehlbach 1988; Green and Anthony 1989; Beltoff and Ritchison 1990; Forsman and Giese 1997; LaHaye et al. 1997; LaHaye and Gutiérrez 1999; Smith et al. 1999
Trochilidae	habitat use	Brown 1992
	habitat selection	Baltosser 1989
Picidae	habitat use	DeLotelle et al. 1987; Renken and Wiggers 1993; Loose and Anderson 1995
	habitat selection	Vierling 1997
	nest-site selection	Kerpez and Smith 1990; Linder and Anderson 1998; Hooge et al. 1999
Furnariidae	nest-site selection	Graves and Arango 1988
Tyrannidae	habitat use	Latta and Wunderle 1996; Martin and Morrison 1999;
	habitat selection	Bergin 1992; Sedgwick and Knopf 1992; Kelly 1993
	nest-site selection	Sakai and Noon 1991; Wilson and Cooper 1998
Hirundinidae	nest-site selection	Rendell and Robertson 1990
Corvidae	habitat use	Burt 1996
	habitat selection	Edwards 1986; VanderWerf 1993
	nest-site selection	Dunk et al. 1997
Paridae	habitat use	Hill and Lein 1989
	nest-site selection	Hatchwell et al. 1999; Ramsay et al. 1999
Troglodytidae	habitat selection	Leonard and Picman 1987
	nest-site selection	Belles-Isles and Picman 1986

Zosteropidae	habitat use	Craig 1990
Sylviidae	habitat use	Craig 1992
Muscicapidae	habitat use	Anders et al. 1998; Vega Rivera et al. 1998; Vega Rivera et al. 1999
	nest-site selection	Martin and Roper 1988; Zamora 1990; Hoover and Brittingham 1998
Laniidae	habitat use	Michaels and Cully 1998
Parulidae	habitat use	Sodhi and Paszkowski 1995; Yong et al. 1998; Burhans and Thompson 1999; Keane and Morrison 1999; Robichaud and Villard 1999
	habitat selection	Sherry and Holmes 1988; Lopez Ornat and Greenberg 1990; Wenny et al. 1993; McShea et al. 1995; Parrish 1995; Hunt 1996; Matsuoka et al. 1997; De la Zerda Lerner and Stauffer 1998; Sodhi et al. 1999
	nest-site selection	Holway 1991; Knopf and Sedgwick 1992; Kilgo et al. 1996a, 1996b
Emberizidae	habitat use	Greenberg 1988
	habitat selection	Zimmerman 1988; Munson 1992; Herkert 1994
	nest-site selection	Filliater et al. 1994; Larison et al. 1998
Icteridae	habitat use	Clark and Weatherhead 1987
	habitat selection	Evans and Gates 1997
	nest-site selection	Dunham 1990
Fringillidae	nest-site selection	Bekoff et al. 1987
Passeriformes (misc.)	habitat use	Yahner 1987; Petit 1989; Darveau et al. 1992; Douglas et al. 1992; Esler 1992; Wunderle and Waide 1993; Yahner 1995; Rappole et al. 1998
	habitat selection	Gutzwiller and Anderson 1987; Sedgwick 1987; Bollinger 1995; Winker 1995; Willson and Comet 1996; Wilson et al. 1998

nest-site selection   Li and Martin 1991; Flashpoler and Laska 1994; Mitchell et al. 1996; Schepps et al. 1999

LITERATURE CITED

Ainley, D.G., C.A. Ribic, and L.B. Spear. 1993. Species-habitat relationships among Antarctic seabirds: a function of physical or biological factors? Condor 95: 806-816.

Anders, A.D., J. Faaborg, and F.R. Thompson III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. Auk 115: 349-358.

Anderson, J.T., and T.C. Tacha. 1999. Habitat use by Masked Ducks along the Gulf Coast of Texas. Wilson Bulletin 111: 119-121.

Andres, B.A. 1998. Shoreline habitat use by Black Oystercatchers breeding in Prince William Sound, Alaska. Journal of Field Ornithology 69: 626-634.

Badyaev, A.V. 1995. Nesting habitat and nesting success of eastern Wild Turkeys in the Arkansas Ozark highlands. Condor 97: 221-232.

Badyaev, A.V., T.E. Martin and W.J. Etges. 1996. Habitat sampling and habitat selection by female Wild Turkeys: ecological correlates and reproductive consequences. Auk 113: 636-646.

Baltosser, W.H. 1989. Nectar availability and habitat selection by hummingbirds in Guadalupe Canyon. Wilson Bulletin 101: 559-578.

Bekoff, M., A.C. Scott, and D.A. Conner. 1987. Nonrandom nest-site selection in Evening grosbeaks. Condor 89: 819-829.

Belles-Isles, J.-C., and J. Picman. 1986. Nesting losses and nest site preferences in House Wrens. Condor 88: 483-486.

Beltoff, J.R., and G. Ritchison. 1990. Nest-site selection by Eastern Screech-Owls in central Kentucky. Condor 92: 982-990.

Bergin, T.M. 1992. Habitat selection by the Western Kingbird in western Nebraska: a hierarchical analysis. Condor 94: 903-911.

Berkelman, J. 1995. Nest-site characteristics of the Madagascar Buzzard in the rain forest of the Masoala Peninsula. Condor 97: 273-275.

Berkelman, J., J.D. Fraser, and R.T. Watson. 1999. Lake selection by Madagascar Fish-eagles. Auk 116: 976-983.

Boe, J.S. 1994. Nest site selection by Eared Grebes in Minnesota. Condor 96: 19-35.

Boettcher, R., S.M. Haig, and W.C. Bridges, Jr. 1995. Habitat-related factors affecting the distribution of nonbreeding American Avocets in coastal South Carolina. Condor 97: 68-81.

Bohall-Wood, P., and M.W. Collopy. 1986. Abundance and habitat selection of two American Kestrel subspecies in north-central Florida. Auk 103: 557-563.

Bollinger, E.K. 1995. Successional changes and habitat selection in hayfield bird communitites. Auk 112: 720-730.

Bolster, D.C., and S.K. Robinson. 1990. Habitat use and relative abundance of migrant shorebirds in a western Amazonian site. Condor 92: 239-242.

Bosakowski, T., D.G. Smith, and R. Speiser. 1992. Status, nesting density, and macrohabitat selection of Red-shouldered Hawks in northern New Jersey. Wilson Bulletin 104: 434-446.

Boulinier, T. 1996. On breeding performance, colony growth and habitat selection in Buff-necked Ibis. Condor 98: 440-441.

Brennan, L.A., W.M. Block, and R.J. Gutiérrez. 1987. Habitat use by Mountain Quail in northern California. Condor 89: 66-74.

Brown, B.T. 1992. Nesting chronology, density and habitat use of Black-chinned Hummingbirds along the Colorado River, Arizona. Journal of Field Ornithology 63: 393-400.

Burger, J. 1987. Physical and social determinants of nest-site selection in Piping Plover in New

Jersey. Condor 89: 811-818.

Burger, J., and M Gochfeld. 1987. Nest-site selection by Mew Gulls (*Larus canus*): a comparison

of marsh and dry-land colonies. Wilson Bulletin 99: 673-687.

Burger, J., and M. Gochfeld. 1988a. Habitat selection in Mew Gulls: small colonies and site

plasticity. Wilson Bulletin 100: 395-410.

Burger, J. and M. Gochfeld. 1988b. Nest-site selection and temporal patterns in habitat use of

Roseate and Common Terns. Auk 105: 433-438.

Burger, J., and M. Gochfeld. 1988c. Nest-site selection by Roseate Terns in two tropical colonies

on Culebra, Puerto Rico. Condor 90: 843-851.

Burger, J., and M. Gochfeld. 1991. Nest-site selection by the Herald Petrel and White-tailed

Tropicbird on Round Island, Indian Ocean. Wilson Bulletin 103: 126-129.

Burger, J., and M. Gochfeld. 1995. Nest site selection by Eared Grebes in a Franklin's Gull colony:

structural stability parasites. Condor 97: 577-580.

Burhans, D.E., and F.R. Thompson, III. 1999. Habitat patch size and nesting success of Yellow-

breasted Chats. Wilson Bulletin 111: 210-215.

Burt, D.B. 1996. Habitat-use pattern in cooperative and non-cooperative breeding birds: testing

predictions with Western Scrub-Jays. Wilson Bulletin 108: 712-727.

Bustnes. J.O. 1996. Is parental care a constraint on the habitat use of Common Eider females?

Condor 98: 22-26.

Call, D.R., R.J. Gutiérrez, and J. Verner. 1992. Foraging habitat and home-range characteristics of

California Spotted Owls in the Sierra Nevada. Condor 94: 880-888.

Carriére, S., R.G. Bromley, and G. Gauthier. 1999. Comparative spring habitat and food use by two

   Arctic nesting geese. Wilson Bulletin 111: 166-180.

Clark, R.G., and P.J. Weatherhead. 1987. Influence of population size on habitat use by territorial

   male Red-winged Blackbirds in agricultural landscapes. Auk 104: 311-315.

Colwell, M.A., and S.L. Dodd. 1997. Environmental and habitat correlates of pasture use by

   nonbreeding shorebirds. Condor 99: 337-344.

Craig, R.J. 1990. Foraging behavior and microhabitat use of two species of white-eyes

   (Zosteropidae) on Saipan, Micronesia. Auk 107: 500-505.

Craig, R.J. 1992. Territoriality, habitat use and ecological distinctness of an endangered Pacific

   Island Reed-Warbler. Journal Field Ornithology 63: 436-444.

Darveau, M., J.L. Desgranges, and G. Gauthier. 1992. Habitat use by three insectivorous birds in

   declining maple forests. Condor 94: 72-82.

Day, R.H., S.M. Murphy, J.A. Wiens, G.D. Hayward, E.J. Harner, and B.E. Lawhead. 1997. Effects

   of the *Exxon Valdez* oil spill on habitat use by birds along the Kenai Peninsula, Alaska.

   Condor 99: 728-742.

De la Zerda Lerner, S., and D.F. Stauffer. 1998. Habitat selection by Blackburnian Warblers

   wintering in Columbia. Journal of Field Ornithology 69: 457-465.

DeLotelle, R.S., R.J. Epting, and J.R. Newman. 1987. Habitat use and territory characteristics of

   Red-cockaded Woodpeckers in central Florida. Wilson Bulletin 99: 202-217.

Douglas, D.C., J.T. Ratti, R.A. Black, and J.R. Alldredge. 1992. Avian habitat associations in

   riparian zones of Idaho's Centennial Mountains. Wilson Bulletin 104: 485-500.

Dunham, M.L. 1990. Nest-site selection by Boat-tailed Grackles. Wilson Bulletin 102: 702-706.

Dunk, J.R., R.N. Smith, and S.L. Cain. 1997. Nest-site selection and reproductive success in

Common Ravens. Auk 114: 116-120.

Edwards, T.C., Jr. 1986. Ecological distribution of the Gray-breasted Jay: the role of habitat.

Condor 88: 456-460.

Erwin, R.M., J.G. Haig, D.B. Stotts, and J.S. Hatfield. 1996. Dispersal and habitat use by post-

fledging juvenile Snowy Egrets and Black-crowned Night-Herons. Wilson Bulletin 108:

342-356.

Esler, D. 1992. Habitat use by piscivorous birds on a power plant cooling reservoir. Journal of Field

Ornithology 63: 241-249.

Espino-Barros, R., and G.A. Baldassarre. 1989. Activity and habitat-use patterns of breeding

Caribbean Flamingos in Yucatan, Mexico. Condor 91: 585-591.

Evans, D.R., and J.E. Gates. 1997. Cowbird selection of breeding areas: the role of habitat and bird

species abundance. Wilson Bulletin 109: 470-480.

Evans, T.J., and S.W. Harris. 1994. Status and habitat use by American Avocets wintering at

Humboldt Bay, California. Condor 96: 178-189.

Filliater, T.S., R. Breitwisch, and P.M. Nealen. 1994. Predation on Northern Cardinal nests: does

choice of nest site matter. Condor 96: 761-768.

Flashpoler, D.J., and M.S. Laska. 1994. Nest site selection by birds in acacia trees in a Costa Rican

dry deciduous forest. Wilson Bulletin 106: 162-165.

Forsman, E.D. and A.R. Giese. 1997. Nests of northern Spotted Owls on the Olympic Peninsula,

Washington. Wilson Bulletin 109: 28-41.

Frederick, G.P., and R.J. Gutiérrez. 1992. Habitat use and population characteristics of the White-

tailed Ptarmigan in the Sierra Nevada, California. Condor 94: 889-902.

Ganey, J.L., and R.P. Balda. 1989. Distribution and habitat use of Mexican Spotted Owls in

Arizona. Condor 91: 355-361.

Ganey, J.L. and R.P. Balda. 1994. Habitat selection by Mexican Spotted Owls in northern Arizona.

Auk 111: 162-169.

Giesen, K.M., and C.E. Braun. 1992. Winter home range and habitat characteristics of White-tailed

Ptarmigan in Colorado. Wilson Bulletin 104: 263-272.

Gilardi, J.D., and C.A. Munn. 1998. Patterns of activity, flocking, and habitat use in parrots of the

Peruvian Amazon. Condor 100: 641-653.

Gloutney, M.L. and R.C. Clark. 1997. Nest-site selection by Mallards and Blue-winged Teal in

relation to microclimate. Auk 114: 381-395.

Goad, M.S., and R.W. Mannan. 1987. Nest site selection by Elf Owls in Saguaro National

Monument, Arizona. Condor 89: 659-662.

Goldin, M.R., and J.V. Regosin. 1998. Chick behavior, habitat use, and reproductive success of

Piping Plovers at Goosewing Beach, Rhode Island. Journal of Field Ornithology 69: 228-

234.

Gonzalez, M.J., H.B. Quigley, and C.I. Taylor. 1998. Habitat use and reproductive ecology of the

Ocellated Turkey in Tikal National Park, Guatemala. Wilson Bulletin 110: 505-510.

Graves, G.R., and G. Arango. 1988. Nest-site selection, nest, and eggs of the Stout-billed Cinclodes

(Cinclodes excelsior), a high Andean furnariid. Condor 90: 251-253.

Green, G.A., and R.G. Anthony. 1989. Nesting success and habitat relationships of Burrowing

Owls in the Columbia Basin, Oregon. Condor 91: 347-354.

Greenberg, R. 1988. Water as a habitat cue for breeding swamp and song sparrows. Condor 90:

420-427.

Gutzwiller, K.J., and S.H. Anderson. 1987. Multiscale associations between cavity-nesting birds and features of Wyoming streamside woodlands. Condor 89: 534-548.

Hagelin, J.C. and G.D. Miller. 1997. Nest-site selection in South Polar Skuas: balancing nest safety and access to resources. Auk 114: 638-645.

Haney, J.C. 1990. Winter habitat of Common Loons on the continental shelf of the southeastern United States. Wilson Bulletin 102: 253-263.

Hatchwell, B.J., A.F. Russell, M.K. Fowlie, and D.J. Ross. 1999. Reproductive success and nest-site selection in a cooperative breeder: effect of experience and a direct benefit of helping. Auk 116: 355-363.

Hayes, F.E., and J.A. Fox. 1991. Seasonality, habitat use, and flock size of shorebirds at the Bahía de Asuncíon, Paraguay. Wilson Bulletin 103: 637-649.

Herkert, J.R. 1994. Status and habitat selection of the Henslow's Sparrow in Illinois. Wilson Bulletin 106: 35-45.

Hill, B.G. and M.R. Lein. 1989. Territory overlap and habitat use of sympatric chickadees. Auk 106: 259-268.

Holway, D.A. 1991. Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. Condor 93: 575-581.

Hooge, P.N., M.T. Stanback, and W.D. Koenig. 1999. Nest-site selection in the Acorn Woodpecker. Auk 116: 45-54.

Hoover, J.P., and M.C. Brittingham. 1998. Nest-site selection and nesting success of Wood Thrushes. Wilson Bulletin 110: 375-383.

Hunt, P.D. 1996. Habitat selection by American Redstarts along a successional gradient in northern hardwoods forest: evaluation of habitat quality. Auk 113: 875-888.

Hunter, J.E., R.J. Gutiérrez, and A.B. Franklin. 1995. Habitat configuration around Spotted Owl

sites in northwestern California. Condor 97: 684-693.

Hustler, K., and W.W. Howells. 1988. The effect of primary production on breeding success and

habitat selection in the African Hawk-Eagle. Condor 90: 583-587.

Jones, M.T., and R.E. Mirarchi. 1990. Habitats used by Common Ground-Doves in southern

Alabama. Wilson Bulletin 102: 137-139.

Keane, J.L., and M.L. Morrison. 1999. Temporal variation in resource use by Black-throated Gray

Warblers. Condor 101: 67-75.

Kelly, J.P. 1993. The effect of nest predation on habitat selection by Dusky Flycatchers in Limber-

Pine-Juniper woodland. Condor 95: 83-93.

Kerpez, T.A., and N.S. Smith. 1990. Nest-site selection and nest-cavity characteristics of Gila

Woodpeckers and Northern Flickers. Condor 92: 193-198.

Kilgo, J.C., R.A. Sargent, K.V. Miller, and B.R. Chapman. 1996a. Nest sites of Kentucky Warblers

in bottomland hardwoods of South Carolina. Journal of Field Ornithology 67: 300-306.

Kilgo, J.C., R.A. Sargent, B.R. Chapman, and K.V. Miller. 1996b. Nest-site selection by Hooded

Warblers in bottomland hardwoods of South Carolina. Wilson Bulletin 108: 53-60.

Knopf, F.L., and J.R. Rupert. 1995. Habits and habitats of Mountain Plovers in California. Condor

97: 743-751.

Knopf, F.L., and J.A. Sedgwick. 1992. An experimental study of nest-site selection by Yellow

Warblers. Condor 94: 734-742.

Krementz, D.G., J.T. Seginak, and G.W. Pendleton. 1995. Habitat use at night by wintering

American Woodcock in coastal Georgia and Virginia. Wilson Bulletin 107: 686-697.

LaHaye, W.S., and R.J. Gutiérrez. 1999. Nest sites and nesting habitat of the Northern Spotted Owl in northwestern California. Condor 101: 324-330.

LaHaye, W.S., R.J. Gutiérrez, and D.R. Call. 1997. Nest-site selection and reproductive success of California Spotted Owls. Wilson Bulletin 109: 42-51.

Laing, K.K., and D.G. Raveling. 1993. Habitat and food selection by Emperor Goose goslings. Condor 95: 879-888.

Larison, B., S.A. Laymon, P.L. Williams, and T.B. Smith. 1998. Song Sparrows vs. cowbird brood parasites: impacts of forest structure and nest-site selection. Condor 100: 93-101.

Latta. S.C., and J.M. Wunderle, Jr. 1996. Ecological relationships of two todies in Hispaniola: effects of habitat and flocking. Condor 98: 769-779.

Lauro, B. and J. Burger. 1989. Nest-site selection of American Oystercatchers (*Haemtopus palliatus*) in salt marshes. Auk 106: 185-192.

Lauro, B., and E. Nol. 1995. Patterns of habitat use for Pied and Sooty Oystercatchers nesting at the Furneaux Islands, Australia. Condor 97: 920-934.

Leonard, M.L., and J. Picman. 1987. Nesting mortality and habitat selection by Marsh Wrens. Auk 104: 491-495.

Li, P., and T.E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108: 405-418.

Linder, K.A., and S.H. Anderson. 1998. Nesting habitat of Lewis' Woodpeckers in southeastern Wyoming. Journal of Field Ornithology 69: 109-116.

Linkhart, B.D., R.T. Reynolds, and R.A. Ryder. 1998. Home range and habitat of breeding Flammulated Owls in Colorado. Wilson Bulletin 110: 342-351.

Loose, S.S., and S.H. Anderson. 1995. Woodpecker habitat use in the forests of southern Wyoming. Journal of Field Ornithology 66: 503-514.

Lopez Ornat, A. and R. Greenberg. 1990. Sexual segregation by habitat in migratory warblers in Quintana Roo, Mexico. Auk 107: 539-543.

Losito, M.P., and G.A. Baldassarre. 1995. Wetland use by breeding and postbreeding female Mallards in the St. Lawrence River Valley. Wilson Bulletin 107: 55-63.

Martin, J.A., and M.L. Morrison. 1999. Distribution, abundance, and habitat characteristics of the Buff-breasted Flycatcher in Arizona. Condor 101: 272-281.

Martin, T.E., and J.J. Roper. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90: 51-57.

Martínez-Morales, M.A. 1999. Conservation status and habitat preferences of the Cozumel Curassow. Condor 101: 14-20.

Marzluff, J.M., B.A. Kimsey, L.S. Schueck, M.E. McFadzen, M.S. Vekasy, and J.C. Bednarz. 1997a. The influence of habitat, prey abundance, sex, and breeding success on the ranging behavior of Prairie Falcons. Condor 99: 567-584.

Marzluff, J.M., S.T. Knick, M.S. Vekasy, L.S. Schueck and T.J. Zarriello. 1997b. Spatial use and habitat selection of Golden Eagles in southwestern Idaho. Auk 114: 673-687.

Matsuoka, S.M., C.M. Handel, D.D. Roby and D.L. Thomas. 1997. The relative importance of nesting and foraging sites in selection of breeding territories by Townsend's Warblers. Auk 114: 657-667.

Maxson, S.J., and R.M. Pace, III. 1992. Diurnal time-activity budgets and habitat use of Ring-necked Duck ducklings in northcentral Minnesota. Wilson Bulletin 104: 472-484.

Mazur, K.M., S.D. Frith and P.C. James. 1998. Barred Owl home range and habitat selection in the boreal forest of central Saskatchewan. Auk 115: 746-754.

McCallum, D.A., and F.R. Gehlbach. 1988. Nest-site preferences of Flammulated Owls in western New Mexico. Condor 90: 653-661.

McShea, W.J., M.V.McDonald, E.S. Morton, R. Meier and J.H. Rappole. 1995. Long-term trends in habitat selection by Kentucky Warblers. Auk 112: 375-381.

Merendino, M.T., and C.D. Ankney. 1994. Habitat use by Mallards and American Black Ducks breeding in central Ontario. Condor 96: 411-421.

Michaels, H.L., and J.F. Cully, Jr. 1998. Landscape and fine scale habitat associations of the Loggerhead Shrike. Wilson Bulletin 110: 474-482.

Mitchell, M.C., L.B. Best, and J.P. Gionfriddo. 1996. Avian nest-site selection and nesting success in two Florida citrus groves. Wilson Bulletin 108: 573-583.

Moorman, C.E., and B.R. Chapman. 1996. Nest-site selection of Red-shouldered and Red-tailed Hawks in a managed forest. Wilson Bulletin 108: 357-368.

Mora, M.A. 1992. Habitat use by foraging Cattle Egrets in the Mexicali Valley, Baja California. Wilson Bulletin 104: 142-147.

Munson, E.S. 1992. Influence of nest cover on habitat selection in Clay-colored Sparrows. Wilson Bulletin 104: 525-529.

Nicholls, J.L., and G.A. Baldassarre. 1990. Habitat associations of Piping Plovers wintering in the United States. Wilson Bulletin 102: 581-590.

Ostrand, W.D., J.A. Bissonette, and M.R. Conover. 1996. Selection of foraging habitat by mourning doves: a structural approach. Journal of Field Ornithology 67: 691-697.

Pampush, G.J., and R.G. Anthony. 1993. Nest success, habitat utilization and nest-site selection of

Long-billed Curlews in the Columbia Basin, Oregon.. Condor 95: 957-967.

Parrish, J.D. 1995. Experimental evidence for intrinsic microhabitat preferences in the Black-

throated Green Warbler. Condor 97: 935-943.

Petersen, M.R. 1990. Nest-site selection by Emperor Geese and Cackling Canada Geese. Wilson

Bulletin 102: 413-426.

Petit, D.R. 1989. Weather-dependent use of habitat patches by wintering woodland birds. Journal of

Field Ornithology 60: 241-247.

Plumpton, D.L., and D.E. Andersen. 1997. Habitat use and time budgeting by wintering

Ferruginous Hawks. Condor 99: 888-893.

Powell, G.V.N. 1987. Habitat use by wading birds in a subtropical estuary: implications of

hydrogeography. Auk 104: 740-749.

Ramos, J.A. and A.J. del Nevo. 1995. Nest-site selection by Roseate Terns and Common Terns in

the Azores. Auk 112: 580-589.

Ramsay, S.M., K. Otter, and L.M. Ratcliffe. 1999. Nest-site selection by female Black-capped

Chickadees: settlement based on conspecific attraction. Auk 116: 604-617.

Rappole, J.H., K. Winker, and G.V.N. Powell. 1998. Migratory bird habitat use in southern

Mexico: mist nets versus point counts. Journal of Field Ornithology 69: 635-645.

Rendell, W.B., and R.J. Robertson. 1990. Influence of forest edge on nest-site selection by Tree

Swallows. Wilson Bulletin 102: 634-644.

Renken, R.B., and E.P. Wiggers. 1993. Habitat characteristics related to Pileated Woodpecker

densities in Missouri. Wilson Bulletin 105: 77-83.

Ritter, M.W., and J.A. Savage. 1999. A predictive model of wetland habitat use on Guam by

endangered Mariana Common Moorhens. Condor 101: 282-287.

Robichaud, I., and M.-A. Villard. 1999. Do Black-throated Green Warblers prefer conifers? Meso-

and microhabitat use in a mixedwood forest. Condor 101: 262-271.

Rodway, M.S., and H.M. Regehr. 1999. Habitat selection and reproductive performance of food-

stressed Herring Gulls. Condor 101: 566-576.

Ryan, M.R., and R.B. Renkin. 1987. Habitat use by breeding Willets in the northern Great Plains.

Wilson Bulletin 99: 175-189.

Sakai, H.F., and B.R. Noon. 1991. Nest-site characteristics of Hammond's and Pacific-slope

Flycatchers in northwestern California. Condor 93: 563-574.

Saliva, J.E., and J. Burger. 1989. Effect of experimental manipulation of vegetation density on nest-

site selection in Sooty Terns. Condor 91: 689-698.

Sánchez-Lafuente, A.M., J.M. Algántara, and M. Romero. 1998. Nest-site selection and nest

predation in the Purple Swamphen. Journal of Field Ornithology 69: 563-576.

Schaffner, F.C. 1991. Nest-site selection and nesting success of White-tailed Tropicbirds (*Phaethon

lepturus*) at Cayo Luís Peña, Puerto Rico. Auk 108: 911-922.

Schepps, J., S. Lohr, and T.E. Martin. 1999. Does tree hardness influence nest-tree selection by

primary cavity-nesters. Auk 116: 658-665.

Schmutz, J.K. 1989. Hawk occupancy of disturbed grasslands in relation to models of habitat

selection. Condor 91: 362-371.

Scott, J.G., M.J. Lovallo, G.J. Storm, and W.M. Tzilkowski. 1998. Summer habitat use by Ruffed

Grouse with broods in central Pennsylvania. Journal of Field Ornithology 69: 474-485.

Seamans, M.E., and R.J. Gutiérrez. 1995. Breeding habitat of the Mexican Spotted Owl in the Tularosa Mountains, New Mexico. Condor 97: 944-952.

Seddon, P.J., and L.S. Davis. 1989. Nest-site selection by Yellow-eyed Penguins. Condor 91: 653-659.

Sedgwick, J.A. 1987. Avian habitat relationships in Pinyon-Juniper woodland. Wilson Bulletin 99: 413-431.

Sedgwick, J.A., and F.L. Knopf. 1992. Describing Willow Flycatcher habitats: scale perspectives and gender differences. Condor 94: 720-733.

Shealer, D.A. 1996. Foraging habitat use and probability in tropical Roseate Terns and Sandwich Terns. Auk 113: 209-217.

Sherry, T.W., and R.T. Holmes. 1988. Habitat selection by breeding American Redstarts in response to a dominant competitor, the Least Flycatcher. Auk 105: 350-364.

Sieg, C.H., and D.M. Becker. 1990. Nest-site habitat selected by Merlins in southeastern Montana. Condor 92: 688-694.

Smith, D.G., T. Bosakowski, and A. Devine. 1999. Nest site selection by urban and rural Great Horned Owls in the northeast. Journal of Field Ornithology 70: 535-542.

Sodhi, N.S., and L.W. Oliphant. 1992. Hunting ranges and habitat use and selection of urban-breeding Merlins. Condor 94: 743-749.

Sodhi, N.S., and C.A. Paszkowski. 1995. Habitat use and foraging behavior of four Parulid warblers in a second-growth forest. Journal of Field Ornithology 66: 277-288.

Sodhi, N.S., C.A. Paszkowski, and S. Keehn. 1999. Scale-dependent habitat selection by American Redstarts in aspen-dominated forest fragments. Wilson Bulletin 111: 70-75.

Sol, D., D.M. Santos, E. Feria, and J. Clavell. 1997. Habitat selection by the Monk Parakeet during colonization of a new area in Spain. Condor 99: 39-46.

Solis, D.M., Jr., and R.J. Gutiérrez. 1990. Summer habitat ecology of Northern Spotted Owls in northwestern California. Condor 92: 739-748.

Sparks, E.J., J.R. Belthoff, and G. Ritchison. 1994. Habitat use by Eastern Screech-Owls in central Kentucky. Journal of Field Ornithology 65: 83-95.

Spear, L.B., and D.W. Anderson. 1989. Nest-site selection by Yellow-footed Gulls. Condor 91: 91-99.

Speiser, R., and T. Bosakowski. 1987. Nest site selection by Northern Goshawks in northern New Jersey and southeastern New York. Condor 89: 387-394.

Squires, J.R., S.H. Anderson, and R. Oakleaf. 1993. Home range size and habitat-use patterns of nesting Prairie Falcons near oil developments in northeastern Wyoming. Journal of Field Ornithology 64: 1-10.

Sutherland, J.M., and W.J. Maher. 1987. Nest-site selection of the American Coot in the aspen parklands of Saskatchewan. Condor 89: 804-810.

Taborsky, B. and M. Taborsky. 1995. Habitat use and selectivity of the Brown Kiwi (*Apteryx australis mantelli*) in a patchy environment. Auk 112: 680-689.

Thibault, M., and R. McNeil. 1994. Day/night variation in habitat use by Wilson's Plovers in northeastern Venezuela. Wilson Bulletin 106: 299-310.

Thogmartin, W.E. 1999. Landscape attributes and nest-site selection in Wild Turkeys. Auk 116: 912-923.

Titus, K., and J.A. Mosher. 1987. Selection of nest tree species by Red-shouldered and Broad-winged Hawks in two temperate forest regions. Journal of Field Ornithology 58: 274-283.

VanderWerf, E.A. 1993. Scales of habitat selection by foraging 'Elepaio in undisturbed and human-altered forests in Hawaii. Condor 95: 980-989.

Varland, D.E., E.E. Klaas, and T.M. Loughin. 1993. Use of habitat and perches, causes of mortality and time until dispersal in post-fledging American Kestrels. Journal of Field Ornithology 64: 169-178.

Vega Rivera, J.H., W.J. McShea, J.H. Rappole, and C.A. Haas. 1999. Postbreeding movements and habitat use of adult Wood Thrushes in northern Virginia. Auk 116: 458-466.

Vega Rivera, J.H., J.H. Rapolle, W.J. McShea, and C.A. Haas. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. Condor 100: 69-78.

Vierling, K.T. 1997. Habitat selection of Lewis' Woodpeckers in southeastern Colorado. Wilson Bulletin 109: 121-130.

Ward, J.P., Jr., R.J. R.J. Gutiérrez, and B.R. Noon. 1998. Habitat selection by Northern Spotted Owls: the consequences of prey selection and distribution. Condor 100: 79-92.

Warkentin, I.G., and P.C. James. 1988. Nest-site selection by urban Merlins. Condor 90: 734-738.

Warnock, S.E. and J.Y. Takekawa. 1995. Habitat preferences of wintering shorebirds in a temporally changing environment: Western Sandpipers in the San Francisco Bay estuary. Auk 112: 920-930.

Wenny, D.G., R.L. Clawson, J. Faaborg, and S.L. Sheriff. 1993. Population density, habitat selection and minimum area requirements of three forest-interior warblers in central Missouri. Condor 95: 968-979.

Willson, M.F., and T.A. Comet. 1996. Bird communities of northern forests: patterns of diversity and abundance. Condor 98: 337-349.

Wilson, R.R., and R.J. Cooper. 1998. Acadian Flycatcher nest placement: does placement influence
reproductive success? Condor 100: 673-679.

Wilson, W.H., Jr., R.E. Zierzow, and A.R. Savage. 1998. Habitat selection by peatland birds in a
central Maine bog: the effects of scale and year. Journal of Field Ornithology 69: 540-548.

Winker, K. 1995. Habitat selection in woodland Nearctic-Neotropic migrants on the Isthmus of
Tehuantepec I. Autumn migration. Wilson Bulletin 107: 26-39.

Withers, K., and B.R. Chapman. 1993. Seasonal abundance and habitat use of shorebirds on an Oso
Bay mudflat, Corpus Christi, Texas. Journal of Field Ornithology 64: 382-392.

Wunderle, J.M., Jr., and R.B. Waide. 1993. Distribution of overwintering Nearctic migrants in the
Bahamas and Greater Antilles. Condor 95: 904-933.

Yahner, R.H. 1987. Use of even-aged stands by winter and spring bird communities. Wilson
Bulletin 99: 218-232.

Yahner, R.H. 1995. Habitat use by wintering and breeding bird communities in relation to edge in
an irrigated forest. Wilson Bulletin 107: 365-370.

Yong, W., D.M. Finch, F.R. Moore and J.E. Kelly. 1998. Stopover ecology and habitat use of
migratory Wilson's Warblers. Auk 115: 829-842.

Zamora, R. 1990. Nest-site selection of the Common Wheatear in high mountain areas of
southeastern Spain. Wilson Bulletin 102: 178-180.

Zimmerman, J.L. 1988. Breeding season habitat selection by the Henslow's Sparrow (*Ammodramus
henslowii*) in Kansas. Wilson Bulletin 100: 17-24.

Zwank, P.J., P.M McKenzie, and E.B. Moser. 1988. Fulvous Whistling-Duck abundance and
habitat use in southwestern Louisiana. Wilson Bulletin 100: 488-494.