



Estimating statewide carrying capacity of bobcats (*Lynx rufus*) using improved maximum clique algorithms

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Abstract

Context Maximum clique analysis (MCA) can approximate landscape carrying capacity (N_k) for populations of territorial wildlife. However, MCA has not been widely adopted for wildlife applications, mainly due to computational constraints and software wildlife biologists may find difficult to use. Moreover, MCA does not incorporate uncertainty into estimates of N_k .

Objectives We extended MCA by applying a vertex cover algorithm to compute N_k over a large (92,789

km²), continuous spatial scale for female bobcats (*Lynx rufus*) in Indiana, USA. We incorporated uncertainty by calculating confidence intervals for N_k across five thresholds of habitat suitability using 10 replicate suitability maps from bootstrapped datasets. For portions of the landscape too large to be solved with the vertex cover algorithm, we compared predictions from a linear model and a “greedy” algorithm.

Results Mean estimates of N_k for female bobcats in Indiana across habitat suitability thresholds ranged from 539 (0.75 threshold) to 1200 territories (0.25 threshold). On average, each 12.5 percentile reduction in the suitability threshold increased estimates for N_k by 1.2-fold. Both the predictive and greedy algorithm produced reasonable estimates of maximum cliques for areas that were too large to compute with the vertex cover algorithm. The greedy algorithm produced smaller confidence intervals compared to the predictive approach but underestimated maximum cliques by 1.2%.

Conclusions Our research demonstrates effective application of MCA to species occupying large landscapes while accounting for uncertainty. We believe our methods, coupled with availability of annotated scripts developed in R, will make MCA more broadly accessible to wildlife biologists.

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Introduction

Estimates of carrying capacity provide key information for the management and conservation of wildlife populations (Del Monte-Luna et al. 2004). Carrying capacity for wildlife populations is often defined as the maximum number of individuals a landscape can support (Del Monte-Luna et al. 2004; Ayllón et al. 2012). Understanding carrying capacity can improve management of recovering or reintroduced populations (Hayward et al. 2007; Lyons et al. 2018; Tinker et al. 2021) and control of invasive species (Yokomizo et al. 2009). Population viability analyses rely on carrying capacity to estimate risk of extinction (Beissinger and McCullough 2002; Leasure et al. 2019). Estimates of carrying capacity are pertinent to predict species responses to climate change (Woodworth-Jefcoats et al. 2017) and increases in habitat loss and human expansion (Brown et al. 2018). Knowledge of carrying capacity is also a core tenet of sustainable timber, fisheries, and game harvesting (Hilborn et al. 1995; Clutton-Brock et al. 2002; Mandujano 2007).

Despite the critical information carrying capacity provides for management of wildlife populations, empirical estimation of carrying capacity is challenging for several reasons. Single factors are insufficient to estimate carrying capacity for most species (Del Monte-Luna et al. 2004). Carrying capacity can be influenced by variation in physical components of the environment such as patch size, or cover type (Goss-Custard et al. 2003, Ayllón et al. 2012). Behavioral interactions within a landscape, such as competition and symbiosis, can also affect carrying capacity (Del Monte-Luna et al. 2004; Morris and Mukherjee 2007; Ayllón et al. 2012). Additionally, because environmental conditions are neither temporally nor spatially static, carrying capacity can change dynamically on a seasonal, annual, inter-patch, or inter-landscape basis (e.g. Goss-Custard et al. 2003). Finally, estimating carrying capacity is logistically difficult over large spatial scales (Donovan et al. 2012), yet inference across such larger extents is often the target of agency management efforts (Millsbaugh and Thompson 2011).

Maximum clique analysis (MCA), a branch of mathematical graph theory, has been applied as a promising approach to approximate carrying capacity of populations of territorial mammals and songbirds

(Donovan et al. 2012; Brown et al. 2018). MCA uses data on home-range size and a measure of habitat suitability to predict the maximum potential number of non-overlapping territories that a landscape can support (Donovan et al. 2012). The resulting metric of landscape carrying capacity (N_k) only includes the portion of the population that is territorial; however, it is a reasonable proxy for carrying capacity when resources within territories are tied to reproduction and survival at the population level. Examples include previous work on territorial male ovenbirds (*Seiurus aurocapilla*) during the breeding season (Donovan et al. 2012; Brown et al. 2018) and female bobcats (*Lynx rufus*, Donovan et al. 2012). An advantage of N_k is that it can be computed from predictive landscape maps based on probabilities of habitat suitability, selection, or occupancy for respective species (Donovan et al. 2012; Brown et al. 2018). Thus, N_k can be estimated from data on species locations and landscape variables typically collected to inform management efforts and modeled using established statistical approaches (Manly et al. 2002; MacKenzie et al. 2006; Guisan et al. 2017).

Despite the potential value of MCA for wildlife conservation and management, to our knowledge only two published studies have applied the methodology (Donovan et al. 2012; Brown et al. 2018). One barrier of MCA for widespread use in wildlife studies is the lack of pre-compiled, ready-to-use software for natural resource scientists who rely on popular commercial operating systems such as Microsoft Windows™. The software ‘Cliquer’ (Niskanen and Östergård 2003), used to conduct maximum clique analysis in previous studies (Donovan et al. 2012; Brown et al. 2018), was developed on Linux and requires some understanding of C and Linux.

Another barrier to adoption of MCA is that computational constraints limit calculations when the possible combinations of the maximum number of non-overlapping territories (maximum cliques) within a landscape is high (class of intractable problems, Garey and Johnson 1979). This is a common occurrence for MCA applied to large continuous areas of high-quality habitat relative to the focal species’ territory size. Donovan et al. (2012) compared two approaches for circumventing this barrier when estimating ovenbird and bobcat N_k in a 1153 km² area in western Vermont. First, they decreased the spatial resolution of predictive landscape maps, thereby

reducing the number of maximum cliques to be calculated. Second, they calculated the maximum territories in smaller, isolated areas and then added up the total number of territories from smaller areas across the larger landscape. However, large landscapes may still contain isolated areas of territories that are too large to compute using MCA (Donovan et al. 2012). Moreover, many large areas (> 50,000 km²) such as states, provinces, and even countries manage wildlife within their borders as single populations of species and according to specific aims (Millspaugh and Thompson 2011). Estimating N_k for species over the large continuous scales of these management units could provide important information to improve current practices and plan for future management scenarios.

Estimates of precision for N_k over large scales should incorporate uncertainty arising from multiple sources. Confidence intervals for N_k based on appropriately propagated uncertainty are critical if estimates will be used to guide management or conservation decisions (e.g. Clutton-Brock et al. 2002; Hayward et al. 2007; Mandujano 2007; Lyons et al. 2018; Tinker et al. 2021). Thus, careful consideration of sources of uncertainty is warranted. Variation in N_k can arise from sampling error in the two types of data inputs required for its estimation, thresholds of habitat suitability and predictive maps. Decreasing habitat thresholds results in higher values for N_k because a higher proportion of the landscape is suitable, permitting a larger number of territories to occupy the same space (Donovan et al. 2012; Brown et al. 2018). Uncertainty in estimates of N_k also arises from predicting habitat suitability, selection, or occupancy for the focal species using statistical models. Beyond data inputs, additional uncertainty can arise if indirect estimates of maximum cliques are used for isolated areas containing so much suitable habitat that numerical computation of the possible number of non-overlapping territories is infeasible.

Bobcats (*Lynx rufus*), like many other mammalian carnivores, present difficulties to estimation of carrying capacity because they tend to be secretive, solitary, and occupy large home ranges (Andersen and Lovallo 2003; Ripple et al. 2014). Large-scale conversion of forests for agricultural use and overexploitation after European settlement (1840–1940s) led to widespread bobcat declines and local extirpations in the midwestern U.S. (reviewed in Johnson et al.

2010). A small remnant population of bobcats began to recover in forested areas of south-central Indiana in the late 1990s (Johnson et al. 2010; Jones et al. 2020). Nonetheless, habitat modifications for agricultural use and human development since their near extirpation appear to represent substantial and unfavorable changes to bobcat habitat in Indiana (Woolf et al. 2002; Martin et al. 2008; Tucker et al. 2008). Thus, bobcat management decisions rely on (1) understanding which remaining habitat in Indiana is suitable and (2) estimating how many territories habitat could provide statewide. Similar challenges are faced by managers in neighboring states and throughout the species' geographic range. Estimates of carrying capacity are particularly crucial when bobcat populations are subjected to harvest (e.g. Jacques et al. 2019).

We extended the approach pioneered by Donovan et al. (2012) and Brown et al. (2018) to compute N_k over large, continuous spatial scales while explicitly incorporating multiple sources of uncertainty in N_k . Our objectives were to (1) create user-friendly R scripts to conduct maximum clique analysis for any scale, (2) predict the maximum number of cliques for areas where direct calculation was infeasible due to computational constraints, and (3) quantify, propagate, and incorporate error of predicted and calculated maximum cliques into estimates of N_k . We apply our approach to bobcats in the state of Indiana, U.S.A.

Methods

Background, maximum clique analysis

Maximum clique analysis enables estimation of N_k , the maximum potential number of territories that a landscape can support, by combining data on (1) home-range size and (2) landscape maps of habitat suitability, selection, or occupancy (Donovan et al. 2012; Brown et al. 2018). We illustrate this process with two examples of landscapes containing two (Fig. 1a–d), and four maximum cliques (Fig. 1e–h), respectively (see also Donovan et al. 2012).

Each pixel in the landscape map is assigned a value predicted by a statistical habitat model fitted to covariates, with a response ranging from 0 to 1. The landscape map is then combined with information on home-range size to create a map

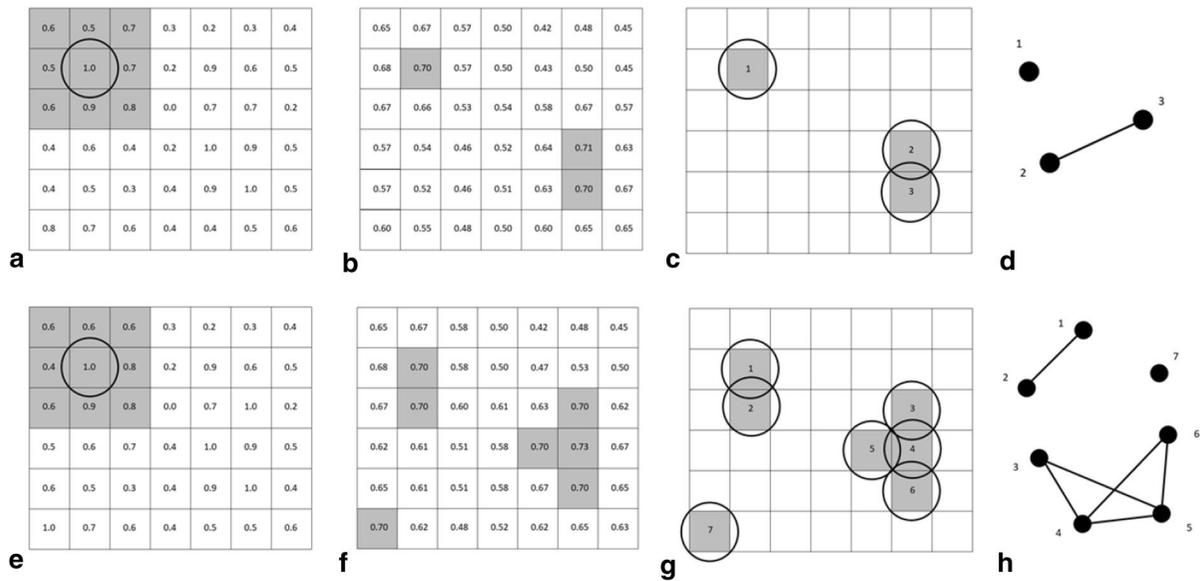


Fig. 1 Two examples of the procedure for converting raster maps of landscape probability (habitat suitability, occupancy, habitat selection) of a territorial species for maximum clique analysis using a vertex cover algorithm. Landscape templates are raster files with cells containing a probability value from 0 to 1. The landscape map is converted to a map of home-range capacity by buffering each pixel in the landscape map by a circular moving window the size of the home range of the target organism (**a** and **e**). Values are averaged within the circular window and the resulting value is assigned to the central pixel, representing the capacity of the area surrounding the central pixel to support a territory (**b** and **f**). Next, threshold

of home-range capacity. Home-range capacity is obtained by buffering each pixel in the landscape map by a circular moving window the size of the home range of the target organism (Fig. 1a and e). Pixel area is always smaller than home range size. Values are averaged within the circular window and the resulting value is assigned to the central pixel, representing the capacity of the area surrounding the central pixel to support a territory (Fig. 1b and f). Next, threshold values for suitability are chosen among home-range capacity values (0.7 in Fig. 1b and f) as potential territories ('pseudo home ranges') across the landscape. Pixels with home-range capacity values below the suitability threshold are deemed unable to support territories and ignored. Pixels with home-range capacity values \geq the threshold are classified as pseudo home ranges and buffered by circles the size of a home range (Fig. 1c, g). Each pseudo home range is then

values for suitability are chosen among home-range capacity values (0.7 in **b** and **f**) as potential territories ('pseudo home ranges') across the landscape. Pixels with home-range capacity values \geq the threshold are classified as pseudo home ranges and buffered by circles the size of a home range (**c**, **g**). Pseudo home ranges are then converted from a spatial location to a point in a mathematical graph and numbered (**d**, **h**). Overlapping pseudo home ranges (points) are connected by edges (lines, **d**, **h**). The maximum clique size is then calculated by subtracting the smallest set of pseudo home ranges that overlap with the rest of the graph from the total number of vertices (two in **d** and four in **h**)

converted from a spatial location to a point in a mathematical graph and numbered (Fig. 1d, h).

Previous studies (Donovan et al. 2012; Brown et al. 2018) used a branch and bound algorithm (Niskanen and Östergård 2003) in which non-overlapping pseudo home ranges are connected by line segments (edges) in the graph. The maximum number of pseudo home ranges (maximum cliques) is then determined as the largest number of non-overlapping territories that can co-exist in the same landscape, which corresponds to finding the maximum size clique of the graph. A challenge with this approach for large domains is that most pairs of pseudo home ranges are non-overlapping over large continuous areas, so the graphs have an extremely large number of edges. Thus, we adopted a vertex cover approach to find the maximum clique and build a graph where only the overlapping home ranges are treated as line segments (edges, Fig. 1d, h). A minimum vertex

cover algorithm (Cormen et al. 2009) finds the smallest set of pseudo home ranges that overlap with the rest of the graph. Intuitively, this involves finding the smallest set of vertices that could not be non-overlapping pseudo home ranges. Because this is the smallest set possible, all the vertices left over are exactly the maximum number of non-overlapping pseudo home ranges. The maximum clique size is then calculated by subtracting these from the total number of vertices (two in Fig. 1d and four in Fig. 1h).

Study design

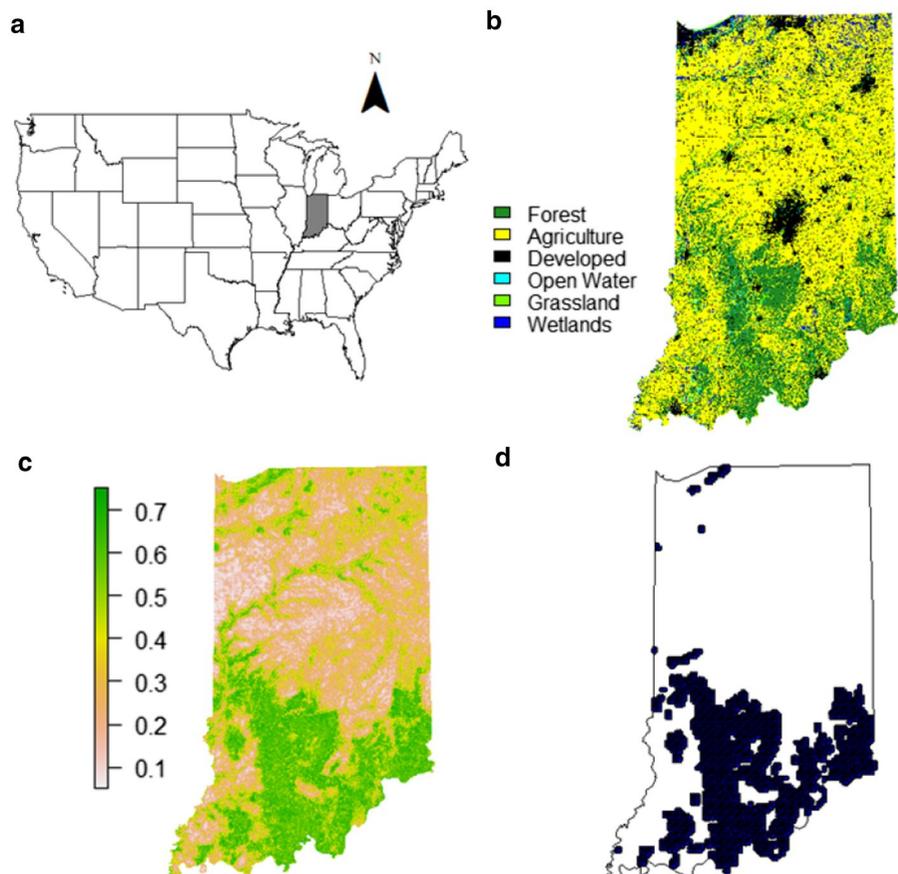
We address our three objectives by analyzing bobcat location data on a large scale encompassing the entire state of Indiana (92,789 km²) in the U.S. We used a statewide habitat suitability map to estimate N_k for bobcats in Indiana (Online Appendix A). We created scripts in R version 3.5.3 (R Development Core Team 2018) to test the feasibility of two algorithms (vertex cover and greedy) to compute maximum cliques

(objective 1). For areas of the state where computation of maximum cliques was infeasible with the vertex cover algorithm, we used a linear model to predict maximum cliques (objective 2). We then compared results of predictions to results from an algorithm that permitted computation of large maximum cliques through a greedy selection strategy (Butenko et al. 2009). To quantify uncertainty, we incorporated the resulting prediction error from the linear model in the statewide estimates of N_k (objective 3). We also created 10 alternate habitat suitability maps from bootstrapped data to quantify uncertainty in estimates of maximum cliques derived from predictions from the statistical model of habitat suitability (objective 3).

Study area

Indiana is located in the midwestern U.S. (Fig. 2a). The landscape is dominated by agriculture (mainly corn and soybeans), which is more concentrated in the northern half of the state (Fig. 2b)

Fig. 2 Map of the United States, highlighting the state of Indiana in grey (a) where landscape carrying capacity (N_k) was estimated for bobcats (*Lynx rufus*). Map of major habitat types for bobcats in Indiana (b). Predictive map for habitat suitability of bobcats in Indiana (c). Portion of Indiana exhibiting overlapping pseudo home ranges for the median threshold of habitat quality for maximum clique analysis (d)



and represents 61.8% of the state by cover type (National Land Cover Database for 2016, Homer et al. 2020). Forest areas are dominated by deciduous hardwood trees, represent 22.9% of the state, and are concentrated in the southern half of Indiana (Fig. 2b). Developed areas, wetlands, open water, and grasslands comprise the remaining cover types (10.4%, 2.5%, 1.4%, and 1.0%, respectively, Fig. 2b).

Data collection and creation of statewide habitat suitability map

We constructed a statewide habitat suitability map for bobcats using 236 point locations from multiple sources acquired between 2010 and 2020. Points included observations reported by bow hunters from 2010 to 2017 ($n=57$), known bobcat mortality locations (excluding road mortalities) between 2010 and 2019 ($n=122$), and additional points from 2017 to 2020 using images captured on game cameras ($n=57$) from various sources (see Online Appendix A). We selected eight predictor variables, including proximity to major roads and proportion of natural habitat (a metric of habitat composition), as well as proximity to six habitat types (forest, agriculture, grassland, developed areas, wetlands, open water), based on available habitat types in Indiana (Jones et al. in press) and findings from other bobcat studies (Woolf et al. 2002; Andersen and Lovallo 2003; Tucker et al. 2008). To estimate statewide habitat suitability for bobcats, we fit an ensemble of small models (ESM) in the Ecospat package in R (Di Cola et al. 2017), due to the low numbers of bobcat observations across the state in our data set for this widespread but secretive carnivore. We obtained importance values and created partial dependence plots for each predictor from output of the final ESM model (Online Appendix A, Fig. S1). We then applied predictions from our ESM to each pixel across Indiana to create a raster map of expected habitat suitability scores, with pixel values ranging from 0 to 1 (Fig. 2c). The resulting spatial map served as our template for statewide home range capacity (see below) in maximum clique analysis (Fig. 2c). Additional details are provided in Online Appendix A.

Maximum clique analysis: general approach

To estimate N_k for bobcats at each scale of our study, we followed the general approach of Donovan et al. (2012), using the steps outlined in Fig. 1. Our goal was to estimate N_k for female bobcats, because the number of females limits reproduction and population growth in this species (Andersen and Lovallo 2003). Additionally, females tend to establish territories based on the smallest area that contains sufficient resources for survival and rearing of offspring, whereas males establish larger territories to improve access to multiple females for mating (Andersen and Lovallo 2003). To estimate N_k for female bobcats across the state, we first converted our raster of predicted habitat suitability into a home-range capacity raster. We applied a moving window analysis centered on each pixel (Fig. 1a and e) with the ‘focal statistics’ tool in ArcMap 10.5.1. We used the median home range of females (radius=2575 m) as the circular moving window, calculated from radio telemetry data at a study site in south-central Indiana (see Jones et al. 2020). Next, we determined habitat suitability thresholds for potential home ranges (hereafter pseudo home ranges) to develop the map of home-range capacity (Fig. 1b and f). We used five threshold levels based on quantile values (25, 37.5, 50, 62.5, 75%). Respective quantiles represented values for modeled habitat suitability from the statewide map of home-range capacity extracted from cells at the 236 bobcat locations used to construct the suitability model (Online Appendix A). For pixels that met selected thresholds, we created circular buffers the size of median home-range values for females to represent pseudo home ranges for female bobcats (Fig. 1c, g). To compute the maximum number of pseudo home ranges (cliques) that a landscape can hold (N_k), we converted these pseudo home ranges to points in a mathematical graph, and numbered them (Fig. 1d, h). We then created a matrix of non-overlapping polygons for pseudo home ranges and calculated the maximum number of non-overlapping polygons (cliques) for respective landscapes or areas.

Statewide estimates of N_k

Processing limits can make it infeasible to compute the maximum number of cliques (territories) a landscape can support when the number of overlapping

pseudo home ranges is high (Donovan et al. 2012). We encountered this limitation in our analyses and applied two solutions proposed by Donovan et al. (2012). First, we increased the pixel size (decreased the resolution) of home-range capacity rasters to decrease the number of overlapping pseudo home ranges for calculation of maximum cliques (Donovan et al. 2012). This method is particularly useful for species with large home ranges that cover a large number of pixels at fine scales, such as bobcats (Donovan et al. 2012). We found the lowest number of overlapping pseudo home ranges for the highest number of maximum cliques with pixel sizes of 2700 m² for the statewide scale (Online Appendix A, Table S3). Second, we broke our landscapes into multiple isolated clusters of overlapping pseudo home ranges and added together the maximum cliques for each cluster instead of considering the landscape as one large cluster (Donovan et al. 2012). We created a custom script in program R to automate and modify the above processes to prepare data for computation in maximum clique analysis (Supporting Information). We used a vertex cover function coded in Java (JDK version 11.0.8) to calculate maximum cliques for bobcats in Indiana (branch and reduce algorithm, Akiba and Iwata 2016). The vertex cover function was incorporated into the R script in Supporting Information via the rJava package (Urbanek et al. 2016).

Even after applying the two solutions proposed by Donovan et al. (2012), i.e., decreasing resolution and breaking the landscape into isolated clusters, 15 of 55 statewide rasters of home-range capacity (see objective 3) contained a single cluster with too many overlapping pseudo home ranges (3039–3825) to feasibly compute maximum cliques using the vertex cover algorithm. For these clusters, we predicted the number of maximum cliques from a model fitted to smaller clusters. Specifically, we fit a linear model to known numbers of maximum cliques as a function of number of overlapping pseudo home ranges in a cluster. We then used the ‘predict’ function to predict maximum clique values.

Additionally, we applied an algorithm designed to find maximum cliques quickly that permitted computation of even the 15 largest clusters in our data set (greedy algorithm). This algorithm greedily builds an independent set (Cormen et al. 2009) in the graph where edges indicate overlap of home ranges, which

identifies a clique in the graph of non-overlapping home ranges. At each step, the algorithm checks for isolated or simplicial vertices, which must appear in any independent set, i.e., these are vertices whose 1-edge neighborhoods form a clique (Butenko et al. 2009). Adding these vertices to the independent set, the algorithm then greedily selects another vertex to add to the independent set based on the distance to the existing independent set. One reason for this is that new sets of pseudo home ranges should be nearby existing sets, but away from any overlap. The drawback of this algorithm, however, is that the maximum cliques it finds are often not the largest (maximum) clique for the entire cluster (Butenko et al. 2009). We compared maximum clique results from a range of clusters (>110 to <3200 pseudo home ranges, N=117) computed with the vertex cover algorithm to results for the same clusters with the greedy algorithm to determine if it could serve as an adequate proxy when maximum cliques cannot be computed with the vertex cover algorithm. We also compared the greedy algorithm to our linear predictions. An additional script in R to run the greedy algorithm to compute maximum cliques through Julia (version 1.6.1) via the JuliaCall package (Li 2019) is also available in Supporting Information.

Quantifying uncertainty in statewide estimates of N_k

Uncertainty in our estimates of N_k for statewide bobcats stemmed from at least two sources. The first source included sampling uncertainty when fitting the ESM to create the map of home-range capacity. We quantified sampling-induced uncertainty by drawing 10 bootstrap samples of presence and background points statewide. For each bootstrap sample, we refit the ESM of habitat suitability, used the resulting model to create predictive landscape rasters, converted predictive landscapes to home-range capacity rasters, and calculated N_k . Mean and standard error (SE) of N_k were computed from bootstrap estimates. For each bootstrapped landscape, we also explored sensitivity of N_k to the choice of habitat thresholds at the statewide scale. We limited creation of bootstrapped landscapes to 10 due the computing time required to replicate ESM models, predict results to landscapes, and compute vertex cover algorithms for MCA.

A second source of uncertainty in estimates of N_k was associated with predicting maximum cliques for clusters of overlapping pseudo home ranges so large that direct computation was infeasible for the vertex cover algorithm. We quantified prediction uncertainty for each bootstrap sample by computing standard errors of prediction for each overly large cluster using the ‘predict’ function for our linear model. Components of variation in N_k from sampling were then added to the mean variation from prediction computed across bootstrap samples to yield an overall estimate of variance in N_k .

Results

Statewide habitat suitability

The final ensemble of small models (ESM) for habitat suitability of bobcats across Indiana produced an AUC (area under the curve) value of 0.83. Proportion of natural habitat within 4 km, distance to forest, and distance to agriculture were the highest-ranked variables by importance value (Online Appendix A, Fig. S1a). Proportion of natural habitat, the variable with the largest importance value, exhibited peak suitability at intermediate values of 0.4–0.7 (Online Appendix A, Fig. S1b). Distance to forest showed peak suitability within forested habitat and < 1 km from forest edge, with a steep decline in suitability outside of forest (Online Appendix A, Fig. S1c). Distance to agriculture exhibited peak suitability 200–500 m outside of agriculture (Online Appendix A, Fig. S1d). Additional results are provided in Online Appendix A.

Statewide estimates of N_k

We used the vertex cover algorithm successfully to compute N_k of female bobcats in Indiana for the majority (three of five) of habitat thresholds. Predicted values for the statewide habitat suitability map based on ensembles of small models (ESM, see Online Appendix A) included 30 m pixel values that ranged from 0.05 to 0.77. The map of home-range capacity, representing values for surrounding resources based on the habitat suitability map, included estimated 30 m pixel values that ranged from 0.08 to 0.66. At the median threshold for home-range capacity (0.57), 16,424,230 pixels met the criteria to

be pseudo home ranges. The number of pixels that were classified as pseudo home ranges was reduced to 2828 after resampling the home-range capacity landscape from 30 to 2700 m². The resulting pseudo home ranges occupied 27 isolated clusters ranging from 2 to 1973 overlapping pseudo home ranges, with a mean \pm SE of 105 ± 74 (Fig. 2d). Computed and predicted maximum cliques for these clusters ranged from 1 to 543, with an N_k estimate of 797 potential female bobcat territories across Indiana at the median threshold.

Only two of five habitat thresholds contained large clusters (3039–3825 pseudo home ranges) that could not be computed with the vertex cover algorithm. However, large clusters for suitability maps at these two thresholds (25%, 37.5%) contained approximately 88% and 89%, respectively, of the total pseudo home ranges at the statewide scale (Table 1). Suitability maps (statewide map and 10 replicates from bootstrapped data) contained 11 large clusters (one per map) for the 25% habitat threshold, but only contained 4 large clusters across maps for the 37.5% threshold (Table 1). Thus, of 55 total maps representing all combinations of 5 thresholds per 11 maps, only 15 (27.3%) contained clusters that could not be computed with the vertex cover method and required prediction of maximum cliques from a linear model based on the number of pseudo home ranges per cluster. Maximum cliques exhibited a strong positive linear relationship with the number of pseudo home ranges per cluster (vertex cover maximum cliques = $2.03 + 0.27$ (pseudo home ranges), $F_{1,451} = 734,200$, $P < 0.001$) with a high adjusted R^2 value (0.999, Fig. 3a). Maximum cliques from predicted clusters ranged from 835 to 1064 (Fig. 3a).

Maximum cliques for large clusters ($N = 15$) computed with the greedy algorithm ranged from 792 to 1009, an average of 4.8% lower than results for predicted clusters. In comparisons between the same clusters computed with the vertex cover and greedy algorithms ($N = 117$), the slope and intercept differed from 1 ($t_{115} = 22.6$, $P < 0.0001$) and 0 ($t_{115} = -3.44$, $P = 0.0001$), respectively. Nonetheless, the magnitude of differences was small, and greedy results underestimated vertex cover results by only 1.2% (vertex cover maximum cliques = $-0.76 + 1.02$ (greedy maximum cliques), $F_{1,115} = 2,057,000$, $P < 0.001$, adj $R^2 = 0.999$, Fig. 3b).

Table 1 Ranges and means of large clusters (3039–3825 pseudo home ranges, PHR) across five thresholds of home-range capacity for bobcats (*Lynx rufus*) in Indiana, U.S.A.

Quantiles for suitability thresholds	Number of clusters		Pseudo home ranges		
	Total	Mean	Range per cluster	Mean PHR	% of total
25.0	11	1	3674–3866	3747.5	87.7
37.5	4	0.36	3033–3103	3064.0	89.3
50.0	0	0	NA	NA	0.0
62.5	0	0	NA	NA	0.0
75.0	0	0	NA	NA	0.0

Thresholds were chosen at specified quantiles for modeled values of habitat suitability extracted from 236 statewide presence locations. Each threshold represents data combined from 11 maps of home-range capacity (statewide map and 10 replicates from bootstrapped data). Combined data represents a total for all thresholds (Total), ranges of values (Range per cluster), or mean values per landscape (Mean, Mean PHR, % of Total). Values for the number of pseudo home ranges per cluster by threshold include the range per cluster, the mean of pseudo home ranges across large clusters per landscape (Mean PHR), and the percent of pseudo home ranges in large clusters divided by the total pseudo home ranges per landscape (% of Total)

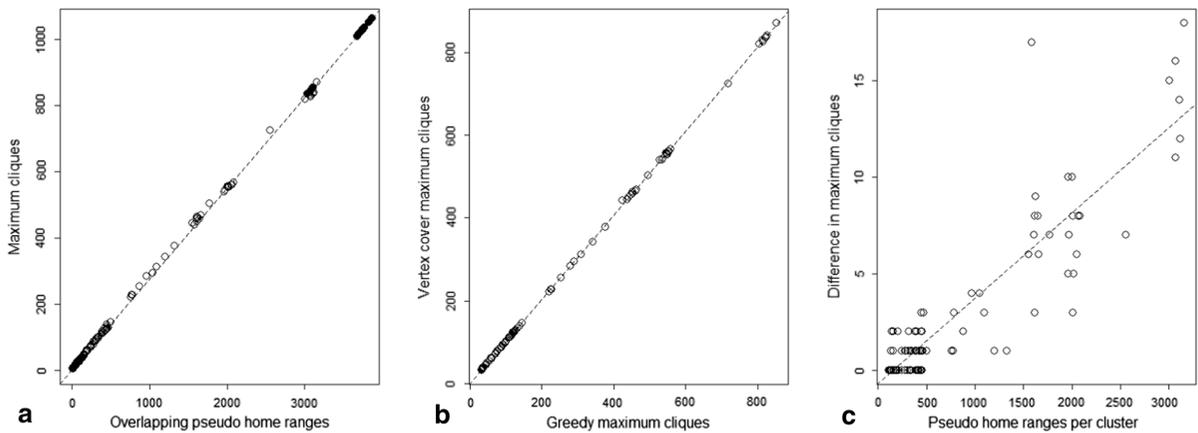


Fig. 3 Relationship between maximum clique values computed by the vertex cover and the number of pseudo home ranges per cluster ($\text{adj } r^2=0.999, P<0.001$) used to estimate landscape carrying capacity (N_k) for bobcats (*Lynx rufus*) in Indiana, U.S.A. (a). Clusters too large for computation (≤ 3158 pseudo home ranges) were predicted by this linear relationship

and are represented by filled in circles. Relationship between maximum cliques computed by the vertex cover and greedy algorithms (b, $\text{adj } r^2=0.999, P<0.001$). Relationship between the difference in maximum clique values computed by the vertex cover and greedy algorithms and the number of pseudo home ranges per cluster (c, $\text{adj } r^2=0.831, P<0.001$)

Greedy results diverged from vertex cover results as the number of pseudo home ranges per cluster increased (difference in vertex cover and greedy maximum cliques = $-0.69 + 0.0044(\text{pseudo home ranges})$, $F_{1,115} = 570.1, P<0.001, \text{adj } R^2=0.831$, Fig. 3c). Thus, an increase of 1000 pseudo home ranges increased the expected difference in maximum clique values between the two algorithms by 4.4. Observed divergence never exceeded 20 maximum cliques (Fig. 3c).

Quantifying uncertainty in statewide estimates of N_k

Mean estimates of N_k for female bobcats in Indiana varied across suitability thresholds, ranging from 539 (75.0% threshold) to 1200 (25.0% threshold, Fig. 4). Suitability thresholds (25.0%, 37.5%, 50.0%, 62.5%, 75%) for home-range capacity were 0.50, 0.55, 0.57, 0.59, and 0.60, respectively. Each 12.5 percentile reduction in the suitability threshold increased estimates for N_k by 1.2-fold on average (Fig. 4). Uncertainty, expressed as 95%

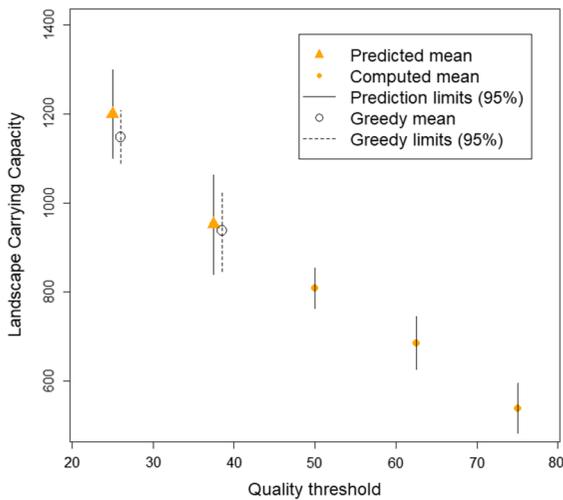


Fig. 4 Maximum clique values (landscape carrying capacity, N_k) at five thresholds of habitat quality for bobcats (*Lynx rufus*) in the state of Indiana, U.S.A. Means and confidence intervals include 15 large clusters (> 3000 pseudo home ranges) for the 25.0% and 37.5% thresholds that were either predicted from a linear regression equation (Predicted) or computed using an algorithm that tended to underestimate true values for maximum cliques (Greedy). Means for the remaining thresholds (50%, 62.5%, 75%) did not require prediction of large clusters (Computed). Quality threshold represents quantiles for modeled values of habitat suitability extracted from 236 statewide presence locations. Results for the greedy algorithm are offset to differentiate from predicted results

prediction intervals, was largest at the lowest habitat suitability thresholds (25.0%, 37.5%, Fig. 4). Averaged across the two relevant thresholds (25.0%, 37.5%), the standard error for computed clusters (38.3) was greater than the standard error for predicted clusters (15.6) and represented 71.1% of the total error (Table 2). Of the two sources of uncertainty for prediction of large clusters, the standard error from estimating landscape suitability on average for the same thresholds was almost three times greater than the standard error associated with prediction (Table 2). Large clusters were only predicted for the 25.0% and 37.5% thresholds and thus, compared to the greedy algorithm only at these two thresholds. Confidence intervals at these two thresholds computed with the greedy algorithm were 38.1% and 18.9% smaller compared to those predicted with the linear model (Fig. 4).

Table 2 Components of uncertainty (SE) associated with landscape carrying capacity (N_k) estimated for 10 replicate landscapes from bootstrapped data across five thresholds of home-range capacity for bobcats (*Lynx rufus*) in Indiana, U.S.A.

Quantiles for suitability thresholds	Computed clusters SE_C	Predicted clusters		All clusters $SE_C + SE_B + SE_P$
		SE_B	SE_P	
25	30.4	16.7	3.8	50.9
37.5	46.2	9.2	1.5	56.9
50	23.4	NA	NA	23.4
62.5	30.4	NA	NA	30.4
75	28.6	NA	NA	28.6

Maximum cliques were computed for clusters < 3000 pseudo home ranges (Computed Clusters) and predicted using a linear model for clusters > 3000 pseudo home ranges (Predicted Clusters). SE of pseudo home ranges for computed clusters (SE_C) was estimated from bootstrapped samples. For pseudo home range estimates obtained by prediction, SE had components due to bootstrap variation (SE_B) and due to prediction with a linear model (SE_P). Thresholds represent quantiles for modeled values of habitat suitability extracted from 236 statewide presence locations

Discussion

Maximum clique analysis is an underappreciated approach to addressing the important challenge of estimating carrying capacity (Chapman and Byron 2018). Our results for bobcats in Indiana highlight how this approach can be extended to populations with a large number of prospective home ranges while explicitly accounting for uncertainty, thus improving its utility for applications to other wildlife species. For clusters of pseudo home ranges too large to compute we devised and validated two solutions. Tradeoffs between our predictive linear approach and greedy algorithm would determine which is best for future applications. Predictions or computations with the greedy algorithm for large clusters may be required to estimate N_k for populations of species that are harvested or of conservation concern within large geopolitical boundaries of management (Millsaugh and Thompson 2011). We also incorporated estimates of uncertainty from two sources to compute confidence intervals for our estimates of N_k for bobcats across Indiana. Upper and lower bounds of confidence intervals for N_k provide important information on the limits of our data to predict potential

carrying capacity of a landscape for a given population and species (Donovan et al. 2012; Brown et al. 2018). Finally, we created and provide R scripts (Supplementary Information) to improve the availability and convenience of maximum clique analysis for future users. Our results for bobcats provide important insights to improve adoption of maximum clique analysis to inform management and conservation efforts for other species.

The lack of user-friendly tools for natural resource scientists has been a barrier to more widespread use of maximum clique analysis. Although the software ‘Cliquer’ (Niskanen and Östergård 2003) used in previous studies (Donovan et al. 2012; Brown et al. 2018) is a branch and bound algorithm that has been optimized to conduct maximum clique analysis, it requires some experience with C and Linux. Alternatively, the R programming language (R Development Core Team 2018) provides a freely accessible software platform that is popular with wildlife researchers (Bolker 2008). The ‘igraph’ package in R (Csardi 2019) is capable of calculating maximum cliques; however, in our study it had difficulty with clusters > 105 pseudo home ranges. Our coding scripts (Supporting Information) to conduct maximum clique analysis using the vertex cover, greedy, and prediction approaches can be modified for use with other species. The scripts require an input map of either habitat suitability (Donovan et al. 2012), probability of occupancy (Brown et al. 2018), or probability of habitat selection that has been converted to a habitat-capacity raster. The scripts include code for methods to improve computation and speed of maximum clique analysis developed by Donovan et al. (2012, reducing raster resolution, breaking landscapes into isolated clusters) and for predicting max cliques of large clusters infeasible to compute via the vertex cover algorithm.

Computation of N_k may be infeasible at large scales where management and conservation decisions are often made such as states, provinces, regions, and countries (Millsbaugh and Thompson 2011). Timely management decisions in the absence of high-quality or population data (e.g. Murphy and Noon 1991) may require estimating maximum cliques for areas within such large landscapes rather than calculating them. A simple linear model based on the number of pseudo home ranges yielded high precision (based on r^2 values), permitting prediction of the number of

maximum cliques for bobcats in Indiana. Precision was high within clusters; however, the main caveat of this method is the assumption that the linear relationship remains unchanged when extrapolating outside of our data for large clusters. It is reasonable to expect this predictive approach can extend to estimating N_k for other species. Predictions for large clusters may also be required to estimate N_k for populations of species that occupy large geographic areas at low densities, such as predatory mammals (carnivores, Dalerum et al. 2009) and birds (raptors, McClure et al. 2018).

The greedy algorithm often underestimated true values for maximum cliques compared to the vertex cover algorithm. Underestimation likely occurred because the greedy algorithm finds local maxima that are not always the maximum clique if the entire cluster were considered simultaneously. Despite this drawback, the greedy algorithm applied to bobcats provided an excellent proxy for the vertex cover algorithm and underestimated true values for maximum cliques by only 1.2%. The greedy algorithm also improved precision of maximum clique estimates relative to linear predictions. The strong performance of the greedy algorithm was aided by a bobcat data set that required computation of only 15 clusters just outside of the range of capabilities for the vertex cover algorithm. The problem of underestimation for the greedy algorithm increases with cluster size, hence, the negative bias of maximum clique estimates will increase accordingly. Predicting maximum cliques with our linear approach may be more advantageous compared to the greedy algorithm for clusters of extreme sizes.

If a “quick-and-dirty” estimate of N_k is sufficient, the rapid calculation time typical of the greedy algorithm provides an additional advantage for its use. In our experience, it typically finished computations for even the largest clusters in a few minutes compared to 30–60 min required by the vertex cover method for the same clusters. Despite its limitations, assessing the utility of the greedy algorithm for maximum clique analysis seems a promising avenue of future study. Such powerful computation approaches are needed because computing power often limits maximum clique analyses in large continuous areas, or when home range sizes are small compared to landscape extent (Donovan et al. 2012; Brown et al. 2018).

Accounting for uncertainty in proxy measures of population estimates such as N_k is critical to managing wildlife populations (Williams et al. 2002). To capture effects of uncertainty in maximum clique analysis, Donovan et al. (2012) recommended conducting sensitivity analyses with input variables (quality thresholds, territory size) to determine a range of estimates of N_k but also acknowledged uncertainty in statistical models used to construct habitat suitability maps. Uncertainty in spatial models can arise from multiple sources, including natural variation, measurement error, systematic error, and sample size (Elith et al. 2002). One way to deal with uncertainty in habitat maps is to create upper and lower bounds (Burgman et al. 2001), which can then be used to produce three maps based on mean, upper, and lower suitability values for further analyses (e.g. population viability analysis, Larson et al. 2004). We quantified uncertainty in habitat suitability and selection maps instead using a bootstrap approach (Elith et al. 2002), creating 10 replicate maps from resampled data. We propagated this uncertainty in landscape predictions and added them to prediction uncertainty for large clusters to calculate overall prediction intervals for estimates of N_k for bobcats in Indiana. Accounting for and propagating uncertainty in proxy measures for population estimates such as N_k provides high and low estimates for animal populations, which are useful for making sustainable management decisions compared to the mean (Burgman et al. 2001; Milner-Gulland and Akçakaya 2001). When managing for populations of harvested animals, estimates of N_k can provide guidance for numbers of harvest permits consistent with harvest objectives (Williams et al. 2002). Estimates of N_k also can help quantify targets to restore or improve strategic habitat for species of conservation concern (Johnson et al. 2009).

Caveats and conservation implications

Although maximum clique analysis provides estimates of landscape carrying capacity (N_k), this metric is not synonymous with population estimates, nor do its assumptions always hold. For bobcats in Indiana, our estimates did not include non-territorial (typically dispersing) individuals or territorial males. MCA can be sensitive to territory size (Brown et al. 2018) and assumes no territory overlap (Donovan et al. 2012). Home-range sizes for female bobcats can differ

from 0.99 to 42.70 km² across studies (reviewed in Ferguson et al. 2009), showing patterns by latitude and ecosystem productivity (Andersen and Lovallo 2003; Ferguson et al. 2009). Additionally, females may share home ranges in highly productive systems (Cochrane et al. 2006), or when space is limited, such as on islands (Diefenbach et al. 2006). Hence, MCA likely provides conservative estimates of N_k for bobcats that can provide comparisons across populations throughout the range of this species because MCA estimates are tied to respective landscapes (Donovan et al. 2011; Brown et al. 2018).

Our bobcat case study aligns well with results from previous studies and has important implications for the broad applicability of clique analysis as an approach for estimating carrying capacity. The predictors that our ESM identified (Online Appendix A) as related to bobcat habitat quality conform with inference from numerous studies, such as the strong association of the species with edge habitat types (Woolf et al. 2002; Andersen and Lovallo 2003; Preuss and Gehring 2007; Tucker et al. 2008; Jones et al. in press). Similar to previous studies (Donovan et al. 2012; Brown et al. 2018), our work demonstrated that MCA is sensitive to thresholds of habitat suitability. This sensitivity could provide important insights for conservation applications. For example, recovering populations of timber wolves (*Canis lupus*) in the northern U.S. (Mladenoff et al. 1999) and Eurasian otters (*Lutra lutra*) in Spain (Clavero et al. 2010) initially colonized high quality habitat and did not utilize lower quality habitat until after populations expanded. Thus, estimating N_k at higher thresholds of habitat quality for recolonizing species may help identify the characteristics of habitat that are most valuable for a species.

An ultimate goal of research should be to verify that variation in habitat suitability is tied to limiting resources with fitness consequences (Morrison 2001), an aim not yet applied to MCA but increasingly targeted in studies of ecology and conservation biology (Aldridge and Boyce 2008; Losier et al. 2015; Catlin et al. 2019; Maresh Nelson et al. 2020). Despite the above caveats, maximum clique analysis provides a conservative estimate of potential population capacity of a given landscape for Indiana bobcats, and it could readily be used for other species. Such knowledge can be particularly critical for management of harvested species that

are territorial, such as other furbearers (Feldhamer et al. 2003). Information on N_k can also direct and maximize costly efforts for the reintroduction of species of conservation concern, such as mammalian carnivores that are secretive but widespread across the landscape (Dalerum et al. 2009). We hope our methodological extensions of maximum clique analysis will inform and motivate future assessments and applications of this tool for wildlife conservation (Chapman and Byron 2018).

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Author contributions All authors contributed to study design and approved the final manuscript. GA, SJ, and CH collected the data. LJ conducted analyses, created code, and wrote the manuscript with contributions from RS and PZ. DG contributed computer algorithms and coding expertise.

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Code and Data Availability Code and data for maximum clique analysis are shared publicly in the Purdue University repository (<https://purr.purdue.edu/publications/4058/1>).

Declarations

Competing interests The authors declare that they have no competing interests.

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