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Economical defence of resources structures territorial space use in a cooperative carnivore

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Ecologists have long sought to understand space use and mechanisms underlying patterns observed in nature. We developed an optimality landscape and mechanistic territory model to understand mechanisms driving space use and compared model predictions to empirical reality. We demonstrate our approach using grey wolves (*Canis lupus*). In the model, simulated animals selected territories to economically acquire resources by selecting patches with greatest value, accounting for benefits, costs and trade-offs of defending and using space on the optimality landscape. Our approach successfully predicted and explained first- and second-order space use of wolves, including the population's distribution, territories of individual packs, and influences of prey density, competitor density, human-caused mortality risk and seasonality. It accomplished this using simple behavioural rules and limited data to inform the optimality landscape. Results contribute evidence that economical territory selection is a mechanistic bridge between space use and animal distribution on the landscape. This approach and resulting gains in knowledge enable predicting effects of a wide range of environmental conditions, contributing to both basic ecological understanding of natural systems and conservation. We expect this approach will demonstrate applicability across diverse habitats and species, and that its foundation can help continue to advance understanding of spatial behaviour.

1. Background

Ecologists have long strived to understand space use and mechanisms underlying patterns observed in nature. This entails investigating why and how animals select home ranges or territories, including how benefits, costs and trade-offs affect space use. Such knowledge would inform basic ecology and conservation efforts, as ecologists could better predict how environmental conditions or management decisions influence animal behaviour.

Commonly employed empirical approaches have advanced understanding of animal space use. Utilization distributions are frequently used to summarize space use as probabilities of where animals will be found at any time [1]. Although time spent does not explain mechanisms driving space use [2], empirical analyses can contribute, for example, extensive information about patterns and possible underlying processes governing territory size and shape, along with space use within home ranges (second- and third-order selection, respectively; [3]). Resource selection functions have been particularly popular for studying space use, but as 'statistical descriptions of the distribution and use of landscapes, … do not necessarily help us to understand why organisms are where they are' [4, p. 271]. Inferences from many empirical approaches are most applicable to the time and place from which data were collected, particularly
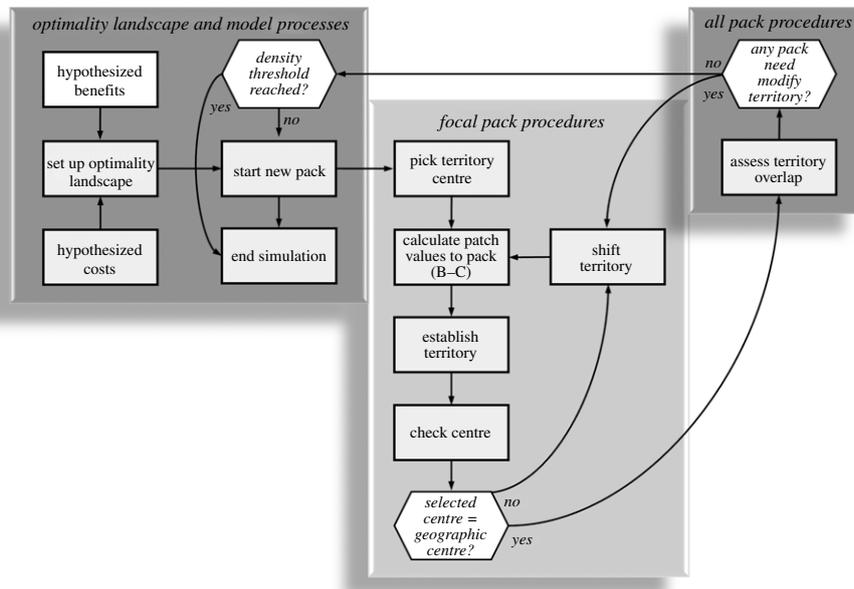
Figure 1. Framework of the mechanistic model for territory selection. Simulated wolf packs were added to an optimality landscape representing Montana. Packs established territories by identifying patches of high value based on benefits and costs of ownership. Territory overlap triggered packs to reassess whether their territories remained economical, leading to territory shifts over time.

when research employs phenomenological models to describe empirically observable patterns without revealing underlying mechanisms [5].

An alternative approach seeks to understand space use that arises from animal movements and interactions [6–8]. Mechanistic home range analysis (MHRA) often uses partial differential equations to simulate third-order movements [3] and resulting territory or home range structure. Space use can be modelled, for example, in relation to the presence of territorial boundaries [9], distance to central place [10], memory capacity [11] or presence of conspecifics [12]. MHRA has advanced understanding of second- and third-order [3] animal space use by testing hypotheses about underlying processes that lead to territory formation. MHRA leaders note, however, that 'a major shortcoming' is that MHRA 'is typically based around testing which model fits the data best out of a set of hypothesized models, without seeking to understand how close the best model is to empirical reality' [6, p. 7] (but see, e.g. [9,13,14]). A related approach uses mechanistic movement models to explore emergent properties through simulations and has demonstrated, for example, the influence of memory on space use [15,16].

An alternative mechanistic approach to investigating space use [8] was presented [17] and recently advanced [18] in the form of mechanistic, spatially explicit, agent-based models that seek to reveal fitness-driven mechanisms underlying space use. These models are founded on optimal foraging theory and thus employ an evolutionary approach to understanding mechanisms driving behaviour [8]. The approach simulates spatial behaviour on an 'optimality landscape' of grid cells that explicitly represents benefits and costs of defending any particular cell for inclusion in a territory. As demonstrated in [18], simulated animals select territories to include grid cells with the greatest net value, accounting for food resources and costs of defending and using a territory (figure 1). This leads to 'economical territories' that maximize benefits over costs of territorial defence [18]. Importantly, simulated animals continually adapt to decisions of neighbouring animals as each attempts to defend the most economical territory possible. This approach represents and tests mechanisms

hypothesized to underlie first-order extent of a species' range and second-order territory selection [3] by predicting what should be observed empirically if the model suitably represents mechanisms underlying territory selection. Subsequent tests of these predictions yielded statistical evidence that grey wolves (*Canis lupus*) select economical territories [19].

The strongest test of this mechanistic approach's hypotheses, predictive capacity and utility would be to extend the model to make quantitative, spatially explicit predictions of space use and further test how well the model predicts empirical reality. Accordingly, here we extend the [18] model to make spatially explicit predictions using an empirically derived optimality landscape, and determine how well the model predicts empirical reality.

An optimality landscape provides a fitness-based currency for studying and understanding mechanisms driving spatial behaviour. Animals almost certainly do not select home ranges (areas for foraging, mating and raising young) or territories (defended portions of a home range) [20] at random or by settling on the first option presented. Instead, animals should be adapted through natural selection [21] to select economical home ranges that maximize benefits and minimize costs of ownership [22–24]. Economical space use should accordingly reflect the distribution of limiting resources [17,25]. These resources are often presumed to be food (the food defence hypothesis) [26]. Researchers have further hypothesized that territorial species are either primarily intrinsically regulated (i.e. numbers are limited by territoriality or strife) [27], or extrinsically regulated (e.g. food limits population growth) [28]. Defence of food would, however, mean that populations are regulated by both extrinsic and intrinsic factors (i.e. through the exclusion of conspecifics from territories selected to defend food resources). An optimality landscape can test these hypotheses of space use and reveal the economic value of selecting different areas for inclusion in a home range, based on benefits and costs of ownership.

Our objective was to demonstrate our approach and test hypotheses about space use on grey wolves in Montana, USA. Wolves are strongly territorial, and wolf
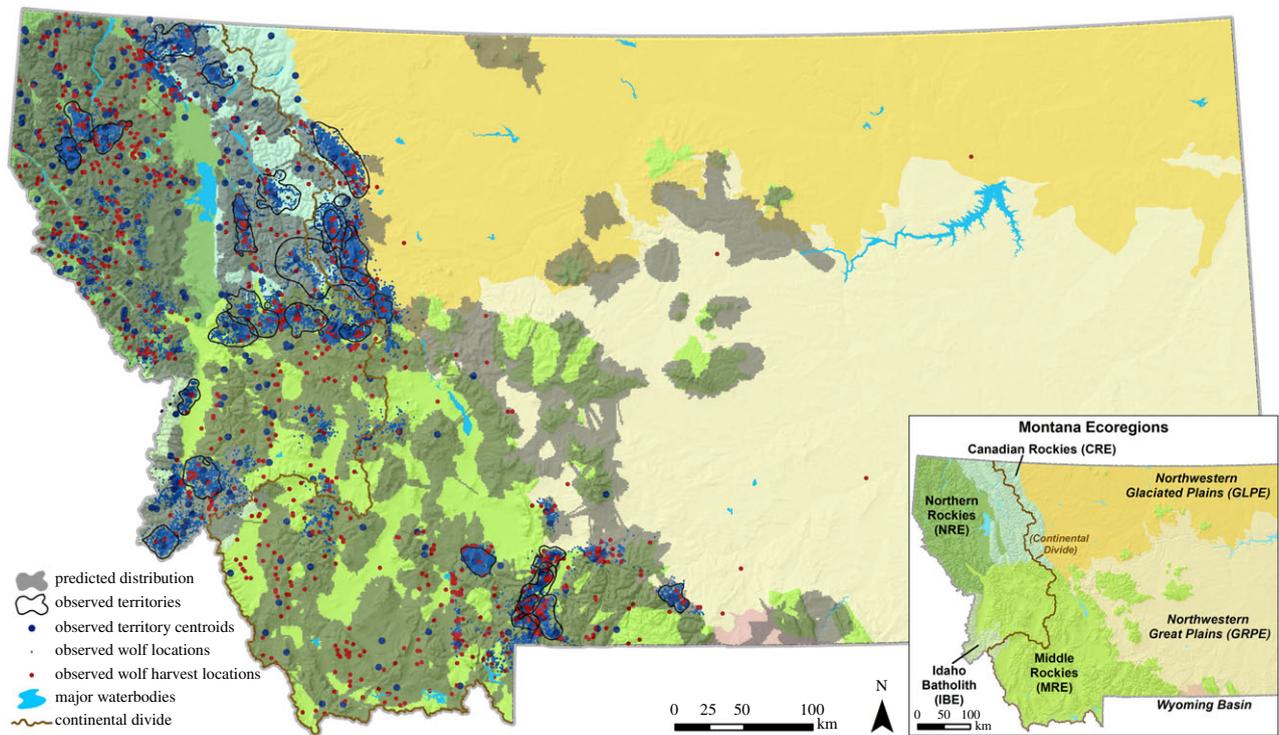
Figure 2. The optimality landscape represented Montana. Various ecoregions characterized Montana (inset map). Model predictions for territory distribution for 2014–2019 are shown on a 1 km² grid (grey shading) alongside observed locations of wolves during this period. (Figure for 2008–2009 provided in electronic supplementary material, p. 31.) (Online version in colour.)

packs cooperatively defend their full home range [29]. We hypothesized that wolves are adapted to select territories economically, and that exclusive access to food resources is the primary benefit of defending and using space [28]. Accordingly, our model represents the food defence hypothesis while incorporating realistic components of the ecosystem and wolf space use. Wolves in North America primarily prey on ungulates [30]. The strongly territorial nature of wolves [29] should make defence (e.g. patrolling, marking, competition for resources) a primary cost of space use. As coursing predators [30], costs associated with traversing the territory (e.g. distance to resources, rugged terrain) are likely also important [19]. Mortality risk may also shape space use, especially if territorial behaviours increase risk of mortality (e.g. via increased movement, vocalizations or visibility). Humans present a primary source of mortality risk for wolves [31] and human presence likely influences costs of mortality risk.

We expected that mechanistically modelling economical territory selection using an optimality landscape to represent these benefits and costs would enable predicting wolf space use. If food is not the primary benefit of wolf space use (as opposed, e.g. to defence of mates, i.e. the mate defence hypothesis [32], or offspring, i.e. the offspring defence hypothesis [33]), we expected the model to perform poorly. We parameterized the optimality landscape with simple indices representing benefits and costs of using and defending space. We applied the model to predict first-order selection (the geographic range of wolves in our study area) and second-order selection (territories of individual packs) [3], and compared the predictions to empirical observations of wolf territories from recent years (2014–2019). We also evaluated the model's ability to predict spatial requirements from an earlier period (2008–2009) when pack densities were lower.

2. Study area

Our study area comprised Montana, USA (figure 2), where elevations were 554 to 3938 m [34] and ecoregions described regionally similar landscapes (epa.gov). Dense forests and a maritime-influenced climate characterized rugged, mountainous terrain of the Northern Rockies Ecoregion. The Canadian Rockies Ecoregion had higher elevation, glaciated terrain. The Northwestern Glaciated Plains Ecoregion had level and rolling terrain with seasonal ponds and wetlands. The Idaho Batholith Ecoregion was mountainous, granitic, and partially glaciated. The Middle Rockies Ecoregion had rolling foothills where shrubs and grasses transitioned to rugged mountains with conifers and alpine vegetation. Grasses and shrubs dominated the xeric Wyoming Basin Ecoregion. Breaks and forested highlands interspersed semiarid, rolling plains of the Northwestern Great Plains Ecoregion.

After extirpation in the twentieth century, wolves successfully recolonized western Montana through natural immigration and reintroductions in the 1980s and 1990s. By 2008, wolf densities in western Montana were estimated at 4–8 wolves/1000 km², and this increased to 11–13 wolves/1000 km² in the 2010s (fwp.mt.gov). Densities in eastern Montana have remained low at less than 2 wolves/1000 km². Food resources included white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), elk (*Cervus canadensis*) and moose (*Alces alces*). White-tailed deer were the numerically predominant species in the Northern Rockies, whereas mule deer and elk generally comprised greater proportions of ungulate populations elsewhere in western Montana. Mule deer were the most common ungulate in eastern Montana, and moose were generally uncommon throughout the state. Most humans lived in western Montana, with a statewide population of just over 1 million in 2018 (census.gov).

3. Methods

We present a general overview of our approach; full details are in the electronic supplementary material.

(a) Optimality landscape and mechanistic model

We developed the model and optimality landscape in NetLogo 6.1.1 [35]. We designed the optimality landscape as a grid of 929×540, 1 km^2 patches representing Montana (electronic supplementary material, p. 2,5,7). Raster data (1 km^2 resolution) were loaded into NetLogo to inform each patch's benefits (B) of food and costs (C) for defending and using patches (details electronic supplementary material, p. 5, values electronic supplementary material, p. 19). Because ungulates in Montana are largely migratory, we represented each patch's seasonal B using ungulate density indices in summer (mid-Apr–mid-Oct) and winter (mid-Oct–mid-Apr). Each patch's C arose as simulated wolf packs selected and competed for patches, but also included raster inputs for terrain ruggedness and human density (electronic supplementary material, p. 6).

The model's individual agents each represented a wolf pack. During simulations (figure 1), a simulated focal pack was added to the optimality landscape at a random patch that served as an initial annual territory centre (electronic supplementary material, p. 8). Possible initial centre patches were at least 5 km from Montana's boundary (to avoid slow simulation speeds due to edge effects as B and C inputs were constrained to the state), unoccupied by other packs, and within 15 km of western Montana ecoregions to simulate realistic dispersal (Northern Rockies, Canadian Rockies, Idaho Batholith and Middle Rockies; figure 2). However, in subsequent model steps, territory centres could be shifted to any location on the Montana landscape (electronic supplementary material, p. 11).

The focal pack next assessed summer and winter values (V) of patches within 45 km of the initial annual territory centre as B–C for each season (electronic supplementary material, p. 9) [18]. Patches of highest V had high B (high summer or winter prey densities) and low C, i.e. were closer to the territory centre and of lower terrain ruggedness (thereby reducing travel costs), not occupied by other packs (reducing competition costs), and had low human densities (reducing mortality risk costs). Conversely, patches more costly to use and own were occupied by other packs, further from the territory centre, or had greater ruggedness or human densities. The pack established a summer territory by selecting patches in order of summer V (patch with highest V, next highest V, etc.) until it acquired sufficient resources for summer (R, i.e. total resources required for survival and reproduction, assumed to be equivalent across packs; electronic supplementary material, p. 10). This was repeated for a winter territory, based on winter V and winter R. The summer and winter territories together comprised the annual territory.

We next needed to determine if the simulated pack should shift its annual territory to maximize its economic value. This was an iterative process until the annual territory centre and the geographic centre aligned, and a simulation requirement to identify a territory with maximal economic value since costs and benefits of patches were determined by testing out possible territory formations. In real life, we expect wolves to explore and learn about their environments in order to ultimately settle in areas of maximal value. For simulations, the pack's territory centre was compared to the simulated territory's geographic centre (as measured by combined extents of summer and winter territories; electronic supplementary material, p. 11). Mismatches of at least 1 km between a selected and geographic territory centre often indicated V could be maximized by shifting that direction. Therefore, if mismatched, the pack discarded its territory, repositioned to this new centre, recalculated V and again selected territory patches. This was repeated until centres aligned.

Next, a new pack was added and the territory selection steps were repeated (figure 1; electronic supplementary material, p. 8). If a pack chose a territory partially overlapping existing packs (thereby increasing costs of competition and reducing V for packs claiming the patch; electronic supplementary material, p. 9), each affected pack reassessed whether their territories remained economical, leading to territory shifts and dynamic, density-dependent competition among packs (electronic supplementary material, p. 13).

During simulations, density thresholds (density) specified per-ecoregion densities of packs per 1000 km^2 to be modelled (electronic supplementary material, p. 8,15). After density was reached and all packs were settled, each pack's final territory was recorded as patches selected based on V plus any crossed to reach selected patches from the territory centre (electronic supplementary material, p. 13,23). Territory size was the number of 1 km^2 patches in the territory and overlap was percentage of the territory overlapping other territories. The model recorded each pack's number of nearby competitors (number of other territory centres ≤ 25 patches from the territory border) [19] and mean human density per territory patch. Summer and winter seasonal territories selected to meet R in the respective season were likewise summarized. Patches recorded the size of the annual territory claiming them (shared patches were assigned the mean territory size of packs claiming them), and final results were saved as 1 km^2-resolution rasters.

(b) Model application

We completed a series of simulations (electronic supplementary material, p. 15). We first calibrated the optimality landscape to identify applicable parameter values for wolves in our system. For this step, we used 26 empirical estimates of territory boundaries [19] derived from global positioning system (GPS) collars deployed on wolves from 2014 to 2019 (figure 2; electronic supplementary material, p. 6). Territories were summarized as 95% volume-adaptive kernel density estimates [1] with a smoothing parameter of 100% of the reference bandwidth. Ecoregions contained five (Northern Rockies), seven (Canadian Rockies), three (Idaho Batholith), nine (Middle Rockies), one (Glaciated Plains) and one (Great Plains) empirically observed territories (figure 2).

Calibration swept across a wide range of parameter values (i.e. low–high weights for C and settings for R; electronic supplementary material, p. 14). This iteratively minimized and maximized R and importance of each C (competition, travel and mortality risk) to test a wide swath of model formulations and associated hypotheses (e.g. competition very important while travel and mortality less so, etc.). Whereas simulated packs normally had no information about locations of real territories, during calibration, we manually placed a pack at each empirically observed territory centre and had them select optimal territories (electronic supplementary material, p. 14). We repeated this while systematically varying the parameters to identify values that minimized average mean squared error in size of predicted versus observed territories. We used the identified values for the remaining model applications.

For our primary simulations, we simulated recent (2014–2019) wolf densities in Montana (electronic supplementary material, p. 15). Because competition among packs influences spatial behaviour [18,19], an approximation of density helped simulate a specific period of space use. To set density, we used empirical data to estimate mean densities of packs that occurred in each ecoregion (electronic supplementary material, p. 6). The population was largely stable in these years with a mean of 127 packs per year and pack densities per 1000 km^2 of 1.6 (Northern Rockies), 1.4 (Canadian Rockies), 1.9 (Idaho Batholith), 0.5 (Middle Rockies), 0.02 (Glaciated Plains) and 0.03 (Great Plains). Once these densities were reached, the

simulation ended. We repeated 50 simulation iterations to capture variability in results (electronic supplementary material, p. 15).

We used the model's simulation results to test our hypotheses and the model's predictive capacity (electronic supplementary material, p. 15). To assess first-order selection, we overlaid raster datasets from the 50 iterations to identify where predicted territories occurred. We overlaid this with an empirically observed distribution of wolves from monitoring data (territory centroids, harvest locations of wolves and resident wolf GPS locations; for 2014–2019, $n = 628$; 915; and 50,601, respectively; electronic supplementary material, p. 6). For second-order selection, we averaged the 50 rasters at each 1 km^2 cell, measured mean territory size predicted within each real territory boundary for 2014–2019 and compared this to the empirically observed size. We also compared sizes of simulated territories versus the 26 real territories in relation to prey density, competition and human density.

To externally test the model (using data omitted from calibration), we simulated an earlier period when pack densities were lower (2008–2009) and GPS data were available (electronic supplementary material, p. 6,15). We set per-ecoregion *density* to that which occurred in these years (electronic supplementary material, p. 7), ran 50 iterations of the model and measured predicted territory sizes for 10 GPS-collared wolves living in nine packs in these years. We plotted first-order selection against the empirically observed wolf distribution in these years and compared simulated territories versus the nine observed territories in relation to prey density, competition and human density (electronic supplementary material, p. 31–34).

Finally, we applied the model across a range of *density* and variable prey B to demonstrate their effects on space use (electronic supplementary material, p. 15,35).

4. Results

Model calibration steps tested model variations that reduced or strengthened importance of the hypothesized primary costs of space use (competition, travel and mortality risk) and settings for R. All C were important for accurate prediction (electronic supplementary material, p. 15).

The model successfully predicted wolf distribution, i.e. first-order space use (figure 2; electronic supplementary material, p. 24–31). Observed and predicted distributions for 2014–2019 were extensive in northwestern Montana and noticeably patchy in southwestern Montana. The model likewise predicted wolf distribution in 2008–2009 (electronic supplementary material, p. 31). Simulated packs largely avoided areas apparently also avoided by real wolves. The model occasionally predicted territories in central Montana (electronic supplementary material, p. 25,26). These areas include island mountain ranges surrounded by ranchlands where human–wolf conflicts can be high, potentially decreasing the odds of packs persisting. The public has reported wolf sightings and harvests in these areas, however (electronic supplementary material, p. 28–30), indicating that wolves indeed use them.

The model demonstrated predictive capacity for second-order selection, despite large variability in real territory sizes (mean 568 km^2, s.d. 420 km^2, median 441 km^2, range 188–2207 km^2). Median differences in predicted versus observed territory sizes was 129 km^2 for 26 packs from 2014 to 2019 (figure 3; mean = 212 km^2, or 158 km^2 omitting one large observed outlier territory.) Specifically, 42.3% of predicted territory sizes were within 100 km^2 of the observed size, 73.1% were within 200 km^2, and 80.8% were within 300 km^2. Additionally, for five of seven observed territories with
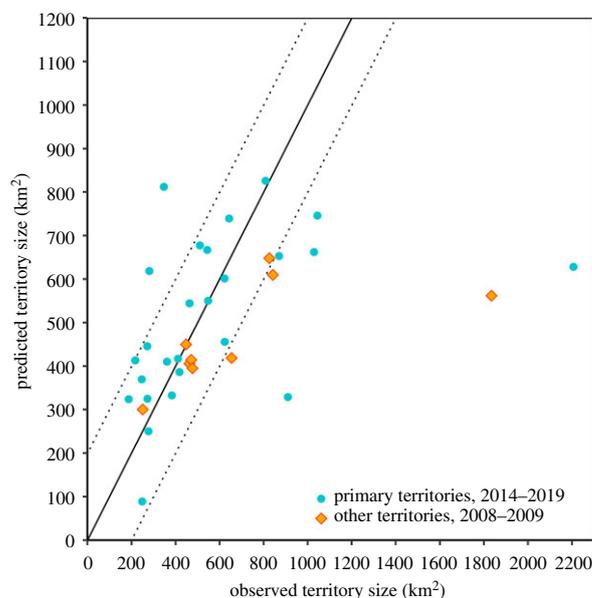
Figure 3. Predicted versus observed territory sizes. Predictions were similar to observations from GPS-collared packs ($n = 26$ in 2014–2019; $n = 9$ in 2008–2009). Solid line delineates perfect precision and dotted lines delineate predictions within 200 km^2 of observed territory sizes. (Online version in colour.)

predictions differing by greater than 200 km^2, concentrated space use was predicted and observed (based on the density of GPS fixes) to be smaller than full territory boundaries estimated empirically (figure 2), an outcome of empirical uncertainty measured by kernel density estimation. The remaining two wolves from this subset were probable breeding females, who tend to use less space than the rest of the pack while raising pups; unsurprisingly, their predicted space use was greater than observed.

Despite highly variable real territory sizes observed for 2008–2009 (mean 696 km^2, s.d. 467 km^2, median 477 km^2, range 251–1835 km^2), median difference in predicted versus observed territory size was 82 km^2 (figure 3). (Mean difference was 240 km^2, or 112 km^2 omitting one large observed outlier territory.) Of the nine territories, 55.6% were within 100 km^2 of observed sizes, 66.7% were within 200 km^2, and only the outlier differed by greater than 300 km^2.

The model predicted empirically observed patterns in space use. As demonstrated for 2014–2019 densities, the model predicted spatial variation by ecoregion (figure 4) and for responses to food abundance, competitor density and human density (figure 5). Territory size declined with increasing food abundance and more neighbouring packs, during which territory overlap was predicted to increase. Territory size was predicted to increase and then decrease curvilinearly with greater human-caused mortality risk (figure 5). The model predicted seasonal territories to be smaller and have less overlap in summer than winter (figure 6). Predictions for 2008–2009 likewise matched empirically observed patterns in space use (electronic supplementary material, p. 31–34).

5. Discussion

We demonstrate how an optimality landscape and mechanistic model centred on optimal foraging theory can advance scientific understanding of mechanisms driving spatial behaviour. Our approach contributes evidence that
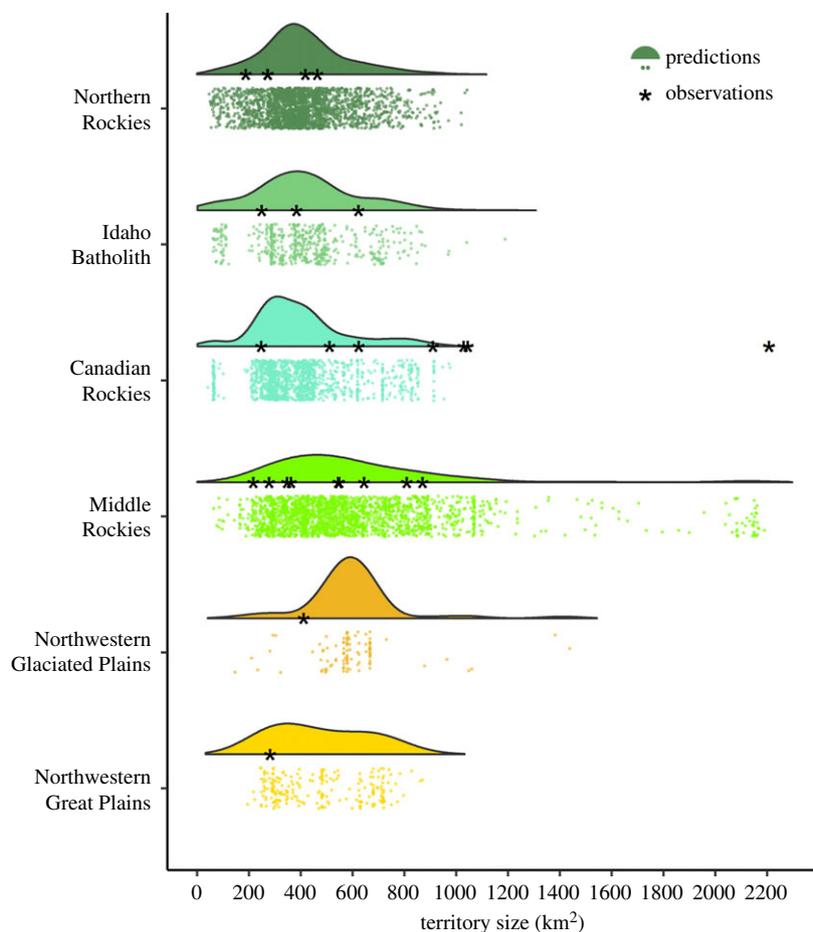
Figure 4. Spatial requirements were predicted to vary by ecoregion, as empirically observed for GPS-collared wolves between 2014 and 2019. Raincloud plots display half-violin plots (kernel probability density of predicted territory sizes) with a jittered-point plot below (raw predicted points contributing to the violin plot). (Figure for 2008–2009 provided in the electronic supplementary material, p. 32.) (Online version in colour.)

economical space use is a mechanistic bridge to animal distribution and density on the landscape. Wolf territories were economical with respect to benefits of food and costs of defending and using space, consistent with the food defence hypothesis [26] and expectation that wolves are regulated by both intrinsic [27] and extrinsic [28] factors. Simple rules for economical selection of patches for inclusion in territories yielded first- and second-order predictions of space use [3] that mirrored reality, including of the distribution of animals (figure 2), their spatial requirements (figure 3), and how these are influenced by prey density, competitor density, human-caused mortality risk and seasonality (figures 4–6). Application of this knowledge can predict behaviour under a wide range of ecological and social conditions (electronic supplementary material, p. 35–38).

Our approach to mechanistic models of space use centres on simple behavioural rules to simulate first- and second-order space use [3] in an effort to understand how and why animals select territories [17,18]. Contrasting MHRA's focus on second- and third-order animal movements and partial differential equations [6], our approach's foundation is in optimal foraging theory [8] and simultaneously integrates dynamic competition among territory holders to account for how competitors influence economics of defending space [6,18]. Building on this foundation, we incorporated an optimality landscape for producing spatially explicit predictions of space use. Importantly, we not only found which model formulation fit the data best but assessed the extent to which emergent properties of the best model

matched empirical reality, for an entire population across an area of greater than 380 000 km^2.

Our model for animal space use predicted the population's distribution and territory sizes of individual packs, absent extensive data for movements and resource availability. It accomplished this for recent (2014–2019) space use by real wolves (whose training data were used during model calibration), and for an earlier, lower density period of wolf recovery (representing new data omitted from model calibration; figure 3). Per-pack predictive accuracy varied but predictions strongly improved on estimates that could be derived from the population's observed territory sizes, which in recent years averaged 568 km^2 and ranged over a greater than 2000 km^2 spread (188–2207 km^2; s.d. = 420 km^2).

Our approach was designed to enable testing hypotheses about carnivore space use. This work contributes evidence that carnivore territories are economical with respect to benefits and costs of space use. In this system, space use appears to be particularly influenced by prey and competition (figure 5; electronic supplementary material, p. 36–37), consistent with the food defence hypothesis [26] and expectation that both extrinsic and intrinsic factors regulate carnivore spatial behaviour and resulting densities. Researchers previously hypothesized that carnivore populations are primarily driven by extrinsic factors (prey) [28] or intrinsic factors (competition) [27]. Support for the extrinsic hypothesis would have been found if model calibration identified minimal or no importance of competition, versus support for the intrinsic hypothesis had predictions mismatched reality (as
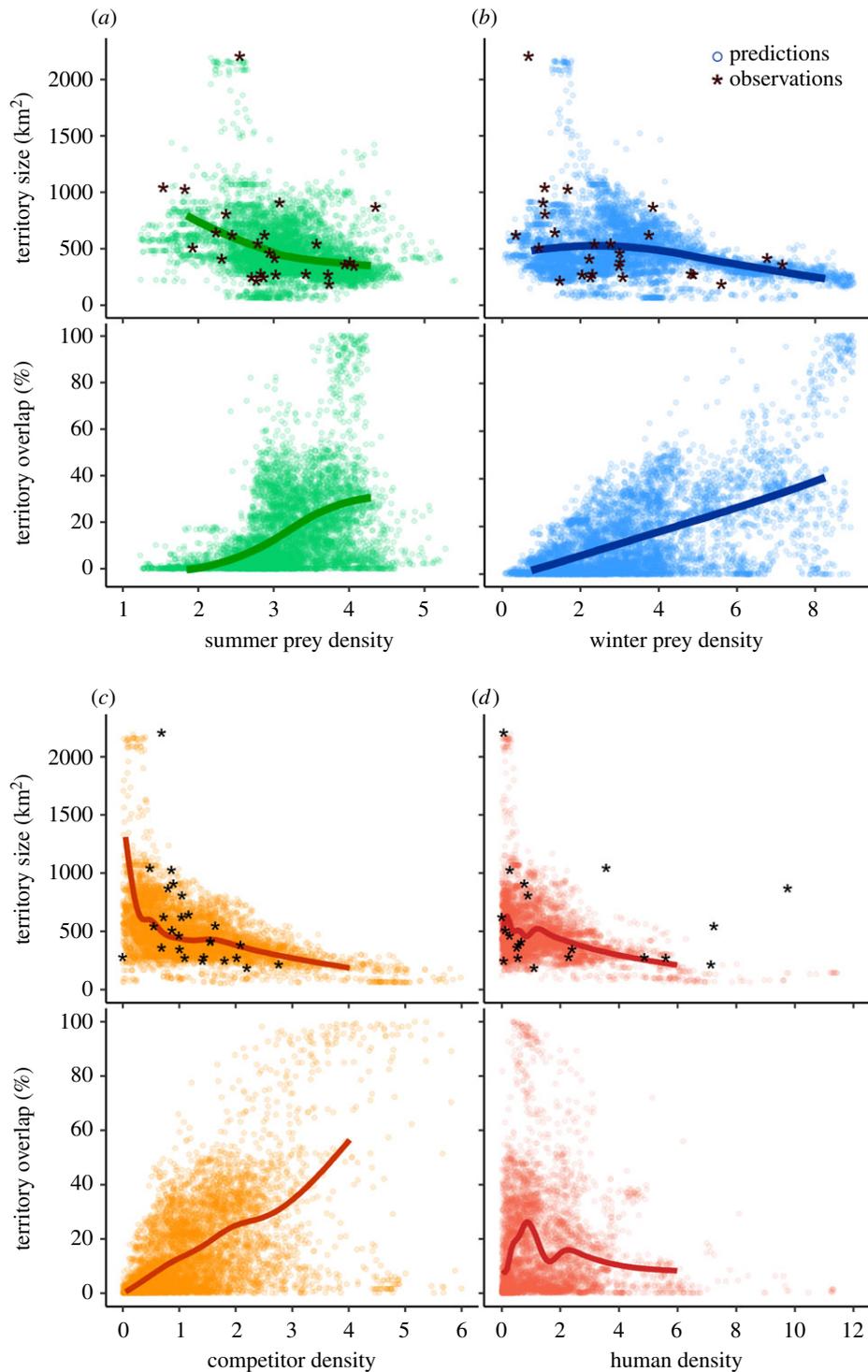
Figure 5. Predicted spatial requirements for 2014–2019 aligned with empirical observations in relation to seasonal densities of ungulates (a,b; ungulates/km^2), competitors (c; no. neighbours/100 km^2 in territory area), and human densities (d; humans/mi^2; three outlier observations had densities of 26, 30 and 72). Lines depict smoothed conditional means for predictions. (Figure for 2008–2009 provided in the electronic supplementary material, p. 33.) Observations of per cent overlap were unavailable as this would require simultaneously deploying collars in every pack in Montana.) (Online version in colour.)

prey comprised the primary benefit for defending space on the landscape). Logically, plentiful food resources reduce spatial requirements when animals select territories to economically meet resource needs; however, these high-value areas attract competitors. Escalating competition imposes added costs of territory defence, which generally causes territories to compress as their peripheries become uneconomical. Overlap among territories simultaneously increases where retaining access to areas relatively rich in food remains economical despite costs of defending these sites. Economical space use leading to numerous, highly compressed territories will

encourage continued jockeying for space and fluctuations in territory boundaries as animals interact to defend food and respond to competitors. These complex dynamics likely underlie spatial drifts of territories over time as observed for wolves [36] and other species [37]. The overall distribution of territories may however appear relatively stable even as territory boundaries shift within (electronic supplementary material, p. 38). Importantly for conservation, this means that a population's distribution is likely to be strongly decoupled from and a poor gauge of population size, growth rate and long-term viability.
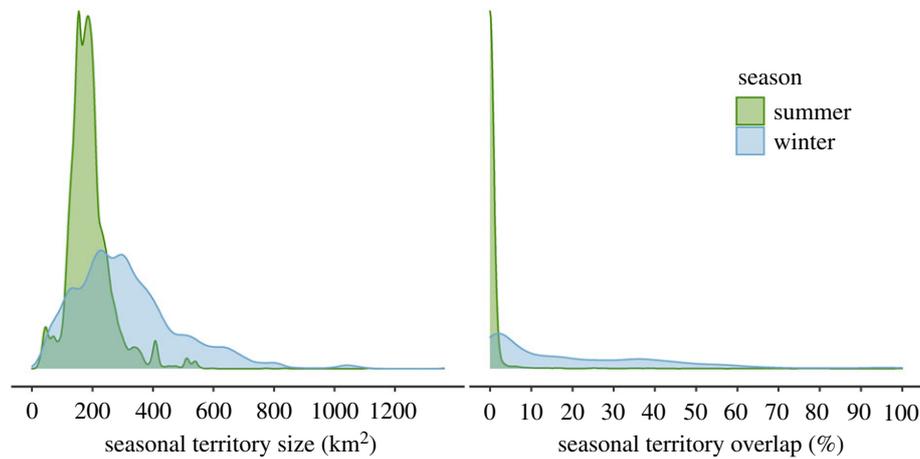
Figure 6. Density plots show that seasonally defended areas were predicted to be smaller and have less overlap in summer than winter. (Figure for 2008–2009 provided in the electronic supplementary material, p. 34.) (Online version in colour.)

Because this work contributes evidence that food defence drives space use in our study system, it offers evidence against mate or offspring defence as sole primary drivers of territoriality, as proposed by the mate defence [32] and offspring defence [33] hypotheses. Because we explicitly modelled defence of food resources, our model's predictive ability would have been low if mate or offspring defence was instead the primary benefit of territoriality. Including mates or offspring in the optimality landscape could strengthen predictive capacity, and our approach provides a foundation for future tests. Interestingly, however, the mate defence hypothesis would predict less territory overlap during winter to protect mating opportunities [32], whereas the model predicted overlap should be greater in winter (figure 6), as has been reported empirically [38]. Additionally, whereas a key prediction of the offspring defence hypothesis was that food should not affect territory size [33], we show that food influences territory size and that our optimality landscape accounting for food resources predicts wolf spatial behaviour (figures 2–5).

Spatial requirements and resulting animal densities are highly variable because local conditions are rarely stable over space and time (figures 4–6; electronic supplementary material, p. 36–38); however, what spatial requirements reveal can be counterintuitive. We may assume that large territories indicate greater success in defending space, but small territories tend to reveal a landscape's most desirable areas when animals economically defend space to satisfy resource requirements. For example, northwestern Montana is densely populated by white-tailed deer that use small home ranges and often have short-distance elevational migrations from winter to summer. This stable resource base enables wolf territories to consistently be relatively small (figure 5; electronic supplementary material, p. 37). Notably, wolves naturally recolonized these same areas first in the 1980s. By contrast, dispersed, fluctuating resources cause relatively large territories, such as observed elsewhere in Montana where migratory elk and mule deer predominate. Large territories reveal economical trade-offs are gained despite paying greater costs to maintain and use more space. A widely dispersed, low-density territory mosaic produced by large territories may have lower costs of defence given fewer neighbouring competitors. Such conditions evidently occurred in southwestern Montana and along the Continental Divide,

where some of the largest territories (figure 4) occurred in dispersed, patchily distributed territory mosaics (figure 2).

Territorial behaviours carry costs of mortality risk (e.g. through increased movement and defensive signalling) that influence the optimality landscape and trade-offs in space use (figure 5). We assumed that data for human densities suitably represented how costs of human-caused mortality risk affect economic values of space, and other data representing these costs may be informative. However, reducing costs of mortality risk on the optimality landscape led simulated animals to settle in valley bottoms densely populated by humans and avoided by real wolves. Such areas were likely economical for wolves prior to exploitation by humans. Extensive range overlap among wolves and humans elsewhere (e.g. Italy, where wolves enter human settlements to forage at night) [30] demonstrates how carnivores adapt to variable costs of mortality risk. We expect this cost is reduced in areas with lower human-caused mortality risk (e.g. national parks). However, reduced mortality risk alone will not make areas economically valuable for defending territories.

Economical space use may affect important dynamics like dispersal and may thus have contributed to the evolution of group living and cooperative behaviour [39]. Tightly packed, highly competitive territory mosaics may make dispersal less economical if not deadly by increasing risks of intraspecific encounters and failure to find vacant space. By contrast, sparse territory mosaics may allow dispersers to capitalize on travel corridors provided by undefended interstitial space. Larger territories may also be less risky for trespassing while occupants are patrolling elsewhere. Accordingly, for territorial species, less economically desirable areas could contribute more dispersers within a population or emigrants to nearby ones. Highly competitive territory mosaics may see more delayed dispersal, reduced dispersal success, or more intraspecific mortality and turnover in territory ownership. Such possibilities provide areas for future research. Delayed dispersal in response to competition for space has been hypothesized to underly the evolution of group living [39], which may well have been the case for animals like wolves. This evolution may have continued through a feedback loop such that delayed dispersal brought added benefits of cooperatively defending space and raising young.

Economical space use has broad implications for the greater ecosystem. The same spatial dynamics affecting dispersal may affect pathogen spread within a population and spillover to other species. Prey and predators also likely structure their own space use in response to that of an intermediate predator. For example, prey populations may take refuge where territory boundaries meet, as hypothesized and observed for deer living among wolf territories [40,41]. Areas with densely packed territory mosaics yield increased densities of predators and prey refuge zones at closer proximity to territory owners. However, extensive boundaries formed by numerous small territories could create plentiful refuge zones for prey to exploit.

As with all models, ours carries various assumptions and provides areas for future work. We assumed that resource requirements did not vary with pack size, based on the hypothesis that wolf packs carve out territories to accommodate large packs [29]; this could be modified in future model iterations. We assumed that natural selection has shaped wolves to instinctively perceive relative costs and benefits of selecting different areas for a territory within the general vicinity. This assumption could likewise be relaxed, but should be reasonable for highly mobile species that appear to explore areas before settling into territories [29]. Other costs or benefits may be informative in future model iterations (e.g. areas for den or rendezvous sites, or alternative prey bases). This would increase the calibration iterations required (electronic supplementary material, p. 14) and data inputs nearly identical in both magnitude and spatial extent would challenge discernment of importance to overall patch values. Application of our model to predict space use for specific years of wolf recovery relied on a means to approximate the degree of competition encountered (electronic supplementary material, p. 6), because competition strongly influences space use [18]. We approximated competition by estimating the density of packs from monitoring effort; alternatives could include modifying the model to simulate selection near estimated territory centroids of observed packs, or developing empirical models of approximate pack densities.

6. Conclusion

Scientific understanding of mechanisms driving spatial behaviour can be advanced using an optimality landscape and mechanistic model centred on optimal foraging theory. Our approach can be applied to systems where extensive monitoring data are impossible or impractical to collect. Knowledge gained from our approach can enhance conservation efforts and predict effects of conservation actions.

The foundation provided by this research can be applied to any species. The approach can be easily adapted to different contexts by modifying model rules or data inputs. Submodels, such as for food resources, dispersal and group size, may increase predictive precision and provide additional avenues for research. Further adaptations may also enable predicting third-order movements within a territory and integration with other mechanistic approaches like MHRA. The approach is not limited to territorial species; minor changes to costs of competition would extend the model to home ranges in general, further expanding the opportunity to study and understand animal spatial behaviour.

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