

SMALL - SCALE BIOLOGICAL PHENOMENA
IN A
MALE NEOTROPICAL MIGRANT SONGBIRD

Space Use, Habitat Use, and Behaviour
Within Territories of Male Cerulean Warblers

By

JENNIFER JANE BARG

A thesis submitted to the Department of Biology
in conformity with the requirements for
the degree of Master of Science.

Queen's University
Kingston, Ontario, Canada
January, 2002

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0-612-65600-4

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ABSTRACT

Cerulean Warblers (*Dendroica cerulea*) are migratory songbirds whose space and habitat use patterns have been little studied, especially at small spatial scales. This study examined the space and habitat use patterns of male Cerulean Warblers within their breeding territories. To this end, detailed location (UTM coordinates), habitat (tree species), and behaviour (e.g. activity, height in tree) data were collected during 30 min 'mapping sessions' on males during the breeding seasons of 1999 and 2000 in southern Ontario.

Kernel density estimation techniques were used to examine the space use patterns of male Cerulean Warblers. Space use patterns rely on the location data only. Kernel estimates of territory size were typically smaller than estimates of territory size obtained through minimum convex polygon techniques, and included less unused space. Kernel estimates also indicated that males were not using space uniformly, and that core areas (small areas of intense use) were present. Kernel estimators assume statistical independence among locations and fidelity of locations over the duration of the study period. These assumptions were tested for our data and indicated that statistical measurements of independence and fidelity may not be necessary or appropriate for this species. The effect of sample size on kernel territory estimates was also examined, and revealed no relationship between the two. Therefore all locations were used to generate territory estimates providing maximum detail to the underlying space use patterns. A technique for delineating core areas was recommended.

Habitat use and behaviour patterns were examined within the afore-mentioned territories and core areas. Within territories, males spent the majority of their time

singing from perches, and tended to use canopy tree species in proportion to their prevalence in our forest. Core areas were important song post clusters for all males. Song posts located in core areas were used for longer singing bouts, were likely to be located higher, and were more often situated in bitternut hickories than in non-core areas. Possible explanations for these core area patterns include choosing singing locations that allow song to travel farther with minimal degradation. Core area habitat structure may be important in the process of selecting habitats.

ACKNOWLEDGEMENTS

No large endeavour is ever accomplished without the help of others, and this thesis was no exception. There are many individuals and organisations that must be thanked, whether they know they helped me or not. Here it goes.

The field assistants: Jason Jones, Bill McLeish, Ryan DeBruyn, Javier Salgado Ortiz, Ben Risk, Jesus Vargus, Andrew Stevens, Kate Girvan, Dev Aiama, and Rob Chisnall; without them I would have had nothing to write about. I must pay exceptional homage to Ryan DeBruyn, who suffered through very long field days with a perfectionist, highly stressed graduate student (me) at his side. His positive outlook, sense of humour, and 'colourful' antics were a welcome break from the birds, and his contributions to the research were great. Here I must also mention Ryan Grant, whose GPS prowess helped Ryan DeBruyn and me fumble our way through AutoCAD and ArcView. Ryan G. also analysed some spatial data for me, at a point where I realised that I had too much data, that he then used in an independent project.

To my colleagues in the department, Scott Tarof and Jason Pither, who were always willing to listen to my thoughts, and encouraged me that I wasn't crazy and I could go on, I thank you for your friendship. Scott was a very important instigator of coffee breaks and heartfelt conversations, which I will always treasure. The members of the Robertson lab have contributed by reading drafts of my data chapters.

I owe many, many thanks to my oh so patient supervisor, Raleigh Robertson, for having faith that I would finish, for supporting me along the way, and for giving me this opportunity. He gets extra points for having sent Jason Jones to speak at the AOU meetings in 1997, where Jason and I met for the first time. My supervisory committee, Laurene Ratcliffe, Roly Tinline, and Katherine Wynne-Edwards, has contributed to the development of this thesis. Roly Tinline was exceptionally helpful in the acquisition of the program ArcView, and in teaching me how to

manipulate spatial data. His interest in this project was so keen, he endured the biting insects to accompany me in the field during my second field season.

The students in the biology department are fortunate to have Joanne Surette and Carol Noel working on their behalf. They have helped me over and above what was required. Joanne went to bat for me on many occasions, for which I am truly grateful.

The Queen's University Biology Station is a wonderful place to do field work. This is largely due to the efforts of Frank and Marg Phelan and Floyd Connor, who provided 'post field' needs each day and allowed us access to their computers and GPS/GIS equipment. Special thanks must go to Turid Forsyth who allowed us access to her land. Allen Keast greeted us every morning with a wink and a smile; without him, our mornings would not have been the same. Ted and Marsha Dwyre provided us with housing during the field seasons of 2000 and 2001, at a time when my family had grown to incorporate several dogs. Happily their housing allowed us to stay together during these summers.

Monetary support for this research came from many sources including an NSERC operating grant to RJR, two Queen's Graduate Awards, the World Wildlife Fund of Canada in the form of the Macnaughton Conservation Scholarship, and two field assistants were paid from funds received from Student Work Employment Program. This project was part of Natural Legacy 2000, a nationwide initiative in Canada to conserve wildlife and habitats in private and public.

My thanks must get more personal at this point, where my mentors and friends need be thanked. Ron Mumme and Dick Holmes gave me my start in the field of avian ecology, and remain sources of advice to this day. Pete Marra, Scott Sillett, Matt Johnson, Al Strong, and Laura Nagy all provided the advice and encouragement to attend graduate school in the first place, and their 'loving' nagging has helped me to see it to completion. Paul Hamel and Ken Rosenberg have both been great cheerleaders and co-sympathisers in the study of Cerulean Warblers. I hope to work with them well into the future.

The personal demons that I faced along the road to completing this thesis did not count on the help I would have in the form of friends, strangers and creatures along the way. Jen MacFarlane Shapka and Katarina Manno helped me to remember how to be a girl. The Queen's rowing team, my Tai boxing classes, and Dr. John and Chuck the therapist served as outlets through which I relieved much frustration and re-empowered myself. I must thank my family for keeping things 'interesting' over the last four years. Though they may not really 'get' why it is I do what I do, their support has never wavered. Strangely and without explanation, I must also thank the horses at Skyland Farm.

Somehow I find myself the owner of four wonderful dogs, none of which were mine when I arrived at Queen's. To Katahdin, Mode, Parker and Ella, I give thanks for unconditional love, the best greetings I've ever had at the end of some miserable days, the reminder that simple things are the best things, increasing my patience threshold, and for helping me to see that life does go on when things aren't perfectly organised.

Lastly, to Jason Jones, my (now) husband. You are mentioned both first and last in my thanks. First, because you helped bring me into the world of Cerulean Warblers. Last, because you helped me to see my thesis through, and you let me do it on my own terms. Now that we've realised that our strength lies in teamwork, there's nowhere we can't go.

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Chapter 1

General Introduction

The terms 'habitat use' and 'habitat selection' are frequently and erroneously used interchangeably by avian biologists (Jones 2001). While habitat use is a straightforward documentation of the way an organism uses habitat to meet its life history requirements (Block and Brennan 1993), habitat selection is more complex; it is a process that results in the disproportionate use of habitat features which influence an individual's survival and fitness (Block and Brennan 1993). Though different in purpose, habitat use and habitat selection investigations are similar in their study design requirements. For both, researchers must carefully choose the spatial scale appropriate to the question at hand.

Birds and other animals select habitats for their use in a series of hierarchical steps that can be viewed according to spatial scale (Johnson 1980). In the process of selecting habitats, choices are made first at large spatial scales (e.g. geographic range), then at meso-scales (e.g. territory location), then at micro-scales (e.g. foraging site); each scale is nested within the previous scale. A researcher studying habitat use or selection should measure variables at a spatial scale appropriate to the question at hand. For example, if the intent of the research is to document the habitat associated with foraging locations of a forest bird species, habitat should not be sampled at the forest patch scale; rather it should be sampled at the habitat surrounding actual locations of foraging birds. The choice of scale can seriously affect the conclusions drawn from a study, as it has

been shown that decisions made at one scale may not be reflective of an organism's decisions at other scales (Wiens et al. 1987).

The choice of spatial scale is but one of the important preliminary decisions to make when designing a habitat use or selection study. After the appropriate scale has been determined, the boundaries of the space to be examined need to be delineated. Ideally, these boundaries should be dictated by the organism in question thereby removing the potential for any human introduced bias to enter into the research (Morris 1987). One way to ensure that the study organism dictates the boundaries of the study area is to incorporate a spatially explicit 'space use' methodology into the data collection. Despite its somewhat common occurrence in the literature, the term 'space use' is rarely defined. The intended definition of space use herein is a description of the distribution of an organism's locations, without any corresponding reference to habitat or behaviour. Incorporating a spatially explicit space use methodology into a habitat use or selection study simply involves the simultaneous collection of coordinate data (e.g. latitude / longitude) associated with an organism's location, with habitat structure data and behaviour information. Space use patterns can then be determined; an organism may use space uniformly, or repeatedly visit certain 'core areas' (small areas of intense use) while other areas are never visited. The emergent patterns are especially important in habitat selection studies where 'used' habitats are compared to 'available' habitats, and knowing exactly where to measure each category of habitat is critical for accurate results.

In avian habitat use and selection studies, space use patterns associated with studies at the scale of the territory are very important. Whether documenting territory selection itself or documenting the use of features within the territory, space use patterns

at this scale can be very revealing with respect to habitat use and selection patterns, and therefore need to be determined as accurately as possible. Many methods exist for describing space use patterns at the scale of the territory, also referred to as territory estimators. These fall into two broad categories: parametric and non-parametric (for review see White and Garrot 1990). While the methods in both categories require that certain assumptions be met prior to their use, parametric territory estimators tend to place very restrictive and unrealistic assumptions on the underlying location data sets; many require an assumption of circularity of the territory and a bivariate normal distribution of locations. For these reasons, non-parametric measures of the territory are generally preferred among avian biologists.

In this thesis, I investigate space use, habitat use and behaviour *within* territories (micro-scale) of male Cerulean Warblers (*Dendroica cerulea*). The Cerulean Warbler is a migratory bird species of conservation concern both in Canada and the United States (Robbins et al. 1992; COSEWIC 2000). This species is currently thought to be an interior forest specialist requiring large areas of contiguous forest in eastern North America for successful reproduction and continued persistence (Wilson 1811; Hamel 2000). Their behavioural restriction to the upper forest canopy has earned them a reputation for being difficult to study, especially with regard to their small-scale habitat use patterns. However, researchers at the Queen's University Biology Station near Chaffey's Locks, Ontario, have had great success studying them. Researchers here have recently examined territory habitat selection (meso-scale) and nest site selection (micro-scale) in this species. By combining accurate techniques of space use documentation with habitat use and behaviour information, I will contribute to the growing body of

knowledge on the breeding biology of Cerulean Warblers. Detailed space use patterns and small-scale habitat affinities will then be revealed in preparation for a larger habitat selection investigation. In addition, the techniques used herein may become examples for others to follow who are interested in asking similar questions.

In Chapter 2, I use a non-parametric territory boundary and space use pattern estimation technique, the fixed kernel density estimation method, to delineate territory boundaries and core areas for male Cerulean Warblers. In the process of using this technique, I assess the importance and relevance of the assumptions inherent to kernel methods, and make suggestions regarding the number of locations needed to accurately generate territory boundaries. I also compare territories generated by kernel methods to those generated by another commonly used technique, the minimum convex polygon.

In Chapter 3, I use the territories calculated by the methods recommended in Chapter 2 to examine within-territory use patterns, both in terms of tree species used and the behaviours associated with each location. These patterns are examined on a territory wide basis and as a comparison between core areas and non-core areas within the territory.

These chapters are intricately entwined, as the accurate depiction of each bird's space use patterns (territory and core area boundaries) are essential for examining the habitat and behaviour patterns within them.

Chapter 2

**Use of a kernel density estimator to determine breeding territory size
and define core areas for a migratory passerine.**

ABSTRACT

Territory and home range size are affected by numerous biotic and abiotic factors. Estimates of these spaces can also be affected by the sampling method and estimation technique chosen by the researcher. Utilisation distribution based estimators of territory size provide information regarding an organism's use of space, and are based on the frequency of encounters with an organism over a period of time. Thus, they are essentially defined by the organism itself. Kernel density estimators are an example of a utilisation distribution technique and are becoming increasingly used in radio tracking studies. Though non-parametric, kernel density estimators do assume that an organism shows site tenacity during the sampling period, and that locations used to generate estimates are independent. Given restrictions imposed by the biology of the organism in question, and logistical constraints imposed by time and personnel limitations, achieving independence is not always possible; additionally, the techniques most frequently used to measure fidelity and independence are not necessarily appropriate in all situations. We used location data from a highly mobile, territorial passerine, the Cerulean Warbler, to estimate territory size and assess the appropriateness of some techniques used to validate the assumptions inherent to kernel density estimators for this and similar species. We compared our kernel generated territory sizes and boundaries to those generated by minimum convex polygon methods using identical data sets. Recommendations on how to define the boundary of core areas from kernel density estimates were addressed. Although our data were statistically autocorrelated and did not satisfy statistical measures of fidelity, locations were biologically independent, overlapped among all collection sessions, and appeared to provide good estimations of territory size and core area

locations during the sampling period. Minimum convex polygon areas did not perform as well. For species with similar ecologies to that of the Cerulean Warbler, we recommend using fixed kernel density estimators to measure territory size and define core areas, especially when used in resource selection studies. Statistical measures of autocorrelation and fidelity do not seem appropriate for this species.

INTRODUCTION

Territories can be defined simply as "any defended area" (Noble 1939:267).

Territory size among individuals of the same species can be highly variable. Within a population, this variation likely reflects a number of factors, including differences in habitat quality, resource distribution, mated status, and experience (Wiens 1969, 1973; Schoener and Schoener 1982; Village 1982; Wiens et al. 1985; Smith and Shugart 1987). Unfortunately, the estimated size and boundary of a territory can also be influenced by the researcher, via the sampling method employed during data collection and the choice of area estimation technique.

Estimation techniques based on an individual's 'utilisation distribution' have become popular, perhaps following on the recommendation by Hayne that "the differing degree of intensity of use of the home range (or territory) is a biologically significant aspect, and should not be neglected while attempting to determine absolute size" (1949:15). A utilisation distribution is a two-dimensional representation of "the relative frequency distribution for the points of location of an animal over a period of time" (Van Winkle 1975:118). These estimation techniques allow investigators to examine aspects of the internal configuration, such as the location of 'core areas' (small areas of intense use), in addition to calculating total area.

Kernel density estimators have been the most heavily promoted utilisation distribution based estimation techniques for territory and home range boundary calculations, since Worton (1989) suggested this application. These techniques estimate the density of a distribution at all points in a given set of locations; the resultant densities are an approximation of the amount of time an organism spent at any location. Kernel

estimators are popular for several reasons: they are non-parametric, produce a density estimate without needing to 'correct' the data, and they are not influenced by grid size or placement like many other utilisation distribution based techniques (Silverman 1986). Research on kernel based estimators has emphasised their performance, mainly in relation to sample size, spatial resolution, degree of autocorrelation in the data, and with respect to other techniques (Worton 1989, 1995; Seaman and Powell 1996; Hansteen et al. 1997; Swihart and Slade 1997). More recently however, they are being used empirically in studies of resource use and behavioural ecology to delineate home range and territory boundaries and areas (Naef-Daenzer 1993, 2000; Tufto et al. 1996; Strong 2000; Thogmartin 2001).

Traditionally, the most commonly used non-parametric estimator has been the minimum convex polygon (MCP) described by Mohr (1947). The MCP can be calculated in various ways, but is usually constructed by connecting the outermost points in a location data set. Given its simplicity and non-parametric nature, it has been an obvious choice for researchers who need to estimate home range or territory size with minimal effort, and it may be the only technique that is entirely comparable between studies (Harris et al. 1990). Its three main disadvantages are that it does not allow the researcher any insight into internal configuration, it is highly affected by locations on the periphery of the area being measured, and it can contain large areas that were never visited by the focal organism (Harris et al. 1990).

A common problem when using any area estimation technique, including non-parametric kernel and minimum convex polygon estimators, is that they assume that the location data used in the analysis are statistically independent. Depending on the

behaviour and biology of the focal organism and the logistical constraints of sampling, achieving statistical independence can be difficult (Heezen and Tester 1967; Smith et al. 1981). Two schools of thought arise here: that data need not be statistically independent, only biologically independent, as defined by "a sampling interval long enough to allow the animal to move from any point in its home range (or territory) to any other point" (Lair 1987:1099) (Holzenbein and Marchinton 1992; McNay et al. 1994; De Solla et al. 1999); the alternative, that data must not be serially autocorrelated (i.e., that the location at time $t + 1$ is not dependent on the location at time t) (Schoener 1981; Swihart and Slade 1985a). Certain studies have indicated that autocorrelated locations may result in underestimated areas (Schoener 1981; Swihart and Slade 1985a), whereas others have disagreed (Anderson and Rongstad 1989; De Solla et al. 1999).

It seems reasonable that if the goal of a study is to both estimate area and examine internal configuration as suggested by Hayne (1949), then eliminating autocorrelation would alter the apparent patterns of the animal, and consequently alter the resultant utilisation distribution. Additionally, current methods commonly used to detect autocorrelation are not necessarily suitable for all organisms (Andersen and Rongstad 1989). Under these methods, no distinction is made between highly mobile species like birds, and more restricted movement organisms like slow moving mammals. In other words, a fast moving bird is likely to have biologically independent locations at short time intervals (though they would be statistically dependent), whereas a slow moving mammal, such as an opossum, would have both biologically and statistically dependent locations at the identical time interval. Therefore, using a sampling methodology that captures biologically independent data, which can be organism specific, is perhaps a

more relevant way of avoiding autocorrelation when using utilisation distribution based estimation techniques. If the criteria for biological independence are determined prior to the collection of data, and the appropriate sampling interval is then used during the study, it could then be argued that statistical measures of autocorrelation are irrelevant.

However, since the actual area of an organism's territory or home range can never really be known and used as a comparison, we must rely on investigators to determine if their sampling regime and associated estimation technique produce values that seem reasonably sound based on their observations in the field.

This investigation used a fixed kernel density estimation technique to create a utilisation distribution, estimate territory size and delineate the location of core areas for breeding season territories of male Cerulean Warblers (*Dendroica cerulea*). We chose Cerulean Warblers because they are highly mobile, territorial, and they are representative of the Neotropical migrants; a group which is frequently the subject of habitat selection studies where accurate territory boundary and size estimation are crucial. The location data we collected were biologically independent, though statistically highly autocorrelated. The objective of this study was to suggest guidelines for using fixed kernel methods and for addressing their inherent assumptions, when estimating territory size and examining internal configuration in similar species with statistically autocorrelated data. Additionally, we examined the differences between areas and boundaries generated by the kernel methods and minimum convex polygons with identical data sets.

METHODS

Study Site and Species

The study was conducted during the breeding seasons of 1999 and 2000 (May-July in both years), at the Queen's University Biological Station (QUBS), Lake Opinicon, Leeds/Frontenac Counties, Ontario, Canada (44°30'N; 76°W). The forest is characterised as second growth mixed-deciduous, between 80-90 years old. The canopy is dominated by *Acer saccharum* (Sugar Maple), *Carya cordiformis* (Bitternut Hickory), and *Fraxinus spp.* (Ash), with the occasional *Quercus spp.* (Oak), *Ulmus spp.* (Elm), *Tilia americana* (Basswood) and *Betula spp.* (Birch); the mid and under-story is primarily *Ostrya virginiana* (Ironwood), and *Acer saccharum* saplings (see Farrar 1995 for authorities). Mean (\pm SE) daily temperatures (1200 EDT) and mean daily rainfall were 21.15 ± 0.60 °C and 3.00 ± 0.93 mm/day for 1999, and 17.62 ± 0.57 °C and 2.97 ± 0.74 mm/day for 2000, during the sampling periods.

Forests within and surrounding QUBS have regularly supported breeding populations of Cerulean Warblers since 1961 (Weir 1989). The focal population occupies a 24 ha area of QUBS property on the Bonwill Tract, known locally as The Bedford Mills Road. This population has been the focus of Cerulean Warbler investigations since 1994, and is part of one of the largest populations across its breeding range (Jones 2000).

Cerulean Warblers are small (~ 10 g), sexually dimorphic, migratory birds. Males use the upper forest canopy almost exclusively (Hamel 2000). Previous work has found that Cerulean Warblers in this population maintain relatively small (~ 1 ha) territories, which are densely packed, giving the appearance of cluster-like aggregations (Oliarnyk and Robertson 1996; Hamel 2000). There is no evidence of polyterritoriality in this species, and males show marked site tenacity between seasons (Jennifer Barg et al.

unpublished data). Males defend the territory both vocally and through physical interactions, and regularly 'patrol' the boundaries, as is typical of most *Dendroica* warblers (Howard 1920; Bent 1953). Defence of the territory is most pronounced in the mornings between 5-11 am; afternoons are quiet with very little noticeable activity, especially in late summer (Woodward 1997; Jennifer Barg personal observation)

Cerulean Warbler preferred breeding habitat has traditionally been characterised as large, contiguous areas of old growth deciduous or mixed-deciduous forest (Wilson 1811). The focal population will incorporate forest-field edge habitat within territory boundaries, occupies second-growth forests, and sometimes occurs in small (10 ha) tracts (Jones 2000).

Field Methods

The study took place from May 13-July 4 in both 1999 and 2000. This sampling period was chosen for several reasons. Territories were established and nest building initiated by May 13 in both years. We also did not detect any newly arrived birds after this time in either year. Therefore, the population was relatively 'settled' in terms of individual territory locations and pairing status by the beginning of our sampling period. This was important because prior to the arrival of females, male territory boundaries shift considerably (Jennifer Barg personal observation). By the conclusion of our sampling period, pairs that had repeatedly failed nests rarely re-nested. Each male used in this study was therefore given equal opportunity to experience all phases of the breeding cycle, before the breakdown of territory boundaries in mid to late July. Although each male was allowed the same temporal 'window' for their sampling period, males that had

successful nests prior to the conclusion of the sampling period were not studied beyond the fledging date since they were no longer defending their territories.

Most un-banded territorial males were captured using target netting techniques, aged, and given a unique colour and Canadian Wildlife Service band combination for easy field identification. Any males that were not caught were identifiable by unique song characteristics within a season (Woodward 1997). Males were never captured within 3 days of location data collection, so that they had time to adjust to their new leg bands. Mated status and nest locations were determined for all males in the population.

An individual's location data was collected in 'bursts'. Burst sampling is commonly used to collect location data when activity budget or habitat use data are desired, or when logistical constraints require the observer to collect many locations in a short amount of time. Typically, successive observations within a burst are separated by short, regular time intervals; between bursts, longer time intervals occur (Dunn and Gipson 1977; Swihart and Slade 1997). The alternative to burst sampling, sequential sampling, is characterised by evenly spaced observations usually collected with longer intervening time intervals (e.g. one location per day). We used burst sampling because it generated large sample sizes in a short amount of time, which was critical since our birds exhibit a very brief breeding season and we were constrained by the number of available researchers. Given that Cerulean Warblers are highly active and can move about their territories quickly (Jennifer Barg personal observation), we also felt this sampling method would best depict within territory use patterns for the generation of utilisation distributions.

A burst consisted of a 30 min session, during which time the focal male was followed via direct observation; its location was recorded every 60 s. This 60 s time interval allowed enough time for a bird to traverse its entire territory if it chose to do so, thus providing biologically independent locations (Lair 1987). We used direct observation to collect our locations because our birds were too small to carry radio transmitters, and it was the only way to be certain we were collecting points within the territory (i.e. defended locations) (Burt 1943). This method yielded a possible total of 30 locations per session per individual. Sessions were conducted between 0530-1030 EDT and commenced 2 min after the observer located and confirmed the identity of the focal male. This time delay was incorporated in order to reduce bias to conspicuous and commonly used sites (Recher and Gebski 1990). Locations were marked sequentially during a session with pre-numbered (1-30) neon surveyor flags; their exact coordinates (grid Universal Transverse Mercator, datum NAD83Canada, zone 18North) were obtained each afternoon using a Global Positioning System (Trimble single antenna fanny pack unit consisting of a TSC1 datalogger with ProXRS receiver employing real-time differential correction), which is accurate to within 1 m. We did not collect coordinate readings if the point dilution of precision (PDOP) was > 4 ; readings greater than four decreased the accuracy of location fixes. If PDOPs were too high, we waited to collect locations at a time they were 4 or less. If a male went 'missing' during a session, any locations that should have been obtained during this time were considered 'lost' points, and were recorded as such into a micro-cassette recorder. Lost points were usually the result of males making long, direct flights unaccompanied by song or other territorial behaviour, and most likely represented extra-territorial forays, which were

beyond the scope of this study. In both years, each male in the population was subjected to six or seven sessions during the sampling period, each separated by 2-7 days, depending on weather and behaviour modifications resulting from nest loss (i.e. the birds ceased singing for several days post depredation). Each male received equal representation in terms of early morning and late morning sessions.

Kernel Density Estimation Technique

A fixed kernel density estimator was used to construct a utilisation distribution (UD) based on the set of two-dimensional locations for each male in the population. Height above ground, the third dimension relevant to the location of males, was not used to calculate territory locations. We chose the fixed kernel over the adaptive kernel because it is computationally simpler, and typically generates values with less bias as evidenced in simulation investigations (Seaman and Powell 1996). The mathematical definition for a bivariate fixed kernel density estimate is

$$\hat{f}(x) = \left[\frac{1}{nh^2} \right] \sum_{i=1}^n K \left\{ \frac{x - X_i}{h} \right\}$$

where n is the number of locations, h is the smoothing parameter, x describes the location where the function is being evaluated, X_i is the series of locations i , and K is the kernel probability density function. The kernel density estimator can be visualised as a sum of 'bumps' placed over the locations themselves; the kernel K determines their shape, the smoothing parameter h determines their width (Silverman 1986). Therefore, if location distributions are non-uniform and multi-modal, the density estimate will be high (many bumps) in areas where concentrations of points occur, and low (few bumps) in areas where there are few (Worton 1989). There are several kernel functions that can be used to generate the kernel estimate. In general, the choice of kernel has very little effect on the

overall density estimate. It is the smoothing parameter h , which can be varied to reveal or obscure details in a data set, which has the most influence on the resulting density estimate (Epanechnikov 1969).

For each male, we used the process of least squares cross validation (LSCV) to determine the optimal value of h for a given kernel and sample size. This process is generally accepted as generating the best value of h for multi-modal data by providing the amount of smoothing that minimises the function

$$M_1(h) = \frac{1}{n^2 h^2} \sum_{i=1}^n \sum_{j=1}^n K\left[\frac{X_i - X_j}{h}\right] + \frac{2K(0)}{nh^2}$$

and represents the minimum score of h corresponding to the smallest mean integrated square error value (Silverman 1986; Worton 1989; Seaman and Powell 1996). It has been shown to perform better and to provide nearly unbiased estimates on non-uniform data as compared to other methods of smoothing parameter selection (Worton 1995; Seaman and Powell 1996).

The utilisation distribution that resulted from each kernel density estimator was used to describe the intensity of use across a male's territory. The UD was plotted as a series of isopleths that connected areas of equal use (Figure 1). Isopleth values describe the likelihood of encountering a male in a particular area. Territory boundaries were established at the 95th density isopleth for each male in order to be consistent with other kernel based studies; territory size therefore, was considered as the area contained within this region.

Sample Size Selection

In order to select the most appropriate sample size (i.e. number of locations) to use in the generation of our utilisation distributions, we followed the procedure suggested by Harris et al. (1990). This procedure suggests using a sample size standardised across individuals, defined at the point where territory size reaches an asymptote with respect to the number of locations used to generate a particular estimate. First, territory area was calculated for each male using the first 50 locations collected. We then added 10 more locations, in collection order, and recalculated territory size. This process was repeated until all locations had been used. We did not calculate territory area at sample sizes below 50; kernel estimators using the LSCV for the smoothing parameter have been shown to perform poorly with small sample sizes, and 50 has been suggested as the lower limit by Worton (1987) (see also Seaman and Powell 1996). We then examined the relationship between sample size and area for each individual, in order to determine at what sample size territory area reached an asymptote. Additionally, we examined the relationship between territory size and the number of locations used across males. Kernel areas used in this analysis were square root transformed to obtain normality.

Meeting the Assumptions: Fidelity and Independence

Although kernel density estimators are non-parametric and make no assumptions regarding the distribution of locations, the method does assume that the locations for each individual show fidelity to a given area over the course of the sampling period, and are not autocorrelated. We evaluated site fidelity by visually inspecting each male's set of locations for overlap among his sessions. Additional criteria used to establish fidelity were the absence of a 'move' or 'shift' (i.e. males did not abandon one area for an area elsewhere with different neighbours).

Additionally, we quantified fidelity using a Multi-Response Permutation Procedure (MRPP), as suggested by White and Garrott (1990). This procedure tests whether two or more sets of locations come from a common probability density distribution, by comparing the average of the within-group pairwise distances to the average irrespective of group (White and Garrot 1990). It is a favourable option with the type of data we collected since it is non-parametric, makes no assumptions about the shape of the underlying distribution, and allows for unequal sample sizes among groups of locations (Zimmerman et al. 1985; Biondini et al. 1988; White and Garrot 1990).

Autocorrelation was evaluated biologically for this species guided by the definition in Lair (1987) prior to the study. However, we did test for statistical independence using Schoener's ratio, for informative and comparative purposes. Schoener's ratio, \bar{r}^2/\bar{r}^2 , where \bar{r}^2 is the mean squared distance between successive observations and \bar{r}^2 is the mean squared distance between each observation and the geometric centre of activity, is commonly used to determine the degree of serial autocorrelation in location data sets (Schoener 1981; Swihart and Slade 1985b). Simulations by Swihart and Slade (1985b) determined that values of $\bar{r}^2/\bar{r}^2 = 2$ indicate independence among points, while values < 2 indicate positive serial autocorrelation, and values > 2 negative serial autocorrelation. After Schoener's ratios were calculated for each male's complete data set, we sub-sampled location data sets at 2 min intervals and recalculated the ratios in an attempt to determine the time at which we would achieve statistical independence for a given male.

Minimum Convex Polygons

Territory size was also estimated for each male using the minimum convex polygon (MCP) method. MCP territory areas were calculated using the identical data sets used in the final kernel estimations, and were considered as the region bounded by the polygon connecting the outermost locations in a given data set. We tested for size differences between kernel and MCP area estimates, and demonstrated the difference in physical space encompassed by each technique's boundary by comparing the percent of MCP area enclosed by the kernel area. Values used in the size comparisons were square root transformed.

Core Area Delineation

Core areas were delineated by the following procedure, which is a modification of the suggestions by Wray et al. (1992), and Harris et al. (1990). For each male, we calculated the area enclosed by kernel density isopleths 10-90, in increments of 10. Area calculations were based on the same sample size and utilisation distributions generated previously. We then calculated the difference in area between successive isopleths. We defined the core area at the first point where the difference in consecutive isopleth differences at least doubled. The core area was then the area bounded by the smaller of the two consecutive isopleths, although areas bounded by the same isopleth needed not be continuous in space (for example see Fig. 1). Core area fidelity over the course of the sampling period was assessed via a visual inspection of overlap among locations from different sessions in the same manner that fidelity was visually assessed for the kernel area calculations.

The resultant core areas for each male were then characterised on the basis of their use patterns in order to confirm their status as 'small areas of intense use'. We

measured the percent of the territory contained within the cumulative core area (% territory), percent of the total locations contained within the cumulative core area (% use), and a relative measure of the intensity of use (% use / % territory), as described by Samuel et al. (1985).

We used the Animal Movement Analysis Program V1.1 (Hooge and Eichenlaub 1997) and Spatial Analyst Extensions to the Geographic Information System Program ArcView V3.2a (ESRI 1999) to calculate and display all kernel utilisation distributions, MCP territory areas and core areas. Grid extents used in the LSCV calculations were generated by the addition of 50% area to each male's set of locations. BLOSSOM Statistical Software (Cade and Richards 2000) was used to perform the Multi-Response Permutation Procedures. JMP IN V4.0.2 (SAS Institute 2000) was used for all other analyses.

RESULTS

We collected location data on 9 of 16 males in 1999 and 16 of 22 males in 2000. Of these, four in 1999 and 10 in 2000 were equally sampled across the defined period. We used these 14 males in all of our analyses. All males were mature (≥ 2 y); two males were unmated and 12 were mated.

Sample Size Selection

There were considerable differences among males in the way territory size was affected by the number of locations used to generate the estimates. Rarely did a male's territory size reach an asymptote; more commonly, it remained small for a time, then increased, even up to the day before nest fledging (for examples see Figure 2). Males

whose territory size did appear to reach a plateau ($n = 3$), did not do so at the equivalent sample sizes.

Across males, we did not find a statistically significant relationship between territory size and the number of locations used (standard linear regression, $r^2 = 0.0078$, d.f. = 13, $P = 0.7647$). Large territories were not the result of more locations; small territories were not the result of few.

Growth of the territory seemed closely associated with hatch day. Of the six males who had nestlings prior to the conclusion of the sampling period, four of those reached their maximum territory size within 2 days of hatching, and the other two began to dramatically increase in size during the same time interval (for examples see Figure 2). Since it was therefore apparent that standardising sample size across males was less important than using locations from all nest cycle stages, and because kernel methods perform best at large sample sizes, we used each male's full complement of locations to generate their utilisation distributions. By using each male's full set of locations, we ensured the inclusion of locations from all phases of a given male's breeding cycle, including hatch day.

Fidelity and Independence

Multi-Response Permutation Procedures indicated that none of our males demonstrated fidelity to a given area over the course of the study ($P < 0.0001$). However, every male used in our analysis had a location data set that was comprised of overlapping sessions (for example see Figure 3). None of our males were polyterritorial, and none moved their territories during the sampling period.

Biologically, all locations collected for each male were independent, as defined by Lair (1987). Males could easily traverse their territories in less time than the 60 s interval we allotted between the recording of locations. Statistically, Schoener's ratio (r^2/r^2) values indicated high levels of autocorrelation for each male's full set of locations (mean \pm SE, 0.30 ± 0.05 ; range 0.08 - 0.71), which was expected. When we sub-sampled the locations in each mapping session in an attempt to attain independence among points, we did not achieve independence even at 10 min intervals, far longer than biological independence would suggest. Additionally, we lost important information concerning locations that were used repeatedly by an individual (see also Reynolds and Laundre 1990; McNay et al. 1994).

Area Estimates

Kernel density estimates of cerulean warbler territory size in our population showed considerable variation (mean \pm SE, 0.70 ± 0.16 ha; range 0.12 - 2.35 ha, untransformed values; Table 1). MCP area estimates likewise showed considerable variation (mean \pm SE, 0.96 ± 0.18 ha; range 0.23 - 2.21 ha, untransformed values; Table 1).

There was a statistically significant difference in the values generated by the two estimation techniques (paired t-test, $t = 3.56$, d.f. = 13, $P = 0.0035$); MCP areas tended to be larger. The physical space bounded by the two methods, measured as percent overlap, differed drastically in certain cases, especially in situations where there were large areas within a territory that were never visited during our data collection sessions (Table 1; for example see Figure 4).

Core Areas

Core areas differed in size across males (mean = 0.07 ha; range = 0.0078 - 0.44 ha), but were similar in number (1 or 2; Table 2). The percent of the territory enclosed by core areas was quite small (mean = 8.0 %; range = 3.0 - 18.6 %; Table 2), while the percent of total locations contained by core areas was large (median = 30.6 %; range = 17.5 - 66.0 %; Table 2). Core areas were visually stable during the sampling period, although they were used more heavily in some sessions than others.

DISCUSSION

Based on our observations in the field, the fixed kernel density estimation technique using LSCV to select the smoothing parameter seemed to provide good estimates of the boundary, area, and location of cores for territories of male Cerulean Warblers, despite the fact that our data did not meet the assumption of statistical independence and statistical fidelity. Kernel area estimates were smaller than those generated by the MCP technique, and more accurately depicted real use patterns. Therefore, we would recommend the use of fixed kernel estimation techniques for investigations that require accurate territory boundary and area estimations for this and other species with similar life history characteristics.

As was mentioned previously (see introduction), the debate on the necessity of complying with certain assumptions inherent to these techniques is ongoing. When we used Multi-Response Permutation Procedures to examine a male's set of locations for fidelity to an area over the course of the study, the tests failed to indicate that each group of locations came from the identical distribution. Intuitively, we knew that none of our birds had 'moved' or 'shifted' any appreciable degree during the sampling period, and we also knew that our birds repeatedly used the same locations over and over throughout the

sampling period. Unfortunately, this intuition was not reflected in the outcome of the MRPP analysis. This procedure did not measure positive fidelity for any of our individuals, even when their session locations overlapped and they remained in a 40 m x 40 m area for the entire sampling period. Possibly, this procedure perceived certain locations as 'outliers', despite the fact that at the small spatial scale we were working, these points were an unappreciable distance from the remainder of the locations. However, we compensated for any possible discrepancies between what we witnessed and what the MRPP suggested by defining the sampling period in such a way as to limit the available individuals to those that had established their territories prior to the study. Once males of this species in this population have established a territory, they do not abandon it until fall migration forces them or they fail to successfully fledge young.

This is not to say that there are not other potentially useful tests that can be used to examine fidelity to an area. Nearest neighbor analysis (Clark and Evans 1954) can be used to look for clustering of locations within a defined boundary, as can a random walk analysis with a Monte Carlo procedure. However, the appropriateness of these techniques for this purpose is debatable. They seem to fall on the opposite side of the sensitivity spectrum to the MRPP. Whereas the MRPP seemed sensitive to the smallest change in use patterns over time for our data, the sensitivity of the nearest neighbor and random walk analysis is entirely dependent on the user's boundary selection. Given these problems, we would recommend that researchers guide their measures of fidelity by educated intuition and an understanding of their study organism, and explain these measures fully. Certainly, we do not recommend the abandonment of fidelity tests, but if

they fail when intuition says they should not, it is possible that the test simply is inappropriate for the data or organism.

Similarly, when we tested for independence among locations in a data set, Schoener's ratios failed to indicate independence in all sets of locations. These results were not surprising given our choice of burst sampling methodology with a short inter-location time interval. During our sessions following male Cerulean Warblers, they could easily, and often did, traverse their entire territory in a matter of seconds. Therefore when sub-sampling locations and recalculating Schoener's index of autocorrelation failed to find independence between points even at 10 min intervals, we knew that this measure was not relevant to the species or data at hand. Even if we had achieved independence through sub-sampling our data, we believed that sub-sampling would eliminate biologically important information needed to create an accurate utilisation distribution for individuals of this species. Additionally, kernel density estimators have proven robust to the presence of serial autocorrelation in similar data (Swihart and Slade 1997; De Solla et al. 1999).

More and more researchers are finding that defining independence biologically instead of statistically is far more relevant to their study organisms, and has a negligible effect on area estimation (Andersen and Rongstad 1989; Reynolds and Laundre 1990; McNay et al. 1994; De Solla et al. 1999). This is an important realisation since most studies are seriously limited by time, either because of personnel issues, or because the biology of the organism at hand dictates a speedy, efficient maximisation of location collection; when this is the case, autocorrelated locations are almost impossible to avoid. Although it is not possible to compare a 'true' Cerulean Warbler territory area to those we

have generated here, we do not feel that our use of autocorrelated data appreciably affected the areas or boundaries we estimated. Indeed, given the substantial variation in territory size that we witnessed in our population, it would be impossible to expect any such 'true' versus 'estimated' comparison to be at all meaningful, even if it were possible.

Selection of the sample size to be used in the generation of a utilisation distribution is typically addressed at the species or population level via the area asymptote/sample size analysis (Harris et al. 1990). However, we found that Cerulean Warblers in our population behaved individualistically, and that a standard sample size for the population would not have provided meaningful area estimates. Additionally, large territories were not the result of using more locations any more than small territories were the result of using few. If we had eliminated locations from the data sets of our birds either because of sub-sampling to achieve statistical independence or to standardise sample size across males, we would necessarily alter the relative contribution of points from different nest cycle stages. Considering our goal, to estimate breeding season territory size not just size during a specific portion of the breeding cycle, and because we witnessed dramatic increases in territory size around the time of hatching, it seemed more important to take nest cycle stage into account than it did to worry about standardising sample size across males. This combined with the fact that kernels perform better with large sample sizes (Worton 1987), is what led us to use the full data set for each male in the generation of his utilisation distribution. Again, it became apparent that strictly defining the sampling period and evenly sampling individuals during this time is important. Of course this recommendation should be used cautiously dependent upon the definition of the sampling period and the question at hand.

The method we chose to establish the boundaries of core areas seemed to reliably represent areas that were intensively used throughout the sampling period, within each male's territory. Their relatively small area and large inclusion of locations (Table 2) exemplified this. Although the delineation of core areas is not an exact science, we feel the method provided here is practical in the sense that it is exactly repeatable among observers and between studies, and results in areas that are neither too small nor too dispersed to be useful for addressing within core area questions. Methods that have been suggested previously where core area boundaries are established by examining area vs. isopleth graphs for a "change in gradient", are open to interpretation and are more difficult to repeat (see Harris et al. 1990).

Many studies have addressed the variation in performance among territory or home range estimation techniques (Van Winkle 1975; Worton 1987). MCP area estimators are known to be highly affected by locations on the periphery of a boundary (Worton 1987). We have shown that this pattern holds with Cerulean Warbler location data. Despite their attractiveness as a 'quick and dirty' area measure, their application could seriously affect research results under certain circumstances. For example, habitat selection studies routinely compare 'used' versus 'available' habitat in an attempt to describe species specific habitat associations and preference (Block and Brennan 1993). Had we used the MCP technique to estimate territory boundaries, and we were interested in addressing habitat selection questions for Cerulean Warblers based on 'used' versus 'available' comparisons, we would have incorrectly designated some areas within the territory as 'used' when in fact they were not (see Figure 4 for example). Unfortunately, this technique has been used extensively in just such situations (Ganey and Balda 1994;

Marzluff et al. 1997; Linkhart et al. 1998; Mazur et al. 1998; Lambert and Hannon 2000). Researchers should revisit their choices when designing habitat selection studies, and opt for the area estimator that will most accurately reflect the choices made by the bird or other organism under investigation. The fixed kernel estimator with a smoothing parameter chosen by LSCV, perhaps modified to reveal extra detail and to avoid over-smoothing caused by large h values (Seaman and Powell 1996), would be a far better choice for such an application.

Cerulean Warblers were an ideal model organism for this study. Their conspicuous behaviours and small territories lent themselves well to the type of data collection methods we used and the questions we asked. Aside from the methodological questions, we were also able to further identify important aspects of this species' breeding season biology. In a very detailed way, we have established extreme variation in territory size for this species, and demonstrated the existence of core areas within their territory boundaries. While further attempting to explain why this variation exists was beyond the scope of this study, our methodology nicely established the preliminary step in any good resource selection study where the 'why' questions could easily and accurately be addressed.

Table 1. Territory sizes for male Cerulean Warblers calculated by both the kernel, and minimum convex polygon (MCP) methods. Also shown are the number of locations (n) used to generate both estimates and the LCSV smoothing parameter (h) used in the kernel estimation. The overlap represents the percentage of the MCP area that is also contained within the kernel territory boundary.

| Male | Year | n | h | Kernel (ha) | MCP (ha) | Overlap (%) |
|------|------|-----|-------|-------------|----------|-------------|
| 1 | 1999 | 137 | 8.35 | 0.5307 | 0.9368 | 48.8 |
| 2 | 1999 | 206 | 7.74 | 0.7067 | 0.7636 | 74.9 |
| 3 | 1999 | 141 | 10.27 | 0.7002 | 1.5070 | 40.6 |
| 4 | 1999 | 97 | 17.47 | 2.3472 | 2.1187 | 68.6 |
| 5 | 2000 | 178 | 9.81 | 1.1584 | 1.1382 | 82.8 |
| 6 | 2000 | 122 | 9.68 | 0.4819 | 0.9084 | 43.4 |
| 7 | 2000 | 168 | 14.41 | 1.0275 | 2.2059 | 37.3 |
| 8 | 2000 | 118 | 14.09 | 1.9604 | 1.4681 | 87.0 |
| 9 | 2000 | 125 | 4.18 | 0.1677 | 0.3548 | 42.2 |
| 10 | 2000 | 119 | 9.56 | 0.5638 | 0.8767 | 50.0 |
| 11 | 2000 | 110 | 5.26 | 0.3364 | 0.3393 | 81.5 |
| 12 | 2000 | 177 | 4.56 | 0.1660 | 0.2328 | 56.5 |
| 13 | 2000 | 96 | 5.81 | 0.3538 | 0.3887 | 73.3 |
| 14 | 2000 | 147 | 3.69 | 0.1177 | 0.2694 | 34.7 |

Table 2. Core area characteristics and their associated use patterns for male Cerulean Warblers.

| Male | Cumulative core area (ha) | Number of core areas | % territory ^a | % use ^b | Intensity ^c |
|------|------------------------------|-------------------------|--------------------------|--------------------|------------------------|
| 1 | 0.0904 | 3 | 17.0 | 62.8 | 3.69 |
| 2 | 0.0298 | 1 | 4.2 | 17.5 | 4.14 |
| 3 | 0.0229 | 1 | 3.3 | 27.0 | 8.24 |
| 4 | 0.4366 | 2 | 18.6 | 66.0 | 3.55 |
| 5 | 0.0708 | 2 | 6.1 | 25.8 | 4.23 |
| 6 | 0.0512 | 1 | 10.6 | 43.4 | 4.09 |
| 7 | 0.0630 | 1 | 6.1 | 31.0 | 5.05 |
| 8 | 0.1321 | 2 | 6.7 | 31.4 | 4.65 |
| 9 | 0.0078 | 1 | 4.7 | 20.8 | 4.47 |
| 10 | 0.0298 | 1 | 5.3 | 30.3 | 5.72 |
| 11 | 0.0101 | 2 | 3.0 | 21.8 | 7.27 |
| 12 | 0.0105 | 2 | 6.3 | 37.9 | 5.98 |
| 13 | 0.0197 | 2 | 5.6 | 29.2 | 5.24 |
| 14 | 0.0165 | 1 | 14.0 | 48.3 | 3.45 |

^a % territory = % of territory contained within the cumulative core area

^b % use = % of total locations contained within the cumulative core area

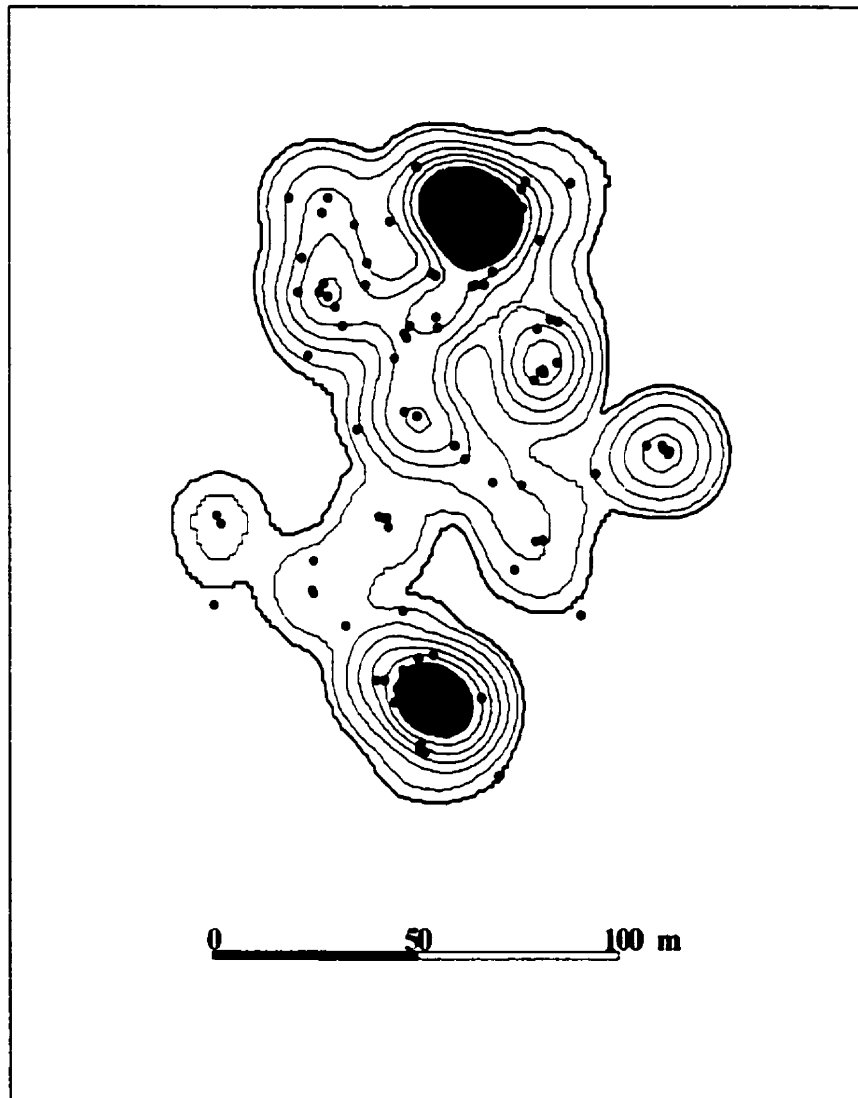
^c intensity = % use / % territory; measure of use intensity within the cumulative core area

Figure 1. Utilisation distribution for Cerulean Warbler male number 5, generated from a fixed kernel density estimator. Dots represent the locations collected for this individual during the sampling period. The outermost line represents the 95th density isopleth and territory boundary. The shaded areas represent the two core areas, which resolved at the 40th density isopleth for this particular individual.

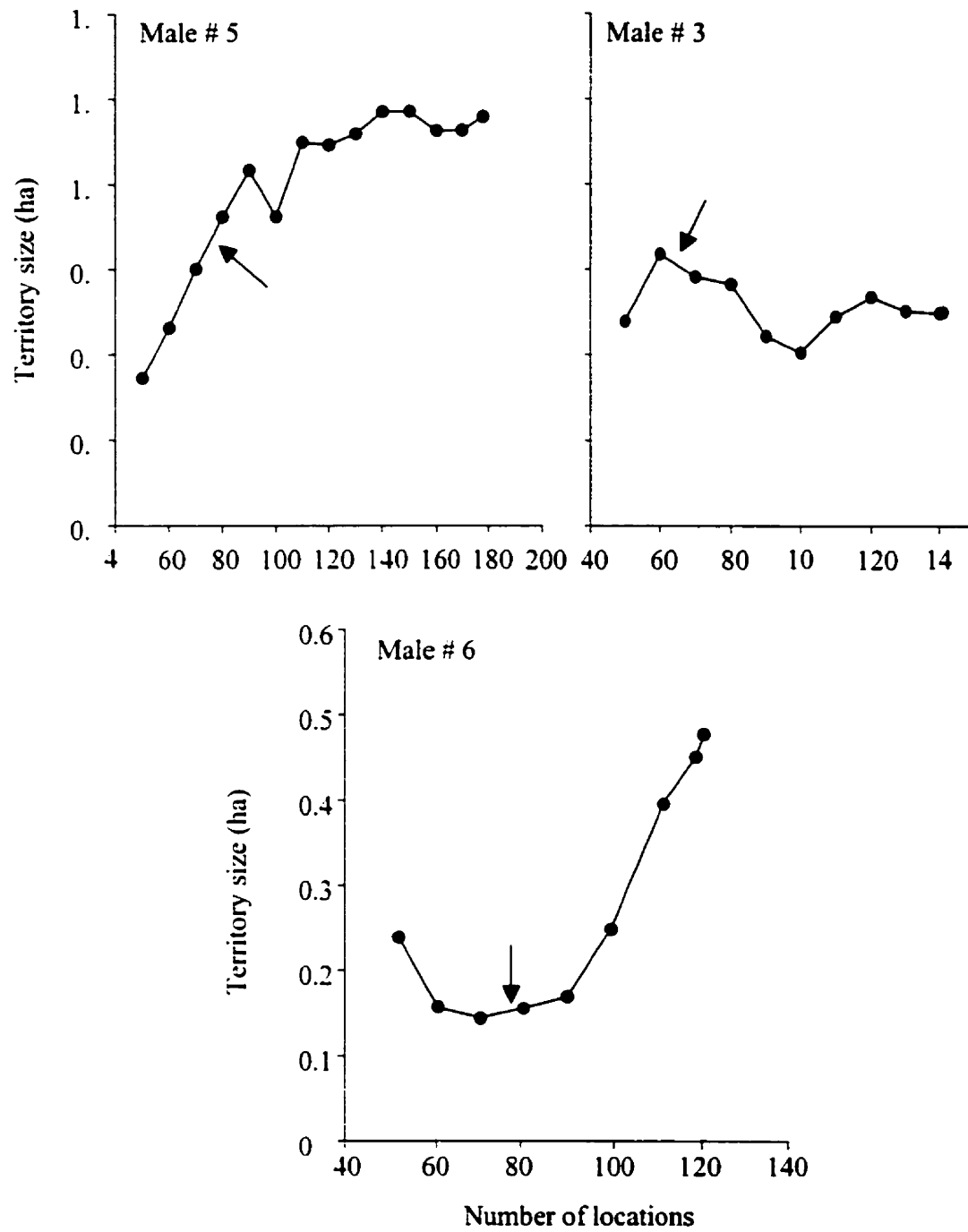
Figure 2. Variation in the behaviour of kernel estimates of territory size with respect to sample size in three different mated males. Arrows indicate the point at which hatching occurred.

Figure 3. Locations collected for Cerulean Warbler male number 14 during the sampling period. Note that the locations occur over a small area and overlap significantly among the seven sessions, suggesting fidelity to this area during the sampling period.

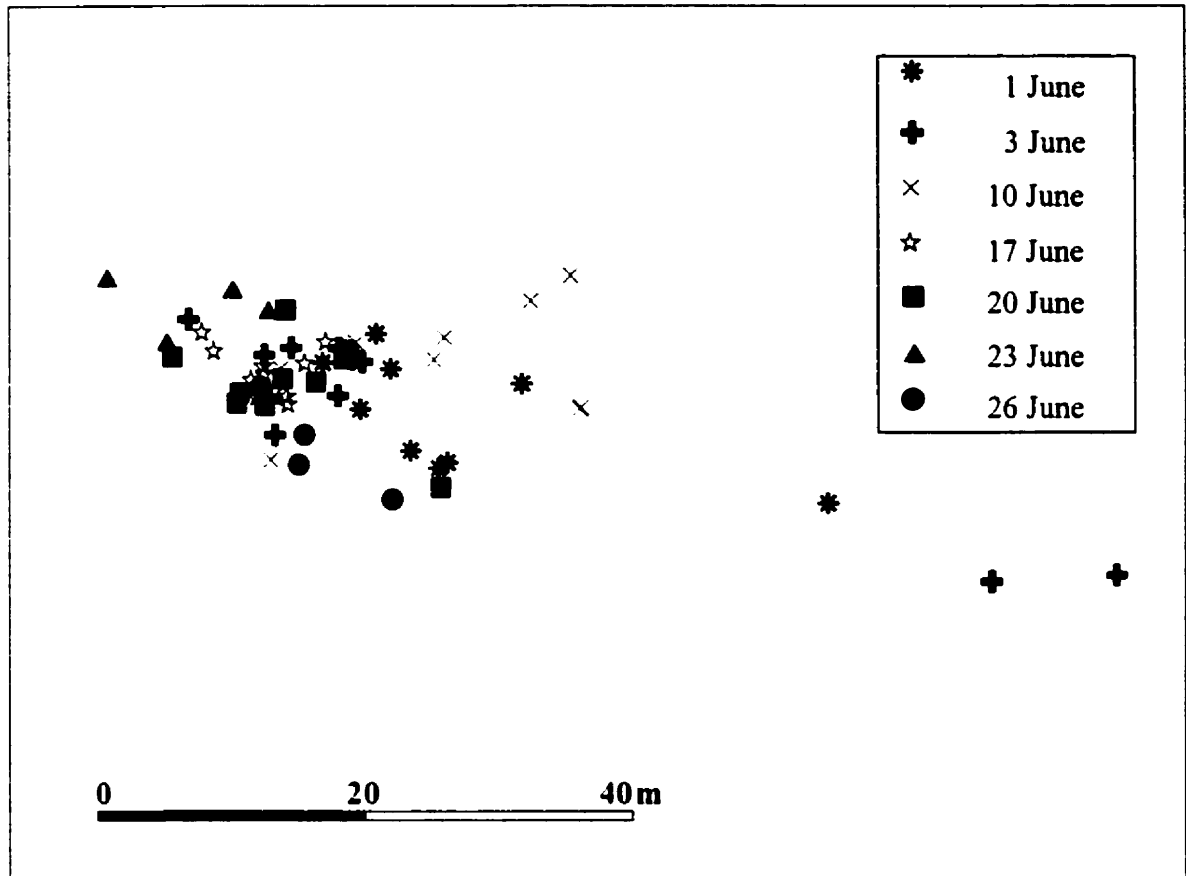
Figure 4. Territory boundaries for a Cerulean Warbler male generated by the fixed kernel density estimator (shaded area) and the minimum convex polygon (outline). Areas enclosed by the minimum convex polygon that do not overlap with the kernel boundaries were contiguous forest habitat, but the individual was never recorded there.

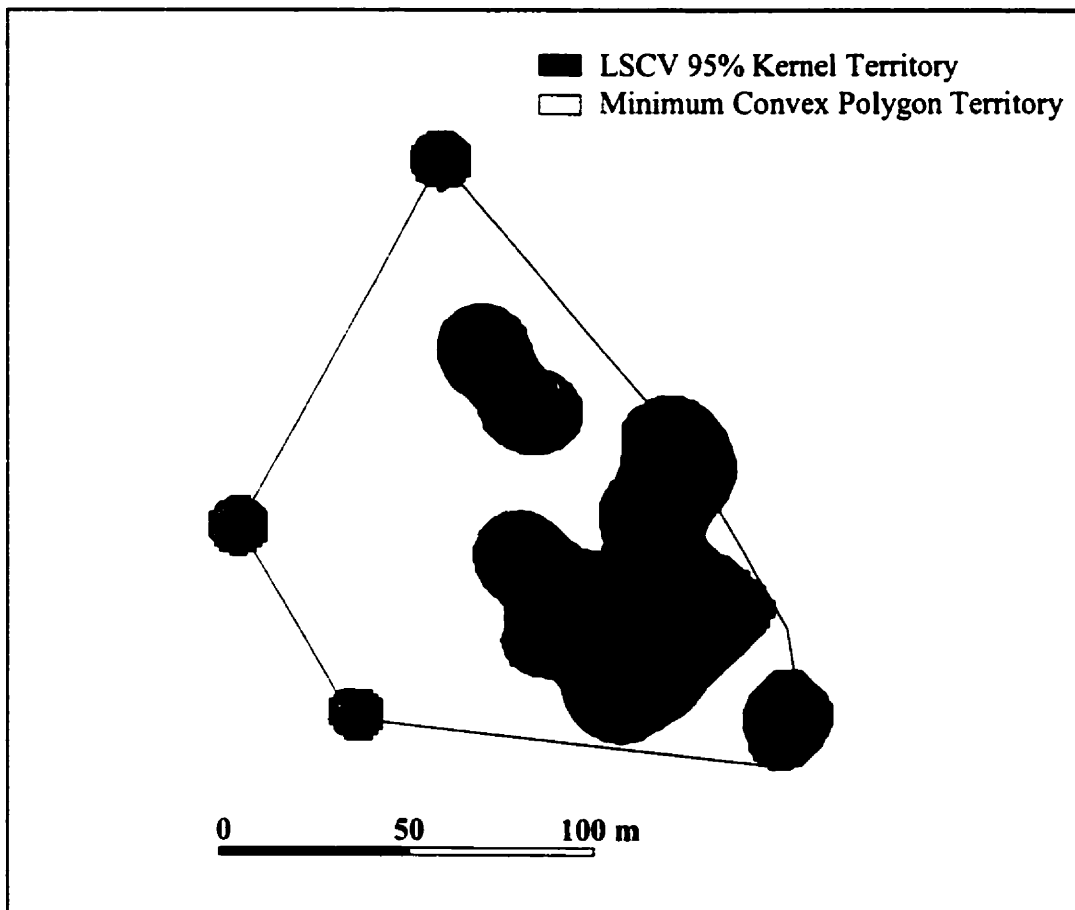


Chapter 2 - Figure 1



Chapter 2 - Figure 2





Chapter 3

**Micro-habitat use and behaviour patterns
within territories and core areas
of male Cerulean Warblers during the breeding season**

ABSTRACT

Habitat selection investigations rely on the identification of habitat use patterns. Current habitat use and selection literature emphasises the importance of multi-scale investigations and avoiding the use of single-scale studies to draw broad scale conclusions, both temporally and spatially. Previous studies of Cerulean Warbler population biology in southeastern Ontario have focussed on multi-scale habitat selection questions, specifically at the scale of the territory (meso-habitat) and nest site (micro-habitat). While these investigations have revealed the habitat characteristics associated with Cerulean Warbler territories, they have also revealed the presence of core areas within these territories. The presence of core areas indicates that within the territory, space is not used uniformly and suggests that some resources may be more important or used more often, than others. The purpose of this investigation was to identify population level habitat use and behaviour patterns of male Cerulean Warblers at two spatial scales: within the territory and within the core area. Within their territories, Cerulean Warbler males spend the majority of their time singing from perches even when they have nestlings, and tend to use canopy trees in proportion to their prevalence in our forest. Core areas seem to be important song post clusters, not foraging centres, for all male Cerulean Warblers. Song posts located in core areas tend to be used for longer singing bouts, are likely to be located higher, and are more often situated in bitternut hickories than they are in non-core areas. Males may be choosing core areas for structural features which maximise the distance song can be transmitted and minimise song degradation. Alternatively, males may be choosing core areas for their proximity to neighbouring males or females.

INTRODUCTION

The detection and description of pattern is the first fundamental step in understanding species-specific habitat associations. Once patterns have been described, their ultimate function and the mechanisms by which they are sustained can typically be determined in light of some selective advantage (Levin 1992). To identify these patterns, one must first describe habitat use: the way in which an organism uses habitat to meet its life history requirements (Block and Brennan 1993). Habitat use patterns then emerge through the examination of the distribution of a set of organisms among habitat types (Hutto 1985). Habitat selection investigations rely on the identification of these habitat use patterns, and take them one step further by quantifying habitat preference and the relative selective advantages preferred habitats confer (Hutto 1985; Block and Brennan 1993; Jones 2001). It is obvious then, that habitat selection cannot be studied without first correctly identifying habitat use patterns.

When embarking on a study of habitat use or selection, it is important to decide *a priori* the scale or scales at which the investigation will take place, and appropriately select and measure variables. Current literature has emphasised the importance of multi-scale investigations and avoiding the use of single-scale studies to draw broad scale conclusions, both temporally and spatially (Morris 1987; Wiens 1989; Orians and Wittenberger 1991; Bergin 1992; Levin 1992; Linkhart et al. 1998). Johnson (1980) developed a list of spatial hierarchical selection levels that describes a continuum of choices made by an organism, that reflects both macro-habitat, or first order selection, (e.g. geographic range) and micro-habitat, or fourth order selection (e.g. foraging tree). Hierarchical documentation of a species' habitat use patterns or habitat selection can

reveal how choices made on one scale influence those made at others (Levin 1992) and can offer a more thorough understanding of an organism's specific habitat associations (Rettie and Messier 2000). In the field of avian ecology, we are beginning to put this hierarchical examination into practice (Orians and Wittenberger 1991; Bergin 1992; Keane and Morrison 1999; Robichaud and Villard 1999; Jones and Robertson 2001).

Global Positioning Satellite (GPS) and Geographic Information System (GIS) technology used to capture and analyse location data have recently become commonly used tools in hierarchical habitat use and selection studies. Locations (e.g. latitude and longitude) of organisms can now be collected with sub-meter accuracy and monitored for the intensity with which they are used, among other applications. Such accurate identification of intensely used spaces, more commonly called core areas, is particularly important for small-scale studies, such as investigations of use within the territory. Density estimation techniques such as the kernel method (Worton 1989) can be used to identify and delineate the boundaries of these core areas, as well as to determine territory or home range limits (Chapter 2). Once identified, these spaces can be examined for particular habitat associations.

Kernel density estimates indicate that male Cerulean Warblers (*Dendroica cerulea*) in southeastern Ontario have core areas within their territories where concentrated bouts of activity take place throughout the breeding season, though the exact purpose and habitat associations of these core areas is unknown (Chapter 2). Previous studies of Cerulean Warbler population biology in southeastern Ontario have focussed on multi-scale habitat selection questions, specifically at the scale of the territory (meso-habitat) and nest site (micro-habitat). Jones and Robertson (2001) have

shown that Cerulean Warbler males choose territories non-randomly; territories tend to have dense canopies, high vertical vegetative complexity, and more large trees than do available, unused areas. Despite the fact that we seem to understand the vegetative characteristics associated with Cerulean Warbler territories, the presence of core areas suggests that within the territory, males do not use space uniformly and therefore some resources may be more important, or used more often than others.

The purpose of this investigation was to continue studying male Cerulean Warbler habitat use patterns at small spatial scales. We set out to identify population level habitat use and behaviour patterns of male Cerulean Warblers at two spatial scales: within the territory and within the core area. Research on other organisms indicates that core areas are usually concentrated foraging 'hot spots' (Lair 1987), song post clusters (Samuel and Garton 1987), or resting sites (Woollard and Harris 1990). The tree species used by our birds were considered the used habitats. In other words, we did not measure habitat features surrounding the used locations, only the used locations themselves. We hypothesised that use patterns and behaviours within core areas would be different from those in the rest of the territory. Aside from documenting nest site selection parameters, little else has been documented on Cerulean Warbler micro-habitat associations.

Understanding habitat selection mechanisms in this species is of particular importance. Cerulean Warblers are a Neotropic-Nearctic migratory passerine that has suffered severe loss of its historical breeding habitat, and perhaps as a consequence, severe declines in number (Robbins et al. 1992). Currently we have only a basic understanding of male Cerulean Warbler habitat associations on rather coarse scales. We hope that identifying habitat use patterns at these small scales will provide a launching

point for further study into their adaptive consequences, and eventually, a better idea of how to manage forests for these birds.

METHODS

Study Site and Species

The study was conducted during the breeding seasons of 1999 and 2000 (13 May-4 July in both years), at the Queen's University Biological Station (QUBS), Lake Opinicon, Leeds/Frontenac Counties, Ontario, Canada (44°30'N; 76°W). Cerulean warbler habitat here is characterised as second-growth mixed-deciduous forest, between 80-90 years old. The canopy is dominated by *Acer saccharum* (sugar maple), *Carya cordiformis* (bitternut hickory), and *Fraxinus spp.* (ash), with the occasional *Quercus spp.* (oak), *Ulmus spp.* (elm), *Tilia americana* (basswood) and *Betula spp.* (birch); the mid and under-story is primarily *Ostrya virginiana* (ironwood), and *Acer saccharum* saplings. Mean (\pm SE) daily temperatures (1200 EDT) and mean daily rainfall were 21.15 ± 0.60 °C and 3.00 ± 0.93 mm/day for 1999, and 17.62 ± 0.57 °C and 2.97 ± 0.74 mm/day for 2000, during the sampling periods.

Forests within and surrounding QUBS have regularly supported breeding populations of Cerulean Warblers since 1961 (Weir 1989). The focal population occupies a 24 ha area of QUBS property on the Bonwill Tract, known locally as The Bedford Mills Road. This population has been the focus of Cerulean Warbler investigations since 1994, and is part of one of the largest populations across its breeding range (Jones 2000).

Cerulean Warblers are small (~ 10 g), sexually dimorphic, migratory birds. Males use the upper forest canopy almost exclusively (Hamel 2000). Males primarily capture food through leaf gleaning, although males will also hover-glean and sally for more

mobile prey (Hamel 2000; Barg personal observation). Males in this population maintain relatively small (< 1 ha) territories, although significant size variation is present (Chapter 2). There is no evidence of polyterritoriality in this species, and males show marked site tenacity between seasons (Barg et al. unpublished data). Males defend their territory both vocally and through physical interactions, and regularly 'patrol' the boundaries, as is typical of most *Dendroica* warblers (Howard 1920; Bent 1953). Defence of the territory is most pronounced in the mornings between 0500-1100; afternoons are quiet with very little noticeable activity, especially in late summer (Woodward 1997; Barg personal observation)

Cerulean Warbler preferred breeding habitat has traditionally been characterised as large, contiguous areas of old growth deciduous or mixed-deciduous forest (Wilson 1811). The focal population will incorporate forest-field edge habitat within territory boundaries, occupies second-growth forests, and sometimes occurs in small (10 ha) tracts (Jones 2000).

Field Methods

Most un-banded territorial males were captured using a playback and target net technique, aged, and given a unique colour and Canadian Wildlife Service band combination for easy field identification. Any males that were not caught were identifiable by unique song characteristics within a season (Woodward 1997). Males were never captured within 3 days of collecting behaviour data, so that they had time to adjust to their new leg bands. Mated status and nest locations were determined for all males in the population.

An individual's location and behaviour data were collected in 'bursts'. Burst sampling is commonly used to collect location data when activity budget or habitat use data are desired, or when logistical constraints require the observer to collect many locations in a short amount of time. We used burst sampling because it generated large sample sizes in a short amount of time, which was critical since our birds exhibit a very brief breeding season and we were constrained by the number of available researchers. Given that Cerulean Warblers are highly active and can move about their territories quickly (Barg personal observation), we also felt this sampling method would best depict within territory use patterns. Typically, successive observations within a burst are separated by short, regular time intervals; between bursts, longer time intervals occur (Dunn and Gipson 1977; Swihart and Slade 1997).

A burst consisted of a 30 min session, during which time a focal male was followed via direct observation; its location was recorded every 60 s. This 60 s time interval allowed enough time for a bird to traverse its entire territory if it chose to do so, thus providing biologically independent locations (Lair 1987). We used direct observation to collect our locations because our birds were too small to carry radio transmitters, and it was the only way to be certain we were collecting points within the territory (i.e. defended locations) (Burt 1943). This method yielded a possible total of 30 locations per session per individual. Sessions were conducted between 0530-1030 EDT and commenced 2 min after the observer located and confirmed the identity of the focal male. This time delay was incorporated in order to reduce bias to conspicuous and commonly used sites (Recher and Gebiski 1990). In both years, each male in the population was subjected to between five and eight sessions during the sampling period,

each separated by 2-7 days, depending on weather and behaviour modifications resulting from nest loss (i.e. the birds ceased singing for several days post depredation). Each male received equal representation in terms of early morning and late morning sessions.

Locations were marked sequentially with pre-numbered (1-30) neon-coloured surveyor flags during a session. If a male went 'missing' during a session, any locations that should have been obtained during this time were considered 'lost' points, and were recorded as such into a micro-cassette recorder. Lost points were usually the result of males making long, direct flights unaccompanied by song or other territorial behaviour, and most likely represented extra-territorial forays, which were beyond the scope of this study. Behaviour and habitat use data were also recorded for each location. After a location was marked with its appropriate flag, the observer recorded the following information into a micro-cassette recorder: point number; behaviour (e.g. singing perched or foraging); tree species used; height above ground; whether or not the bird had moved from the perch used for the previous location; and whether or not the bird had moved from the tree used for the previous location. Heights were estimated by eye to the nearest meter. Observers trained themselves to estimate heights reliably by using a range finder to check their estimates against real distance values. These estimates were good to within a meter of the true value. Any information that could not reliably be determined was recorded as unknown.

Song posts were defined post hoc as locations where a bird remained on the same perch in the same tree, singing, for at least two consecutive minutes. Prey 'snatching' while at this perch site was considered opportunistic and did not occur very frequently; we considered the dominant behaviour in these cases as 'singing perched'. We recorded a

male's behaviour as 'foraging' if, when the point capture time occurred, the bird was engaged in a foraging bout. We defined our behaviours in this manner since at any one second, the behaviour a male might be exhibiting was ambiguous, and because males were almost always singing. We overcame this problem by recording the dominating behaviour surrounding the point capture time as described above.

The exact coordinates of each flagged location (grid Universal Transverse Mercator, datum NAD83Canada, zone 18North) were obtained each afternoon using a Global Positioning System (Trimble single antenna fanny pack unit consisting of a TSC1 datalogger with ProXRS receiver employing real-time differential correction), which is accurate to within 1 m. We did not collect coordinate readings if the point dilution of precision (PDOP) was > 4 ; readings greater than four decrease the accuracy of location fixes. If PDOPs were too high, we waited to collect locations at a time they were 4 or less.

Spatial delineation of territory boundaries and core areas

The boundaries of territories were calculated using 95% inclusion kernel density estimation techniques. Only those males whose data sets were evenly sampled across all nest cycle stages during the defined study period were used to calculate kernel territories, and each male's complete location data set was used to generate his territory (see Chapter 2 for details). The utilisation distribution (UD) that resulted from each kernel density estimator was used to describe the intensity of use across a male's territory. The UD was plotted as a series of isopleths that connected areas of equal use (for example see Figure 1). Isopleth values describe the likelihood of encountering a male in a particular area. Territory boundaries were established at the 95th density isopleth for each male in order

to be consistent with other kernel based studies; the territory was considered as the area contained within this region.

Core areas were delineated empirically by the following procedure. For each male, we calculated the area enclosed by kernel density isopleths 10-90, in increments of 10. Area calculations were based on the same utilisation distributions generated previously. We then calculated the difference in area between successive isopleths. We defined the core area at the first point where the difference in consecutive isopleth differences at least doubled. The core area was then the area bounded by the smaller of the two consecutive isopleths, although areas bounded by the same isopleth needed not be continuous in space (Figure 1). Locations that fell within the boundaries of the core areas were referred to as core area locations; locations that fell outside the core area but within the territory boundaries were referred to as non-core locations. For a more complete description of these procedures see Chapter 2.

Analysis

We used the Animal Movement Analysis Program V1.1 (Hooge and Eichenlaub 1997) and Spatial Analyst Extensions to the Geographic Information System Program ArcView V3.2a (ESRI 1999) to calculate all kernel utilisation distributions and core areas. JMP IN V4.0.2 (SAS Institute 2000) and Microsoft Excel 2000 (Microsoft Corp. 1999) were used for all other analyses. Before performing analyses, data were tested to see if test assumptions were met. The only variable that required transformation was song post density (log transformed). Values presented are means \pm 1 SE.

RESULTS

We collected location data on 9 of 16 males in 1999 and 16 of 22 males in 2000. Of these, four in 1999 and 10 in 2000 were equally sampled across the defined period and were suitable for calculating comparable territory boundary and core areas using kernel density estimators (Chapter 2). We used these 14 males in all of our core area / non-core area analyses. However, 18 males were used for the territory wide comparisons, which did not require the calculation of kernel area estimates and the meeting of their inherent assumptions. Data from both years were pooled since we were interested in population wide parameters and not temporal variation between seasons. All males were mature (≥ 2 y); 2 males were unmated and 16 were mated.

Territory-wide comparisons

Behaviours

The overall observations for each male, which were irrespective of nest stage and mated status, showed that 16 of 18 males had a higher percentage of singing than foraging observations (Table 1). However among males, the proportion of time spent either singing or foraging was not consistent ($\chi^2 = 170.64$, $df = 17$, $P < 0.0001$; Table 1). If we compare the percentage of singing and foraging observations collected during the incubation stage of mated males (to eliminate any possible effect of nestling provisioning), 16 of 16 males sang more than they foraged (Table 1). Observations collected on mated males during the nestling period had less consistent results. Ten males were followed during their nestling periods, 4 of which reversed their pre-nestling trends and had a greater percent of foraging than singing observations; 1 foraged and sang in equal proportions, and 5 still sang more than they foraged (Table 1). Of these same 10 males, 4 demonstrated a significant effect of nest stage on behaviour and

exhibited an increase in the percent of their foraging observations during the nestling period (Fisher's Two-tailed Exact Test, $P < 0.05$, data not shown). We then examined the relationship between Julian date and the proportion of foraging observations across each male's mapping sessions, in an attempt to determine whether time of season might also have had an effect on percent foraging observations. Three showed a significant relationship between date and percent foraging observations (2 positive and 1 negative; Table 2). However, 13 of the 18 males showed a positive trend to forage more late in the season, and only 5 showed a negative trend (Table 2).

Tree Species Use

When we combined the observations of all 18 males irrespective of behaviour, nest stage or mated status, the five most commonly used tree species in decreasing order were sugar maple, bitternut hickory, white ash, oak, and American elm (Table 3). Ten of 18 males used these tree species in significantly different proportions for singing and foraging within their respective territories (Table 4). If we limit this same comparison to observations collected during the incubation stage of mated males (to eliminate any possible effect of nestling provisioning), 7 of 16 used tree species in significantly different proportions for singing and foraging within their respective territories (Table 4).

Height

Within each male's set of observations irrespective of nest stage or mated status, males tended to sing higher above the ground than they foraged (13 of 18 males), although only 7 of these were statistically significant differences (Figure 2). The same trend holds when restricted to incubation observations only for mated males. Ten of 16

tended to sing higher than they foraged, although only 5 of these differences were statistically significant (Figure 3).

Combining the observations of all males irrespective of nest stage or mated status, singing observations were significantly higher above ground than foraging observations (foraging height 12.8 ± 0.21 m; range 5.0 - 25.0 m, $n = 367$; singing height 15.0 ± 0.09 m; range 5.0 - 25.0 m, $n = 1412$; $t = 10.43$, $df = 1777$, $P < 0.001$).

Commonalities

We examined tree species use with respect to behaviour across all males in an attempt to determine if there were population wide patterns. Despite significant differences among males in tree species selected for foraging ($\chi^2 = 358.2$, $df = 153$, $P < 0.0001$; Table 5), the diversity of trees *commonly* used among males was quite low. Sixteen of 18 males used either sugar maple (8 males) or bitternut hickory (8 males) as their number one foraging tree species (Table 5). Twelve of 18 males used sugar maple (6 males) or bitternut hickory (6 males) as their second most commonly used foraging tree species (Table 5). Similarly, despite significant differences among males in tree species selected for singing ($\chi^2 = 1362.98$, $df = 153$, $P < 0.0001$; Table 6), the diversity of trees commonly used was quite low. Sixteen of 18 males used either sugar maple (8 males) or bitternut hickory (8 males) as their most commonly used tree from which to sing. Fourteen of 18 males used either sugar maple (9 males) or bitternut hickory (5 males) as their second most commonly used singing tree (Table 6).

Eleven of 18 males used the same tree species as their most common foraging and singing tree, while 7 did not (Tables 5 and 6). Of the 15 males who used either sugar maples or bitternut hickories the most for foraging and singing, 5 males used bitternut

hickories the most for both behaviours, 5 used sugar maples the most for both behaviours, 2 used bitternuts the most for foraging and sugar maples the most for singing, and 3 used sugar maples the most for foraging and used bitternut hickories the most for singing (Tables 5 and 6).

When singing observations were put in the context of song posts (see definition in Methods section this paper), only 2 of the 18 males did not use either sugar maple (9 males) or bitternut hickory (7 males) as their most common song post tree species (Table 7). The distribution of the number of song posts with respect to tree species was again different among males ($\chi^2 = 220.26$, $df = 329$, $P < 0.0001$; Table 7).

Core area vs. non-core area comparisons

Behaviours

Five of 14 males exhibited significant differences in the distribution of behaviours between core and non-core areas within their respective territories (Fisher's Two-tailed Exact Test, $P < 0.05$, data not shown). This comparison was made using each male's complete set of observations irrespective of nest stage. Of these 5 males, 4 had a greater percent of singing observations in their respective core areas than in their non-core areas. Four of the remaining 9 males also sang more in their core areas, although these trends were non-significant, and four showed no difference. Because males tended to forage far less than they sing overall (see territory wide comparisons this section), and because core areas did not appear to be foraging 'hot spots', we focussed the remaining core area/non-core area comparisons on singing observations.

We chose to examine singing behaviour in the context of song posts in order to alleviate the violation of independence brought about by birds choosing to sing

repeatedly from the same location during our 30 min mapping sessions. All core areas had significantly greater song post densities than did non-core areas (Paired *t*-test; $t = -16.265$, $df = 13$, $P < 0.0001$). Core area and non-core area song post densities (untransformed values) were 303.9 ± 77.4 song posts/ha and 34.0 ± 8.5 song posts/ha, respectively. Song posts also tended to be used for longer singing bouts in core areas vs. non-core areas. Three of 14 males demonstrated significantly longer song post bout durations in core areas over non-core area song post bouts (Figure 4). Eight of the remaining 11 males showed a similar trend to sing for longer periods of time at core area song posts, although there was some overlap and the trends were not significant.

Tree Species Use

We compared the percent of non-core song posts to the percent of core area song posts with respect to tree species among males, using only the top 5 most commonly used tree species (as determined from the territory wide analysis). The difference in the distribution of the top five tree species used for song posts in non-core areas vs. core areas was significant ($\chi^2 = 12.5$, $df = 12$, $P = 0.01$). Among all tree species used as song posts, most non-core song posts were maples, while most core area song posts were bitternut hickories (Table 8). The diversity of tree species used for song posts was also greater in non-core areas (12 species) than in cores (7 species; Table 8). Sample sizes were too small to compare song post tree species use within a male to examine whether individuals were shifting their song post tree species use patterns between their core and non-core areas.

Height

We compared the relative heights of song post perches between core areas and non-core areas for each male. For this analysis, we combined the elevation (meters above sea level) at each song-post location with the estimated height above ground, then compared these 'true' heights to each other, with each male's lowest song post set equal to zero meters. Two of 14 males sang significantly higher at core area song-posts; 1 male sang significantly higher in his non-core area (Figure 5). However, 8 additional males demonstrated a non-significant tendency to sing higher in cores than in non-cores (Figure 5). We then looked solely at song post elevation between core and non-core areas. The two males who had significantly higher relative core area song post heights also had significantly higher core area song-post elevations, no males sang at significantly higher elevations in non-core areas, and 9 males demonstrated a non-significant tendency to sing at higher elevations in core vs. non-core areas (Figure 6).

Commonalities

We then examined the distribution of song post tree species used across all males in an attempt to determine if there were population wide patterns of use in core areas and in non-core areas. We restricted these analyses to the top 5 most commonly used tree species. In core areas, the distribution of tree species used as song posts among males were significantly different from each other ($\chi^2 = 138.958$, $df = 52$, $P < 0.0001$). The distribution of tree species used as song posts among males in non-core areas was also significantly different from each other ($\chi^2 = 100.219$, $df = 52$, $P < 0.0001$).

DISCUSSION

Territory-wide comparisons

Cerulean Warbler males spend the majority of their time singing from perches even when they have nestlings. Foraging tends to increase for some males during the nestling period, and for some, later in the season. Whether the increase in foraging is caused by males needing to provide for nestlings as well as themselves, pre-migration hyperphagia late in the season, or some combination is unknown, though the tendency to increase foraging rates while provisioning nestlings is a common phenomenon among male warblers (Morse 1989). We recognise that our sampling regime provided data from the morning hours only, and it is possible that temporal variation in behaviour and habitat use exists for this species (i.e. perhaps foraging rates are greater in the afternoons). Generally speaking however, peak activity periods for wood warblers are in the early mornings and late afternoons (Robbins 1981), so it is likely that our morning data collection sessions were representative of overall patterns. Morning data collection was essential in this particular study, since we do see a drastic reduction in singing activity in the afternoons, and singing is the most reliable indicator of a defended (within the territory) location (Burt 1943).

In general, the tree species most commonly used by male Cerulean Warblers, sugar maple and bitternut hickory, were used in proportion to their abundance in our forest canopy (Jones et al. 2001). Since Cerulean Warbler males use the forest canopy almost exclusively (Hamel 2000), it is not surprising that males in our population are using the most common canopy trees in our forest with the greatest frequency. Given that habitat heterogeneity exists within our study site (Jones and Robertson 2001), not all males have access to the identical distribution of tree species within their territories. Hence, it is equally unsurprising that males are not using the same tree species in

identical proportions for the same behaviours. In fact, the data suggest that certain males may lack the more commonly used canopy trees within their territories, and are replacing them with other, available canopy trees (e.g. male 14, Tables 5-7). However, it is interesting that among males, there is a split in their use patterns; for some, tree species are used in different frequencies for foraging than they are for singing, while for others they are used in the same proportions. While these tendencies need to be interpreted with caution due to the small number of foraging observations for each male, this result could be suggestive of variable foraging patch or song post qualities within territories which are either tree or tree species specific. Variable foraging patch quality at the individual tree level has been reported for other bird populations (Naef-Danzer 1994; 2000).

Overall, Cerulean Warbler males sing on perches higher above the ground than they forage. If singing serves to both attract mates and defend the territory from intruders, males should try to situate themselves in the best position to propagate these songs. Height may be a good way to achieve this and has been shown to be important to other similar species (Mathevon et al. 1996; Schieck 1997; Robichaud and Villard 1999). This will be discussed in more detail in the next section.

Core area and non-core area comparisons

Our data indicate that core areas are not foraging centres within male Cerulean Warbler territories. Other passerines have shown similar core area behavioural use patterns (Samuel and Garton 1987). Cerulean Warbler core areas tend to encompass a greater proportion of 'singing perched' observations than foraging observations, and more so than in non-core areas. This difference became much more obvious when we compared song post densities between core and non-core areas. Cerulean Warbler males

have greater song post densities in their core areas than in their non-core areas. Song posts located in core areas tend to be used for longer singing bouts, are likely to be located at higher elevations, and are more often situated in bitternut hickories than they are in non-core areas. Despite these tendencies, comparisons among males do not show a clear song post tree species use pattern for the population, and most of the trends we report, though obvious, are not significant.

What is clear is that core areas seem to be important song post clusters for all male Cerulean Warblers that we observed. What speculations might we make about their adaptive significance? If core areas are clusters of song posts, and song posts are used to propagate song, then song transmission ability must be a fairly important consideration for male Cerulean Warblers when selecting these singing locations. Since sound transmission is affected by sound structure, frequency, the surrounding habitat and environmental conditions (Mathevon et al. 1996; Fotheringham et al. 1997; Kime et al. 2000), males who must send reliable, far-reaching messages should carefully choose the locations from which they send them (sing), to maximise their specific potential.

Cerulean Warbler songs in our population have bandwidths ranging from 3 - 8 kHz, and usually consist of 2 or 3 non-repeating frequency syllables (Woodward 1997). The physical and abiotic environment surrounding the locations where Cerulean Warblers broadcast these songs will affect their propagation in somewhat predictable ways. High frequencies attenuate faster in relation to distance in forested environments, and are more easily degraded by reverberations off foliage than are lower frequencies (Marten and Marler 1977; Lemon et al. 1981). The upper frequencies in a Cerulean Warbler song would be affected by these factors. While Cerulean Warblers may somewhat ameliorate

the problem of reverberation-induced song degradation by structuring their songs within the 2 - 7 kHz range, and by avoiding the repetition of rapidly repeating signals (Wiley and Richards 1982), they may be choosing singing *locations* (core areas) to lessen the effects of foliage on both reverberation and song attenuation. Reverberation effects on frequencies > 4 kHz have been shown to be stronger in trees with leaves than in trees without leaves, and attenuation has been shown to be dependent on vegetative structure (Wiley and Richards 1982; Schieck 1997). Given this information, it would be possible to test whether core area song posts are in areas with less dense vegetation to optimise the propagation of songs to 'biologically important receivers' (Lemon et al. 1981).

It does not appear that Cerulean Warbler males are choosing core area song post locations in a tree species, specific manner. At first glance, it seems that more core area song post trees are bitternut hickories than are non-core area song post trees, however this overall difference is likely due to the observations of a few individuals who used bitternut hickories exclusively in their core areas. This is not to say that bitternut hickories are not good song post trees. Bitternut hickories, with their fairly open canopy architecture, leafing patterns, and late leaf-out tendencies, might more often make better song post locations than maples, which tend to have thick, densely foliated canopies, and achieve full leaf out earlier in the spring (Barg personal observation). As a consequence, song post locations in bitternut hickories may experience less serious effects on Cerulean Warbler song reverberation and attenuation. In other situations, bitternut hickories may not make the best song post locations. For example, a maple in a canopy gap, or which has suffered significant canopy damage may allow better song propagation than any bitternut hickory within the territory. If this latter situation is true, then perhaps core area

song post locations are chosen based on structure-specific over species-specific cues, though some of the identifying structural cues may reflect taxonomic distinctions. Most likely, core area song post locations are chosen in a more complicated fashion, based on a set of criteria which maximises song propagation to intended receivers, and minimises the negative effects of the surrounding vegetation given the limits imposed by Cerulean Warbler song structure.

If song propagation ability were an important criterion for choosing a core area, then the height of the song posts within the core area would also be important. Assuming Cerulean Warbler males are primarily sending messages to conspecifics, the location of song post perches in the canopy is essential, since this is where Cerulean Warblers spend the majority of their time. Another advantage of using high perches for song posts is that high frequency song transmitted from high above the ground has been shown to travel farther and maintain its structure better than song broadcast from closer to the ground, regardless of the location of the receiver (Mathevon et al. 1996; Schieck 1997). In our population, the trend to sing higher at core area song posts over non-core song posts is certainly the norm. Despite a general lack of statistical differences in core and non-core song post heights, males appear to be maximising the topographical variation available to them. Elevations within our study site only range from 128 m to 170 m above sea level. Within any one territory, it is unusual to encounter these extremes, and the range of elevations within a territory is much tighter. Because we know that males sing significantly higher than they forage, an indication that height is an important component to singing, and since males appear to be maximising the height that is available to them, song post height is a potentially important factor for Cerulean Warbler males. In other

parts of the Cerulean Warbler breeding range, populations experience much more varied topography (e.g. Cumberland Mountains, Tennessee; Barg personal observation). These may be better locations for examining song post height selection in this species.

Our data indicate that song posts are used both within and outside the core area, although the pattern of song post use within core areas is arguably different from the patterns of song post use outside cores. This discussion is not meant to discount these non-core area song posts. However, non-core area song posts may be used at whim over the course of the data collection period, while core area song posts, by the very nature of the core area definition (see Chapter 2), are used repeatedly throughout the study period. This suggests that core areas are very important spaces and that selection of these spaces is perhaps as critical as the selection of appropriate nest locations.

At a very coarse level, our study has demonstrated that core areas function as singing areas within male Cerulean Warbler territories. We have also highlighted physical factors that may be used by Cerulean Warblers as selection criteria when choosing core area locations. We have not discussed the ultimate purpose these core areas may serve. Males sing to attract mates and defend their territories; core areas seem to be the location where they perform these activities the most intensely. Therefore, there are four possible functions for Cerulean Warbler core areas: (1) defence of the territory; (2) defence of social nest sites; (3) defence of /communication with social mate; and (4) advertisement for extra-pair copulations. It should be noted that in no way do we consider any of these to be mutually exclusive, and that while we have not tested any of these hypotheses, some seem more plausible than others.

On a spatial level, the core areas we delineated did not typically encompass social nest sites, nor were they more likely to be associated with the edge or centre of a territory (for example see Figure 1; Barg personal observation). Therefore, if proximity is important, it is unlikely that they serve to defend a nest site, an incubating or brooding female, or the territory boundaries. Non-core area song posts may be more effective at boundary defence, since they are scattered throughout the territory. Males typically defend their social mates while they are fertile by following them intensely, chasing them, soliciting copulations, and communicating through contact calls (Barg et al. unpublished data). During these times, males are not typically using core area locations as intensively. While females are incubating, the pair rarely comes in contact (Barg et al. unpublished data). Males will sometimes approach the nest area to 'cue' incubating females to commence an 'off bout' during the incubation and nestling periods, and frequently will then remain vigilant near the nest until she resumes incubating or brooding (Barg et al. unpublished data). Once she resumes, he eventually returns to his core area activities.

This leaves us with two most likely scenarios for future study. Either core areas are chosen based on their ability to propagate song to a maximum number of conspecifics, or they are chosen based on their ability to propagate song to specific or to a maximum number of *female* conspecifics for the purpose of advertising for extra-pair copulations. We have witnessed extra-pair copulations and have genetic evidence of extra-pair fertilisations (Barg et al. unpublished data). Though the prevalence of extra-pair activity in our population is not yet known, our observations, together with findings

on other *Dendroica* (Chuang-Dobbs et al. 2001), lead us to suspect that the incidence is high.

Regardless of which of these latter two scenarios proves to be the most important, it is evident that core areas have potentially important implications for Cerulean Warbler population dynamics and habitat selection, and their ultimate purpose, spatial arrangement and specific habitat associations need further investigation. Because core areas seem to be important singing stages for all the males we examined in our population, it is possible that the features which create these micro-habitats (good core areas) are chosen at a much larger scale, possibly when males choose forest patches to occupy or territories to defend. In fact small-scale habitat features that are potentially limiting, may drive larger scale habitat selection (Rettie and Messier 2000). If subsequent investigations reveal that habitat structure of core areas is consistent among males, then perhaps we could use these structural features together with habitat structure of territories and nest sites, and eventually foraging locations, to predict occupancy and suitability of forest patches by Cerulean Warblers. This would be an exceptionally useful tool to apply to forest management strategies for this species.

Table 1. Distribution of foraging and singing activity for male Cerulean Warblers.

Values are sample sizes (*n*) followed by percentages of observations when a male was foraging (F) or singing-perched (SP). Incubation and Nestling totals do not necessarily add up to Overall total as some points included in the Overall category were from watches during an uncertain nest stage. Blank cells indicate that no watches were done during a particular stage.

| Male ID | Mated? | Overall | | | Incubation | | | Nestling | | |
|---------|--------|----------|------|------|------------|------|------|----------|------|------|
| | | <i>n</i> | F | SP | <i>n</i> | F | SP | <i>n</i> | F | SP |
| 1 | Y | 114 | 7.9 | 92.1 | 114 | 7.9 | 92.1 | | | |
| 2 | Y | 157 | 22.9 | 77.1 | 157 | 22.9 | 77.1 | | | |
| 3 | Y | 100 | 19.0 | 81.0 | 100 | 19.0 | 81.0 | | | |
| 4 | Y | 71 | 57.8 | 42.2 | 18 | 38.9 | 61.1 | 20 | 60.0 | 40.0 |
| 5 | Y | 144 | 18.8 | 81.3 | 135 | 17.0 | 83.0 | 9 | 44.4 | 55.6 |
| 6 | Y | 101 | 5.9 | 94.1 | 65 | 4.6 | 95.4 | 36 | 8.3 | 91.7 |
| 7 | N | 144 | 22.9 | 77.1 | | | | | | |
| 8 | Y | 98 | 16.3 | 83.7 | 90 | 15.6 | 84.4 | 8 | 25.0 | 75.0 |
| 9 | Y | 92 | 29.4 | 70.7 | 42 | 4.8 | 95.2 | 50 | 50.0 | 50.0 |
| 10 | Y | 113 | 31.9 | 68.1 | 113 | 31.9 | 68.1 | | | |
| 11 | Y | 84 | 27.4 | 72.6 | 59 | 6.8 | 93.2 | 24 | 79.2 | 20.8 |
| 12 | N | 166 | 17.5 | 82.5 | | | | | | |
| 13 | Y | 68 | 51.5 | 48.5 | 21 | 9.5 | 90.5 | 47 | 70.2 | 29.8 |
| 14 | Y | 133 | 12.0 | 88.0 | 23 | 8.0 | 91.0 | 22 | 9.1 | 90.9 |
| 15 | Y | 151 | 11.9 | 88.1 | 151 | 11.9 | 88.1 | | | |
| 16 | Y | 124 | 25.0 | 75.0 | 24 | 25.0 | 75.0 | 23 | 13.0 | 87.0 |
| 17 | Y | 132 | 43.2 | 56.8 | 132 | 43.2 | 56.8 | | | |
| 18 | Y | 101 | 25.0 | 75.0 | 88 | 20.5 | 79.5 | 13 | 62.0 | 38.0 |

Table 2. Relationship between Julian Date and percentage of observations foraging for male Cerulean Warblers measured with Pearson's correlation coefficients. Bold face *P*-values are significant.

| Male ID | Number of mapping sessions | <i>r</i> | <i>P</i> -value |
|---------|----------------------------|----------|-----------------|
| 1 | 6 | 0.41 | 0.43 |
| 2 | 7 | 0.22 | 0.64 |
| 3 | 7 | -0.19 | 0.68 |
| 4 | 6 | 0.19 | 0.72 |
| 5 | 7 | 0.69 | 0.09 |
| 6 | 6 | 0.54 | 0.27 |
| 7 | 6 | 0.51 | 0.30 |
| 8 | 7 | -0.52 | 0.23 |
| 9 | 7 | 0.84 | 0.02 |
| 10 | 7 | -0.25 | 0.59 |
| 11 | 6 | 0.76 | 0.08 |
| 12 | 6 | 0.57 | 0.24 |
| 13 | 6 | 0.89 | 0.02 |
| 14 | 7 | 0.03 | 0.95 |
| 15 | 8 | -0.21 | 0.63 |
| 16 | 6 | 0.04 | 0.93 |
| 17 | 5 | -0.95 | 0.02 |
| 18 | 5 | 0.87 | 0.06 |

Table 3. Distribution of observations (foraging and singing-perched combined, $n = 2034$) across tree species for male Cerulean Warblers.

| Species | # Observations | % Total Observations |
|---------------------|----------------|----------------------|
| sugar maple | 743 | 36.5 |
| bitternut hickory | 601 | 30.0 |
| white ash | 245 | 12.1 |
| oak spp. | 165 | 8.1 |
| American elm | 115 | 5.7 |
| Basswood | 46 | 2.3 |
| paper birch | 42 | 2.1 |
| large-toothed aspen | 35 | 1.7 |
| ironwood | 29 | 1.4 |
| other | 13 | 0.1 |

Table 4. Comparison of tree species use by male Cerulean Warblers for foraging and singing-perched activities within their territories. All tree species were included. Values are for the entire data set (Overall) and for the Incubation period. Bold-faced *P*-values are significant at $\alpha < 0.05$.

| Male ID | Overall | | | Incubation | | |
|---------|----------|----|--------------------|------------|----|--------------------|
| | χ^2 | df | <i>P</i> | χ^2 | df | <i>P</i> |
| 1 | 23.05 | 5 | 0.0003 | 23.05 | 5 | 0.0003 |
| 2 | 20.98 | 4 | 0.0003 | 20.98 | 4 | 0.0003 |
| 3 | 7.62 | 4 | 0.11 | 7.62 | 4 | 0.11 |
| 4 | 16.46 | 7 | 0.02 | 8.95 | 3 | 0.03 |
| 5 | 2.56 | 6 | 0.86 | 1.17 | 6 | 0.98 |
| 6 | 3.34 | 3 | 0.34 | 1.38 | 2 | 0.50 |
| 7 | 19.75 | 5 | 0.001 | | | |
| 8 | 11.03 | 7 | 0.14 | 9.95 | 5 | 0.08 |
| 9 | 12.78 | 3 | 0.005 | 6.07 | 1 | 0.01 |
| 10 | 15.06 | 4 | 0.005 | 15.06 | 4 | 0.005 |
| 11 | 17.46 | 5 | 0.004 | 10.66 | 4 | 0.03 |
| 12 | 13.65 | 4 | 0.009 | | | |
| 13 | 13.77 | 4 | 0.008 | 0.42 | 2 | 0.81 |
| 14 | 10.06 | 6 | 0.12 | 1.86 | 6 | 0.40 |
| 15 | 2.84 | 5 | 0.73 | 2.84 | 5 | 0.73 |
| 16 | 6.31 | 4 | 0.18 | 5.01 | 2 | 0.08 |
| 17 | 27.91 | 6 | < 0.0001 | 27.91 | 6 | < 0.0001 |
| 18 | 3.73 | 6 | 0.71 | 6.24 | 6 | 0.40 |

Table 5. Territory-wide distribution of male Cerulean Warbler foraging observations among tree species. Values are row percentages. There were no foraging observations in paper birch. The two most commonly used species for each male are in bold.

| Male ID | <i>n</i> | sugar maple | bitternut | white ash | oaks | American elm | basswood | large-toothed aspen | ironwood |
|---------|----------|-------------|-------------|-------------|-------------|--------------|-------------|---------------------|----------|
| 1 | 9 | 33.3 | 55.6 | 0.0 | 0.0 | 0.0 | 0.0 | 11.1 | 0.0 |
| 2 | 31 | 52.8 | 8.3 | 0.0 | 2.8 | 0.0 | 22.2 | 0.0 | 13.9 |
| 3 | 19 | 26.3 | 47.4 | 15.8 | 10.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 4 | 37 | 20.6 | 23.5 | 32.4 | 2.9 | 5.9 | 0.0 | 0.0 | 11.7 |
| 5 | 27 | 25.9 | 44.4 | 7.4 | 7.4 | 14.8 | 0.0 | 0.0 | 0.0 |
| 6 | 6 | 33.3 | 66.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 7 | 33 | 30.3 | 42.4 | 3.0 | 6.1 | 15.2 | 3.0 | 0.0 | 0.0 |
| 8 | 16 | 37.5 | 0.0 | 0.0 | 31.3 | 25.0 | 0.0 | 0.0 | 0.0 |
| 9 | 27 | 51.9 | 29.6 | 14.8 | 3.7 | 0.0 | 0.0 | 0.0 | 0.0 |
| 10 | 36 | 27.8 | 44.4 | 5.6 | 13.9 | 8.3 | 0.0 | 0.0 | 0.0 |
| 11 | 19 | 43.5 | 30.4 | 0.0 | 0.0 | 0.0 | 4.4 | 0.0 | 17.4 |
| 12 | 29 | 20.7 | 34.5 | 6.9 | 24.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| 13 | 32 | 40.0 | 34.3 | 8.6 | 8.6 | 0.0 | 0.0 | 0.0 | 8.6 |
| 14 | 16 | 0.0 | 0.0 | 25.0 | 50.0 | 12.5 | 6.3 | 6.3 | 0.0 |
| 15 | 16 | 68.8 | 6.3 | 0.0 | 0.0 | 25.0 | 0.0 | 0.0 | 0.0 |
| 16 | 27 | 50.0 | 25.0 | 21.4 | 0.0 | 0.0 | 0.0 | 0.0 | 3.6 |
| 17 | 40 | 18.6 | 23.3 | 20.9 | 0.0 | 23.3 | 2.3 | 0.0 | 7.0 |
| 18 | 16 | 75.0 | 12.5 | 6.3 | 0.0 | 0.0 | 6.3 | 0.0 | 0.0 |

Table 6. Territory-wide distribution of male Cerulean Warbler singing observations among tree species. Values are row percentages. There were no singing observations in ironwood. The two most commonly used species for each male are in bold.

| Male ID | <i>n</i> | sugar maple | bitternut | white ash | oaks | American elm | basswood | paper birch | large-toothed aspen |
|---------|----------|-------------|-------------|-------------|-------------|--------------|----------|-------------|---------------------|
| 1 | 105 | 32.4 | 9.5 | 43.8 | 1.0 | 0.0 | 13.3 | 0.0 | 0.0 |
| 2 | 121 | 74.4 | 19.0 | 0.0 | 0.8 | 0.0 | 3.3 | 0.0 | 0.0 |
| 3 | 81 | 48.2 | 23.5 | 19.8 | 3.7 | 4.9 | 0.0 | 0.0 | 0.0 |
| 4 | 30 | 36.7 | 23.3 | 13.3 | 0.0 | 10.0 | 10.0 | 0.0 | 0.0 |
| 5 | 117 | 28.2 | 32.5 | 11.1 | 8.6 | 17.1 | 0.0 | 0.0 | 0.9 |
| 6 | 95 | 20.0 | 55.8 | 6.3 | 17.9 | 0.0 | 0.0 | 0.0 | 0.0 |
| 7 | 111 | 30.6 | 27.9 | 11.7 | 25.2 | 0.9 | 3.6 | 0.0 | 0.0 |
| 8 | 82 | 42.7 | 3.7 | 3.7 | 12.2 | 29.3 | 3.7 | 0.0 | 4.9 |
| 9 | 65 | 18.5 | 67.7 | 12.3 | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 |
| 10 | 77 | 31.2 | 61.0 | 6.5 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| 11 | 61 | 34.4 | 49.2 | 3.3 | 0.0 | 0.0 | 0.0 | 13.1 | 0.0 |
| 12 | 137 | 23.4 | 49.6 | 4.4 | 2.9 | 0.0 | 0.0 | 19.7 | 0.0 |
| 13 | 33 | 21.2 | 66.7 | 0.0 | 12.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| 14 | 117 | 1.7 | 1.7 | 32.5 | 33.3 | 7.7 | 0.0 | 0.0 | 23.1 |
| 15 | 122 | 75.4 | 4.9 | 4.1 | 0.8 | 13.9 | 0.0 | 0.0 | 0.8 |
| 16 | 87 | 44.8 | 33.3 | 10.3 | 8.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| 17 | 66 | 27.3 | 53.0 | 15.2 | 0.0 | 1.5 | 0.0 | 0.0 | 0.0 |
| 18 | 71 | 60.6 | 8.5 | 18.3 | 1.4 | 2.8 | 7.0 | 0.0 | 0.0 |

Table 7. Tree species used for song posts by male Cerulean Warblers across nest stage.

Values are row percentages and the two most commonly used species for each male are in bold. Only the five most commonly used tree species are included.

| Male ID | <i>n</i> | sugar maple | bitternut | white ash | oaks | American elm |
|---------|----------|----------------|-------------|-------------|-------------|-----------------|
| 1 | 19 | 36.8 | 15.8 | 47.4 | 0.0 | 0.0 |
| 2 | 22 | 86.4 | 13.6 | 0.0 | 0.0 | 0.0 |
| 3 | 27 | 44.4 | 22.2 | 22.2 | 7.4 | 3.7 |
| 4 | 9 | 44.4 | 33.3 | 11.1 | 0.0 | 11.1 |
| 5 | 28 | 25.0 | 35.7 | 10.7 | 7.1 | 21.4 |
| 6 | 15 | 33.3 | 40.0 | 6.7 | 20.0 | 0.0 |
| 7 | 25 | 48.0 | 20.0 | 16.0 | 16.0 | 0.0 |
| 8 | 14 | 42.9 | 7.14 | 7.1 | 14.3 | 28.6 |
| 9 | 12 | 8.3 | 75.0 | 16.7 | 0.0 | 0.0 |
| 10 | 22 | 40.9 | 50.0 | 9.1 | 0.0 | 0.0 |
| 11 | 13 | 30.8 | 61.5 | 7.7 | 0.0 | 0.0 |
| 12 | 21 | 38.1 | 52.4 | 4.8 | 4.8 | 0.0 |
| 13 | 7 | 28.6 | 71.4 | 0.0 | 0.0 | 0.0 |
| 14 | 27 | 3.7 | 3.7 | 37.0 | 44.4 | 11.1 |
| 15 | 29 | 75.9 | 3.5 | 3.5 | 0.0 | 17.2 |
| 16 | 16 | 43.8 | 37.5 | 12.5 | 6.3 | 0.0 |
| 17 | 14 | 50.0 | 28.6 | 21.4 | 0.0 | 0.0 |
| 18 | 13 | 76.9 | 7.7 | 15.4 | 0.0 | 0.0 |

Table 8. Summary table of tree species used by male Cerulean Warblers for song posts in non-core ($n = 195$ observations) and core ($n = 106$) areas for all nesting stages combined. All tree species used as song posts are included.

| Tree Species | Non-core (%) | Core (%) |
|---------------------|--------------|-----------|
| sugar maple | 67 (34.4) | 30 (28.3) |
| bitternut hickory | 43 (22.1) | 39 (36.8) |
| white ash | 28 (14.4) | 13 (12.3) |
| oaks | 10 (5.1) | 16 (15.1) |
| American elm | 11 (5.6) | 4 (3.8) |
| basswood | 5 (2.6) | 0 |
| paper birch | 3 (1.5) | 1 (0.9) |
| large-toothed aspen | 4 (2.1) | 0 |
| ironwood | 1 (0.5) | 0 |
| yellow birch | 1 (0.5) | 0 |
| American beech | 1 (0.5) | 0 |
| snags | 2 (1.0) | 1 (0.9) |
| un-identified | 19 (9.7) | 2 (1.9) |

Figure 1. Territory (solid lines) and core area (shaded areas) boundaries calculated for 14 male Cerulean Warblers using the fixed kernel method. Note core areas do not have to be continuous in space. Stars represent each male's social nest locations for the study period. In all but 3 cases, core areas were not associated with nest sites.

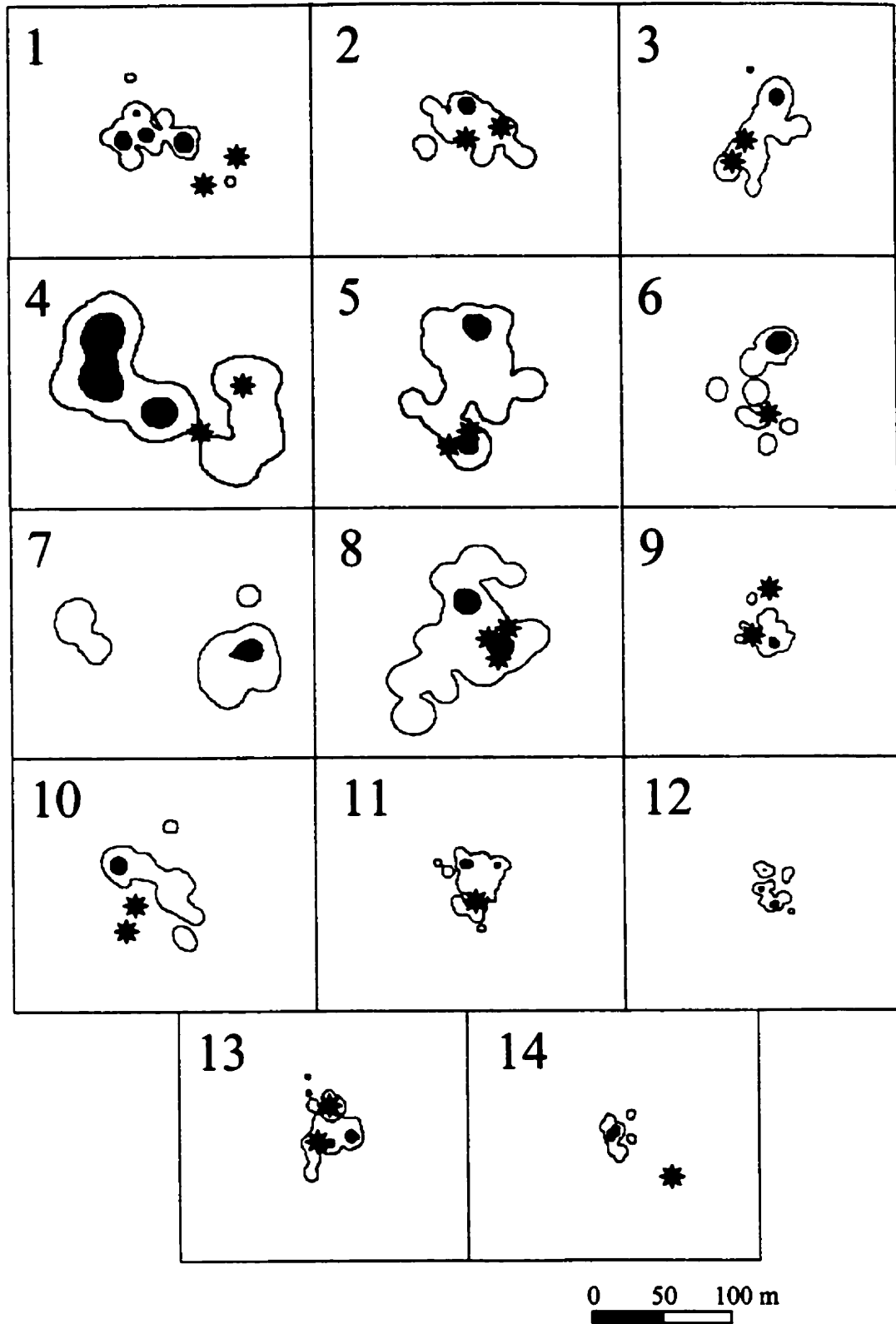
Figure 2. Foraging and singing heights (m) of male Cerulean Warblers across all nest stages. Values depicted are mean \pm SE. Differences between foraging and singing heights were tested for significance using Mann-Whitney *U* tests. Heights for males with boxed ID numbers were significant at $\alpha < 0.05$.

Figure 3. Foraging and singing heights (m) of mated male Cerulean Warblers for incubation period locations only. Values depicted are mean \pm SE. Differences between foraging and singing heights were tested for significance using Mann-Whitney *U* tests. Heights for males with boxed ID numbers were significant at $\alpha < 0.05$.

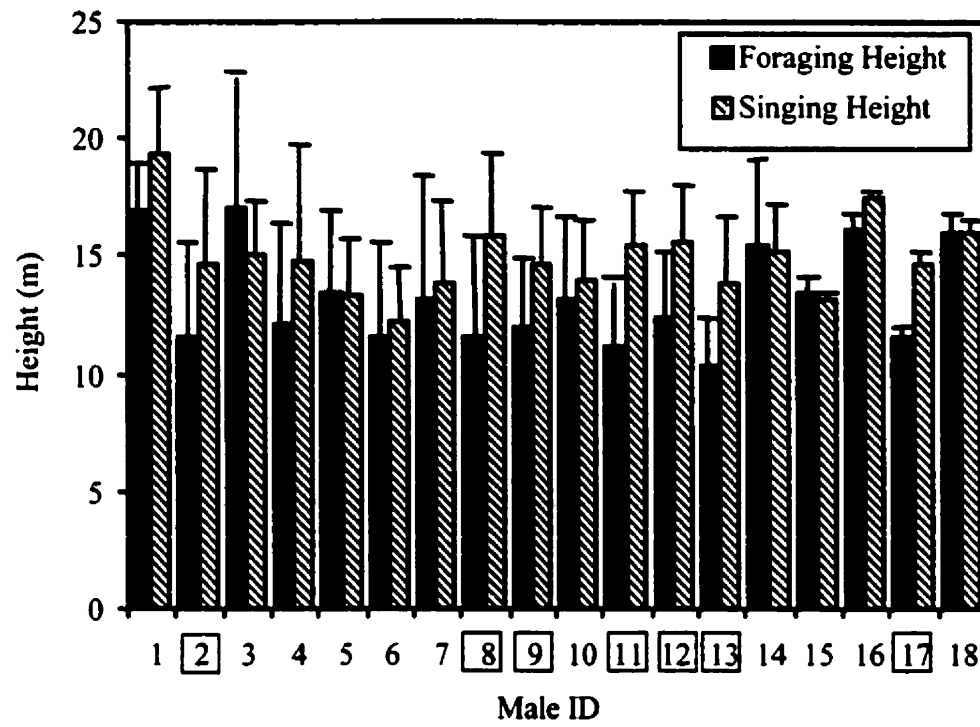
Figure 4. Song bout duration between non-core and core song post locations across all nest stages for male Cerulean Warblers. Bout length is the number of consecutive times a bird was recorded at a song post perch before moving to a new location and is depicted as mean \pm SE. Differences between non-core and core values are significant (based on Mann-Whitney *U* tests) at $\alpha < 0.05$ for males with boxed ID numbers.

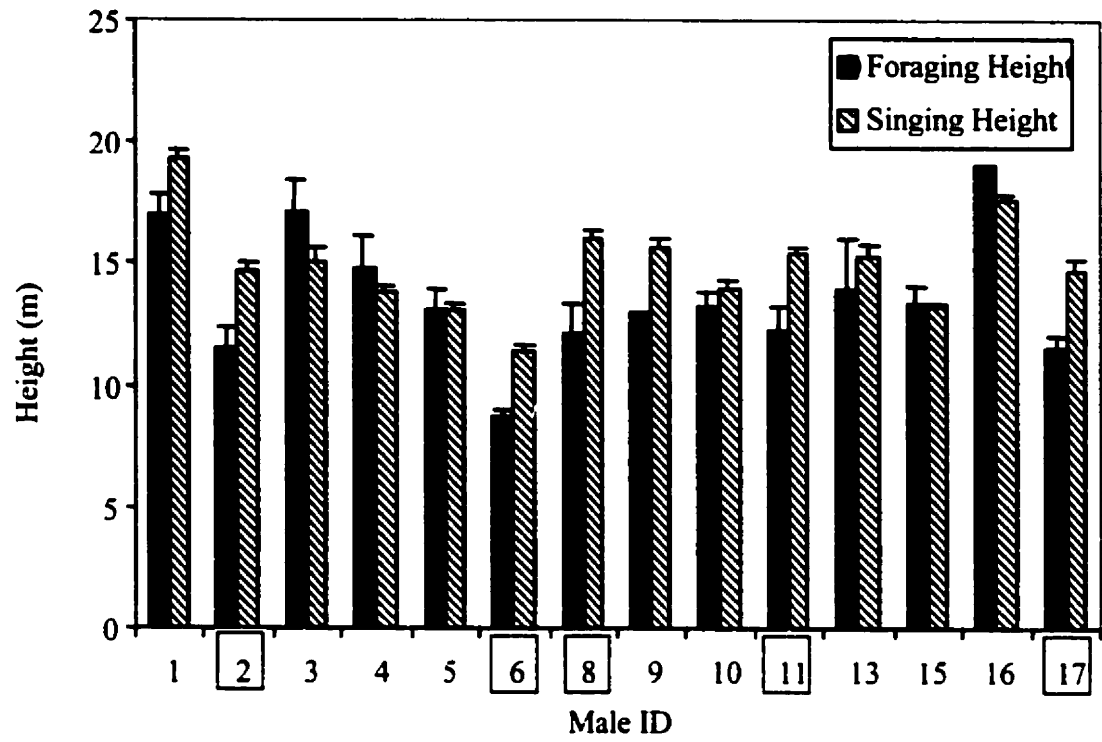
Figure 5. Relative heights (m) of song post perches for non-core and core area song post locations across all nest stages for male Cerulean Warblers. Heights were estimated by summing the elevation and the perch height. The lowest song post perch in the territory of a given male was set at 0m. Values shown are mean \pm SE. Differences between non-core and core values are significant (based on Mann-Whitney *U* tests) at $\alpha < 0.05$ for males with boxed ID numbers.

Figure 6. Elevations (m) at each song-post location in non-core and core areas across all nest stages for male Cerulean Warblers. Values shown are mean \pm SE. Differences between non-core and core values are significant (based on Mann-Whitney *U* tests) at $\alpha < 0.05$ for males with boxed ID numbers.

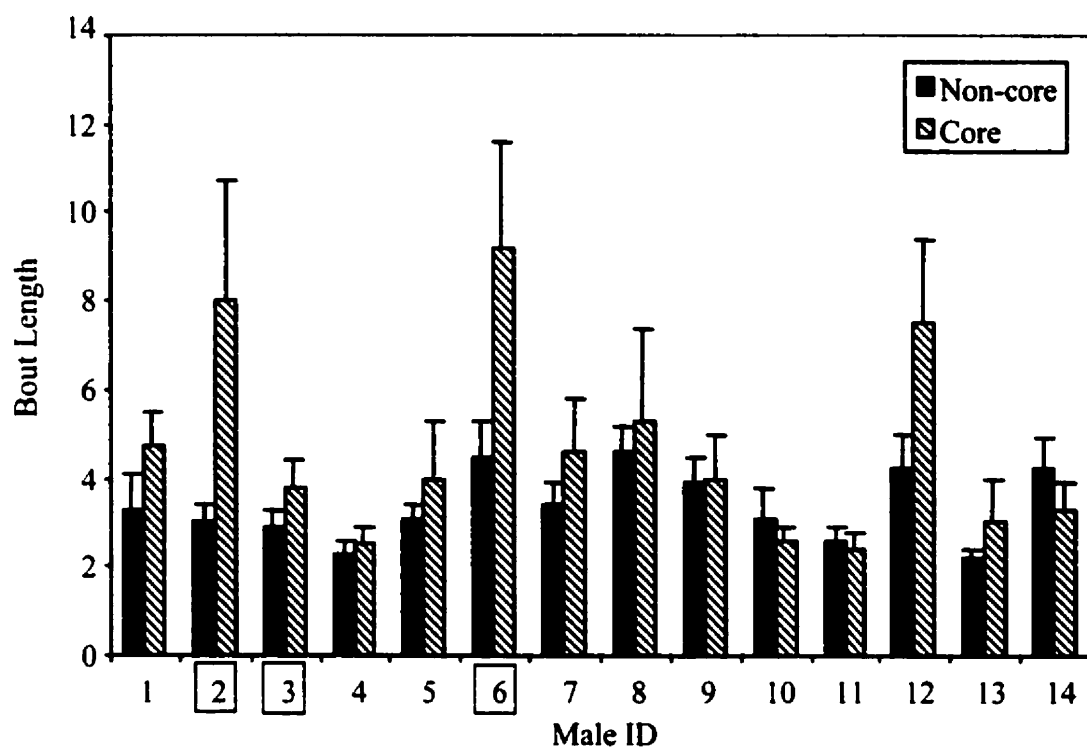


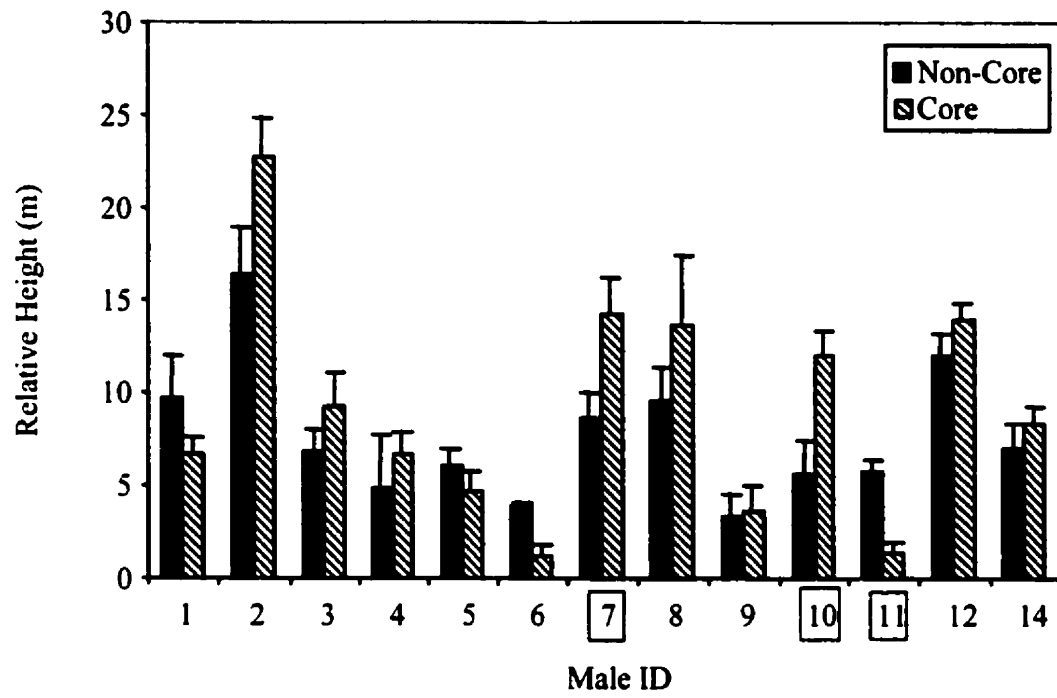
Chapter 3 - Figure 1

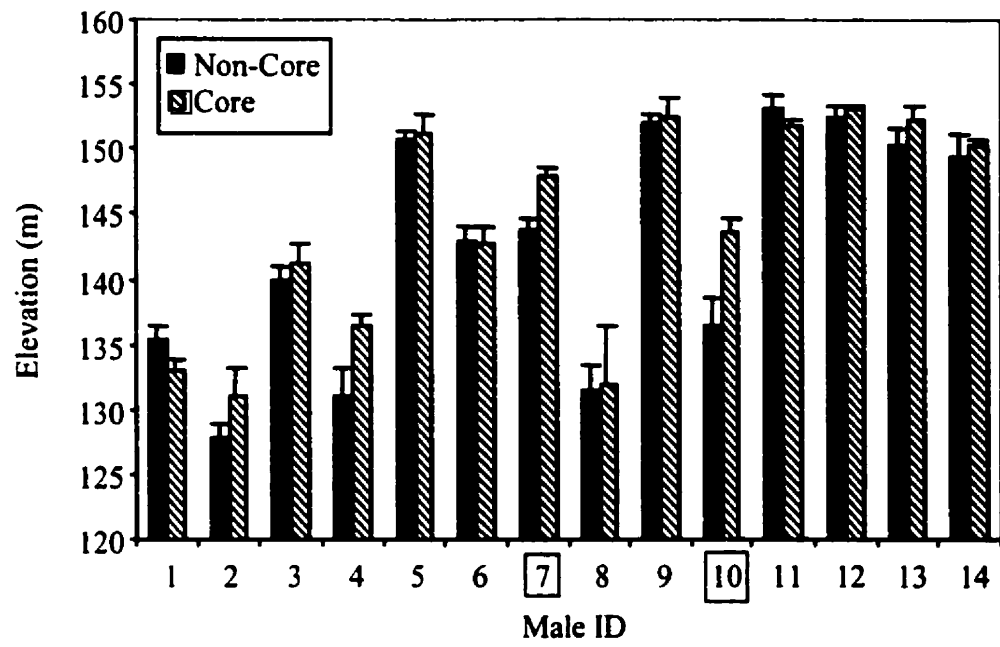




Chapter 3 - Figure 3







Chapter 4

General Discussion

The idea for an investigation on male Cerulean Warbler space, habitat and behavioural use was born out of my interest in understanding exactly how males use their territories, and what particular small-scale habitat features are important to them in their daily activities. My field observations of males repeatedly using the same trees during the breeding season, primarily for singing purposes, lead me to believe in the existence of core areas for this species. During the course of this study, I witnessed returning males singing from the same trees in different years, as well as new males singing from the same trees occupied by different males in the previous year. It then became clear that good singing locations might be valuable to all Cerulean Warbler males, and that they may be associated with distinct habitat features, much like good nest locations are distinct from other, random locations in the territory (Oliarnyk 1996). The eventual examination of core area habitat selection required me to begin at the beginning, however, by documenting their existence and use; these two steps alone have occupied the whole of my thesis.

Major findings in this Thesis

The first step in the process of quantifying these patterns was to choose an appropriate sampling regime and analytical technique that would most closely resemble actual spatial distributions of bird locations, the latter purely in an empirical sense. Regarding the sampling regime, I found it possible to monitor bird locations via direct

observation, and found that 'burst sampling' allowed for the collection of reasonably large sample sizes as well as accurate depictions of a bird's true space use patterns (Chapter 2). Of the analytical techniques available that were appropriate to my data, I found that the fixed kernel density estimation technique, using the least squares cross validation method for choosing the smoothing parameter, produced territory boundaries that closely conformed to actual bird locations (Chapter 2). This non-parametric technique uses a bird's set of locations to produce an estimate of the density of the frequency distribution at each location; the resultant densities are an approximation of the amount of time the bird spent at any location (Silverman 1986). While learning to use this technique to define bird territories, I showed that conventional assumptions regarding the number of locations needed to generate accurate kernel estimates (e. g. sample size) and the independence of those locations (e. g. degree to which position at time $t + 1$ is affected by position at time t) may not be as important as total sample size and an even sampling of locations across nest cycle stages (Chapter 2). I also demonstrated the effectiveness of this technique by comparing the territories calculated with this method to those calculated by the commonly used minimum convex polygon technique. Minimum convex polygon territories were larger and contained large areas that were never used by the territory owner (Chapter 2). This finding lead me to conclude that minimum convex polygons are not appropriate in territory boundary delineation for this species, certainly not when conducting studies of resource selection.

Kernel based territory estimates not only more accurately depict territory boundaries, they also allow for the examination of the internal configuration of a territory. This was important to the aims of this study because it provided a way to

quantitatively define the areas where I observed birds repeatedly - the core areas. I designed a repeatable, unambiguous method for defining core areas based on suggestions in other studies (Wray et al. 1992; Harris et al. 1990) (Chapter 2). This method yielded the location of each male's core area that I could then examine in terms of habitat and behavioural use patterns.

Chapter 2 provided more information on male Cerulean Warblers than just the technical aspects of boundary and core area delineation however. My results clearly demonstrated large variation in territory size within our population (Figure 1, Chapter 3), and non-uniform space use within each male's territory. The fact that territory size is so variable raises more questions than I attempted to answer here. In similar species, territory size variation has been attributed to habitat, male quality, resource distribution, and competition (see Wiens et al. 1985; Smith and Shugart 1987 and discussions therein). While investigating territory size variation was not a goal of this particular study, these causal factors should also be considered for Cerulean Warblers in future investigations.

In Chapter 3, we used the territories and core areas determined in Chapter 2 to examine their associated behaviour and habitat use patterns. Most locations where we recorded birds were associated with singing, not foraging, behaviours and were located in the most common canopy trees within our study area, sugar maple and bittersweet hickory. Males did not appear to have preferences for any particular tree species for either of these behaviours. Core areas were localised singing centres for all males in the population. Males tended to sing from higher perches (both as a function of location in the tree and elevation within the territory), for longer periods of time, and were more often found in bittersweet hickories in core areas, than in those locations outside the core (Chapter 3).

The results from Chapter 3, though straightforward, suggest interesting possibilities on the selection of core area locations. Given that all males considered here had core areas and used them for the same purpose, they may play an important role in male biology. It follows logically that there may be consequences to their selection, and possibly consequences to selecting territories that contain better or poorer core areas. I have proposed that choice of core area, either in spatial position or habitat association, may affect song transmission to intended receivers, and subsequently affect territory defence ability and/or effective advertisement to neighbouring females for the purpose of extra-pair copulation. To address the latter possibility, I am currently constructing a finely detailed habitat profile of the entire study area, which will be used to examine core area habitat selection. I hope to follow this up with a test of song transmission ability comparing songs broadcast from used core area locations and from random non-core locations within a male's territory. In order to address the spatial positioning hypothesis, I am going to attempt to quantify the spatial relationships between core area location, social nest site, neighbour nest site, and territory boundary.

Future work based on our findings

The research presented here is but the cornerstone in our understanding of male Cerulean Warbler micro-habitat selection. There are many new research avenues to pursue based on these findings, some of which I have outlined below.

1. What habitat features affect male Cerulean Warbler territory size? Why do we see such size variation in our population?
2. Core area habitat selection- Is there some measurable habitat association with core areas? *In Progress*

3. Ultimate purpose of core areas- Are core areas chosen based on their ability to allow song to travel farther and more reliably? Are core areas chosen based on their proximity to neighbouring females?
4. Core area / song post persistence- Are the same core areas and song posts used by returning males between years? When males fail to return in the spring, do new males utilise the former occupants' core areas and song posts? *In Progress*
5. Similarities in song post / core area use and habitat structure across breeding range?

Contributions to the field

There are many difficulties associated with detailed habitat use studies on small birds. They are fast, they are secretive, and if they inhabit the forest canopy, they can be elusive. While radio-transmitters can make this type of study simpler, birds still need to be reliable to capture, and transmitter studies do not always allow the investigator to witness *exactly* where the bird was, or what it was doing. Not to mention the difficulties associated with the transmitters themselves: their size, their battery life, and their cost. This investigation has demonstrated a feasible technique for examining detailed habitat use on a species that has a reputation for being difficult. The sampling and analytical methodologies presented herein have wide applicability to other species in various environments, and eliminate the expense and 'guess work' associated with radio tracking studies.

The exact nature of the male Cerulean Warbler territory had not been documented until the present study (Hamel 2000). The fact that core areas exist in male Cerulean Warbler territories leads us to assume that they may exist for other forest dwelling

passerines as well. While habitat selection studies typically document selection on the scale of the territory, nest site, or foraging patch, core areas have long been either ignored in this process or not identified at all. My findings indicate that there may be another layer of complexity that bears examination in habitat selection investigations. If appropriate core area habitat structure is important to males, its presence or absence could influence patch occupancy and territory selection, and could be just as critical as the presence of appropriate nesting habitat.

Eventually, we hope to identify the specific habitat features of good core areas (in progress, see future studies #2). The birds studied in this investigation are part of one of the largest, most successful Cerulean Warbler populations across the breeding range (Oliarnyk 1996; Jones 2000). Therefore, habitat features that are important to these birds should have applicability to Cerulean Warblers elsewhere, at least within southern Ontario, and can be justifiably used to structure local forest management practices. It is our hope that core area habitat features will eventually be incorporated into forest stand management techniques together with what we already know about territory and nest-site habitat selection for this species. The demand for such a comprehensive management program across the Cerulean Warbler's breeding range is great. If Cerulean Warbler breeding season habitat selection in Ontario proves to have similarities across the geographic range, we may eventually be able to develop a general model for Cerulean Warbler habitat selection that could be used to manage forests across the breeding range. With this ultimate goal in mind, we continue to put together the pieces.

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