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The Value of Remotely-Sensed Data in Terrestrial Habitat Corridor Design for Large Migratory Species

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Sharing Our Work

The value of remotely-sensed data in terrestrial habitat corridor design for large migratory species[1]

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Abstract

Cost-effective conservation program design to support seasonal migratory species is urgently needed, but to-date has received little attention by economists. Conserving migratory corridors is a complicated design problem because of the large spatial scales over which migratory species can travel and the weakest-link characteristic of the problem. If one section or area of a potential migratory corridor is unable to support species movement, the migration through that route will not be successful. We develop and apply an integer-programming modeling approach that leverages innovative new data products to propose a cost-effective, landscape-scale conservation planning approach. We apply our approach to the Cody elk herd range within the Greater Yellowstone Ecosystem (GYE), leveraging satellite data on crop type and density over time and GPS collar data on elk migrations. We provide empirical evidence that using new satellite data products can avoid unconnected corridors and increase the cost effectiveness of corridor construction. In the Cody context, we estimate that achieving the conservation outcome associated with using satellite data on both costs and benefits would cost close to twice as much when using satellite benefit data but only limited cost data and about three times as much when using satellite cost data but only limited benefit data. Empirical work across additional herds is needed to provide additional insights into characteristics of contexts under which we expect gains from satellite and/or GPS collar data.

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1 Introduction

The design of habitat corridors for large migratory species has been identified as a critical and understudied aspect of terrestrial conservation planning needed to ensure the survival of these species in the face of threats from habitat destruction and fragmentation (Wilcove and Wikelski, 2008; Bauer and Hoye, 2014). Recent work by ecologists has demonstrated the importance of agricultural land in providing habitat for "stopover sites" for migratory ungulate species that traverse both private and public land in their seasonal migrations (Sawyer and Kauffman, 2011; Middleton et al., 2020), underscoring the challenges associated with the unique spatial scale and connectivity required in conservation policy design for these species (Sawyer et al., 2009). Furthermore, climate change and shifting habitats are putting additional pressure on migratory species and increasing the urgency to identify policy solutions (Bauer and Hoye, 2014; Díaz et al., 2019).

In recent years, corridor planning to provide habitat for species including elk (*Cervus candadensis*), mule deer (*Odocoileus hemionus*), and pronghorn antelope (*Antilocapra americana*) has received increasing national attention by policymakers in the United States (US) and become the subject of two secretarial orders (Secretarial Order 3356, 2017; Secretarial Order 3362, 2018), bipartisan congressional legislative efforts (e.g. U.S. Congress (2019)), and millions of dollars in support. For instance, the recently passed Infrastructure Investment and Jobs Act allocates $350 million to provide grants for projects to reduce wildlife-vehicle collisions and improve habitat connectivity (U.S. Congress, 2021), and the USDA's Grasslands Conservation Reserve Program has also begun prioritizing land in the Greater Yellowstone Elk Migration Corridor.[2] This federal-scale emphasis and funding is intended to complement and provide support for coordination among various state and regional organizations also working to improve migratory habitat (e.g. Wyoming Game and Fish Department (2019); Western Governors' Association (2019); Governors and Premiers (2016)).

The substantive scale and required connectivity of migratory habitat makes conservation planning methodologically challenging (Bauer and Hoye, 2014). Specifically, the expansive geographies that

[2]See https://www.fsa.usda.gov/news-room/news-releases/2021/usda-announces-dates-for-conservation-reserve-program-grasslands-signups.

comprise migratory species' habitat result in the involvement of a wide variety of stakeholders, including government agencies at the local, state, tribal, and federal level, private landowners with working lands, and non-governmental organizations (NGOs) representing both conservation interests and landowners. Private land has been identified as an essential component of successful migratory corridors and scholars have acknowledged the need to more explicitly integrate landowner impacts into the planning process (Morse and Clark, 2019; Middleton et al., 2020). An additional challenge to any program design arises due to the required connectivity of the migratory path that introduces a weakest-link public good aspect wherein the species' status is a function of the entire migratory route (Hirshleifer, 1983; Albers et al., 2021; Buchholz and Sandler, 2021). Specifically, if there are any points of the route the species cannot pass through, connectivity breaks down and the value of that entire route may be lost (Albers et al., 2021).

Securing the conservation of large-scale migratory corridors through a mixed-use landscape is an expensive proposition (Middleton et al., 2021). Given limited budgets available to conservation agencies relative to conservation goals, being efficient with conservation funding for a given project is crucial to support additional conservation actions. Cost-effectiveness is also an important metric used in habitat corridor construction and biodiversity conservation planning more broadly (see e.g. (Boyd et al., 2015)). Cost effectiveness is important in conservation planning because per-project cost savings enable a given agency or NGO to achieve a larger impact with the same budget (additional conservation) or larger scope of work (i.e. additional corridors/projects). Government agencies and private NGOs such as The Nature Conservancy (TNC) are known for their strategic pursuit of cost-effective fee-simple and easement purchasing strategies (Parker and Thurman, 2011).

Relatively little empirical work on migratory species planning that includes cost effectiveness as an outcome has been done to-date. Exceptions include recent work in the reserve site selection literature that focuses on identification of a set of reserve sites to target for purchase that will structurally link two sites within the landscape – typically a summer and winter range – via a habitat corridor. Conrad et al. (2012) model grizzly bear conservation as a site selection problem that maximizes habitat quality along a path linking two core habitat areas, subject to a budget constraint and heterogeneous site costs. Dilkina et al. (2017) expand this model to include two migratory species, each requiring a path between two areas. This literature focuses on advances in computational methods using relatively coarse data on potential conservation benefits and on the costs of including in a migration corridor. Coarse habitat maps provide proxies for conservation benefits, while county-level average agricultural land values (scaled by parcel acres) are used to estimate the costs of including parcels in a corridor plan.[3]

Critically, the science of conservation planning has not yet incorporated advances in ecology and in remote sensing that enable more accurate measurement of costs and benefits. The use of GPS collars has enabled ecologists to track species' precise movements at fine temporal scales, yielding the ability to estimate high-resolution "utilization distributions" for individual species across entire landscapes (Sawyer et al., 2009; Kauffman et al., 2021). At the same time, advances in remote sensing of satellite imagery have led to widely accessible annual estimates of vegetative cover, land use, and crop choice at scales as small as 30×30 meters (Han et al., 2012).

Incorporating these improved data can improve the cost effectiveness of corridor design in several ways. First, by providing spatial precise, continuous measures of conservation benefits, GPS collar data can help avoid including low-benefit parcels in conservation plans, freeing up budget for higher-benefit sites. Second, satellite data on land use can be used to infer important cost heterogeneities across a landscape, making cost estimates more realistic. If policymakers attempt to implement proposed corridors with naive or inaccurate measures of parcel costs, they may be forced to re-design corridors, or worse, fail to establish connectivity altogether. Ultimately, the gains from using satellite data to improve cost and benefit estimates will vary across contexts depending on ecological factors and land use heterogeneity.

In this paper we model migratory species conservation planning in a well-known, empirically rich, and policy-relevant context: migratory ungulates in the Greater Yellowstone Ecosystem (GYE). The GYE is one of the world's only remaining large-scale ecosystems, harboring critical habitat for a number of species including bison (*Bison bison*), mule deer, pronghorn, wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and elk (Haggerty et al., 2018). Yellowstone and Grand Teton National Parks provide significant

[3]Under the assumption that sites are purchased outright and used exclusively for conservation.

protected areas that serve as high-elevation summer ranges with higher precipitation and abundant food, but are inhospitable for most ungulates in winter. Recent research has revealed that the 20,000 GYE elk spend as much as 36% of their time on private land as they migrate to lower-elevation winter ranges with less food but more tolerable winter weather (Rickbeil et al., 2019). Once there, they may spend up to 80% of their time on private land (Middleton and White, 2020).

We develop estimates of the value of satellite data in terrestrial habitat corridor design and discuss how our results provide insight into the potential for gains across larger spatial scales, for other species, and in other geographies as our primary input. This paper provides a estimates the value of improvements in satellite data to design migratory corridors for elk in the Cody, Wyoming region along the South Fork of the Shoshone River. Our focus on the Cody Elk Herd provides a proof-of-concept that can be scaled across the GYE, and ultimately, to other migratory conservation contexts. We describe how satellite data use can enable more cost effective corridor design for policymakers and NGOs by i) providing more realistic estimates of parcel-specific costs to landowners and ii) providing improved estimates of the conservation benefits of including a specific parcel in a corridor plan.

This analysis is also a first step in developing systematic planning tools to inform emerging "pop-up" conservation techniques (also called habitat leasing and dynamic conservation). In contrast to conventional fee-simple acquisition of protected areas that engender more rigid conservation strategies, pop-up approaches are designed to compensate landowners for temporarily providing habitat at specific times in specific places. These approaches, while complex to design, can result in substantial cost savings relative to fee simple corridor construction. Moreover, conservation plans using this approach can be flexibly updated as species' habitat needs change. Our approach takes a necessary first step in this direction by using season-specific estimates of habitat utilization by elk that are derived from GPS collar data.

Migratory species conservation also fits within the broader conservation planning context, where better data to inform to planning models has been identified as a critical ingredient for improving cost effectiveness (e.g. Armsworth (2014)). Agricultural land values, although readily and freely available in the US, have been specifically identified as poor proxies for realized costs (Armsworth, 2014). Recent empirical work on the cost of land purchase in the US has shown that the often-used coarser cost estimates can underestimate the true cost of conservation, suggesting better cost estimates can improve conservation targeting (Nolte, 2020). Recently there have been calls to use GPS tracking and other real-time data sources to support migratory species conservation (Albers et al., 2021), but no analysis including costs has been conducted.

2 Background and Study Context

2.1 Migrations in the GYE

We focus on migratory elk in the Greater Yellowstone Ecosystem (GYE). Elk are one of several big game migratory species with a higher-elevation summer range that generally has higher precipitation and more food but is inhospitable in winter, and a lower-elevation winter range with less food but more tolerable winter weather. Animals must migrate between the seasonal locations, and past work has shown that the migration route is important habitat for species survival, especially in the spring when the animals follow the "green up," moving at a rate to enable prime vegetation consumption as it the landscape greens (e.g. (Bischof et al., 2012; Merkle et al., 2016; Aikens et al., 2017)).

Although ungulate migrations in the GYE were previously known, recent discoveries and technological developments have dramatically increased researchers' appreciation for their extent and importance (Middleton et al., 2020; Rickbeil et al., 2019). Figure 1 depicts the scope of the major elk migrations of the GYE, as mapped using GPS collar data over the past two decades. Thus far, the science of optimal spatial conservation planning has not incorporated these new insights and accompanying spatial data. Whereas existing methods focus on connecting seasonal ranges utilizing coarse "habitat suitability" measures to weight different routes (e.g. Conrad et al. (2012)), there is mounting evidence that "not all routes are created equal" in terms of their ecological outcomes (Sawyer et al., 2019).

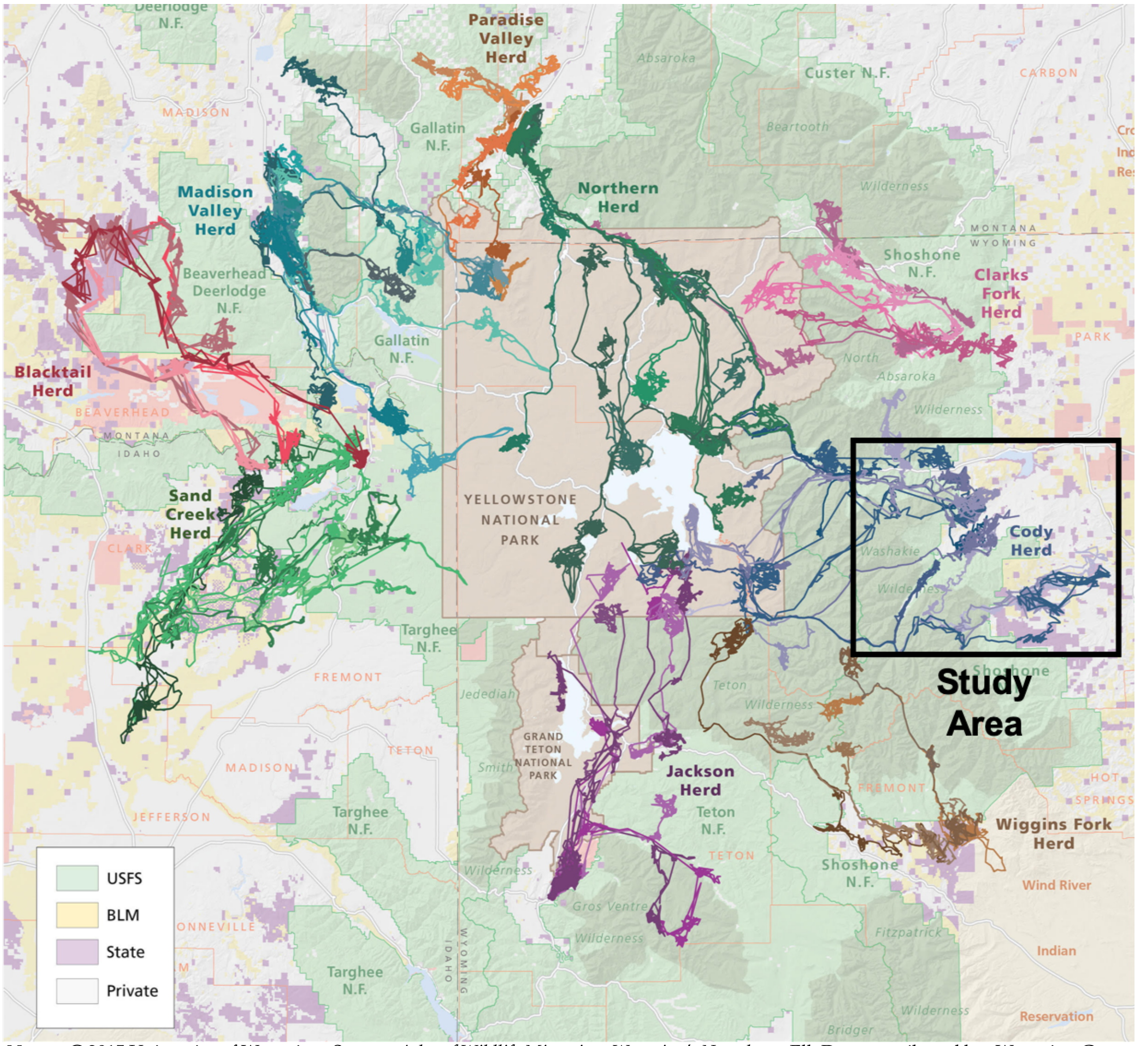
Specifically, recent research demonstrates i) the critical importance of "stopover sites" along a corridor for maintaining fitness (Sawyer et al., 2009); ii) larger winter ranges than previously realized (Sawyer et al., 2009); iii) a link between the length of migration routes and exposure to anthroprogenic risk (Sawyer et al., 2016); and iv) a link between route choice and mortality within a herd (Sawyer et al., 2019). Hence, conservation corridors are more likely to succeed if they are fully planned *ex ante* to incorporate the importance suitability of habitat and the extent of disturbances along the each potential route. Existing approaches that rely on ad hoc, opportunistic acquisition of parcels may fail to deliver expected conservation benefits. Systematic corridor planning approaches may also fail in practice if they rely on unrealistic assumptions about the costs of enrolling landowners or overlook important differences in habitat quality between routes.

Multiple NGOs such as TNC and government organizations including USDA are committed to conservation in the GYE, but larger-scale planning recommendations have yet to be developed. Specifically, this work can inform the structure of an incentives under USDA's working lands programs, Environmental Quality Incentives Program (EQIP) and Conservation Stewardship Program (CSP). EQIP practices may include fence removal, new fencing or modification to current fence designs, weed control, crop prioritization, and other potential habitat enhancements. The current Regional Conservation Partnership Program (RCPP) program "Securing the Grass Highway for Wyoming Migrations"provides an excellent example of the decision-making context that our approach can inform. This is a partnership between USDA, TNC, private foundations, and researchers at several universities including UC Berkeley and the University of Wyoming. The Wyoming RCCP's goal is to create conservation corridors in Wyoming that protect large-scale migrations for several species across the state. An explicit aim of the program is to "achieve the highest return on investment for every conservation dollar spent."

2.2 Cody, Wyoming and the South Fork of the Shoshone

This paper focuses on the Cody Elk Herd that migrates along the South Fork of the Shoshone River to the south of Cody, Wyoming, leveraging GPS collar data collected by Arthur Middleton and colleagues. The focus area is depicted in Figure 2. The approach developed here can be applied to other elk herds across

Figure 1: Migrations of the Greater Yellowstone Ecosystem

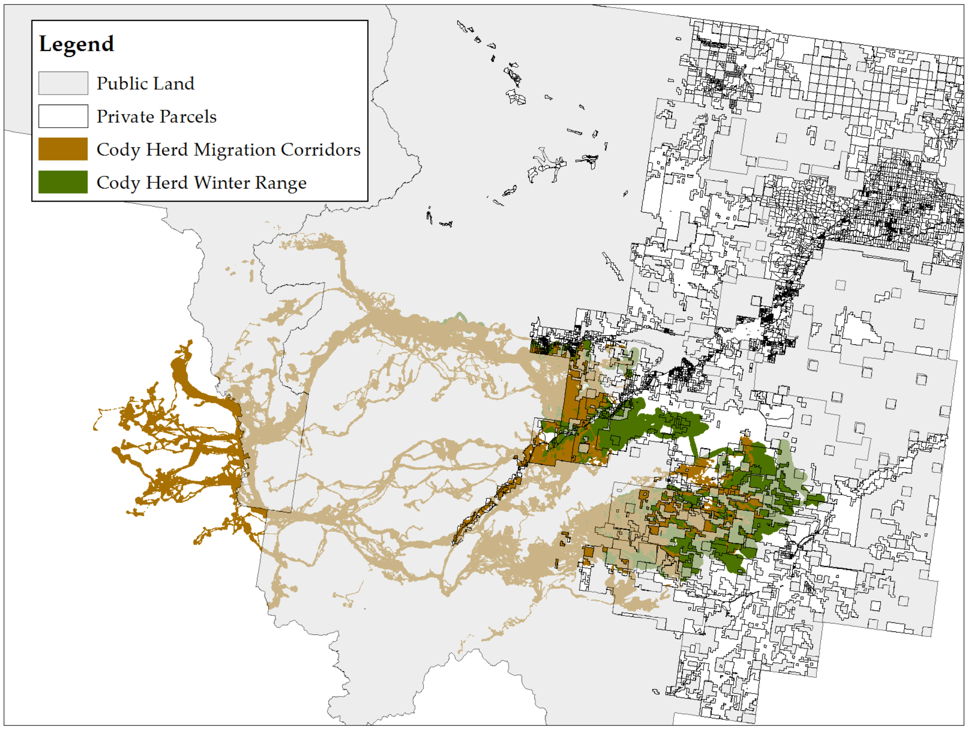


Notes: ©2015 University of Wyoming. Source: *Atlas of Wildlife Migration: Wyoming's Ungulates*. Elk Data contributed by: Wyoming Game and Fish Department; Montana Fish, Wildlife, and Parks; Idaho Fish and Game; National Park Service, US Fish and Wildlife Service, Wildlife Conservation Society, Wyoming Cooperative Fish and Wildlife Research Unit, Iowa State University, and Yale School of Forestry and Environmental Studies.

the GYE with the cooperation of state agencies and university stakeholders who manage access to highly sensitive GPS collar data on elk migrations.

The Cody Elk Herd migrates from their high-elevation summer range in Yellowstone National Park and the Shoshone National Forest to their lower-elevation winter range along the South Fork of the Shoshone river each fall (see Figure 2). The South Fork of the Shoshone river flows northeast out of the national forest through the primarily rural valley that supports ranching and agriculture. Flanked by public lands managed by the Forest Service, the Bureau of Land Management, and the state of Wyoming, the

Figure 2: Study Area: Park County, Wyoming



Notes: This figure depicts private and public land ownership and seasonal elk ranges in Park County, Wyoming. Gray shaded areas represent public lands. Green shaded areas represent elk winter ranges, while brown shaded areas indicate major migratory corridors.

South Fork also supports fishing, hunting, hiking, and various other recreational pursuits. The valley's landowners who host migratory ungulate herds on their working lands face various costs including forage loss, fence damage, increased predation from wolves and grizzlies, and the risk of brucelosis transmission. A recent survey of landowners in Paradise Valley, Montana (Tilt, 2020) revealed important insights for understanding the costs faced by landowners who would potentially be included in a migratory corridor. First, land ownership—even solely within ranching—is highly variable. Some ranchers own fewer than 160 acres, while others manage more than 5,000, with many falling somewhere in between. Second, 40% of landowners derive nearly all of their income from ranching/agriculture while another 40% derive less from ranching and agriculture. Taken together, these findings suggest that costs associated with elk utilization of private lands may be very different for different types of landowners. If so, existing approaches in the literature that base cost estimates on average farm value per acre are likely to misrepresent the true costs of a given corridor. Indeed, Tilt (2020) finds substantial heterogeneity in landowners' self-reported costs associated with elk utilizing their property for migratory/winter habitat (see Tilt 2020, Chart 7).

3 Modeling Strategy

Our modeling framework allows for ex ante estimation of the value of satellite data — in terms of cost effectiveness — to a policymaker making decisions about which sites within the landscape to enroll in a habitat corridor. The policymaker must decide how to protect key migratory routes by supporting land uses that facilitate elk migration across contiguous parcels. In practice, this would likely amount to preventing new or further development and ensuring herds could migrate through privately owned ranches, "working lands," and other open spaces by compensating landowners for losses associated with elk migrations, described above (Haggerty et al., 2018; Gude et al., 2007). Compensation instruments include an easement, habitat lease, or "occupancy agreement." We will compare decisions made under the baseline scenario in the absence of satellite data to decisions made using inputs from two satellite data sources: elk movement data from GPS collars (e.g., Rickbeil et al. (2019)) and remote-sensed estimates of land-use from USDA's Cropland Data Layer (CropScape).

We assume there is a budget-constrained policymaker that must decide on compensation to offer private landowners due to costs they incur from elk migrations. We solve for the optimal plan/policy by using a previously developed mixed integer programming method to solve the habitat connectivity problem (specifically (Conrad et al., 2012)). Operationally, the approach in Conrad et al. (2012) requires dividing the landscape up into a grid, and then selecting grid cells to include in a conservation corridor to maximize habitat quality over the route/path that satisfies a connectivity constraint between the two end points of a migratory route (typically Winter and Summer range) and that the budget is not exceeded. We solve this optimization problem under four scenarios: limited vs. satellite data on site-specific costs of conservation activities in each grid cell and limited vs. satellite data on the conservation benefits associated with each grid cell.[4]

There are 4 key parameter inputs to the computational model that must be estimated from data:

1. Adjacency of grid cells

[4]This approach makes sense when the benefits an animal receives from occupying a site during migration are not perfectly correlated with the costs to the landowner; which is true in our empirical application.

2. Starting/ending points (Winter and Summer ranges)

3. A conservation benefit or "utility" for each grid cell: $\vec{U} = [u_1, u_2, ..., u_N]$ (see Middleton et al. (2018))

4. A cost of including each grid cell in the route: $\vec{C} = [c_1, c_2, ..., c_N]$

In practice, the grid used for optimization is either arbitrarily created by the researcher or is based on an available parcel map; this input does not change across our two approaches. In both scenarios, we assume that public lands (identified using the US Protected Area Database) are available to migratory species at zero cost. GPS collar data from Rickbeil et al. (2019)), described in more detail below, are used to define starting and ending points for the migration based on estimated Winter and Summer Ranges.

We contrast limited data vs. satellite data for inputs 3 (conservation benefits) and 4 (costs), resulting in four different scenarios, depicted in Figure 3. Below, we describe how we estimate cell-specific benefits and costs under each scenario.

For our **Limited-Data Cost Estimate**, we assign costs that are proportional to county agricultural land values, a typical assumption in past modeling efforts (e.g. Conrad et al. (2012)). We calculate c_i as an annualized rental rate based on the the product of the county average land value and the number of private acres in the grid cell i: $c_i = r \times \overline{LandVal} \times Acres_i$.[5] For $\overline{LandVal}$, we use average farm value per acre in Park County, WY from the 2017 U.S. Census of Agriculture. We calculate $Acres_i$, the amount of private land in each grid cell, by overlaying our grid with the Protected Areas of the United States (PADUS) database to remove public land from our calculations.

We also develop a **Satellite-Data Cost Estimate** using remote-sensed data to calculate cell-specific crop revenues that reflect heterogeneity in land use decisions (and therefore costs of conservation). Rather than treating all private land as equally valuable, we utilize CropScape data—provided by USDA/NASA and available at a 30m resolution—to estimate a value of site-specific potential forage loss that varies based on the crops grown on a given site. This differentiates costs based on crop value rather than treating all

[5]This approach uses ex ante estimates of private costs to estimate what a planner may pay to achieve conservation outcomes via an easement or lease payment that is some fraction $\alpha \in [0, 1]$ of the land's total value. In our empirical work we choose α such that the average cost per grid cell is equal across the Limited-Data and Satellite Data cases. In other words, the cost of purchasing the entire landscape is equal for each planner. This ensures that our results are driven by the degree of heterogeneity of costs across the landscape under the two data assumptions, rather than differences in scaling. We leave exploring the impact of α on results and implications for policy and planning for future work.

Figure 3: Limited vs. Satellite Data Approaches

		Costs	
		County Farm Values	Total Revenue (CropsScape)
Benefits	Coarse Critical Habitat Overlay	Limited Benefits, Limited Costs	Limited Benefits, Satellite Costs
	Utilization Distribution (GPS)	Satellite Benefits, Limited Costs	Satellite Benefits, Satellite Costs

parcels as homogeneous. An example of this data is provided in Figure 4.

We use CropScape to estimate the opportunity cost of supporting migratory species instead of agriculture crop sales with the following formula:

$$c_i = \sum_{k=1}^{N} Acres_k \times Y_{k,2017} \times P_{k,2017} \tag{1}$$

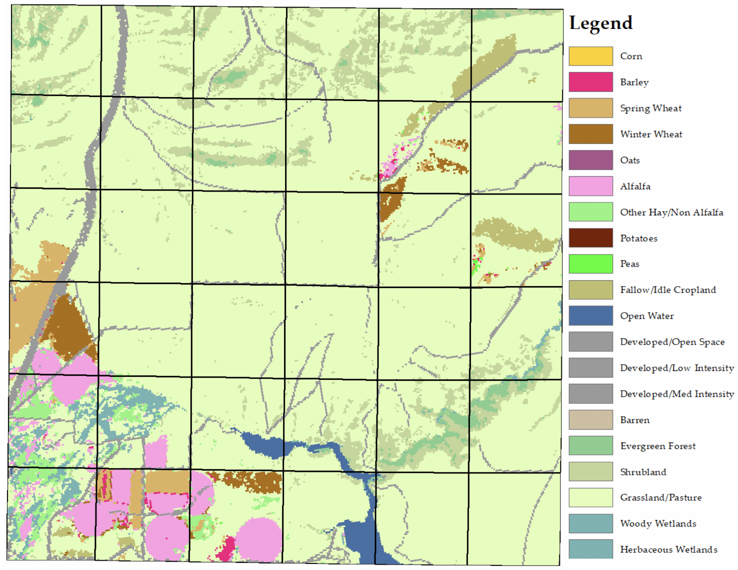
where $Acres_k$ denotes the total acres of crop k grown on parcel i (estimated using CropScape), $Y_{k,2017}$ is the estimated yield for crop k in Park County, WY (from the 2017 Census of Agriculture), and $P_{k,2017}$ is the price of crop k in 2017 (also from the Census of Agriculture). We adopt the simplifying assumption that conserved parcels bear the full opportunity cost of foregone crop revenue .[6] We calculate $Acres_k$ for each crop using only private land within each grid cell, under the assumption that no crops are produced on public land.

For the **Limited-Data Benefits Estimate**, we use broad polygons depicting "critical habitat areas" for elk, obtained from the Wyoming Fish and Game Department (brown shaded areas in Figure 5).[7] We overlay these critical habitat areas with our grid to calculate the percentage of each grid cell that falls within a critical habitat area, and use this as a coarse measure of the conservation benefits associated with a grid cell. This method of using relatively coarse habitat maps to derive conservation benefits is closely in line with Conrad et al. (2012).

[6] An alternative approach would be to use forage rates from the ecology literature (measured in "Animal Unit Months"—AUMs) to estimate the crop-specific value of the biomass landowners will lose (in expectation) if their parcel is included in a corridor.

[7] See https://wgfd.wyo.gov/Wildlife-in-Wyoming/Geospatial-Data/Big-Game-GIS-Data.

Figure 4: Example Land Use Data

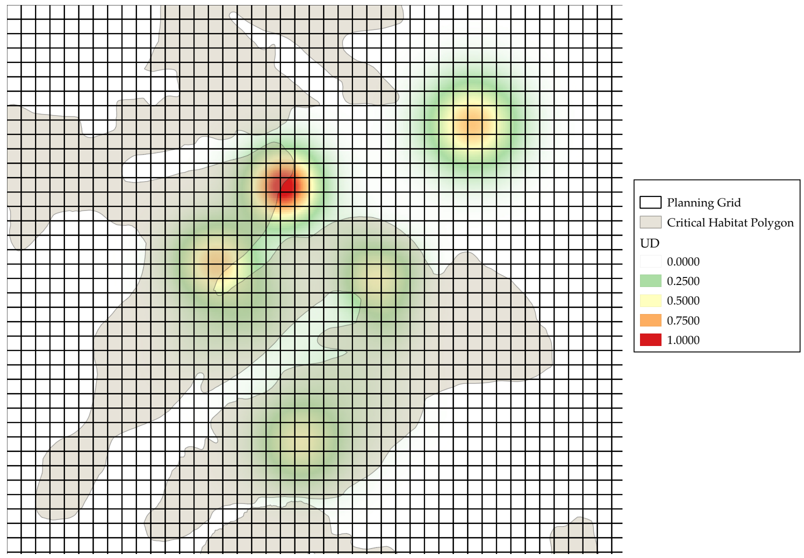


Notes: This figure depicts the CropScape satellite data on land use (in 2018) as well as the 1-mile grid cells used for our analysis.

Finally, we develop a **Satellite-Data Benefits Estimate**. To do so, we rely on high-resolution GPS collar data generously provided by the Arthur Middleton Lab at UC Berkeley. The satellite benefits data are constructed in several steps following Rickbeil et al. (2019). First, helicopter net-gunning and darting were used to capture elk on their winter ranges between 2001-2015. These elk were then fitted with GPS collars that took locations once every 30 minutes to 24 hours for one to three years. Second, net-squared displacement models were used to identify migration start and end dates to distinguish winter ranges, summer ranges, and migratory (fall and spring) ranges. Third, dynamic Browning Bridge Movement Models were used to estimate a utilization distribution (UD) across the landscape at a 180-meter resolution (depicted with colored shading in Figure 5). Finally, we sum the UD index within each grid cell to estimate the benefits of including that cell in a corridor, based on observed elk behavior in the recent past. Figure 5 depicts both the Limited-Data and the Satellite Data benefits estimates.

The corridor selection problem is to choose grid cells on which to purchase an easement to maximize species "fitness" while meeting budget and connectivity constraints. The objective function value is the sum of the u_i within the corridor. Changes to u_i affect contribution of each grid cell to the overall objective function. Changes to c_i affect the budget constraint the planner uses when planning. Additionally,

Figure 5: Example Benefits Data



Notes: This figure depicts an example of the Limited-Data Benefits Estimate (brown shaded "critical habitat areas") and the Satellite Data Benefits Estimate (elk Utilization Distributions based on GPS collar data).

using poorer quality cost information can result in sites the planner expects to include in the corridor not being included because the compensation offered by the planner based on the poorer-quality cost data is below the damages incurred by the landowner.

We assume that the satellite benefit and costs data are accurate estimates of costs and benefits and do not model uncertainty over either benefits or costs. By construction, the Satellite Data Approach using satellite benefit and costs data will correspond to the optimal corridor because it relies on the most accurate cost and benefit estimates available. We then measure the performance of the Limited Data Approach relative to the Satellite Data Approach. This allows us to explore the impact of substituting the poorer quality limited-data inputs for costs and benefits, which is ultimately an empirical question.

3.1 Mixed Integer Programming Model Formulation

We follow Conrad et al. (2012) and represent the landscape as a graph $G = (V, E)$, with a set of vertices V and directed edges E (Figure S1). We represent landscape cells in the model using their centerpoint, or vertex. We also follow Conrad et al. (2012) and introduce a source vertex x_0 with outgoing flow n into the node at which we designate the migration to begin at. The flow is inserted into the model at this node. Vertices in the landscape are indexed $V = 0, 1, ..., n$, and we introduce a binary integer x_j equal to one if the vertex is in the final solution, and 0 otherwise. Each vertex has an associated cost of inclusion c_j and fitness — or utility — benefit u_j. Connectivity is defined based on edges between vertices. Flow from vertex i to j is represented as a nonnegative value y_{ij}.

In addition to the root node, there is a terminal node where the migration ends. The variables associated with the source vertex, beginning node, and terminal node are all constrained to be equal to one — i.e., flow must occur through these vertices ($x_0 = 1$, $x_r = 1$, $x_t = 1$). We also include a variable z_0 that functions like a slack variable. At the source vertex we introduce flow equal to *n*, which is the maximum outgoing flow.

The objective given on line (1) represents the goal of maximizing the value from, or utility of, the migration. Constraint (2) is the budget constraint ensuring that the cost of the vertices selected does not exceed total budget C and constraint (3) requires that, for y_{ij} to be positive, the node x_j must be part of the solution set. The constraint on line (4) requires that only vertices in the solution have positive flow; i.e., vertices not in the solution do not have any flow. Additionally, the constraint on line (5) requires that each vertex in the solution consumes one, and only one, unit of incoming flow. Finally, the equation on line (6) requires that all flow inserted into the system equals that absorbed by the system.

$$\text{Max}_{x_j} \sum_{j \in V} u_j x_j$$

s.t.

$$\sum_{j \in V} c_j x_j \leq C \tag{2}$$

$$z_0 + y_{0,root} = n \tag{3}$$

$$y_{ij} - n x_j \leq 0 \quad \forall\, i, j \in V \tag{4}$$

$$\sum_{i:(i,j) \in E} y_{ij} = x_j + \sum_{l:(j,l) \in E} y_{jl} \quad j \in V \tag{5}$$

$$\sum_{j \in V} x_j = y_{0,root} \tag{6}$$

$$y_{ij} \geq 0 \tag{7}$$

$$z_0 \leq n \tag{8}$$

$$x_0 = 1, \quad x_r = 1, \quad x_t = 1 \tag{9}$$

$$x_j \in \{0, 1\} \quad \forall\, j \in V \tag{10}$$

We use data from the area of the GYE displayed in the box in Figure 1. A decision applying the model to our GYE setting is the choice of vertices and edges. One common approach to this decision is to lay a uniform grid over the landscape. In our case we lay a 1-mile by 1-mile grid across the landscape, orienting the grid such that the winter (ending node) and summer ranges (beginning node) are at opposite top and bottom edges of the grid, respectively.

We leverage local knowledge of the landscape and animal migration patterns to simplify the computational complexity of the problem. First, we assume migrating species will never move in the opposite direction of the grounds they are trying to reach. Specifically, an animal migrating from winter to summer grounds may move up to the left, up to the right, or straight forward, but not backward toward the wintering grounds (Figure S1).

3.2 Value of Satellite Data

Because these corridors have not yet been implemented, we perform an *ex ante* assessment of the gains from using satellite data. Applying the method from (Conrad et al., 2012), we compare the value of the optimized objective function and the associated costs from each approach. This amounts to calculating the overall conservation benefits—measured in units of "species fitness"—that are the explicit goal of policy proposals (Secretarial Order 3356, 2017; Secretarial Order 3362, 2018) and legislative efforts (e.g. U.S. Congress (2019)) for a given budget under each approach.

Our assessment of the gains from satellite data is based on comparing the cost effectiveness of using satellite data versus other data types, which is the metric often used by conservation NGOs to assess performance. We do this in two steps. First, we solve the optimization problem for a range of budgets and for the four data scenarios described in Figure 3. As a benchmark, we consider the costs of including *all* grid cells in the landscape and compare the performance of each scenario to this maximum-conservation outcome. We choose budgets that range from a a small fraction of the total cost of all sites within the landscape to up to 60% (6.25%, 10.42%, 16.67%, 20.84%, 31.26%, 41.68%, and 62.51%).

At the same time, we cap the number of sites the planner can actually select at 50, to focus on cases where the planner is unable to purchase most or all of the landscape and therefore will need to focus on achieving connectivity (arguably the conservation planning problem that exists in many real-world contexts today). We use the optimization outputs to calculate the realized conservation benefits (the sum of u_i for all parcels included in the corridor — with parcels for which the planner's limited data cost estimate is lower than the satellite cost estimate eliminated) relative to the conservation benefits of including all grid cells in the "corridor."

This allows us to trace out a functional relationship between the planner's budget and the conservation benefits for each scenario. Differences in the benefits for a given budget between the Satellite Data Approach and any of the three Limited Data Approaches represent the increase in conservation value associated with the satellite data. We expect higher conservation benefits from the scenario using only satellite data for any given budget expenditure because this approach eliminates the possibility that the planner over-pays for any given parcel—enabling them to ultimately include more parcels for the same total cost—while also enabling the planner to target the most ecologically beneficial parcels along a given route.

Differences in simulated conservation benefits are difficult to value. Hence, in the second step of our calculation, we invert the functional relationship estimated in Step 1 to develop a cost-effectiveness measure. In other words, rather than comparing simulated benefits from each approach for a given budget, we can compare the cost of achieving any given conservation outcome under each approach. The difference between the cost of achieving conservation outcomes under the Limited Data vs. the Satellite Data approach provides a direct measure of the value of satellite data in terms of its impact on cost effectiveness in conservation planning. This is depicted in Figure 6, where V_{sat} is the cost savings from using satellite data rather than limited data.

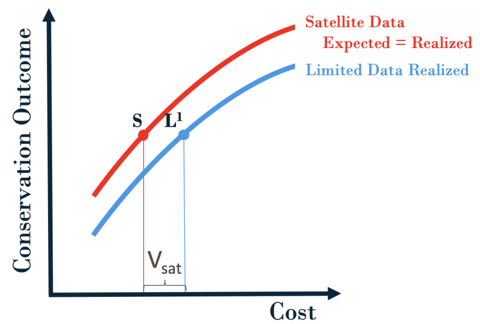


Figure 6: The difference in cost between the two approaches, holding conservation outcome constant, provides a monetary estimate of the value of satellite information (here $C(L) - C(S)$).

4 Results

There are notable differences in the spatial distributions of cost and benefit estimates from the different data inputs. In Figure S2 we show the heterogeneity in the gridded cost and benefit estimates for the different data types. Both the benefits (panel (a)) and costs (panel (b)) of including a given grid cell in the corridor differ depending on whether satellite or non-satellite data are used. As expected, there is more heterogeneity in benefits when satellite data are used. In particular, there is a high-benefit area that overlaps with farmland. The critical habitat benefits layer is quite flat and bimodal. Similarly, there is greater heterogeneity in costs across grid cells in the satellite-based cost estimates than in the estimates that assume a constant land-value per acre. In particular, there is a high-cost section of the grid that runs along the river. Whether these improved cost and benefit data substantially changes the cost of corridor construction, holding benefits constant, is an empirical question we explore in the remainder of this section.

We begin by plotting the realized conservation benefits for each of eight budgets for each of the four information scenarios in Figure 7. The scenario using satellite data on benefits and costs performs best. We obtain a smooth curve that levels off when the budget is around 30% of that which is required to purchase all sites in the landscape. Beyond this point, the constraint that the planner cannot purchase more than 50 sites becomes binding, rendering further increases in budget moot. Prior to this point, the shape of the curve suggests that there are diminishing marginal benefits as the budget increases. Specifically, for lower budgets an increase in budget results in a larger gain in benefits than the gain in benefits as the budget is increased the same amount at higher budget levels. Also as expected, the scenario with limited benefit and cost data performs the worst. The two intermediate scenarios with limited cost or benefit data perform similarly, but with a critical difference in connectivity that we discuss more below.

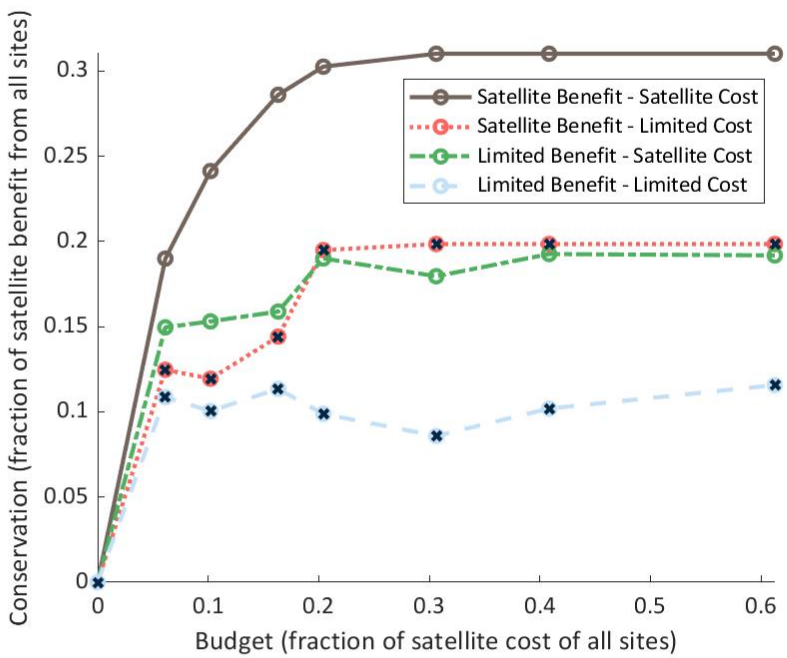


Figure 7: Comparison of conservation outcomes across data scenarios and budgets. The fitness associated with each scenario is measured as the percentage of the total fitness associated with purchasing every grid cell. Similarly, the budget for the corridor is measured as a percentage of the total cost to purchase every grid cell. All results are based on models that limit the number of selected sites to 50 out of the 459 in the grid. Additionally, points marked with an X represent cases where the actual corridor will not be connected.

Figure 8 provides insight into the the drivers of the differences in the performance of each scenario with one or more non-satellite data inputs. Specifically, Figure 8 shows that the actual benefits achieved through these approaches differ from what planners expect to achieve. Differences arise through three pathways. First, limited benefit data can result in the under or over-estimate of the benefits of a cell to the herd. Depending on the magnitude of these errors, actual benefits may ultimately be higher or lower than expected. We see this with the case based on satellite cost data and limited benefit data. For low budgets expected benefits are higher than actual; for larger budgets actual benefits are higher than expected.

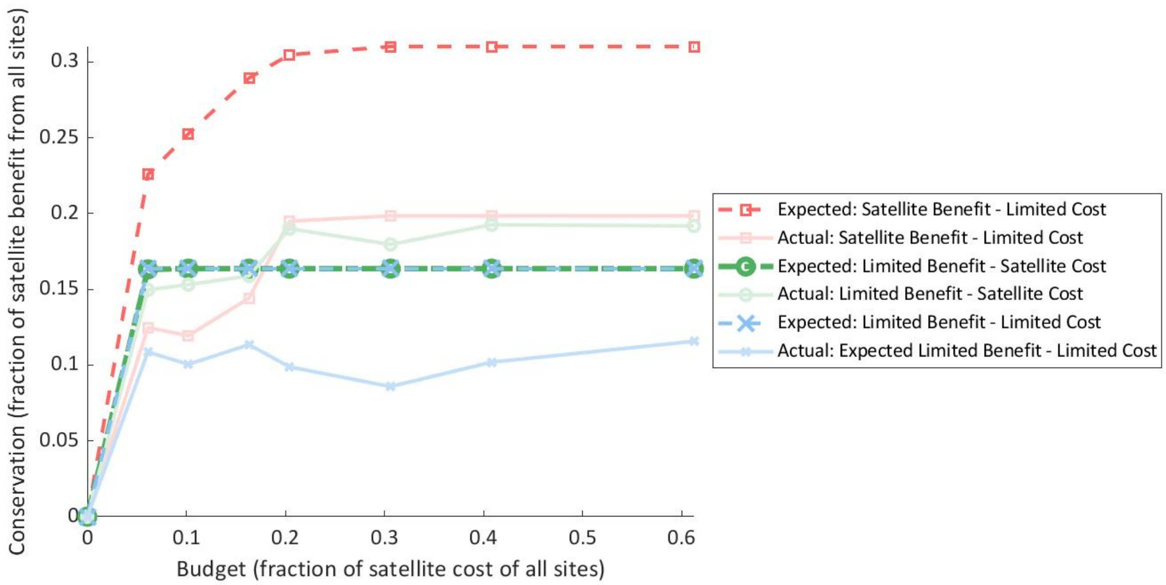


Figure 8: Differences between actual, or realized, outcomes and expected outcomes for each of the three scenarios using limited data. Differences arise through three pathways. First, limited benefits data may under or over-estimate of the benefits to the herd. Second, mis-estimating costs due to limited data can result in an underestimate of benefits because the planner will offer too low an incentive for a private landholder to engage in the conservation program. Third, limited cost data can result in an overestimate of site costs resulting in under-utilization of the budget.

The other two pathways through which expected and actual benefits can be driven apart relate to the cost data and related assumptions. Mis-estimating costs due to limited data can result in an underestimate of benefits because the planner will offer too low an incentive for a private landholder to engage in the conservation program, and our assumption is that these sites are dropped from the corridor, resulting in zero benefits from these sites. The last pathway is that limited cost data can result in an overestimate of site costs resulting in under-utilization of the budget. In other words, if selected sites have above average costs, they will ultimately not be included in the corridor. On the other hand, if selected sites have below average costs, the planner may construct a corridor that does not exhaust the budget, leaving conservation benefits on the table.

The substantial impact of mis-estimation of costs can be observed in the difference between the expected and actual benefits from the satellite benefit and limited cost data scenario. In this scenario the planner expects to do almost as well as the planner with satellite cost and benefit data, but falls short by about one-third. Additionally, in this scenario we observe a limit to the impact of increasing the budget. For budgets equal or greater to 20% of the budget needed to select all sites, the planner does not change their site selection. The planner identified the 50 sites bringing the highest benefit and the planner believes they can afford this set of sites; therefore, increases in budget do not change site selection and the total benefits generated. For for these high budgets the difference between expected and actual benefits is due to sites being dropped from the corridor and not the last pathway related to over-estimation of costs.

The scenario with limited benefit data and actual cost data highlights how coarse benefit data can limit planner performance. This landscape contains sites with bimodel benefit values with sites either being high or low benefit. Even at a low budget of 6.25% of the cost of all sites in the landscape, this planner is able to identify 50 relatively high-value sites that the planner is able to purchase. Increases in budget result in small changes in site selection, but with coarse benefit data this planner is not able to identify the sites that, based on the satellite data, represent the high-benefit cluster of sites. Similarly, the planner with limited cost and benefit data is unable to identify high-benefit sites and therefore, has a cap on performance. Moreover, this planner does not have good cost data, so some sites the planner plans to pay for are infeasible due to their cost estimate being below the satellite cost and this planner performs worst of all.

Another way to analyze the impact of poor cost data is to explore the implications for corridor connectivity and what a planner would need to pay to include all the sites in a corridor they planned to. Figure 7 shows that each scenario with limited cost data results in an incomplete corridor at all nonzero budgets under the assumption that the planner's budget is capped and that sites for which estimated cost is below actual will be dropped from the corridor. Figure 9 shows the percentage increase in site cost associated with including all the sites the planner expected to include in the corridor. For low budgets the percentage increase is over 150%; for higher budgets the planner with limited cost and benefit would need to pay about 50% more and the planner with limited benefit data but satellite cost data would need to pay about 20% more.

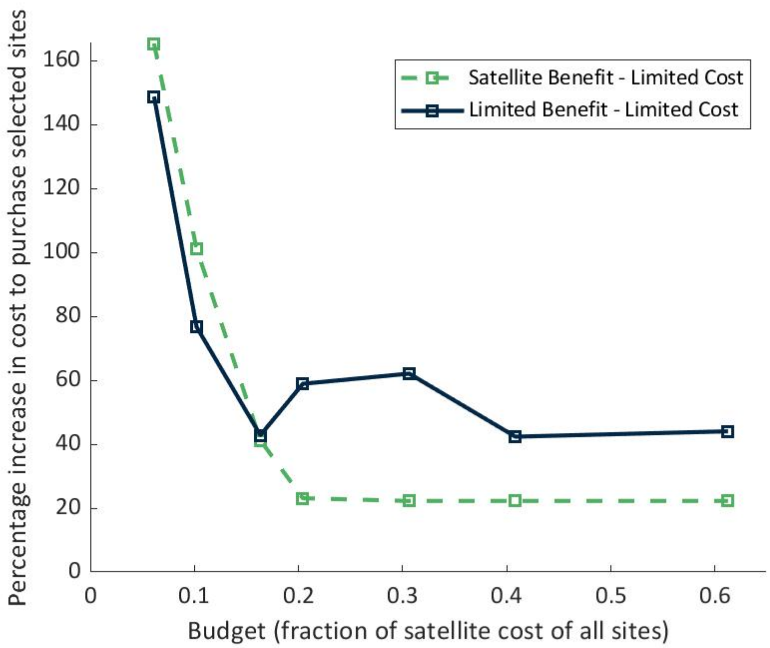


Figure 9: Additional ex post payment needed (increase in cost) for planners with limited data to purchase the corridor they selected. limited data can result in an underestimate of benefits because the planner will offer too low an incentive for a private landholder to engage in the conservation program.

Although the higher budgets are helpful in understanding some of the drivers of outcomes, in reality conservation budgets are small relative to need. Therefore, for our discussion of value of satellite data we focus on lower budgets that are about 10% of the budget needed to select all sites in the landscape. Our first main empirical result is that unconnected corridors emerge without satellite cost data under the assumption that the planner's budget is capped and that sites for which estimated cost is below actual will be dropped from the corridor. This can be remedied by acquiring satellite cost data or by using additional budget ex post to pay the difference between the estimated and true cost for sites where the estimated is less than the actual cost. This can be expensive though, especially at lower budgets where the percentage difference in the cost of including all planned sites is particularly high.

For the case with satellite benefit data but limited cost data, achieving the expected connected corridor with about 20% of the available conservation benefit (achieved by the planner with satellite cost and benefit data with 10% of the total budget needed to purchase all sites) the planner will need to pay close to double the amount of that the planner using satellite cost data pays *to achieve the same level of benefit* (Figure 7, Figure 8, and Figure 9).

Finally, we can explore the benefit of satellite benefit data comparing the outcomes for the planner with satellite benefit and cost data to those associated with the planner with limited benefit data and satellite cost data. The planner with limited benefit data but satellite cost data does complete their corridor, representing a key advantage of the cost data (Figure 7). However, for this planner to reach 20% of the available conservation benefit requires approximately triple the budget required by the planner with both satellite benefit and cost data. The planner with limited cost *and* benefit data does so poorly that they never achieve 20% of the available conservation benefit, either in expectation or in reality.

5 Conclusion

Recent advances in ecology have demonstrated the substantial spatial extent of many migrations globally, as well as their importance for protecting biodiversity (Bauer and Hoye, 2014). In the US, ungulate migration in the GYE is a highly salient example thanks to the ongoing use of GPS collar data to document and study migration behavior at a fine scale (Middleton et al., 2020). However, the science of conservation planning and optimal reserve site selection methods have not kept pace. This paper fills a critical gap in conservation science and planning emphasized in Sawyer et al. (2009) by providing empirical evidence that utilizing GPS collar data in conjunction with remote-sensed land use and vegetative cover data can result in improved migration corridor design.

The impact of incorporating better cost and benefit data capturing land and landowner heterogeneity exists at relatively low budgets — the case typically encountered in the real world. Using poorer cost data in this context results in incomplete corridors. We also show that using satellite data results in substantial differences in cost effectiveness. Achieving the same conservation outcome as that using both satellite cost and benefit data will cost close to twice as much when satellite benefit data are used but only limited cost data are available. Additionally, achieving the same conservation outcome as that using both satellite cost and benefit data would cost about three times as much when satellite cost data are available but only limited benefit data are available.

Empirical work across additional herds is needed to provide additional insights into characteristics of contexts under which we expect gains from satellite and/or GPS collar data. Specifically, patterns in private versus public land likely influence the returns to different types of information.

While the empirical application we focus on for this paper is elk migrations in the GYE, the methods developed here are designed to be applicable to any setting where heterogeneity across landowners affects the cost of assembling contiguous habitat preserves. Our approach advances conservation science by i) making use of the best available knowledge; ii) creating a blueprint for satellite-based site selection in other contexts; and iii) providing insight into when utilizing satellite data in conservation planning generates a large return on investment.

Our work also lays the foundation for extensions that can capture additional system complexities. First, the focus of the current model is on structural connectivity, assuming the species will use the corridor if it is created. The collar data also provide information on functional connectivity — i.e. whether the species will use the space and the fitness associated with the use — and this could be more fully developed. More information on the fidelity and plasticity of path choices to determine whether the structurally connected path is functionally connected from the species' perspective could enhance the model (Albers et al., 2021). Additionally, uncertainty about how climate change will shift annual habitat creates an incentive to explore how to conserve multiple pathways to provide resilience if climate change lowers or eliminates functional connectivity in or across protected areas (e.g. Ando and Mallory (2012)). We also assume that the costs are exclusively those to landowners and the benefits accrued are to species only, and hence we likely miss important benefits. Work to estimate the value of these conservation outcomes to humans is ongoing and beyond the scope of this project, though we note that visitor surveys indicate wildlife viewing is a primary motivation for visiting Yellowstone and Grand Teton National Parks (Cullinane and Koontz, 2016).

Another important area of research needed to fully leverage models like the one developed here relates to program design. Specifically, there is no consensus over how to design policies and programs that engage private landowners; instead more work to explore how to do this in a cost effective manner has been called for (Haggerty et al., 2018; Middleton and White, 2020). More broadly, migratory species are an important context in which to explore the design of large-scale programs aimed at temporary conservation programs (e.g. Reynolds et al. (2017)). Our work supports integrating satellite data into the design of these programs.

Finally, many of the challenges associated with conservation planning for migratory species are similar to those identified over the last approximately 30 years associated with Ecosystem Based Management (EBM). These include large spatial scales and long time periods with complicated system dynamics as well as an emphasis on key ecological processes rather than structural components of ecosystem such as species (Yaffee, 2011). On one hand, experiences implementing EBM can be leveraged to improve migratory species planning as proposed by Yaffee (2011). On the other hand, in the longer run migratory species should be considered as a species within an ecosystem and be included in EBM frameworks supporting a more holistic approach to large-scale landscape planning. This would explicitly require consideration of multiple species interactions and other landscape complexities that are beyond our current model.

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Supporting information for **The value of remotely-sensed data in terrestrial habitat corridor design for large migratory species**

Figure S1: Network representation of gridded space.

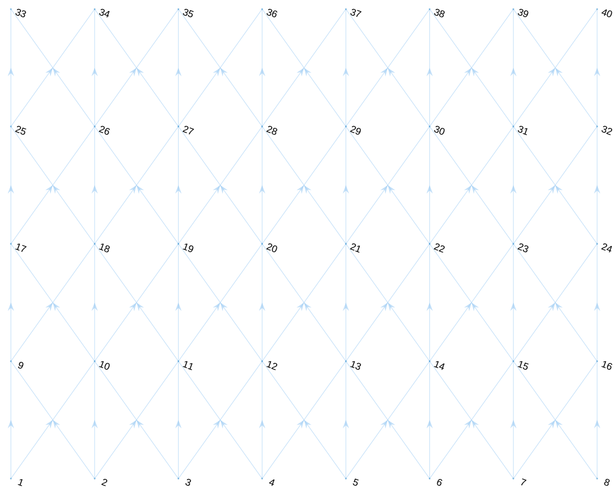
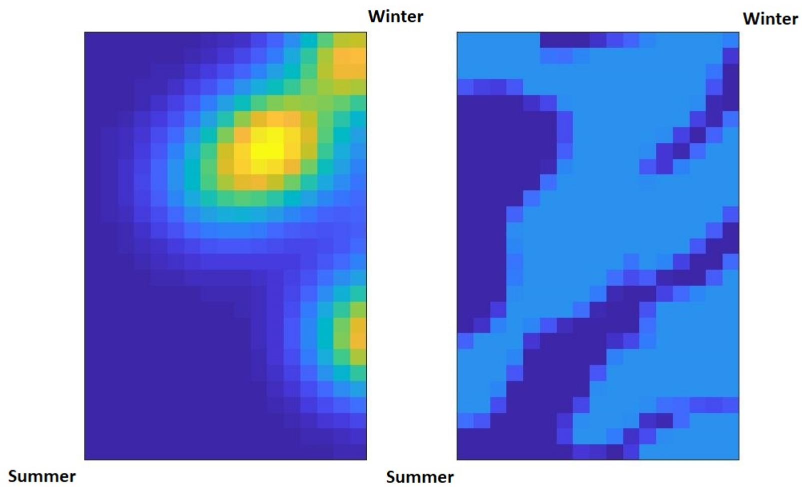
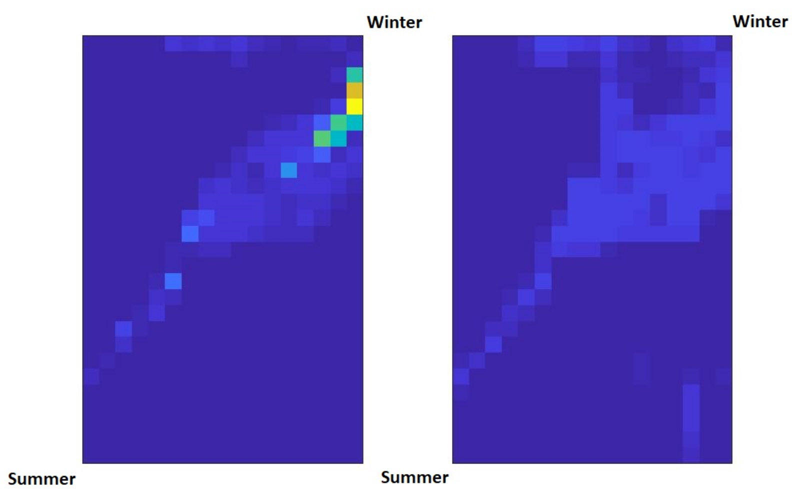


Figure S2: Comparison of spatial distribution of relative costs and benefits calculated with and without satellite data. The average cost per grid cell is standardized so that the average cost is equal across the two cost scenarios. The difference is in the distribution of costs across the landscape. Similarly, we standardize the benefits (fitness) associated with each grid cell so that the average is equal across the two scenarios.

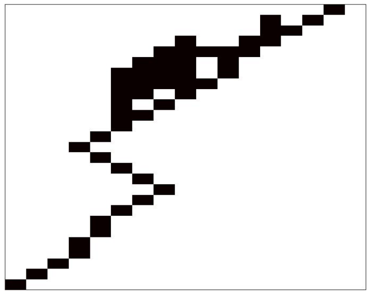


(a) Comparison of fitness benefits of each grid cell to migratory elk using satellite data (left) and critical habitat maps (right).

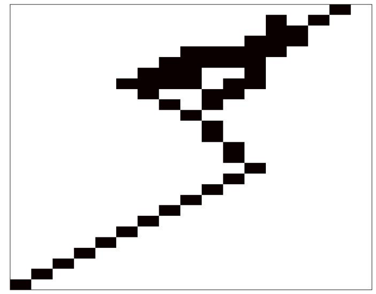


(b) Comparison of the relative cost of each grid cell using satellite data (left) and average county farmland values (right).

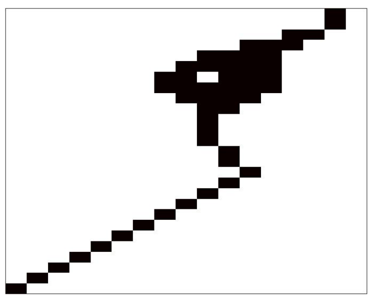
Figure S3: Site selection by budget using satellite data for benefits and costs.



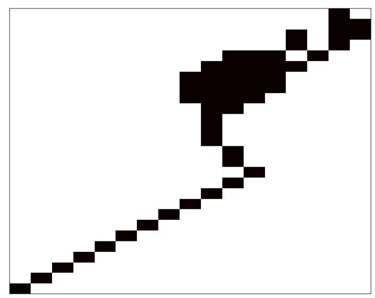
(a) Budget 6.25% of the total cost of all sites.



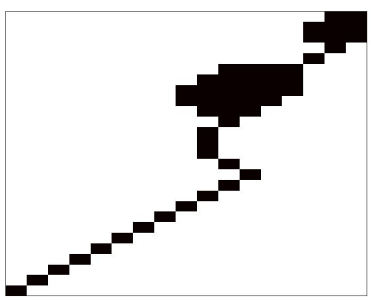
(b) Budget 10.42% of the total cost of all sites.



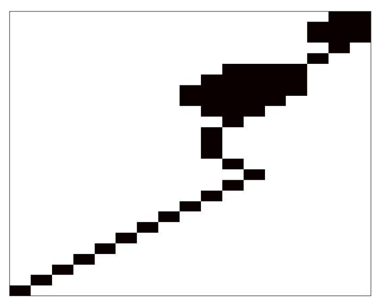
(c) Budget 16.67% of the total cost of all sites.



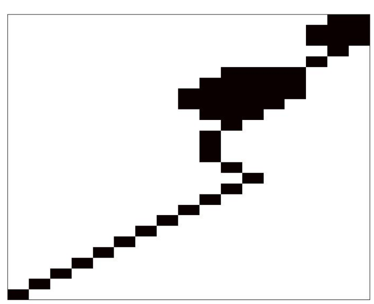
(d) Budget 20.84% of the total cost of all sites.



(e) Budget 31.26% of the total cost of all sites.

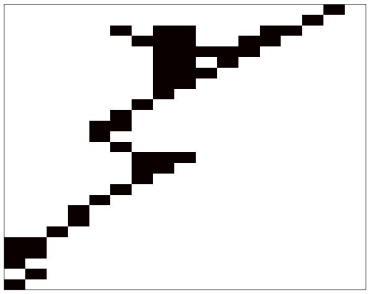


(f) Budget 41.68% of the total cost of all sites.

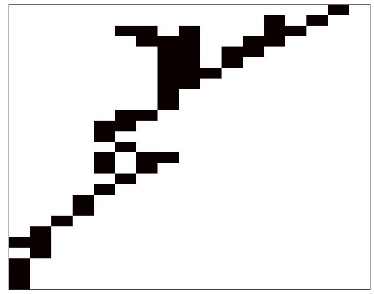


(g) Budget 62.51% of the total cost of all sites.

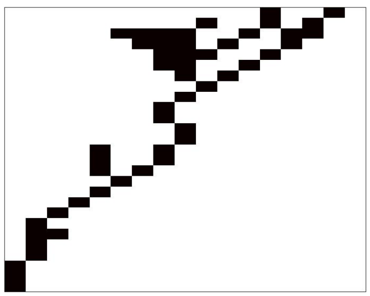
Figure S4: Site selection by budget using satellite data for benefits and costs.



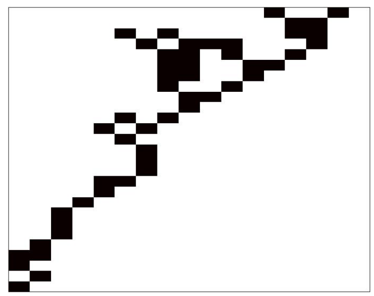
(a) Budget 6.25% of the total cost of all sites.



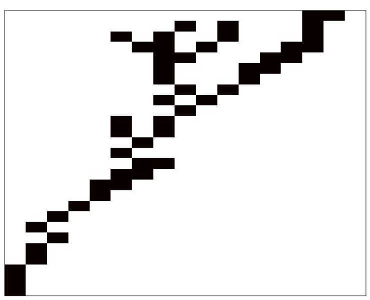
(b) Budget 10.42% of the total cost of all sites.



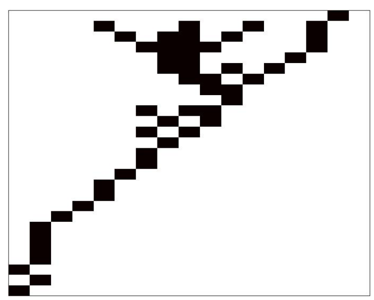
(c) Budget 16.67% of the total cost of all sites.



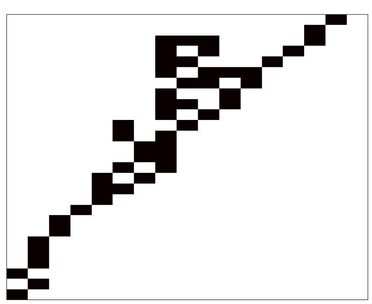
(d) Budget 20.84% of the total cost of all sites.



(e) Budget 31.26% of the total cost of all sites.

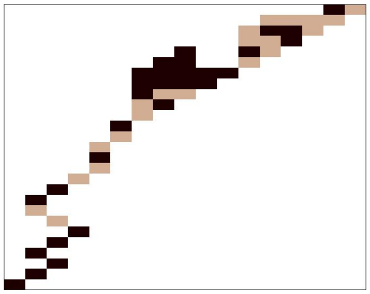


(f) Budget 41.68% of the total cost of all sites.

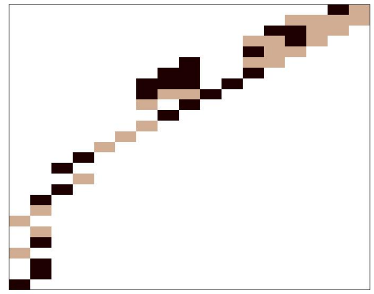


(g) Budget 62.51% of the total cost of all sites.

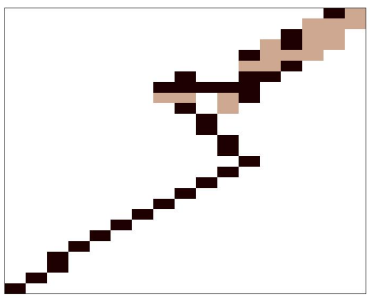
Figure S5: Site selection by budget using satellite benefit data and limited cost data. Pink cell satellite costs are greater than naive cost estimates.



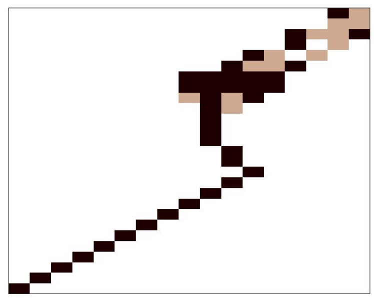
(a) Budget 6.25% of the total cost of all sites.



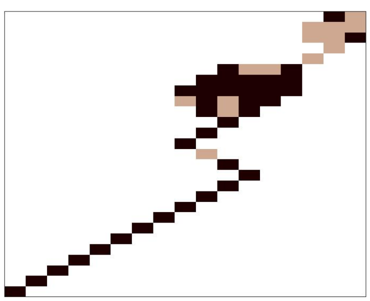
(b) Budget 10.42% of the total cost of all sites.



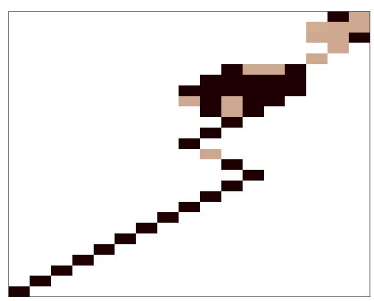
(c) Budget 16.67% of the total cost of all sites.



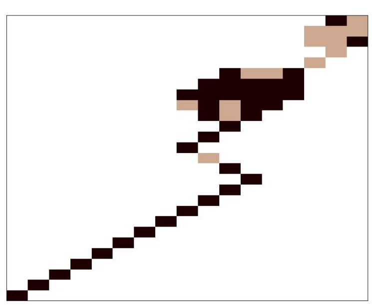
(d) Budget 20.84% of the total cost of all sites.



(e) Budget 31.26% of the total cost of all sites.

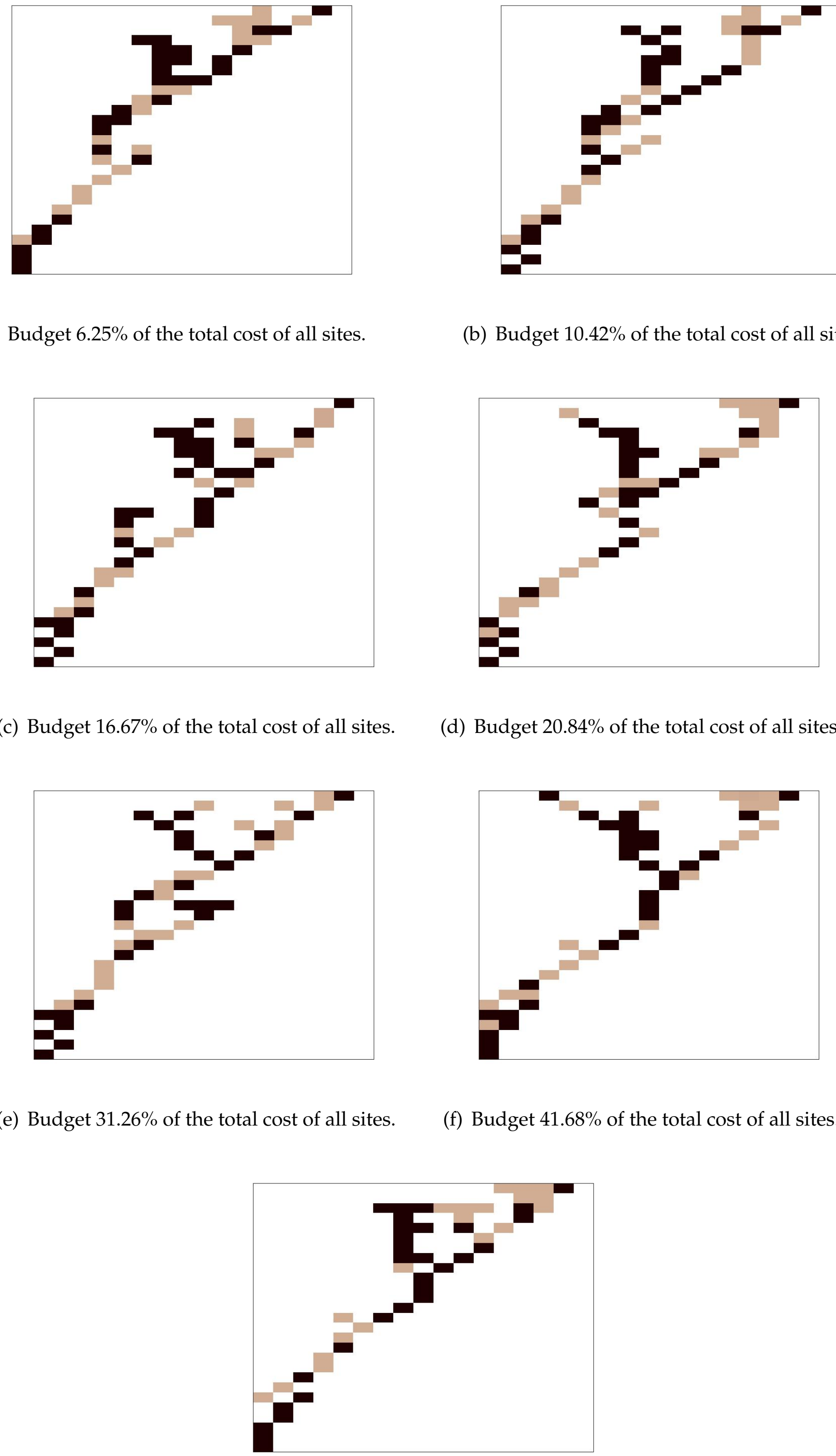


(f) Budget 41.68% of the total cost of all sites.



(g) Budget 62.51% of the total cost of all sites.

Figure S6: Site selection by budget using limited benefit data and limited cost data. Pink cell satellite costs are greater than naive cost estimates.



(a) Budget 6.25% of the total cost of all sites.

(b) Budget 10.42% of the total cost of all sites.

(c) Budget 16.67% of the total cost of all sites.

(d) Budget 20.84% of the total cost of all sites.

(e) Budget 31.26% of the total cost of all sites.

(f) Budget 41.68% of the total cost of all sites.

(g) Budget 62.51% of the total cost of all sites.