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Contributed Paper

Reserve design to optimize functional connectivity and animal density

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Abstract: Ecological distance-based spatial capture–recapture models (SCR) are a promising approach for simultaneously estimating animal density and connectivity, both of which affect spatial population processes and ultimately species persistence. We explored how SCR models can be integrated into reserve-design frameworks that explicitly acknowledge both the spatial distribution of individuals and their space use resulting from landscape structure. We formulated the design of wildlife reserves as a budget-constrained optimization problem and conducted a simulation to explore 3 different SCR-informed optimization objectives that prioritized different conservation goals by maximizing the number of protected individuals, reserve connectivity, and density-weighted connectivity. We also studied the effect on our 3 objectives of enforcing that the space-use requirements of individuals be met by the reserve for individuals to be considered conserved (referred to as home-range constraints). Maximizing local population density resulted in fragmented reserves that would likely not aid long-term population persistence, and maximizing the connectivity objective yielded reserves that protected the fewest individuals. However, maximizing density-weighted connectivity or preemptively imposing home-range constraints on reserve design yielded reserves of largely spatially compact sets of parcels covering high-density areas in the landscape with high functional connectivity between them. Our results quantify the extent to which reserve design is constrained by individual home-range requirements and highlight that accounting for individual space use in the objective and constraints can help in the design of reserves that balance abundance and connectivity in a biologically relevant manner.

Keywords: connectivity conservation, conservation planning, functional connectivity, integer linear programing, mathematical optimization, reserve design, spatial capture–recapture

Diseño de Reservas para Optimizar la Conectividad Funcional y la Densidad Animal

Resumen: Los modelos de captura-recaptura espacial (CRE) basados en distancias ecológicas son un método prometedor para estimar la densidad animal y la conectividad, las cuales afectan los procesos poblacionales espaciales y, en última instancia, la persistencia de las especies. Exploramos cómo se puede integrar a los modelos CRE en los marcos de diseño de reserva que explícitamente reconocen tanto la distribución espacial de los

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individuos como su uso del espacio resultante de la estructura del paisaje. Formulamos el diseño de reservas de vida silvestre como un problema de optimización de presupuesto limitado y realizamos una simulación para explorar 3 diferentes objetivos de optimización informados por CRE que priorizaron diferentes metas de conservación mediante la maximización del número de individuos protegidos; la conectividad de la reserva y la conectividad ponderada por la densidad. También estudiamos el efecto sobre nuestros objetivos de hacer que los requerimientos individuales de uso de espacio fuesen satisfechos por la reserva de manera que se pudiese considerar que los individuos estaban protegidos (referidos como restricciones de rango de hogar). La maximización de la densidad de la población local resultó en reservas fragmentadas que probablemente no contribuyan a la persistencia de la población a largo plazo, mientras que la maximización de la conectividad produjo reservas que protegían al menor número de individuos. Sin embargo, la maximización de la conectividad ponderada por la densidad o la imposición preventiva de restricciones de rango de hogar en el diseño de reservas produjo reservas compuestas por conjuntos de parcelas mayormente compactas espacialmente que cubrían áreas de densidad alta en el paisaje con alta conectividad funcional entre ellas. Nuestros resultados cuantifican la extensión a la cual el diseño de reservas esta limitado por los requerimientos de rango de hogar individuales y resaltan que la consideración del uso de espacio individual en el objetivo y limitaciones puede ayudar al diseño de reservas que equilibren la abundancia y la conectividad de manera biológicamente relevante.

Palabras Clave: captura-recaptura espacial, conectividad funcional, conservación de la conectividad, diseño de reservas, optimización matemática, planeación de la conservación, programación entera lineal

摘要: 基于生态距离的空间捕获-重捕模型 (spatial capture-recapture model, SCR) 有望同时估计动物密度和连接度, 这两者通过影响种群空间过程, 最终影响着物种续存。我们探究了如何将 SCR 模型整合到保护区设计框架中, 以兼顾个体的空间分布和对景观结构的空间利用。我们认为野生动物保护区设计可以看作是受预算限制的最优化问题, 并且模拟了三种基于 SCR 信息实现保护目标最优化的情况, 即优先考虑保护个体数目最大化、保护区连接度最优化以及密度加权的连接度最优化。我们还分析了在保护区满足个体空间利用需求的前提下这三个目标受到的影响, 这个条件是为了确保个体受到有效保护 (即家域约束) 。实现局部种群密度最大化会导致保护区破碎化, 这可能不利于种群的长期续存;而考虑连接度最优化则会导致保护区覆盖的个体数最少。然而, 考虑密度加权的连接度最优化, 或在保护区设计中优先加入家域约束, 则保护区会含有大量空间上紧密的斑块以覆盖景观中种群密度高的地区, 斑块之间功能连接度也较高。本研究结果量化分析了个体的家域需求的限制对保护区设计的影响程度, 并强调了在保护区设计的目标和限制中考虑个体空间利用将有助于设计出生物学意义上平衡丰度和连接度的保护区。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 功能连接度, 保护区设计, 保护规划, 连接度保护, 空间捕获-重捕模型, 整数线性规划, 数学最优化

Introduction

Habitat loss and fragmentation has accelerated as natural land cover has been altered by humans, resulting in population declines and increased extinction risk for many species (Krauss et al. 2010). One strategy for conserving individual species or biodiversity in general is to designate reserves (protected areas, wilderness areas, etc.) where human land use is limited. One Aichi biodiversity target established by the Convention on Biological Diversity (2010) is to conserve at least 17% of terrestrial natural areas by 2020 through well-connected reserve systems. These reserves must protect sites that support the long-term persistence of species by maintaining general ecological functioning within the reserve. Largely, this has been approached through the development of reserve-design models that incorporate spatial attributes (i.e., reserve size, shape, connectivity, and proximity) that are thought to be representative of species' probabilities of persistence over time (Williams et al. 2004).

Population density and functional landscape connectivity are both central to population persistence (Tischendorf & Fahrig 2000; Cushman et al. 2010). Moreover, methods that simultaneously estimate local densities and resistance to individual movement, such as the ecological distance parameterization of spatial capture–recapture models (SCR) (Royle et al. 2013), capture interdependencies between density and connectivity that could ultimately affect population viability (Cushman et al. 2010). Specifically, SCR-based landscape connectivity metrics (Sutherland et al. 2015; Morin et al. 2017; Royle et al. 2018) describe the capacity of individuals to move through the landscape with respect to their distribution across the landscape and thus are valuable objectives for a reserve-design optimization framework. For example, density-weighted connectivity (Sutherland et al. 2015; Morin et al. 2017), which can be derived from population densities and functional connectivity estimated from SCR models, was recently used as an optimization objective in landscape conservation (Xue et al. 2017). These metrics provide an alternative to traditional reserve-design approaches in which species abundance and connectivity are decoupled and treated as separate objectives (Williams et al. 2004).

Reserve designs must also explicitly address individual-level resource requirements, which affect processes such as habitat selection and population dynamics. Past approaches have used habitat area and quality (Berglund et al. 2012) or number of territories (Haight & Travis 2008; Önal et al. 2016) to estimate the number of individuals of a target species protected by purchasing a given land unit. More generally, and even for nonterritorial species, home ranges are commonly used to describe animals' spatial resource requirements, delineating areas used by individuals to access the resources needed to survive, reproduce, and persist (Burt 1943). Therefore, an underlying motivation for protecting entire territories or home ranges is the assumption that all resources in an individual home range are necessary for survival or conversely that protecting only a portion of a home range may jeopardize the persistence of individuals located there if the unprotected parts are lost to land-cover change. One strategy could be to develop reserve-design optimization procedures that explicitly select entire home ranges obtained using a home-range estimation approach and select as many home ranges as possible to increase the chances that conservation actions taken in the near term result in population persistence in the long run. However, this approach has not yet been widely studied.

A wide variety of algorithmic methods are available for systematically selecting reserve sites that optimize a specified conservation goal. Many early methods were iterative heuristics that construct a reserve by sequentially selecting sites according to a rule (Williams et al. 2004), such as adding the site with the largest increment in conservation value at each step. Other approaches, including the widely adopted Marxan software, employ randomized local search methods such as simulated annealing (Ball et al. 2009) or evolutionary algorithms (Wu et al. 2011). Such heuristic strategies typically provide solutions quickly even for problems with large numbers of candidate reserve sites, but they do not guarantee the solutions are globally optimal in terms of the conservation objective (i.e., at least as good as any other feasible solution). However, optimization problems formulated as integer linear programs (ILPs) can be solved to optimality using the branch and bound algorithm (Lawler & Wood 1966). If an optimal solution is found, the decision maker knows that no other set of actions would result in a higher conservation benefit. If an optimal solution is not found due to, for example, time constraints, the algorithm returns the best solution that was found and an optimality gap that quantifies the quality difference between this solution and the unknown optimal solution. These optimality guarantees come at the price of longer runtimes, but it has been shown that many realistically sized problem instances can be solved in a reasonable amount of time on modern desktop computers (Önal et al. 2016; Dilkina et al. 2017). The ILP formulations are also remarkably flexible in terms of the conservation objectives and constraints that can be expressed. They have been used to enforce a variety of reserve-design requirements such as representation, aggregation, compactness, and connectivity (Beyer et al. 2016; Jafari et al. 2017) and were also employed to maximize density-weighted connectivity within a landscape (Xue et al. 2017).

We developed ILP formulations for budget-constrained reserve design based on landscape metrics estimated using spatial capture–recapture, namely, realized density of individuals of a target species (RD), potential connectivity (PC) of the landscape, and density-weighted connectivity (DWC) of the landscape. An ILP-based approach was presented in Xue et al. (2017) for dynamically maximizing DWC over an entire landscape by modifying resistance to animal movement between select pairs of adjacent land units and by using sophisticated strategies for solution space sampling to scale up the method. In contrast, we focused on maximizing different objectives enabled by SCR-estimated values (RD, PC, and DWC) over only the reserved land units rather than the whole landscape, specifying that reserve quality be evaluated based only on individuals or land units protected by the reserve design. We also included requirements for explicitly enforcing the protection of a specified area of the home ranges of individuals in a reserve.

We applied our method to a simulated data set with 2 levels of habitat fragmentation to assess how different conservation objectives may perform in the context of reserve design in areas with different amounts of existing fragmentation. Using our ILP formulations, we sought provably optimal solutions to these reserve design problems. We studied the trade-offs of considering different conservation objectives enabled by SCR-estimated values and the effect of explicitly enforcing space-use requirements as constraints for an in-depth analysis of how these choices affect reserve outcomes. We sought to highlight opportunities and practical considerations for extending the utility of SCR models to systematic conservation planning and to compare 2 biologically relevant reserve-design strategies for obtaining compact reserves with both high population density and high functional connectivity.

Methods

We developed a mathematical optimization-based method for selecting land parcels to incorporate into a wildlife reserve for protecting a single simulated target species. Without loss of generality, we assumed the land parcels are individual pixels in a raster because irregularly shaped parcels can be modeled as pixels that are constrained to be purchased as a set. Each pixel is characterized by the local density of individuals, resistance to animal movement dependent on local landscape covariates, and a known purchasing cost. Density and resistance can in practice be estimated from empirical data obtained from capture–recapture studies (Sutherland et al. 2015). We assumed allocation of a fixed budget for simultaneously purchasing all pixels in the reserve design. We defined the most cost-effective reserve as the collection of land parcels or pixels that provides the greatest conservation benefit without exceeding the budget. Specifically, we attempted to design reserves that maximize various metrics, including the number of protected individuals and functional connectivity of the reserve.

Ecological Model of Space Use

Following Royle et al. (2013), we assumed that each individual in the target species population has an activity center, which depends on the biology of the species, but can be regarded as the centroid of an animal's home range or the centroid of an individual's activities during the time of sampling. We represented the landscape as a raster of G pixels of unit area indexed by g or s, where s is a pixel containing an activity center. The realized population density $N(s)$ of pixel s is then the number of individuals whose activity centers are located within that pixel. Each pixel g also has an associated movement cost $e^{\alpha_2 z(g)}$ related to the local resistance caused by pixel-specific landscape covariate values $z(g)$, where α_2 parameterizes the extent to which landscape structure increases resistance to animal movement. The ecological distance $d_{\text{ecol}}(g, s)$ between a pair of pixels is measured as the sum of movement costs along the least-cost path between them (Royle et al. 2013; Sutherland et al. 2015). The probability that a pixel g is used by an individual whose activity center is in pixel s is modeled using a Gaussian kernel:

$$\Pr\left(g,\ s\right) = \exp\left[-\alpha_1 d^2_{\text{ecol}}\left(g, s\right)\right], \tag{1}$$

where α_1 is $1/(2\theta^2)$ and θ is the radius of a home range and the distance at which an individual could be detected from their activity center. Thus, $\Pr(g,\ s)$ describes the probability of use for pixels based on their distance from an individual's activity center (modulated by α_1) and the resistance to movement across pixels (modulated by α_2), resulting in an asymmetrical home-range kernel representing how individuals utilize space around their activity centers. Further details on SCR model assumptions and estimation are in Royle et al. (2013) and Sutherland et al. (2015).

Reserve Design Optimization with Integer Linear Programing

Given a fixed budget, the purchasing cost of each pixel, and pixel-wise estimated local population densities and use probabilities, the goal of the budget-constrained reserve design optimization problem is to select a set of pixels to purchase that has the greatest conservation value. We formulated this problem as an ILP in which decisions about selecting pixels are encoded in binary variables, the limited budget is expressed as a mathematical constraint, and the value of a set of purchasing decisions is quantified in terms of the number of protected individuals and functional connectivity of the resulting reserve.

We defined a binary decision variable x_g for each pixel g in the landscape to encode the decision of whether it is purchased for the reserve (i.e., if pixel g is selected, $x_g = 1$; otherwise, $x_g = 0$). Given the purchasing cost of each pixel c_g, we also required that the total cost of the selected pixels not exceed the budget B. A feasible solution to the reserve design ILP is an assignment of binary values to each x_g variable such that the total purchasing cost of those pixels with $x_g = 1$ is within the budget B.

We expressed our conservation goals as optimization objectives to be maximized. Our first conservation objective was to maximize the number of individuals protected by the reserve design. This is similar to the maximum coverage site selection problem (Church & ReVelle 1974) in which the goal is to protect as many conservation targets as possible with finite resources. The full ILP for maximizing the number of individuals within the reserve, given by the protected realized density (RD) objective, is

$$\max \sum_{g\in G} x_g \cdot N\left(g\right), \tag{2}$$

$$\text{s.t.} \quad \sum_{g\in G} x_g \cdot c_g \le B, \tag{3}$$

$$x_g \in \{0, 1\} \quad \forall\, g \in G. \tag{4}$$

The expression in Eq. (2) sums the estimated local population density over purchased pixels g indicated by $x_g = 1$, excluding density from unpurchased pixels with $x_g = 0$. This is based on the assumption that purchasing a pixel g is sufficient to protect the $N(g)$ individuals with activity centers located within that pixel. The constraint in Eq. (3) ensures the cost of the purchased pixels is within budget B. Equation (4) constrains the x_g variables to binary values.

Another objective was to maximize the extent to which conserved individuals can access the purchased pixels. Reserve-design approaches that minimize functional distance between conserved sites often use least-cost path modeling (Wang & Önal 2016), which provides a way to characterize the impact of landscape features on animal movements and resulting population-level attributes, such as genetic differentiation (Cushman & Lewis 2010). We used potential connectivity (Sutherland et al. 2015; Morin et al. 2017) as a landscape-scale measure of functional connectivity. We define the protected potential connectivity (PC) objective as

$$\max \sum_{\mathrm{g}\in \mathrm{G}} \sum_{\mathrm{s}\in \mathrm{G}} \Pr\left(\mathrm{g},\ \mathrm{s}\right) \cdot \mathrm{x_g} \cdot \mathrm{x_s}. \tag{5}$$

This objective maximizes the accessibility of the reserve sites (for which $x_g = 1$) to individuals inhabiting protected pixels (for which $x_s = 1$). The full ILP for maximizing PC combines the above objective function with the constraints in Eqs. (3) and (4). Although Eq. (5) is an accurate formulation of the PC optimization objective, the expression involves products of decision variables x_g and x_s, violating the requirements of a linear program, but the objective can be easily linearized (see Supporting Information for details). This allows us to leverage state-of-the-art linear programing solvers such as CPLEX (IBM 2013), Gurobi (Gurobi Optimization 2018), or SCIP (Achterberg 2009) that can solve problems with thousands of decision variables efficiently thanks to decades of algorithmic enhancements.

It may be preferable to evaluate a density-weighted variant of connectivity, which favors conserving areas that are highly accessible from sites with high local abundance. This can be quantified by density-weighted connectivity (Sutherland et al. 2015; Morin et al. 2017). We defined the protected density-weighted connectivity (DWC) objective as

$$\max \sum_{g \in G} \sum_{s \in G} \Pr\left(g,\ s\right) \cdot x_g \cdot x_s \cdot N\left(s\right). \tag{6}$$

In other words, this objective maximizes the probability of selected pixels (for which $x_g = 1$) being used by individuals in the reserve (for which $x_s = 1$) and is weighted by the estimated local population density $N(s)$. We linearized the objective in Eq. (6) with the same strategy we used for the PC objective.

Home Ranges and Individual Resource Needs

In the above formulations, individuals were considered protected by a reserve design if their activity centers fell within a purchased pixel. However, in finer-resolution landscapes, the pixel containing an individual's activity center might encompass only a fraction of the area utilized by the individual to meet daily and seasonal requirements for survival. If pixels outside the reserve become inaccessible or undergo land-use change, individuals relying on those areas for resources may face increased mortality risk, even if their activity centers are located within the reserve. Thus, it may be advantageous to explicitly enforce the protection of activity centers as well as the surrounding high-use pixels to ensure that individual resource requirements are comprehensively met.

One mechanism for modeling space use by individuals is the concept of home ranges. The size and geometry of an individual's home range are directly determined by its movements about its activity center and thus depend on resistance to movement exerted by the surrounding landscape features. Thus, use probabilities in Eq. (1) provide a means of delineating the home ranges of individuals based on how they utilize space. Following Sutherland et al. (2015), given an activity center in pixel s, we referred to the corresponding H% home range kernel as the set of pixels g such that the use probability $\Pr(g,\ s) \geq (1 - \frac{H}{100})$. The 95% home range is commonly reported as delineating the entire home range of an individual (Dickson & Beier 2002), and we assumed that protecting the entire home range would meet all of an individual's needs to survive and persist.

We augmented our optimization model to indicate whether the full home range of an individual is protected by a set of purchased pixels. We used $A^{95\%}(s)$ to denote the set of pixels belonging to the 95% home range with activity center at s, comprising any pixels used by individuals at s with probability of at least 0.05. We also defined another binary decision variable h_s for each pixel s in the landscape representing whether the home range centered at pixel s is protected by the reserve design. Then, if the pixels belonging to the set $A^{95\%}(s)$ are all purchased, the full 95% home range centered at pixel s is conserved and we set $h_s = 1$; otherwise, $h_s = 0$.

Under the assumption that only individuals whose full home range is within the reserve can be considered protected, the full ILP for maximizing the protected realized density objective with home-range constraints (RD-H) becomes

$$\max \sum_{s \in G} h_s \cdot N\left(s\right), \tag{7}$$

$$\text{s.t.} \quad \sum_{g \in G} x_g \cdot c_g \leq B, \tag{8}$$

$$x_g \geq h_s \ \forall\, g \in A^{95\%}\left(s\right), \quad \forall\, s \in G, \tag{9}$$

$$x_g \in \{0, 1\} \quad \forall\, g \in G, \tag{10}$$

$$h_s \in \{0, 1\} \quad \forall\, s \in G. \tag{11}$$

Equation (9) ensures that for any protected home range ($h_s = 1$), all pixels g in that home range are purchased ($x_g = 1$). Equation (11) ensures that the decision variables h_s take only binary values. We added these constraints to the protected potential connectivity and protected density-weighted connectivity maximization problems as well to get the home-range constrained versions (PC-H and DWC-H), whose objective functions are as follows:

$$\max \sum_{\mathrm{g} \in \mathrm{G}} \sum_{\mathrm{s} \in \mathrm{G}} \Pr\left(\mathrm{g},\ \mathrm{s}\right) \cdot \mathrm{x_g} \cdot \mathrm{h_s}, \tag{12}$$

$$\max \sum_{g \in G} \sum_{s \in G} \Pr\left(g,\ s\right) \cdot x_g \cdot h_s \cdot N\left(s\right). \tag{13}$$

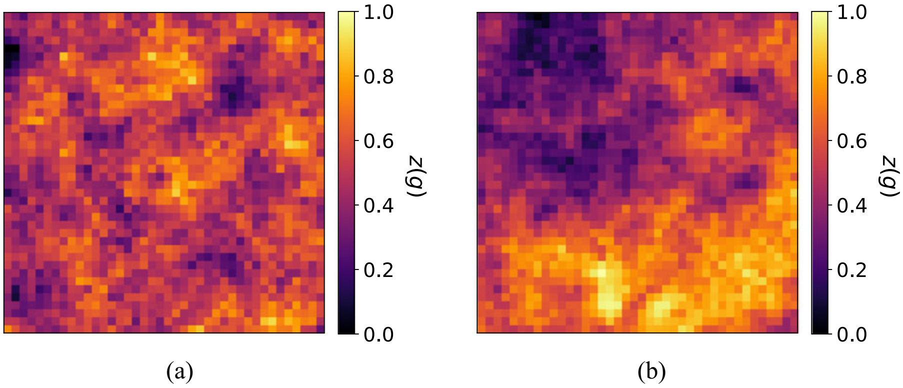

Figure 1. Simulated landscapes showing (a) high and (b) low habitat fragmentation, where higher values of covariate z(g) correspond to areas with less favorable habitat for a hypothetical species.

Simulated Landscape Experiments and Evaluating Reserve Designs

We created simulated landscapes with the type of estimated population density and landscape resistance data that would be used in practice as inputs to the reserve design problem. We created 2, 40×40 pixel gridded landscapes over which we simulated a continuous landscape covariate at 2 levels of habitat fragmentation (low or high) (Fig. 1) approximating levels of fragmentation found for protected areas in the literature. We kept total amount of habitat constant (see Supporting Information for details). We simulated data for a population of $N = 100$ individuals distributed over the landscape according to an inhomogeneous point process; low values of the covariate corresponded to greater local population densities. We modeled animal movement in our landscapes after the SCR model (Royle et al. 2013; Sutherland et al. 2015) in which the movement cost through a pixel g with covariate $z(g)$ is given by $e^{\alpha_2 z(g)}$ and the ecological distance between pixels g and g' is calculated by least-cost path. We set $\alpha_2 = 2.25$ (Morin et al. 2017). The use probabilities are related to ecological distance as shown in Eq. (1); parameter $\alpha_1 = 2.85$ and $\alpha_1 = 1.36$ for the low and high fragmentation landscapes, respectively, resulting in mean home ranges of 89 and 95 pixels for a hypothetical species. We simulated spatial capture–recapture data with a fixed detector array and then estimated pixel-wise realized densities $\hat{N}(s)$ and use probabilities $\widehat{\Pr}(g,\ s)$ with the SCR ecological distance model (Royle et al. 2013) (details in Supporting Information).

For each landscape, we formulated ILPs as described above based on the 3 objective functions (RD, PC, and DWC) with and without home-range constraints (95% home range or only activity center respectively). All pixels were assigned unit costs, although these could be generalized to reflect different land values or pixel availabilities. We varied the available budget from 0 to 1600 land units in increments of 100, resulting in 204 optimization problems. The resulting ILPs were solved using IBM ILOG CPLEX Studio version 12.6 in <5 minutes per problem. We evaluated each solution in terms of the design's protected realized density, potential connectivity, and density-weighted connectivity. Additionally, we evaluated the designs optimized without the home-range constraints against the 95% home-range area requirement to determine how disregarding home-range requirements might compromise reserve design quality. For example, we recomputed the protected realized density of the design obtained by maximizing RD without home-range constraints, but in this case only included individuals with complete home-range coverage when calculating protected realized density. This yields a more conservative estimate of the protected density than the objective value for maximizing RD without home-range constraints by incorporating the assumption that individuals whose 95% home ranges are not fully protected by the reserve are not adequately protected by the design. Finally, we compared the spatial composition of the designs in terms of percent overlap between designs obtained by maximizing different objectives and by calculating the number of patches and aggregation index of the designs with the SDMTools R package (VanDerWal et al. 2014).

Results

Conservation Objectives and Outcomes

We obtained optimal solutions for all 204 optimization problems. This meant each reserve quality measure was greatest when the corresponding objective was maximized (Fig. 2); for example, protected realized density was greater for designs maximizing RD than for those maximizing PC or DWC. Without imposing home-range constraints, the purely density-driven reserve designs had the lowest protected potential connectivity, whereas the purely connectivity-driven reserve designs protected the lowest realized density out of solutions obtained using the 3 objectives. Meanwhile, maximizing the DWC objective resulted in a compromise between maximizing the number of protected individuals and maximizing the potential connectivity between the purchased pixels.

The spatial configuration of reserves obtained by different optimization objectives was dramatically different.

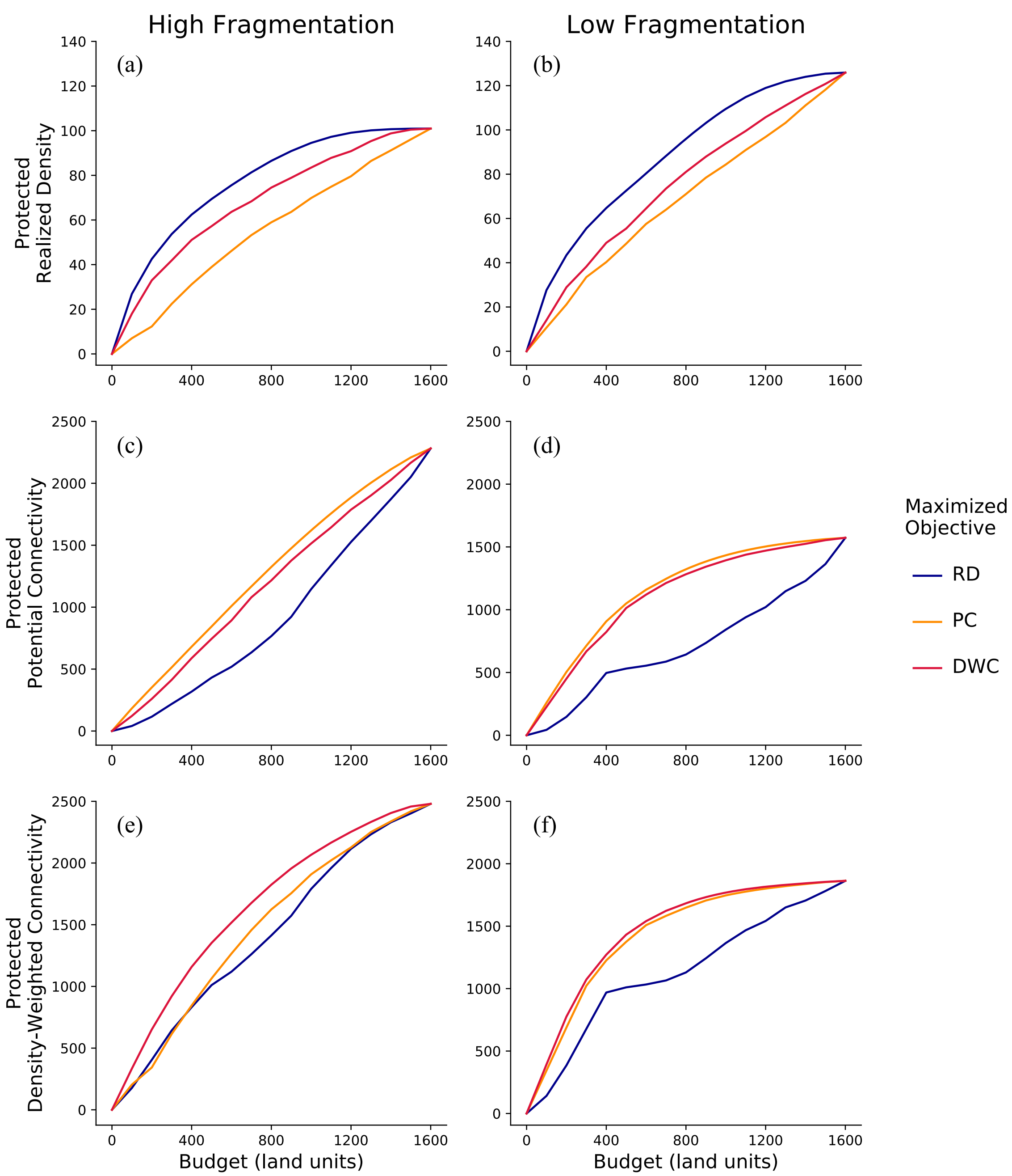

Figure 2. Protected realized density (a and b), protected potential connectivity (c and d) and protected density-weighted connectivity (e and f) of reserves obtained by maximizing either realized density (RD), potential connectivity (PC), or density-weighted connectivity (DWC) with different land-unit budgets. Results are for a simulated landscape with high habitat fragmentation and a simulated landscape with low habitat fragmentation.

Maximizing RD produced reserves with the lowest aggregation index and the greatest number of patches (Table 1 & Fig. 3). Reserves maximizing PC always had the highest aggregation index and typically had the lowest number of patches (Table 1). Maximizing the DWC objective yielded reserves with intermediate aggregation index values and a comparable number of patches to the PC-optimal reserves (Table 1). The different objectives also prioritized different parts of the landscape for protection. Reserves maximizing RD had relatively little overlap with those maximizing PC, despite the existence of a positive correlation between high-density and high-connectivity areas within our simulated data set. The DWC-optimal reserves overlapped significantly with both RD-optimal and PC-optimal reserves, partly by protecting nearly all of the pixels important to both RD and PC.

Table 1. Number of reserve patches and aggregation index (AI) as calculated by SDMTools for optimal reserves obtained by maximizing realized density (RD), potential connectivity (PC), or density-weighted connectivity (DWC) without home-range constraints at select budgets and percent overlap between optimal reserves obtained for each objective.

Fragmentation level & budget (land units)	Maximize RD		Maximize PC		Maximize DWC		Overlap (%)			
	no. patches	AI	no. patches	AI	no. patches	AI	RD–PC	RD–DWC	PC–DWC	RD–PC–DWC
High										
400	22	72.60	2	95.65	2	91.57	34.00	63.00	49.00	29.25
600	22	77.32	2	95.57	3	92.70	40.83	63.17	62.17	36.17
800	14	80.10	2	95.33	2	92.68	51.25	65.38	82.25	50.38
1000	5	86.21	1	96.75	2	93.80	62.00	75.00	84.60	61.20
1200	1	91.42	1	98.20	1	95.75	73.67	84.50	84.58	69.17
Low										
400	14	79.71	1	99.47	1	95.26	54.50	67.25	85.25	54.00
600	13	79.84	1	99.22	3	96.61	51.67	58.50	89.83	51.17
800	13	82.96	2	97.54	3	96.18	50.63	56.88	90.88	50.63
1000	7	85.43	1	98.40	5	96.07	60.50	69.30	90.40	60.40
1200	4	88.50	3	98.15	2	96.31	70.92	78.17	90.75	69.08

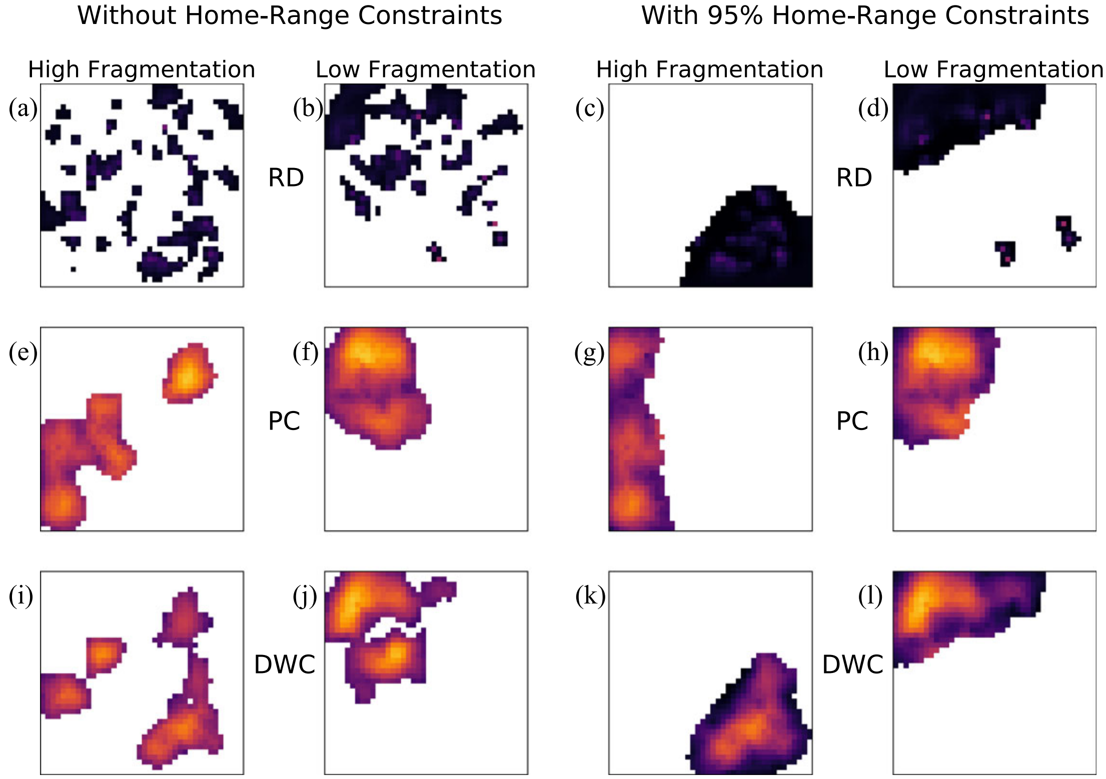

Figure 3. Reserve designs for simulated landscapes with high and low fragmentation obtained by maximizing the protected realized density (RD) in terms of total number of protected target species individuals in the reserve (a–d), potential connectivity (PC) of the reserve (e–h), and density-weighted connectivity (DWC) of the reserve (i–l) with a budget of 400 land units and either no home-range constraints or 95% home-range constraints.

Individual Resource Requirements

We compared reserves obtained assuming that purchasing the activity center is adequate to protect an individual with those obtained with the 95% home-range requirements. Adding home-range constraints created more aggregated reserve designs by requiring the incorporation of pixels surrounding activity centers into the design. This was especially evident in reserves maximizing the RD objective: without 95% home-range constraints these designs were patchy because there is nothing inherent in density that naturally provides for connectivity or aggregates designs. With home-range constraints, the designs had far fewer patches (Fig. 3). Moreover, maximizing density through the RD objective and including 95% home-range constraints achieved very different designs from combining density and connectivity by using the DWC objective alone (without home-range requirements).

Imposing home-range constraints on the reserve-design process made it more challenging to achieve reserve designs with high objective value scores, reflecting the increased cost of protecting each individual's home range compared to just their activity center. For any given budget level, the optimal reserve design objective value (for RD, PC, and DWC) was lower with home-range constraints than without them (Fig. 4, 95% vs. activity center) because only the density or connectivity from fully conserved 95% home ranges counts toward the objective when home-range requirements are considered. When reevaluating the reserve designs obtained without the home-range constraints in terms of their objective values when the 95% home range was used as the criterion for protection, designs obtained without home-range constraints had drastically lower protected RD, PC, and DWC over only the fully protected home ranges, particularly at low budget values (Fig. 4, activity center reevaluated with 95% vs. activity center). The reduction in reserve-quality measures was substantially greater compared with when home-range area constraints were incorporated in the optimization (Fig. 4, activity center reevaluated with 95% vs. 95%).

Discussion

Given the high economic and political costs associated with designing reserves, it is important to test sensible reserve design objectives that are related to population persistence. Our reserve designs considered both local population density and connectivity objectives with the goal of designing reserves that protect individuals and provide functional connectivity for those individuals. Aspects of species behavior such as resource selection and movement determine how individual animals interact with the surrounding landscape and thus influence both short-term survival of individuals and long-term persistence of the population. Our results showed that designing reserves based solely on population density can result in fragmented, patchy designs with low connectivity between reserve parcels, whereas designs that maximize only functional connectivity may achieve a small protected population size. Greater amounts of patch isolation can deter long distance dispersal (Fahrig 2007; Cote et al. 2017) and result in decreased population sizes, inbreeding, and genetic drift when both immigration and emigration are limited (Keller & Waller 2002). This is of particular concern when areas excluded from the reserve could undergo land-use changes that could further increase resistance to movement. Although resistance to dispersal may differ from resistance to daily home range movements (Keeley et al. 2017), failed dispersal attempts through a dangerous matrix may alter the learned or evolved behavior of future dispersers, effectively reducing the connectivity or magnifying the isolation of a reserve network over time (Baguette & Van Dyck 2007). Instead, maximizing an objective that combines both density and connectivity, or preemptively imposing home-range constraints on the reserve design are 2 ecologically meaningful strategies that yield reserves composed of spatially compact sets of parcels covering high-density areas in the landscape with high functional connectivity between them.

Density-weighted connectivity fuses functional connectivity with local population densities in an ecologically meaningful manner, rather than treating density and connectivity as 2 separate objectives in a reserve-design optimization framework. Using DWC as a conservation objective ensures that the resulting reserved parcels offer the most utility to the target population or that the probability of the conserved areas being used by protected individuals is maximized. Density-weighted connectivity is similar to the "realized connectivity" quantity described by Watson et al. (2011), which has been linked to metapopulation persistence. Although we do not explicitly consider population dynamics or dispersal distances in this work, the DWC objective could easily be extended to this setting, for instance, by only counting connectivity between protected sites that are close enough in ecological distance for dispersal. Additionally, both the connectivity-based objectives in our model naturally result in compact reserves by maximizing the total probability of species moving between selected sites or equivalently minimizing the functional distance between selected sites (Wang & Önal 2016). When the stronger condition of contiguity is required for, say, a terrestrial species, the potential connectivity and density-weighted connectivity metrics can be modified to count only connectivity between sites that have a fully-protected path between them (Önal et al. 2016; Jafari et al. 2017).

Our model allowed us to examine the impact of designing reserves with or without explicit provisions for individual resource needs. In early reserve-design models, species occurrence was largely treated as static and the patches or sites under consideration were much larger than average home ranges (Cabeza & Moilanen 2001). To estimate landscape resistance from individual movement using SCR, we used relatively fine-resolution landscapes in which it is more realistic to model individuals as using multiple sites. Our model can accommodate varying the area or fraction of the home range to use more or less conservative thresholds (e.g., 95% vs. 85% home-range extents) for whether or not an individual is considered protected by the reserve design. This can be a useful framework for conservation policy makers tasked with deciding how much habitat to protect in order to support a given population. Reserves designed with home-range constraints exchange the capacity to cover a large

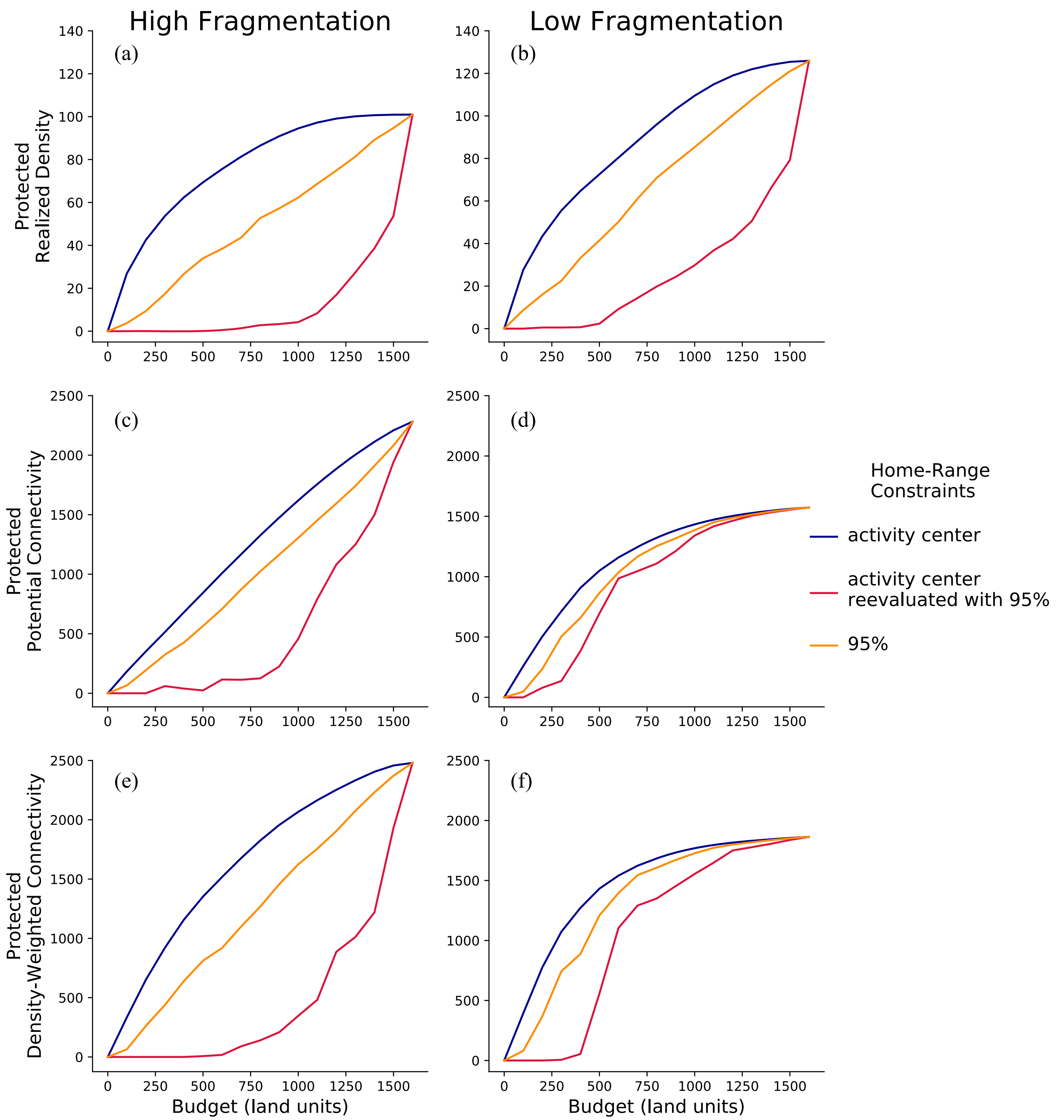

Figure 4. Protected realized density (a and b), protected potential connectivity (c and d), and protected density-weighted connectivity (e and f) of reserves obtained with different land-unit budgets by maximizing protected realized density (RD), potential connectivity (PC), or density weighted-connectivity (DWC) respectively without home-range constraints (activity center), with 95% home-range constraints (95%), or without home-range constraints and reevaluating RD, PC or DWC in terms of only the full home ranges in the design (activity center reevaluated with 95%).

population for potentially greater certainty that a smaller population will persist. However, reserves designed without these constraints could overestimate their conservation value, which could be undesirable for a risk-averse planner. Our approach makes these trade-offs clear and thus helps decision makers compare a range of alternatives that can be obtained by varying the home-range-extent requirement. Conceivably, then, the framework we proposed could be implemented as part of a study focused on an umbrella species.

Our approach could potentially be extended to encompass more varied reserve design goals. For example, one can address the design of reserves for multiple species using techniques from multi-objective optimization. Given estimated pixel-wise densities and pixel-to-pixel use probabilities for several target species within the landscape of interest, one can assess the objective value (such as DWC) of a given reserve design for each species separately, as we did for our single hypothetical target species. Optimizing the reserve design for multiple species simultaneously requires a weighting or ranking of target species in order of conservation priority. For a relatively small number of target species, one can construct an optimization objective as a weighted sum of objectives for each species (Dilkina et al. 2017). With linear objectives and constraints, the same powerful ILP solver tools can be applied to this modified problem. Alternatively, spatial contiguity (Jafari et al. 2017) could be incorporated in addition to home-range constraints. Our framework for reserve design provides decision makers with a tool for obtaining optimal designs that protect ecologically significant space-use patterns at the individual and landscape scales.

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Supporting Information

Further details about the ILP linearization (Appendix S1), the landscape generation and SCR simulation process (Appendix S2), and the code (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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