

Estimating landscape carrying capacity through maximum clique analysis

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Abstract. Habitat suitability (HS) maps are widely used tools in wildlife science and establish a link between wildlife populations and landscape pattern. Although HS maps spatially depict the distribution of optimal resources for a species, they do not reveal the population size a landscape is capable of supporting—information that is often crucial for decision makers and managers. We used a new approach, “maximum clique analysis,” to demonstrate how HS maps for territorial species can be used to estimate the carrying capacity, N_k , of a given landscape. We estimated the N_k of Ovenbirds (*Seiurus aurocapillus*) and bobcats (*Lynx rufus*) in an 1153-km² study area in Vermont, USA. These two species were selected to highlight different approaches in building an HS map as well as computational challenges that can arise in a maximum clique analysis. We derived 30-m² HS maps for each species via occupancy modeling (Ovenbird) and by resource utilization modeling (bobcats). For each species, we then identified all pixel locations on the map (points) that had sufficient resources in the surrounding area to maintain a home range (termed a “pseudo-home range”). These locations were converted to a mathematical graph, where any two points were linked if two pseudo-home ranges could exist on the landscape without violating territory boundaries. We used the program Cliquer to find the maximum clique of each graph. The resulting estimates of $N_k = 236$ Ovenbirds and $N_k = 42$ female bobcats were sensitive to different assumptions and model inputs. Estimates of N_k via alternative, ad hoc methods were 1.4 to >30 times greater than the maximum clique estimate, suggesting that the alternative results may be upwardly biased. The maximum clique analysis was computationally intensive but could handle problems with <1500 total pseudo-home ranges (points). Given present computational constraints, it is best suited for species that occur in clustered distributions (where the problem can be broken into several, smaller problems), or for species with large home ranges relative to grid scale where resampling the points to a coarser resolution can reduce the problem to manageable proportions.

Key words: bobcat; graph theory; landscape carrying capacity; *Lynx rufus*; maximum clique; occupancy modeling; Ovenbird; resource utilization; *Seiurus aurocapillus*.

INTRODUCTION

Knowledge of the current and potential future population size, N , of a target species is of fundamental importance in developing effective management plans. Methods such as mark–recapture analyses and distance sampling have been developed to estimate current population sizes (reviewed in Borchers et al. 2002), but are difficult to apply across the large geographical extents that are increasingly the focus of conservation planning and management (Millspaugh and Thompson 2009). Given these challenges, decision makers and land managers require tools that estimate N or proxies of N across both time and space. These tools are urgently

needed in light of rapid land-use change and climate change, which are expected to alter animal and plant distributions globally (Vitousek et al. 1997).

Habitat suitability (HS) maps are widely used tools in wildlife science and establish a link between wildlife populations and landscape pattern (Boyce and McDonald 1999, Larson et al. 2004). In general terms, HS maps are generated from mathematical models that return a score for each pixel on a landscape map in terms of resources needed for survival or reproduction. Examples of resources—and factors that affect them—include habitat type, habitat amount, distance to water or roads, and patch size. The HS score at a pixel represents the collective value of resources for a given location; it is a continuous variable that often (but not always) ranges between 0 and 1. For example, the U.S. Fish and Wildlife Service’s Habitat Suitability Index models return a score between 0 and 1 based on expert opinion

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(USFWS 1996), while resource selection functions return a score that is proportional to the probability of use (Manly et al. 1993). Maps that predict probability of occupancy for a given species at a given location (MacKenzie et al. 2006) can also be interpreted as HS maps under the assumption that probability of occupancy is directly related to habitat suitability (Martin et al. 2010).

While HS maps do not reveal the current population size, N , in a landscape, they can be used to estimate N_k , defined as the maximum potential population size a given landscape is capable of supporting (i.e., carrying capacity). Linking HS maps to N or N_k is crucial because many conservation objectives use population sizes as indicators (Rosenberg and Blancher 2005). Boyce and McDonald (1999) outlined two aspatial approaches for linking HS models (and maps) to N or N_k for an area of interest. The first approach involves using a reference area of known N , determining the habitats and amounts used by the population, and then applying this information to estimate N in new areas. The second approach involves obtaining a resource-selection probability function for each pixel for a given area, scaling the pixel value relative to density of an individual, and then summing the scaled pixel values over the area of interest to estimate N_k . These approaches have been used to model timber wolf populations (*Canis lupus*) in the northeastern United States (Mladenoff 1997) and bird populations in the midwestern United States (Larson et al. 2004). For some species, however, establishing a reference population of known size can be exceedingly difficult, and the spatial variation of resources within a home range may be a critical determinant of whether a location is used by a species of interest. Downs et al. (2008) recognized the latter issue and created proximity-based HS maps to identify potential territories of Sandhill Cranes (*Grus canadensis*). They then used “uncovering algorithms” (Moon and Chaudry 1984), a class of integer programming optimization approaches, to estimate N_k under the constraint that territories must be separated by at least 3000 m (Downs et al. 2008).

Here, we extend the work of Boyce and McDonald (1999), Mladenoff (1997), Larson et al. (2004), and Downs et al. (2008) by demonstrating how HS maps for territorial species can be used to estimate N_k with maximum clique analysis. A *territorial species* is defined as a species that defends a specified area against conspecifics for at least part of its life cycle (Begon et al. 2006), which sets the temporal limits of the clique analysis. Here, the *territory* is defined as the portion of the home range that does not overlap with the territories of conspecifics, recognizing that home ranges are often much larger than the defended areas (Burt 1943). While N_k may exceed the actual population size, N , at any given time, it provides a spatially explicit, straightforward metric that allows decision makers to compare the

potential influence of various land-planning scenarios on target species.

BACKGROUND

Given a habitat suitability (HS) map with pixel that size is smaller than a home range (Fig. 1A), the first step is to convert the map so that pixel scores depict the home-range capacity (HRC-HS; Fig. 1B; sensu Compton et al. 2006). This is achieved by assuming each pixel is the center of a hypothetical home range (termed a *pseudo-home range*), and computing a score so that the pixel value now reflects the suitability of the pixel itself plus the surrounding area in terms of supporting a territory for the target species (Fig. 1B). We use the term “pseudo-home range” broadly to represent either the portion of the home range that is actively defended or, in the absence of active defense, the area of the home range that does not overlap with areas used by conspecifics. Second, the HRC-HS map is filtered so that only those locations that contain sufficient resources to constitute a pseudo-home range are retained; locations not meeting this threshold are eliminated (Fig. 1C). Third, the suitable cells are assigned a unique number, and then buffered to simulate the actual boundaries and locations of all possible pseudo-home ranges on the landscape (Fig. 1C). Although Fig. 1C shows circular buffers of equal size, it is important to note that the polygons can take on different shapes and sizes, depending on spatial arrangement of resources in the landscape. For example, the pseudo-home range polygon may be small if the encompassed area is very high quality and larger if the spatial distribution of required resources is more dispersed. Finally, the carrying capacity of the landscape is estimated by counting the maximum number of nonoverlapping pseudo-home ranges. For large geographic areas that contain hundreds or thousands of pseudo-home ranges, this is a challenging task. What is needed is an analytical method that provides this count with certainty.

In order to count nonoverlapping pseudo-home ranges, we introduce the mathematical notions of graphs and cliques. *Graphs* are mathematical abstractions that can be used to model relationships between objects, and are increasingly being used to investigate biological phenomena (Fortin and Dale 2005). They arise, for example, in the study of transportation networks and social relationships (West 2001), and have been used in landscape connectivity and corridor design analyses (Fortin and Dale 2005). Formally, a graph consists of a set of objects called *points* (also called *vertices*) along with a set of edges that link the points (Fig. 2A). Each edge indicates a relationship between its associated pair of points. Two points so linked are said to be *adjacent*. The drawings in Fig. 2A, B represent the same graph. We have drawn this graph in two different ways to emphasize that the positions of the points are immaterial; all that matters is that the same pairs of points are adjacent in each drawing. A *clique* in a graph is a subset

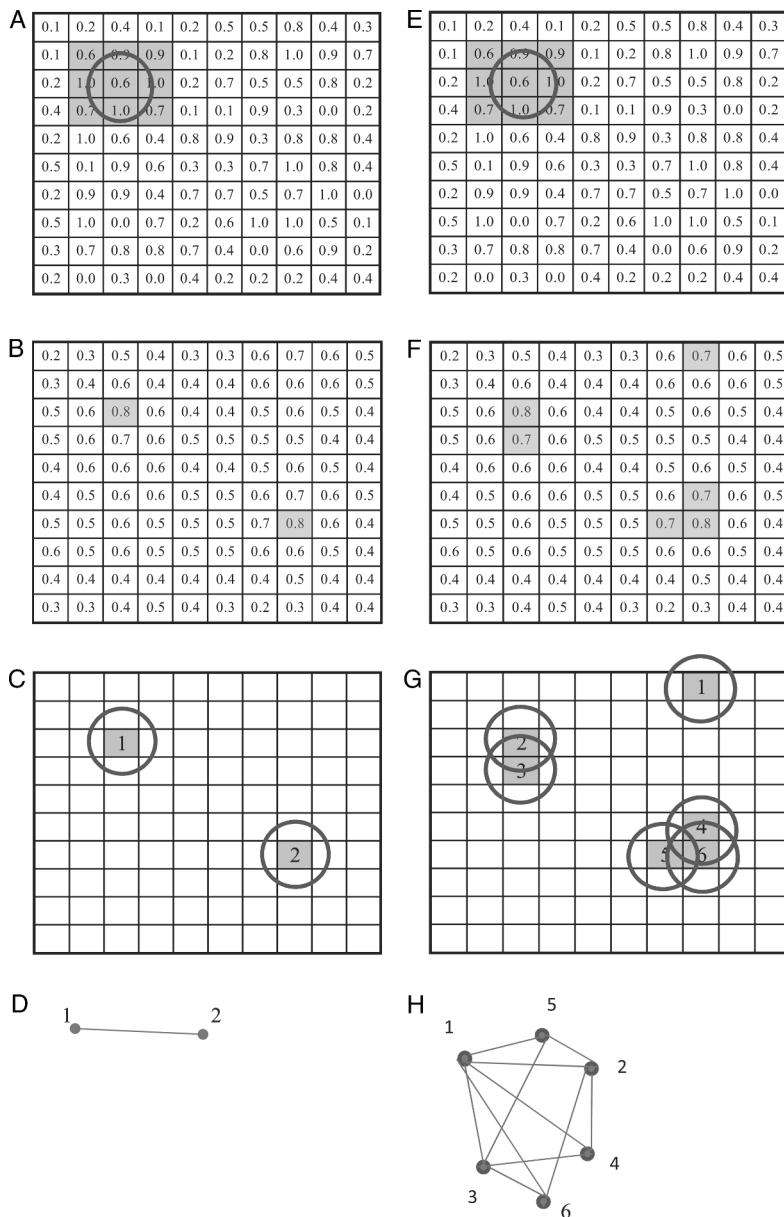


FIG. 1. (A) Hypothetical habitat suitability (HS) map showing pixel values that range between 0 and 1. A focal pixel in row 3, column 3 has an HS score of 0.6. The circle represents a buffered polygon that simulates a home range. (B) Hypothetical home range capacity (HRC)-HS map based on Fig. 1A, in which the HRC-HS score is the average of the focal pixel plus the eight surrounding cells. All pixels that are greater than or equal to a hypothetical pseudo-home range threshold of 0.8 are shaded. (C) The two locations that meet the HRC-HS threshold are retained, numbered 1 and 2, and buffered to simulate the placement of pseudo-home ranges on the landscape. In this example, we used circular buffers to simulate pseudo-home ranges of the same size, resulting in a maximum of two territories that can coexist on the landscape without overlap, and $N_k = 2$, where N_k is the maximum potential population size a given landscape is capable of supporting. (D) The pseudo-home range locations are de-spaced and converted to points on a graph, and edges are drawn between points that can coexist without overlapping boundaries. A maximum clique analysis of this graph yields $N_k = 2$. (E) The same HS map as in panel (A) is duplicated for a new analysis. (F) A new hypothetical HRC-HS map is created with a hypothetical pseudo-home range threshold of 0.7. (G) The six locations that meet the 0.7 threshold are retained and numbered 1–6. (H) The pseudo-home range locations are de-spaced and converted to points on a graph as in panel (D). The maximum clique of this graph (N_k) is 3. The maximum clique (N_k) can be achieved in six ways: examples include points 1, 2, and 4 and points 1, 3, and 5.

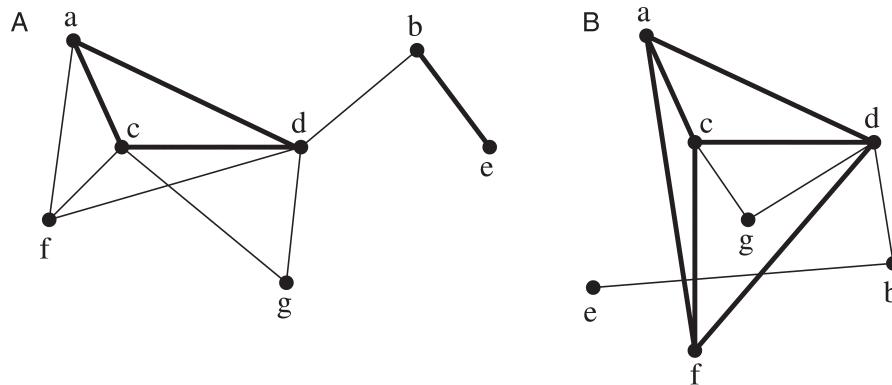


FIG. 2. Two drawings of a single graph with seven points, a–g (also called vertices). Points are joined by an edge if they have a specified relationship; edges are displayed here with lines (either thin or thick lines). In this study, the points represent the center of a pseudo-home range on the landscape; an edge is drawn between two points if the two points can co-exist on the landscape, i.e., their pseudo-home range polygons do not overlap. Point “a” can coexist with points f, d, and c. Its pseudo-home range boundaries overlap with points b, e, and g; therefore “a” is not joined with these points. Point “b” can coexist with points e and d only; its pseudo-home range boundaries overlap with points a, c, f, and g. (A) A clique of size two (points b and e) is highlighted with thick lines, indicating that points b and e can coexist on the landscape. A clique of size three is also highlighted (points a, c, and d), indicating that all three points can co-exist on the landscape. (B) The same graph as (A), just re-oriented, highlighting the maximum clique for this seven-point graph (points a, c, d, and f).

of the points in which every pair of points is adjacent. For example, in a social network in which points indicate people and edges indicate friendships, a clique would correspond to a group of mutual friends. Cliques of size two and three are highlighted in Fig. 2A. A clique is said to be “maximum” if a clique with more points does not exist. A maximum clique of size four is highlighted in Fig. 2B.

An estimate of a landscape’s carrying capacity, N_k , can be made with maximum-clique analysis using the set of all points on the landscape that represent pseudo-home ranges with respect to the chosen threshold (e.g., Fig. 1C). Two points are linked by an edge (i.e., made adjacent) if the corresponding locations can support pseudo-home ranges without overlapping or violating territory boundaries (Fig. 1D). Finally, the maximum clique size of the resultant graph is ascertained. Thus, the problem of counting the maximum number of nonoverlapping pseudo-home ranges translates to the well-studied problem of finding the size of a maximum clique in an associated graph. This size provides an estimate of the landscape’s carrying capacity, N_k .

Our goal is to use maximum-clique analysis to estimate the landscape carrying capacity of two very different species, the bobcat (*Lynx rufus*) and Ovenbird (*Seiurus aurocapillus*), in a large geographical area. Specifically, our objectives are to (1) develop an HS map for each species across the study area; (2) develop an HRC-HS map for each species; (3) convert the HRC-HS map to a mathematical graph, and estimate the landscape carrying capacity N_k for each species via a maximum-clique analysis; (4) compare estimates of N_k obtained with maximum-clique analysis with the results of alternative methods that do not rely on optimization; and (5) evaluate the sensitivity of maximum-clique N_k to

changes in the HRC-HS threshold score, and to the number of pseudo-home range points in the graph.

METHODS

Study area

Our study area was located in the Vermont’s Wildlife Management Unit F1, a 1153-km² area in western Vermont (USA) that borders Lake Champlain (Fig. 3). F1 includes land within 15 towns, including five Wildlife Management Areas, four state parks, and several locally conserved parcels. We chose this area due to both the availability of the data necessary for developing habitat suitability (HS) models and its diversity in land cover. Land cover imagery from 2001 (Homer et al. 2004) suggests F1 is approximately 6% developed, 50% agriculture, 20% forest, 18% water and shoreline, and <2% non-forested wetland and scrub/shrub land cover types.

Ovenbird

The Ovenbird is a Neotropical migrant warbler that requires primarily deciduous or mixed forest for nesting; the home range size varies between 0.5 and 4 ha (Porneluzi et al. 2011). The study area is located in the northeastern portion of its range, which extends across Canada and the eastern United States.

For Objective 1, we derived raw HS maps for singing males from single-season occupancy models, described fully in Schwenk and Donovan (2011). Briefly, birds were surveyed at 693 points across the state of Vermont in either 2003 or 2004. Six environmental resources (covariates) were quantified for each point: (1) forest or not forest; (2) topographic wetness index; (3) distance to edge of a different land-cover type; (4) percentage evergreen forest within 300 m; (5) percentage forest

within 1 km; and (6) road density within 1 km. Thirty-two models, consisting of various combinations of the six covariates, were analyzed in a single-season occupancy framework (MacKenzie et al. 2002). Models were compared and evaluated in an AIC framework (Burnham and Anderson 2002), which estimated the weight of support for each model (scaled such that the sum of weights = 1).

We derived an Ovenbird HS map (Objective 1) by first calculating a covariate value for each 30×30 m pixel on the F1 landscape. Then, for the 13 most highly ranked models (comprising >95% of the AIC weight of support), we developed probability-of-occupancy maps for each pixel based on that pixel's covariate values and model-specific coefficient estimates. Finally, we weighted each model-specific map's probability of occupancy by its corresponding AIC weight, and then added these results across all 13 maps to yield the final Ovenbird HS map (Burnham and Anderson 2002).

Bobcat

The bobcat is a medium-sized carnivore that utilizes a wide range of habitats in its role as a generalist predator. The bobcat range extends from southern Canada to Mexico and includes much of the conterminous United States. Home range size varies between males and females, with males having home ranges of up to 100 km² (Hansen 2006). Females maintain much smaller home ranges that may overlap with multiple males (Hansen 2006). Although females may overlap their home ranges, the degree of overlap is minimal during the breeding season (Lovallo and Anderson 1996). We focus our analysis on females in an attempt to estimate the landscaping carrying capacity of breeding females, which may be important for managers to estimate the potential number of offspring a landscape can support.

We derived a bobcat HS map (Objective 1) by integrating kernel home range analysis with resource-utilization functions for 14 GPS-collared bobcats in northwest Vermont, described fully in Donovan et al. (2011). Briefly, kernel home-range analysis provides an estimate of both the home-range size and a probability density function (also known as the "utilization distribution" or UD) that quantifies where the individual is most likely to occur within the home-range boundary (Silverman 1986, Worton 1989, Seaman and Powell 1996). Similar to the Ovenbird analysis, 18 environmental covariates were quantified for each 30-m^2 pixel in each home range. For each bobcat, 24 models, consisting of various combinations of the environmental covariates, were evaluated to estimate the association between the UD percentile and the level of a given spatially defined resource at the same location in the home range (Marzluff et al. 2004, Millsbaugh et al. 2006). For each bobcat, the 24 models were compared in an AIC framework (Burnham and Anderson 2002) and model-averaged coefficient estimates (betas) were retained. Following Marzluff et al. (2004), we averaged

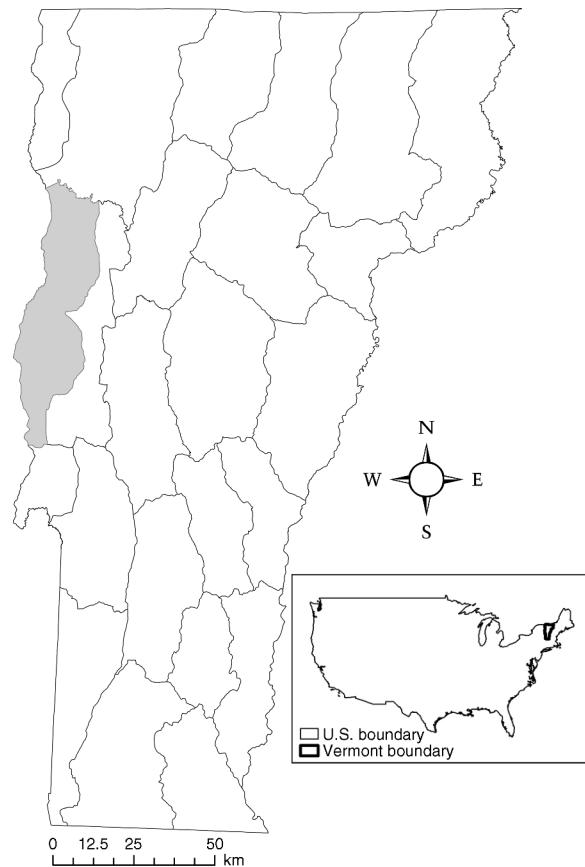


FIG. 3. A map of Vermont, USA, divided into its 24 Wildlife Management Units, of which the gray-shaded on is our study area F1, a 1153-km² area in western Vermont that includes 15 towns, including five Wildlife Management Areas, four state parks, and several locally conserved parcels. Lake Champlain borders northwestern Vermont, including F1.

these model-averaged coefficient estimates across bobcats on a resource-by-resource basis. This process revealed that, in Vermont, the shape of the UD surface was strongly associated with five different land-cover resources (conifer, deciduous, mixed forest, wetland, and shrub habitat) within 1 km of each pixel in the home range, plus two measures of road density at the 1-km scale (Donovan et al. 2011); other covariates carried little weight. We then constructed a bobcat HS map for the study area by measuring the level of each of the seven resources within 1 km of that location, multiplied by the corresponding population-level beta coefficient. Thus, each 30-m^2 pixel on the HS map revealed the cumulative score of bobcat resources based on empirical home-range data.

HRC-HS maps and maximum-clique analysis (Objectives 2 and 3)

For the Ovenbird, we converted the HS map from Objective 1 to an HRC (home range capacity)-HS map with the focal statistics tool in ArcGIS 10 (ESRI 2010).

We set the neighborhood shape to “circle” with a radius of 77.6 m to simulate a circular pseudo-home range of 1.89 ha (which falls within reported home-range size estimates, Porneluzi et al. 2011), and computed the HRC-HS for each pixel as the median HS score within the 77.6-m radius neighborhood. We then used the raster calculator tool to dichotomize the map, where the number 1 indicated cells that contained sufficient habitat for a pseudo-home range (HRC-HS > 0.76), and 0 otherwise. The threshold of 0.76 was determined by calculating such scores in locations where Ovenbirds were known to occur with certainty in Vermont based on singing-male surveys (Schwenk and Donovan 2011). Thus, our Ovenbird analysis focuses on estimating the carrying capacity, N_k , of territorial males. Pixel locations for pseudo-home ranges that met the 0.76 threshold were converted to points in a GIS shapefile.

At this stage the Ovenbird data (points and their relationship to other points in terms of polygon overlap) were ready for maximum-clique analysis. However, in graph theory, finding the maximum size of a clique falls into the generally intractable class of NP-hard problems (Garey and Johnson 1979); i.e., there are algorithms to compute the maximum clique size, but there are unlikely to be any efficient algorithms that provide the answer expeditiously. Consequently, as a practical matter it is only possible to compute the maximum clique size for graphs with sufficiently few points (e.g., <1500 for typical personal computers). Given the very large number of Ovenbird pseudo-home range points in F1, our study area, we handled this challenge in two ways. First, to reduce the total number of vertices for the clique analysis, we used the resample tool in ArcGIS to resample the shapefile to a 60-m grid, retaining only those points closest to the 60-m grid intersection (see *Discussion: Clique analytical considerations*, below, for a brief discussion on how resampling biases N_k). The final set of points was linked if the pseudo-home range polygons did not intersect, where links between any two points indicated nonoverlapping pseudo-home range boundaries. Second, where there were spatially disjoint clusters of pseudo-home ranges (i.e., where no edges existed between points in different clusters, such as the three clusters shown in Fig. 1G), we divided the maximum clique problem into several, smaller analyses to find the maximum clique for each cluster separately; N_k for the study area was then the sum of the maximum clique sizes across clusters. We used an ArcGIS ModelBuilder program written by J. Yu at the University of Vermont to automate the sequence of GIS steps described.

A similar process was used to convert the bobcat HS map to an HRC-HS map. We used a home-range size of 22.9 km² (2700-m radius) and a threshold HS score of -0.05 (a logit score) to identify the pixels that contained sufficient habitat to represent pseudo-home ranges. The threshold of -0.05 was determined by estimating the

average HS scores with the home ranges of four female bobcats (Donovan et al. 2011). We used these estimates because the home-range data were collected in or near the study area. We assumed the female home-range overlap was minimal (Lovallo 1993). Lovallo and Anderson (2003) report mean annual home range sizes of 28.5 km² in Wisconsin (USA), and note that home-range size in summer decreases to ~20 km². Similar to the Ovenbird, this process resulted in an excessive number of points for clique analysis. We reduced the total number of points by resampling the original points to a 900 m grid. All of the points within F1 for bobcats were located in a single cluster. Points were linked if the pseudo-home range polygons did not intersect. We used the public domain C software Cliquer to find the maximum clique size for each Ovenbird cluster and the bobcat graph (Niskanen and Ostergard 2003).

Comparison of estimates of N_k (Objective 4)

We compared the estimates of Ovenbird N_k from maximum clique analysis with the “sum across the grid” approach used by Larson et al. (2004), who used literature to determine the number of individuals that could exist in 1 pixel of optimal habitat (where HS = 1), and then multiplied that number by the habitat suitability of the corresponding pixel, which provided the maximum number of individuals each pixel in the landscape could hold. This result was then summed across the map to provide an estimate of N_k . We followed this same protocol to estimate N_k for Ovenbirds and compared it to the estimate from clique analysis.

We also estimated N_k for both species with an ad hoc approach based on the pseudo-home range polygons that exceeded the HRC-HS threshold. In this approach, we estimated N_k for each species by calculating the total area of F1 that consisted of the union of all pseudo-home range polygons, divided by the home-range area.

Sensitivity of maximum clique N_k to changes in threshold and number of points analyzed (Objective 5)

We evaluated the sensitivity of N_k to changes in the threshold level used to identify points for clique analysis (Ovenbird only). For Ovenbirds we let the threshold vary from 0.6 to 0.8 in increments of 0.01 and repeated the analyses previously described. As the threshold level decreased, the number of points and edges in the graph increased to such an extent that even individual clusters contained too many points for clique analysis. However, we could obtain upper and lower bounds for N_k by dividing each cluster into pieces small enough for maximum clique analyses. We obtained the upper bound by obtaining the maximum clique size for each piece and then summing the sizes. This represents an upper bound because selected pseudo-home ranges along the adjacent boundaries of cluster pieces may in fact overlap. We obtained the lower bound by sequentially obtaining the maximum clique for a piece, removing from consider-

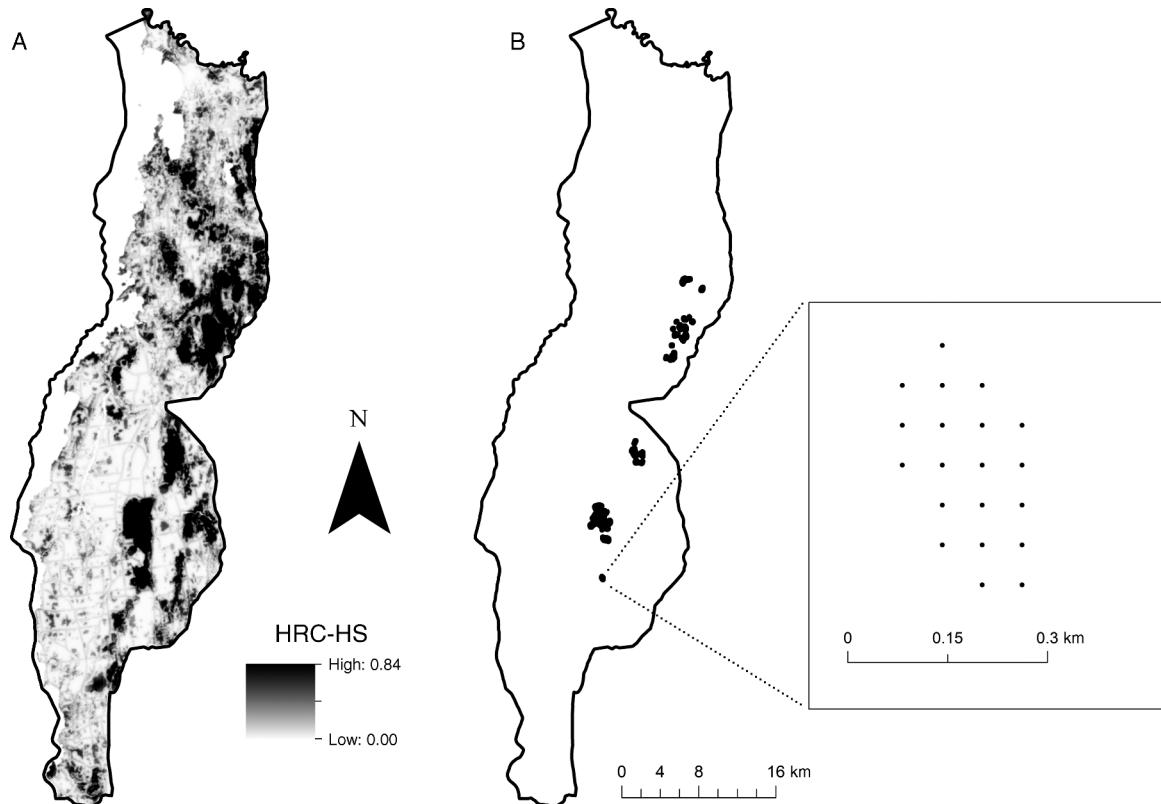


FIG. 4. Ovenbird (*Seiurus aurocapillus*) home range capacity (HRC) and habitat suitability (HS). (A) Ovenbird HRC-HS model, with highest quality habitats depicted in black and lowest quality habitats depicted in white. (B) HRC-HS map in which only those points that met the 0.76 threshold are retained. The points, buffered by a 77.6-m radius to simulate the actual placement of pseudo-home ranges, were spatially aggregated into 22 clusters. The inset shows an enlargement of one cluster of 20 points (which points are analyzed in the clique analysis). The goal is to estimate the maximum number of nonoverlapping pseudo-home ranges within each cluster. The carrying capacity N_k for the study area F1 is the sum of each of the maximum cliques across clusters.

ation any pseudo-home ranges in the remaining pieces that overlapped the clique, and then repeating the process until a maximum clique was obtained for each piece. The union of these cliques still represents a clique, but it may not be a maximum clique because a more efficient way to select pseudo-home ranges for the entire cluster may exist. Therefore, the sum of the maximum clique sizes in this approach yields a lower bound.

Additionally, given a single threshold level, we evaluated the sensitivity of N_k to changes in the number of points analyzed as a result of sampling (bobcats only). We resampled original bobcat points with grid sizes that varied from 900 m² to 3900 m² in increments of 300 m², where only those points located near grid intersections were retained for clique analysis.

RESULTS

Ovenbird

Pixel values in the raw (original) probability-of-occupancy map for Ovenbird ranged from 0 to 0.896 (Objective 1). Probability of occupancy was greatest in locations that were highly forested, had low road

density, and were far from forest edge (see Schwenk and Donovan 2011).

Pixel values in the HRC-HS (home range capacity habitat suitability) map ranged between 0 and 0.839 for the study area (Objective 2; Fig. 4A). Within that map, 5976 points met the 0.76 threshold for designating a pseudo-home range. After resampling to a 60 m grid, the number of points was reduced to 1491. These were spatially aggregated into 22 disjoint clusters of between 94 and 781 points, which had a total buffered area of 762.8 ha (Fig. 4A, B). The maximum clique sizes for these clusters ranged from 16 to 111, with a resulting N_k estimate of 236 (Objective 3). Thus, given our model assumptions, the carrying capacity of the study area landscape was 236 male Ovenbird territories.

We found considerable differences in estimates of N_k between the maximum clique method ($N_k = 236$ territories), the “sum across the grid method,” and the ad hoc method (Objective 4). Using the methods outlined by Larson et al. (2004), we estimated Ovenbird density to be 0.529 Ovenbirds/ha (based on a 1.89-ha home range). Given a pixel size of 0.09 ha (30 m²), the

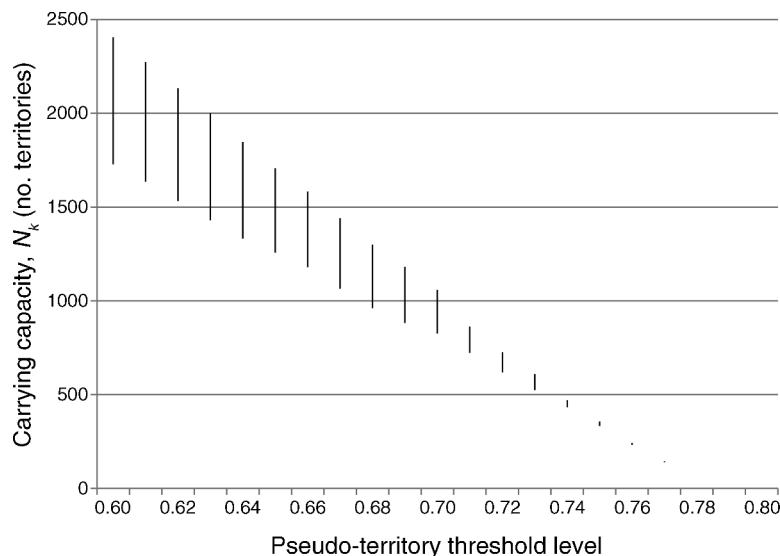


FIG. 5. Sensitivity of N_k to changes in pseudo-home range threshold (0.6–0.8) for Ovenbirds in study area F1. As the threshold decreased (e.g., 0.60), the number of pseudo-home ranges increased, creating very dense mathematical graphs with too many points to be tractable and requiring the upper and lower bounds of N_k to be estimated (depicted by the vertical bars). See *Methods: Sensitivity of maximum clique N_k to changes in threshold and number of points analyzed (Objective 5)* for description.

maximum number of Ovenbirds per HSC-HS pixel under optimal conditions was 0.048 birds. Multiplying the HRC-HS grid by 0.048 and then summing across the grid yielded an N_k estimate of 8050 Ovenbirds. This same approach yielded an estimate of 417 territories when only those pixels that exceeded the 0.76 threshold were considered. Our ad hoc approach of estimating N_k as the total area within F1 that consisted of buffered, pseudo-home ranges (762.8 ha) divided by the home range area (1.89 ha) yielded an estimate of $N_k = 404$ territories, which is 1.71 times higher than the maximum clique estimate.

N_k was sensitive to changes in the threshold level used to define pseudo-home range locations; as the threshold increased, N_k decreased (Objective 5). N_k estimates varied from 26 (the threshold of 0.8) to 2405 (the upper bound for a threshold of 0.6; Fig. 5). The upper and lower bounds of N_k diminished as the threshold increased in a highly predictable way (for the upper bound, $N_k = -12\,729(\text{threshold}) + 9981.6$; $R^2 = 0.99$; for the lower bound, $N_k = -8910.1(\text{threshold}) + 7045.6$; $R^2 = 0.99$).

Bobcat

Pixel values in the raw (original) logit map for bobcats ranged between -1.70 and 1.44 (Objective 1). This map was transformed into an HRC-HS map, where the HR-HS score for each pixel ranged between -0.58 and 0.43 (Objective 2; Fig. 6A). Within that map, 1 012 511 locations met the -0.05 pseudo-home range threshold (Fig. 6B). After resampling to a 900-m grid, the resultant graph consisted of 1116 points and 580 526 edges. Analysis of this graph indicated the maximum clique size was 46; thus the carrying capacity of the study area

landscape was 46 female bobcat home ranges. There were over 4 billion different, potential maximum cliques of size 46 (see Fig. 6C for one example).

Our ad hoc approach of estimating N_k as the total area within F1 that consisted of buffered, pseudo-home ranges ($151\,705\text{ km}^2$) divided by the home range area (22.9 km^2) yielded an estimate of $N_k = 66$ home ranges, which is 1.44 times higher than the maximum clique estimate.

The maximum clique N_k was sensitive to the grid size used to reduce the total number of points for clique analysis. For each 1000-m increase in resample grid-cell length, N_k decreased by 6.2 individuals (Fig. 7).

DISCUSSION

We demonstrated how a widely used tool in wildlife science, a habitat suitability (HS) map, can be analyzed with graph-theoretic methods to estimate the carrying capacity of a landscape for supporting a territorial species. Though N_k —the maximum potential population size a given landscape is capable of supporting (i.e., carrying capacity)—is not an estimate of the actual population size, N (N may be lower than N_k), it provides the upper limit a landscape can support and directly links landscape pattern to population metrics; this has many utilities for management. For example, in terms of formally evaluating the effect of different land-use scenarios in a decision-making context, N_k could become the objective function (e.g., maximize N_k by changing the landscape pattern, subject to various constraints). Less formally, N_k is a more straightforward metric for stakeholders to grasp than pixel values in a HS map when comparing outcomes of different land-use scenarios.

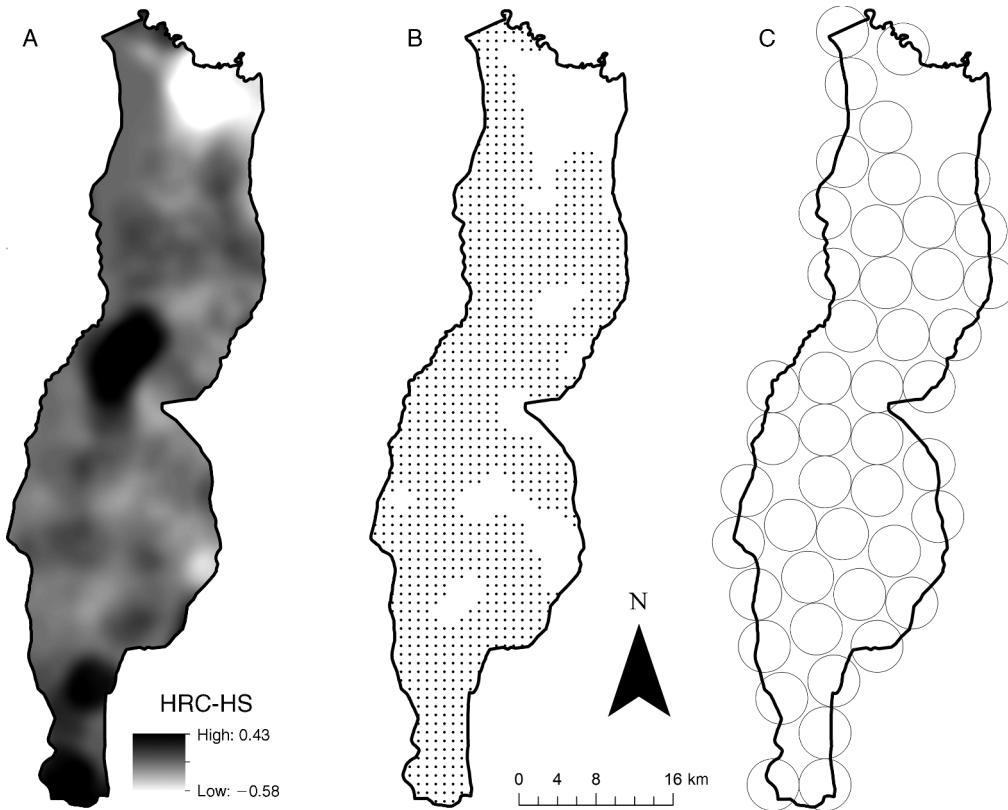


FIG. 6. (A) Bobcat (*Lynx rufus*) HRC-HS map, with highest quality habitats depicted in black and lowest quality habitats depicted in white. (B) Locations (black dots) of pseudo-home ranges in the F1 study area, which identify positions in F1 that have sufficient resources in the surrounding radius to constitute the placement of a 22.7-km² pseudo-home range; the remaining white spaces have insufficient territory resources. (C) Buffered pseudo-home ranges that simulate the actual locations and boundaries of pseudo-home ranges, with one example of a maximum clique of size 46 (the 46 pseudo-home ranges are the gray-outlined circles).

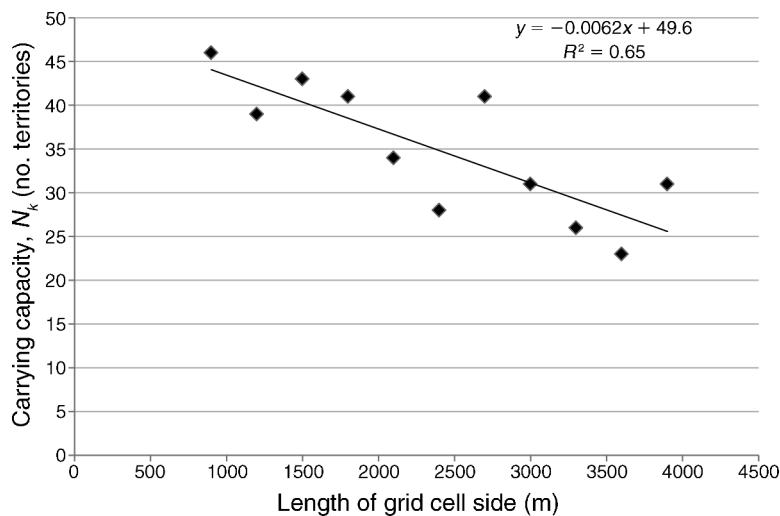


FIG. 7. Sensitivity of bobcat N_k to changes in the scale in which pseudo-home range points are resampled to reduce the total number of points for clique analysis. The x -axis represents one side of a grid cell, where only the point closest to the grid intersection is retained for clique analysis. The figure shows the final N_k estimate as a function of the size of the grid; e.g., for a grid cell of 1500 × 1500 m, the N_k estimate is 43 territories.

Our method builds naturally on methods outlined in Boyce and McDonald (1999) and Larson et al. (2004) in that it begins with an HS map that can be formulated by many different statistical methods and conceptualized at many different spatial scales and ends with an estimate of N_k . However, estimates of N_k via these alternative approaches were 1.4 to >5 times greater than the maximum clique estimate. Approaches that involve calculating the number of animals that a pixel can support (density) and then summing across the map (sensu Larson et al. 2004) are largely aspatial; the spatial arrangement of HS scores on a map is assumed to be unimportant in calculating N_k , such that a pixel contributes to N_k regardless of whether it is clustered near other high-quality pixels (to form a territory) or not. This contributed to the very high estimate of N_k for Ovenbirds ($N_k = 8050$) using the Larson et al. (2004) method compared to the spatially explicit, maximum clique method ($N_k = 236$ territories). These estimates can be made to be more concordant by relaxing the threshold in designating which locations constitute a pseudo territory in the clique analysis (to a threshold lower than 0.76), or by establishing a threshold for inclusion in the Larson et al. analysis (e.g., $N_k = 417$ when only those pixels >0.76 were summed). Our ad hoc method of estimating N_k provided estimates that were up to 1.7 times the maximum clique estimate. Thus, different approaches lead to different estimates of N_k , and each approach has unique assumptions.

Our methods are most similar to the methods used by Downs et al. (2008), who developed HRC-HS maps similar to ours for Sandhill Cranes. They identified all locations in the study area that met the home-range requirements for breeding cranes, and then used an integer programming method to maximize the number of possible breeding locations, under the constraint that the selected territories be at least 3000 m from each other. The clique analysis has the same goal: find the maximum number of territories that can coexist without violating territorial boundaries. Rather than specifying a strict distance separation, we used GIS to place pseudo-home range boundaries across the study area (polygons), and then identified whether any two polygons overlapped or not. The advantage here is that pseudo-home ranges can take on a number of sizes and shapes, and overlap (rather than distance) is part of the selection criteria. Thus, pseudo-home range polygons created under different assumptions (e.g., territory shape, territory size, threshold) can become part of a single analysis. A benefit of using the program Cliquer is that all possible maximum clique combinations are provided in the output (this may be possible with many integer programming packages as well), providing a suite of alternative solutions that can be vetted by decision makers to maximize conservation efforts.

Which method should be employed in estimating N_k depends on the question being asked and the characteristics of the species and landscapes being analyzed.

Computationally simpler approaches, such as the methods of Larson et al. (2004), may suffice as an index of population change over time. For instance, a recent analysis of Breeding Bird Survey trends with respect to HS maps across the Midwestern United States suggests that the Larson et al. (2004) method reasonably tracks fluctuations in bird abundance over time (Bonnot et al. 2011). However, when the population size that a landscape can support is of direct interest, particularly when the spatial arrangement of resources and habitat quality vary substantially across a landscape, the approach we present has considerable advantages.

Sources of uncertainty

Although the estimate of N_k via maximum clique analysis has no sampling error, there are several sources of uncertainty that should be considered to provide a reasonable range of N_k . That is, we recommend conducting assumption and sensitivity analysis with respect to model inputs to obtain a range of N_k estimates. In terms of assumption analysis, for illustration purposes we assumed that territory shape is circular and fixed in size, an assumption that is not strictly upheld in nature. Not only are home range sizes difficult to estimate (Hayne 1949, Odum and Kuenzler 1955), they also change as a function of resource level in both space and time (McLoughlin 2000). Moreover, estimating the nonoverlapping core areas (i.e., defended territory) between individuals is challenging because it requires spatial-temporal habitat-use patterns of nearby individuals; this information is lacking for most species and assumptions must be made about territory size, shape, and minimum resource levels. Our approach can readily test these assumptions, for example, by allowing territory sizes that vary as a function of local resource availability.

Other sources of uncertainty enter the analysis in constructing the HS map, and apply to all methods for estimating population sizes with HS maps. HS maps based on expert opinion require methods for limiting subjective judgment (Ray and Burgman 2006). In contrast, HS maps derived from empirical data, such as the Ovenbird and bobcat maps in this study, are highly dependent on the actual size of the population when the field data were collected and on sample size, to name just two influential factors (Elith et al. 2002). Ecological theory predicts habitat-suitability models constructed from observations when population size is low will be very different than models constructed from observations collected when population size is high (Fretwell and Lucas 1970). Assuming habitats are heterogeneous, at low population sizes individuals will occupy only the best habitats, while at high population sizes the best habitats are monopolized and excess individuals are forced to occupy suboptimal habitat (e.g., Cody 1985, Andren 1990). Moreover, ecological trap theory suggests that organisms may select suboptimal habitat over available, optimal habitat for a

variety of reasons (Robertson and Hutto 2006), resulting in inaccuracies in an empirically derived HS map. Using data from multiple years if available may assist in understanding a realistic range of N_k values.

In addition to these ecological processes, sampling processes play a large role in the precision of coefficient estimates thought to influence animal distribution patterns (Quinn and Keough 2002). As a result of these uncertainties, several authors have incorporated the concept of “bounds” as part of the HS construction process (Burgman et al. 2001) and incorporate them throughout the analytical process (Larson et al. 2004).

Clique analytical considerations

In addition to these biological and sampling uncertainties, our analyses showed that, for any given threshold, N_k is sensitive to the total number of points actually used in the clique analysis, which greatly affects computational speed. As mentioned, the problem of finding maximum cliques in a graph is computationally very difficult. Cliquer uses a branch-and-bound algorithm that relies on a given vertex ordering. The computation time is very sensitive to this ordering. Cliquer applied methods that tend to provide good orderings, but no technique exists for providing an optimal ordering. The expected computation time also increases exponentially as the number of points increases (for fixed edge density). For example, computation time for small clusters of Ovenbird points was negligible (<0.05 s), but considerable for large clusters (e.g., 3.5 days for a 781-point cluster on a 3GHz, 64-bit machine). Similarly, for a fixed number of points, increasing the edge density will on average increase the computation time. Thus, any processing of the data that reduces either of these numbers will speed computation.

We employed several approaches to address limitations in computation time. Breaking the graphs into clusters, which effectively reduces the number of vertices of each graph that Cliquer analyzed, substantially reduced processing time while still yielding the analytically correct solution. Another approach we used was to re-scale the grid to a coarser resolution, thereby reducing the number of vertices in the resulting graph. We believe this approach is reasonable, particularly when home-range size is large compared to the original grid resolution. However, we found evidence of a trade-off between decreased computation speed (resulting from imposing a resampling grid) and the certainty of N_k . Processing speed for fine-resolution grids was much slower, in some cases prohibitively so, but coarse-resolution grids tended to “lose” pseudo-home ranges that were tallied at the finer resolutions. Splitting large clusters into smaller pieces also substantially reduced processing time, but resulted in less certain estimates of N_k . We were able to successfully demonstrate a method for estimating upper and lower bounds on N_k in this approach, however. Parallel programs that run on computer clusters should also be helpful. Another

option would be to implement a hill-climbing algorithm (or some other approximation algorithm). Such an algorithm would not give the maximum clique size but might give useful approximations even for very large problem instances.

Given these limitations, it appears that estimating N_k through maximum clique analysis is best suited for species that occur in clustered distributions (where the problem can be broken into several, smaller problems), or for species with large home ranges where resampling the points to a large grid size can reduce the problem to manageable proportions. For other species, however, it may be most feasible to compute upper and lower bounds only.

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